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How is a cricket like a rat? Insights from the application of cybernetics to evasive food protective behaviour

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Robbing and dodging is a well-documented food protective behaviour in rats. Recently, we demonstrated that a simple cybernetic rule, gaining and maintaining a preferred interanimal distance, can account for much of the variability in dodging by rats. In this paper, the field cricket, *Teleogryllus oceanicus*, was used to test whether or not the same or similar cybernetic rules are used by animals of different lineages and body plans. Pairs of female crickets were tested in a circular arena with a clear glass surface. A small food pellet was given to one of the crickets and the attempts to rob the food by the other were videotaped from beneath. The results show that, although crickets, unlike rats, use a variety of defensive strategies, all of the cases in which they use evasion to protect a portable food item conform to the same cybernetic rules used by rats.

Robbing and dodging, heretofore described in rats, involves one animal (the defender) possessing a portable piece of food, while another animal (the robber) attempts to steal that food. The defender evades the robbing attempts by pivoting laterally, thus dodging away from the robber (e.g. Whishaw 1988; Whishaw & Tomie 1988). Robbing and dodging in rats has been used as a model to investigate a number of issues related to the neural control of behaviour (Whishaw & Oddie 1989; Whishaw et al. 1990; Field et al. 1996, 1997a, b, 2004, 2005; Pellis et al. 2006).

We recently demonstrated that robbing and dodging in rats, rather than resulting from a stimulus–response algorithm, with which defenders calculate fixed dodging angles based on food and partner characteristics, can be succinctly accounted for by appealing to a simple cybernetic rule: gain and maintain a preferred interanimal distance (Bell & Pellis 2011). Stimulus–response algorithms produce fixed motor responses to specific sensory stimuli; that is, when a particular sensory stimulus is experienced by an organism (e.g. an approaching robber), the behaviour that it produces as a result is the same every time (e.g. to pivot a set number of degrees away from approaching robber). In contrast, the term ‘cybernetic’ implies the use of negative feedback to continuously modify behaviour in order to compensate for changing environmental information; that is, variable behaviour is used by the organism in the service of achieving biologically relevant goals (Wiener 1943; Powers 1973). The distinction is that, instead of using the same set of movements to evade a robbing attempt every time, which would be easy for the robber to learn and defeat, something that almost never happens (H. C. Bell, unpublished observations), the cybernetic rule involves using only the same general tactic. The cybernetic control of interanimal distance, which can be achieved by an almost infinite combination of movements, is, by virtue of its unpredictability, much more difficult for the robber to learn and defeat. In terms of behavioural output, this means that the range of angles traversed during dodging is more variable than the range of interanimal distance, as the former is varied to regulate the latter (Bell & Pellis 2011).

In light of our discovery of the existence of a cybernetic rule in rats when dodging, we determined to test whether or not other animals operate using the same principles in similar contexts. For several reasons, we chose field crickets, *Teleogryllus oceanicus*, to conduct this investigation. First, cybernetic rules have previously been used to explain some aspects of cricket behaviour (Pellis et al. 2009). Second, as crickets have also been observed to perform dodges in response to robbing attempts made by other crickets (B. Gorny & I. Q. Whishaw, unpublished observations), the same overt behaviour could be compared across the two species. Third, although they seem to perform dodges to protect food in a similar fashion, crickets have a different body plan than rats, with Arthropoda and Chordata having diverged at least 500 million years ago

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(Ayala & Rzhetsky 1998). For example, rats use their forepaws to hold their food, requiring them not only to shift their body weight onto their hindlegs, but also limiting their defensive movements to only two of their feet (Whishaw 1988). In contrast, crickets hold their food with their mandibles (Manton & Harding 1964), leaving all six limbs free for locomotion when evading the robber. Such differences in posture and motor strategies across the species could produce significant differences in the organization of food protection.

Four hypotheses were tested in the present paper. The first two major hypotheses were (1) that crickets use a cybernetic rule during food protective behaviour and (2) that crickets use the same 'gain and maintain a minimum interanimal distance' rule in the same way that it is used by rats; that is, despite all of the differences mentioned above between the two species, crickets and rats defend food using the same underlying principle (see Table 1). The second two minor hypotheses, dependent on the main hypotheses, were (3) that, in addition to controlling interanimal distance, defenders also control their body orientation relative to robbers, and (4) that approach orientation of the robber is related to the type of evasive action used by defenders (see Table 1).

One issue with respect to the first hypothesis is that for crickets, and for arthropods in general, rapid defensive and offensive actions are thought to be ballistic, allowing little opportunity for modification once their behaviour is initiated (Schöne 1984; Bell 1991). If arthropods act solely in a ballistic fashion, cybernetic mechanisms, because they rely on feedback, could not be a fundamental component of the organization of cricket behaviour. However, the same algorithmic, nonupdateable type of rule was also previously thought to apply to the dodging behaviour of rats (Whishaw & Gorny 1994). Fortunately, ballistic and cybernetic rules produce distinct behavioural outcomes. If defender crickets respond only ballistically to the stimulus of the robber's approach, their behaviour should be relatively stable through time and independent of the specific movements used by the robber. Conversely, if crickets are able to use feedback to compensate for changing conditions, then defender responses should not only be variable, but should also be correlated with the specific movements used by the robber.

With respect to the second hypothesis, if the goal of the defender is to control a two-dimensional interanimal distance, then, as was discovered in the rats, interanimal distance should be less variable than any other measured variable (Bell & Pellis 2011). Furthermore, interanimal distance should not be correlated with the actions of the robber; that is, interanimal distance should remain relatively constant even though the movements of the robber do not, which is also characteristic of the rat dodging system (Bell & Pellis 2011). Finally, the same pattern of relationships between all measured variables that was present in the rats, such as a correlation between the movement of the robber and the movement of the defender, should also be present in the crickets.

With respect to hypothesis 3, our initial observations indicated that, like rats (Field et al. 1996), cricket defenders faced away from robbers at the end of interactions. We predicted that, if defender body orientation relative to robber were controlled, specifically, if the 'facing away' orientation were preferred, then the 'facing away' orientation should be favoured over other defender orientations at the end of interactions.

With respect to hypothesis 4, unlike rats, crickets do not rely solely on dodging (i.e. pivoting away from the robber) as an evasive strategy. In many instances, crickets simply walk or run directly away from the robber. Crickets also differ from rats in the variety of approach angles that are used by robbers. A rat primarily approaches another rat holding food from a parallel orientation, with its head moving along the flank, in the direction of the defender's head. Thus, in the majority of encounters, the defender is confronted with a similar robbing orientation. In contrast, in their approach to rob, crickets do so from virtually any orientation, and this difference could account for the differing evasive strategies used by crickets. Therefore, we predicted that the point on the body of the defender targeted by the robber is related to the type of evasive strategy adopted (i.e. dodging versus running).

METHODS

Subjects

All procedures in this paper conform to the University of Lethbridge Animal Welfare Committee protocol number 0708. Ninety-two female field crickets (46 pairs), *Teleogryllus oceanicus*, that were born and reared at the University of Lethbridge were used in total; however, not all animals were used for every analysis. All animals were housed in rooms maintained at 25 °C and 70% relative humidity, on a 12:12 h light:dark cycle, with lights on at 1200 hours. Hatchlings were placed into large plastic bins (51 cm long × 37.5 cm wide × 35.5 cm high) containing layers of cardboard egg cartons for shelter, glass shell vials filled with water and stoppered with cotton for moisture, and ground and pelleted cat chow (Iams® Original with Chicken) ad libitum. Water vials were changed weekly and additional food was given as needed. Female nymphs were separated from the colony during their penultimate instar (final juvenile instar) and were then housed in groups of 10 to 20 individuals in containers (29.5 cm long × 19 cm wide × 12.5 cm high) with layers of cardboard egg cartons for shelter, and water and food provided as before. Following their final moult, the animals were placed, individually, into round plastic containers (9 cm diameter × 8 cm high). Half of the animals were randomly assigned to be subjects, defending the food, and the other half were assigned to be robbers. Half of both the defenders and the robbers were marked with a dab of typewriter correction fluid on their pronotum. Each cricket destined to be a defender was randomly assigned a partner that would act as the robber. Although isolated, the animals were housed in the colony room from which they would have been able to see, hear and smell conspecifics. Thirteen of the original 46 pairs were eventually

Table 1
Competing hypotheses and predictions tested

Hypothesis 1	Crickets use cybernetic rules to protect food from robbers	Crickets use ballistic rules to protect food from robbers
Predictions*	1. *Defender responses to robbing attempts are variable* 2. *Defender and robber movements correlated*	1. Defender responses to robbing attempts are invariant 2. Defender and robber movements not correlated
Hypothesis 2	Crickets use the same rule as rats to protect food from robbers	Crickets do not use the same rule as rats to protect food from robbers
Predictions	1. *Interanimal distance is invariant* 2. *Interanimal distance is not correlated with robber movement* 3. *The same pattern of relationships among all variables seen in rats is seen in crickets.*	1. Interanimal distance is variable 2. Interanimal distance is correlated with robber movement 3. The same pattern of relationships among all variables seen in rats is not seen in crickets.
Hypothesis 3	Defender body orientation is a controlled variable	Defender body orientation is not a controlled variable
Predictions	1. *Defender body orientation is the same at the end of every interaction*	1. Defender body orientation is variable at the end of every interaction
Hypothesis 4	Initial robber orientation predicts evasive strategy used	Initial robber orientation has no bearing on evasive strategy used
Predictions	1. *Initial robber orientation and evasive strategy are correlated*	1. Initial robber orientation and evasive strategy are not correlated

* Predictions that were supported are *italicized*.

excluded from the study due either to one of the pair dying or escaping, or to lack of sufficient data to include in the analyses (i.e. too few interactions).

Given that different cricket pairs interacted at different rates, the number of interactions contributed by each pair differed. To ensure that the patterns discerned were not a product of overcontribution by a few pairs, only four examples from each pair were used, and so, all pairs contributed an equal number of interactions, yielding a balanced data set for testing. Moreover, since some pairs interacted more than four times, to avoid bias in selecting examples, for each pair, the first four interactions for each type of defence that met the criteria of occurring away from the walls were selected. Comparisons involving the whole data set (unbalanced) are only presented if validated by a balanced analysis.

Testing

Robbers and defenders were deprived of food for 6 days prior to testing, but given water ad libitum during that time. Prior to conducting this experiment, female field crickets were subjected to varying degrees of food deprivation. Preliminary testing showed that 6 days of food deprivation was required to produce sufficient motivation for animals to attempt to steal food from one another without affecting the mortality rate (K. A. Judge, unpublished observations). Previous research also indicated that field crickets can be deprived of food for up to 7 days without an increase in mortality (Adamo & Hoy 1995). On the testing day, each subject (the defender) and its partner (the robber) were introduced into the testing chamber, a 12.6 cm diameter Plexiglas cylinder situated on top of a clear platform with a mirror underneath at a 45° angle. The animals were allowed to habituate to the enclosure for 2 min, at which point, a small piece of cat chow (approximately 3 mm in diameter) was placed, using forceps, in front of the defender. The trial began when the defender picked up the food with its mandibles, and ended when the defender had finished eating the food, when the robber succeeded in stealing the food from the defender, or when 12 min had elapsed. Trials were conducted in the dark, and were filmed from below through the mirror using a Sony High Definition digital video camera in the infrared spectrum. Following the trials, the animals were returned to their home containers, in which cat chow and water were available ad libitum for 1 day, after which the cat chow was removed, and the animals were again deprived of food for 6 days. Trials were always performed using the same pairings of animals, and the cycle of trials was repeated three times. Following the experiment, approximately half of the surviving crickets were returned to the main colony, and the other half were euthanized by freezing and placed in individual vials containing a 70% EtOH solution so that body size measurements could be taken. The crickets that were euthanized were chosen randomly from the entire sample. Both members of the original pair were euthanized so that there was an equal number of robbers and defenders, and so that body size differences within pairs could be compared. As the body size measurements were used for a subsequent study on combat behaviour, they are not reported in the current paper.

Video Analysis

All video was initially viewed at full speed. Instances of fighting and evading were counted (see below for descriptions of the different types of behaviours in these two categories). All instances of evading were digitally clipped from the main video, and individually analysed frame by frame using tracking software (Vicon Motus, Vicon Motion Systems, Centennial, U.S.A.). Several measurements were made with that system (see below). Although the majority of the analysis was performed by the first author of this paper, a subset of the interactions were reanalysed by a naïve observer and scores were correlated to ensure that the full analysis was unbiased. Specifically, the angles swept through by both the robber and dodger were correlated across observers during dodging interactions ($r_4 = 0.871$, $P = 0.02$ and $r_4 = 0.862$, $P = 0.03$ respectively), indicating that when the animals were digitally tracked, the starting and end points of the tracking were the same across observers. Paired Wilcoxon tests showed that the mean angles traversed by both robbers and dodgers did not differ between observers (both results were $V = 5$, $P = 0.3125$), which was further supported by dependent-samples t tests ($t_5 = -1.609$, $P = 0.169$ for dodge angle and $t_5 = -1.403$, $P = 0.216$ for robbing angle). Unfortunately, because the Motus system was calibrated differently, distance measurements could not be directly compared across observers. To ensure that the main analysis was consistent, the balanced subset of dodges was split into two groups. Welch's independent samples t tests showed no difference in dodging or robbing angles ($t_{52.655} = -0.5307$, $P = 0.5979$ and $t_{46.317} = 0.2509$, $P = 0.803$, respectively). Additionally, no difference was seen across samples in the mean interanimal distance ($t_{53.944} = 1.229$, $P = 0.2245$).

Differing Types of Defence

Crickets use two main types of defensive techniques during food protection, fighting and evading. Fighting involves one of two tactics, grappling, in which the defender faces the robber and the pair wrestles with interlocked mouthparts and kicking, in which the defender faces away from the robber and kicks at it with its hindlegs (Adamo & Hoy 1995). Evading involves the defender either laterally swerving away from the robber (i.e. dodging) or running directly away from the robber. The number of different types of defences that were used by each animal was counted. Because what was of interest was comparing cricket to rat behaviour, and because rats use only evasion to protect food items, fighting in crickets will not be discussed further in this paper.

Dodging and Running

When comparing species, a methodological problem arises. Species may differ in the behaviour of interest because the opportunity to perform that behaviour may differ between species. For example, in fighting in rodents, the actual frequency of use of class-common defensive tactics may vary, in part, because of the location in which the attacks occur. If a defender remains wedged in a corner facing its opponent, the kind of attack possible differs from a case in which the defender flees in an open space. Similarly, the tactic adopted may differ in structure if used in a constrained versus an unconstrained context (Pellis et al. 1992). In the robbing and dodging paradigm, these problems can be solved by only comparing dodges during which rats are at least one body length away from a wall (Field et al. 1996). This was the methodological approach used for our previous study of robbing and dodging in rats (Bell & Pellis 2011), and is the one that was used for the crickets in the present study.

The one difference between rats and crickets, as already noted, is that in crickets, attackers can approach from any orientation, rather than the more restricted one typical of rats. To adjust for this difference, in crickets, evasions from different orientations were separately measured and evaluated in case the orientation of approach produced differences in evasive strategies. Once the evasions had been selected, Vicon Motus software was used to track the position, digitally, of the most anterior point on the head and the most posterior point on the abdomen of both the robber and defender during the behaviour. The evasion was said to have begun in the first frame in which the defender began to move. The evasion was completed in the final frame of the defender's movement. As is the case in rats, the robber always stopped robbing before the defender stopped dodging or running.

Several measures were extracted from the digitized tracking data. For dodging only, the angle traversed by the defender (the dodging angle) was used, but unlike in our study on rats, the angle traversed by the robber was not used. This was because, in rats, the robber tends to pivot along with the defender, whereas in crickets, the robber tends either to stop once the defender begins to pivot, or follows in a straight line. Therefore, measuring the angle traversed by the robber would not have been meaningful. For all evasions, be they dodges or runs, the path lengths and maximum instantaneous velocities of both the robber and the defender were measured, as well as the distance between the heads of the two animals (the interanimal distance). To ensure that the data on the crickets could be compared to that of the rats, the sequences of robbing and dodging from Bell & Pellis (2011) were reanalysed to measure the path length traversed by both robbers and dodgers.

As in Bell & Pellis (2011), interanimal distance was used both as a continuous measure (tracked through the entirety of the dodge) and at three specific time points. The initial interanimal distance, d_i, was measured in the first frame in which the evasion began. The interanimal distance when the robber stopped robbing, d_r, was measured in the last frame in which the robber pursued the defender. The final interanimal distance, d_f, was measured in the last frame in which the defender evaded the robber, and was taken as the measurement of the distance between the current position of the defender and the position of the robber at the d_r time point. d_f was calculated in this way to account for any lag time in the updating of the information available to the defender. In addition, we wanted to ensure that any irrelevant movement on the part of the robber after the end of its pursuit of the defender, such as walking in the opposite direction, would not be included in the measurement of d_f. See Bell & Pellis (2011) for further details.

In addition to the tracking data, the orientation of the robber with respect to the defender was recorded both at the initiation of the evasive manoeuvres and at their completion. The initiation and the termination of the evasive manoeuvre were defined, respectively, as the first frame in which the defender began to move and the last frame in which the defender moved (see above). We also recorded three categories of approach orientation: the robber could approach from the front (f), facing the head of the defender; from the side (s), facing the defender's flank; or from the rear (r), facing the rear of the defender's abdomen (see Fig. 1).

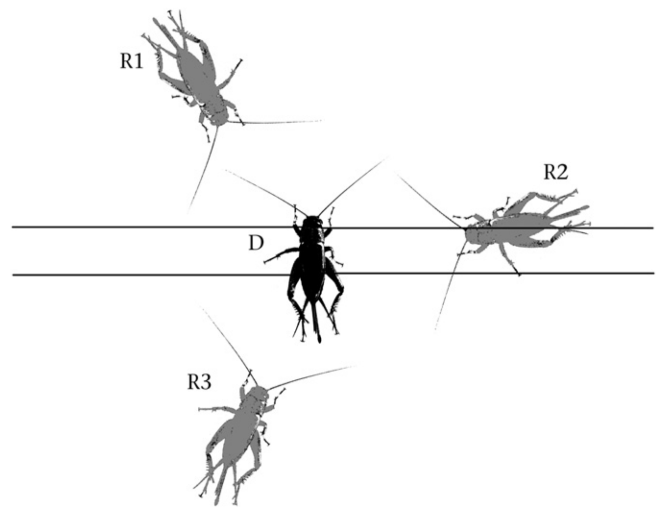

Figure 1. Illustration of how the robber orientation was determined. D is the defender; R1 is a robber in the front orientation; R2 is a robber in the side orientation; R3 is a robber in the rear orientation. Horizontal lines denote the cutoff criteria used.

RESULTS

The results are presented below. See Table 1 for a summary of the predictions made and the results obtained.

Are Crickets Cybernetic Agents?

If crickets use a ballistic rather than a cybernetic rule then, the amount of movement made by each defender in response to a robbing attempt should be static. However, for both running and dodging, in balanced subsets of the first four interactions per animal (the same subsets used hereafter, unless otherwise indicated), the amount of movement (path length) was variable (see Fig. 2). Overall, running crickets had path lengths ranging from 0.919 to 31.188 cm, with a mean ± SD of 10.008 ± 4.685 cm. The coefficient of variation, $\frac{\sigma}{\mu}$, for running crickets was 0.465. For dodging crickets, the range was 3.346–28.404 cm, with a mean ± SD of 10.424 ± 4.708 cm. The coefficient of variation was 0.452.

If, as in rats, dodging were a coupled system in crickets, the movement of the defender and the movement of the robber should be correlated. Using the path length of each animal as a measure of movement, the prediction was supported for the whole data set (running plus dodging) ($r_{279} = 0.634$, $P < 0.001$); (see Fig. 3a). For dodging alone, the rob path versus defender path analysis yielded $r_{54} = 0.548$, $P < 0.001$, and for running, the rob path versus defender path produced $r_{82} = 0.732$, $P < 0.001$.

Are Crickets the Same as Rats?

It was predicted that, if, as was the case in rats, interanimal distance were a controlled variable, the variation for interanimal distance should be less than for any other measure. The coefficient of variation, $\frac{\sigma}{\mu}$, was used, so that variables measured using different scales could be directly compared (Lehner 1996). The prediction was supported (Table 2).

Also, as in rats, if interanimal distance were a controlled variable, it should not be correlated with the movement of the robber. As predicted, the path length of the robber was not correlated with interanimal distance for the entire data set ($r_{279} = 0.18$, $P = 0.762$); (see Fig. 3b). The absence of a correlation was not an artefact of having insufficient data, as further analysis showed that there was sufficient power to detect even a small effect ($P(r \geq 0.2) = 0.923$). Additionally, for dodging alone, rob path versus distance produced $r_{54} = 0.001$, $P = 0.995$, and for running alone, $r_{82} = -0.045$, $P = 0.681$.

If crickets use the same rule for organizing evasive behaviour as rats, one would expect that the pattern of correlations between certain variables would be the same for crickets as they are for rats. Using path lengths from the rat data (Bell & Pellis 2011), the variables measured were compared with the analyses of the crickets when they both dodged and ran. Irrespective of the evasive tactic used, the same pattern was found in crickets, and this pattern matched that of rats when they dodged in almost all comparisons (Table 3). The one exception was that, for rats, interanimal distance and maximum instantaneous dodge velocity were correlated, whereas this was not the case in crickets for either running or dodging.

As with the rats, in the crickets, the initial interanimal distance, d_i, was shorter than the distance after the robber had ceased robbing, d_r, and these were both shorter than the final interanimal distance, d_f (see Fig. 4). The relationships between d_i with d_f, for both the running

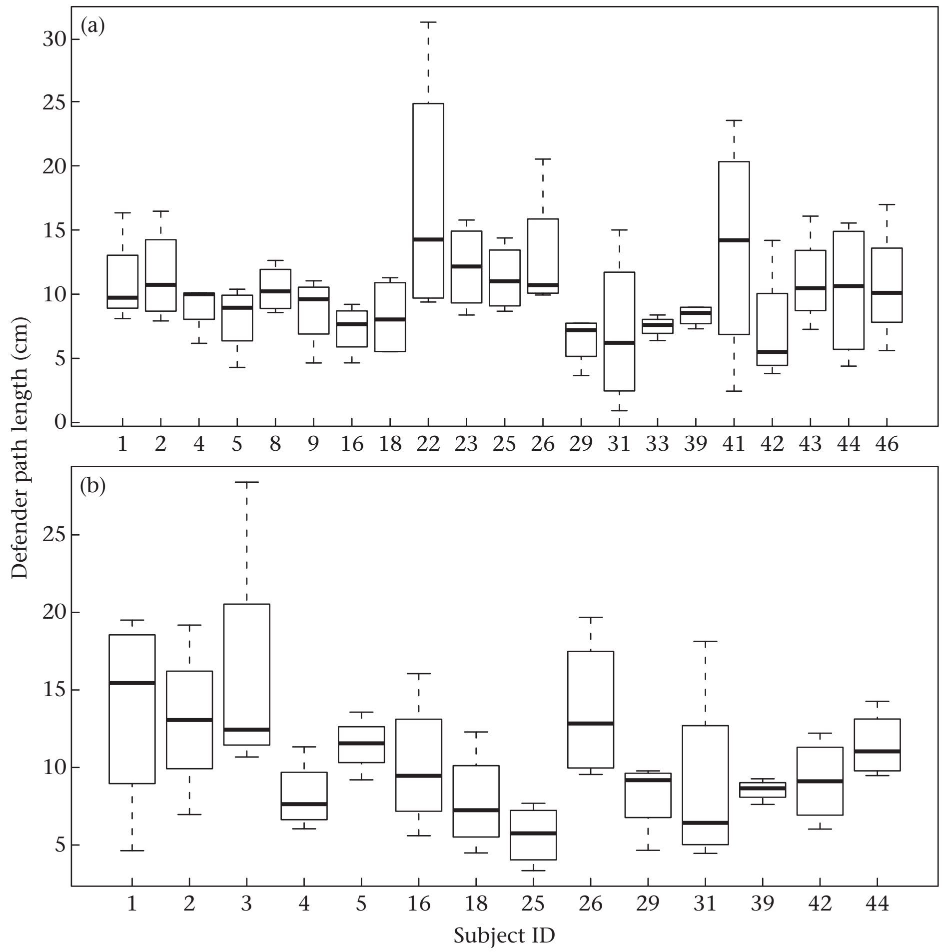

Figure 2. (a) Variability in path length in running crickets over four interactions. (b). Variability in path length in dodging crickets over four interactions. Whiskers indicate range; boxes are first and third quartiles; centre bar is the median.

and dodging conditions, were tested using correlations, neither of which were significant ($r_{82} = 0.023$, $P = 0.832$ and $r_{54} = 0.094$, $P = 0.491$, respectively). This mirrors what was found in rats. In contrast, d_r and d_f were significantly correlated for both running and dodging ($r_{82} = 0.627$, $P < 0.001$ and $r_{54} = 0.648$, $P < 0.001$, respectively), again, as was found in rats.

Is Defender Orientation a Controlled Variable?

It was also predicted that, in addition to interanimal distance, the final orientation of the defender to the robber would be facing away, as was the case in rats (Field et al. 1996). This is what was found (Table 4).

Does Approach Orientation Determine the Type of Evasive Strategy Used?

Using the full data set, the frequencies of the initial orientation of the robber with respect to the defender were recorded (Table 5). A chi-square goodness-of-fit test indicated that defenders that were approached from the front would almost always use dodging as an evasive strategy; whereas defenders that were approached from the rear would almost always use running as an evasive strategy. Defenders that were approached from the side were equally likely to dodge or run ($\chi^2_2 = 222.41$, $P < 0.001$).

Given that the robbers could initiate attacks from different orientations (Fig. 1), and that different approach angles were associated with different evasive tactics (Table 5), approach angle could potentially influence the ability of the defender to coordinate its movements with those of the robber. As shown in the above analysis, the variation in the distance gained from d_i to d_f is partly dependent on the movement performed by the defender concurrently with that of the robber (d_r). Therefore, the strength of the correlated movements by robbers and defenders should be greatest when the robber approaches from an orientation in which the two animals are equally able to counter each other's movements. Approaching from the side would seem to be such an orientation as the defender is equally likely to run or dodge, but, in either case, as the defender moves, the robber can countermove, keeping a constant orientation. Conversely, frontal approaches invariably lead to dodging, and, as pivoting around a vertical axis moves the head away faster than the walking or running needed to maintain the orientation of the robber, this approach orientation should afford the robber the least opportunity to counter the defender's movements finely. The data support these expectations (Table 6). The correlation for defender path versus robber path was strongest for side approaches and weakest for frontal approaches, with rear approaches yielding an intermediate value. With regard to final distance and movement by the defender (defender path versus distance), the strongest correlation was when the robber

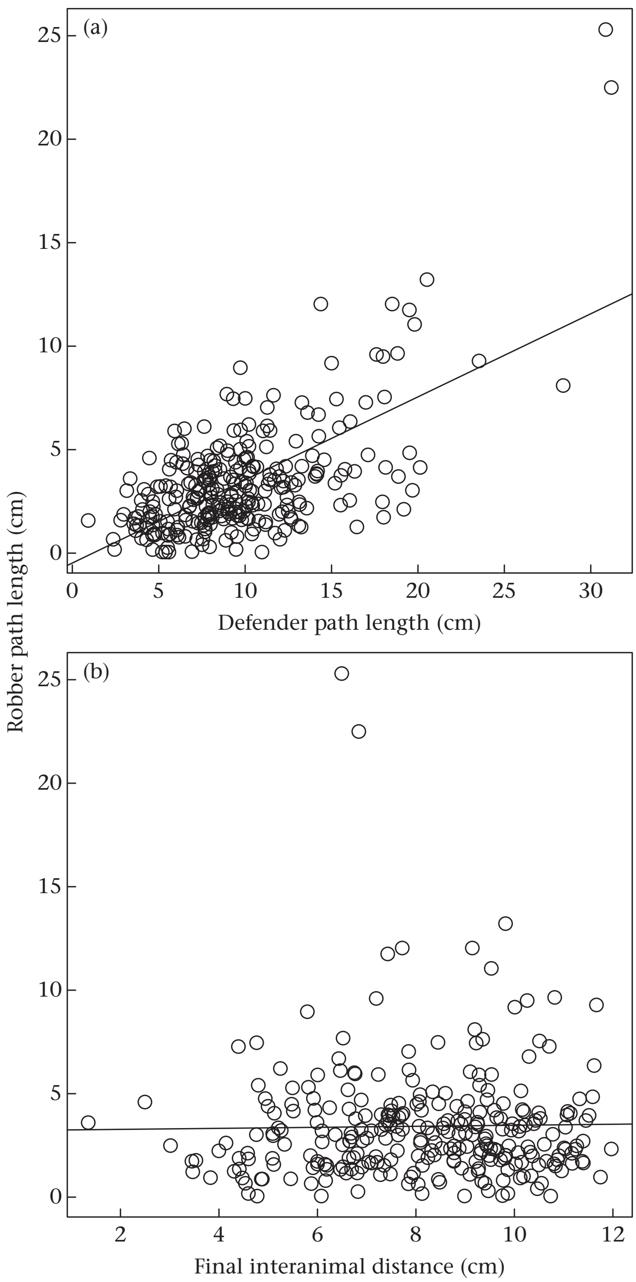

Figure 3. (a) Correlation between robber path length and defender path length. (b). Correlation between robber path length and interanimal distance.

approached from the front. That is, when approached from the front, most of the change in distance from d_i to d_f was determined by the movement of the defender, with little contribution by the movement of the robber.

Table 2

Coefficients of variation, $\frac{\sigma}{\mu}$

Measure	Dodging crickets*	Running crickets†	Rats‡
Dodge path length (cm)	0.452	0.465	0.463
Rob path length (cm)	0.759	0.872	0.867
Distance§ (cm)	0.341	0.193	0.392

* $N = 56$.
† $N = 84$.
‡ $N = 246$.
§ Final interanimal distance, d_f.

Table 3

Pattern of correlations among variables for crickets and rats

Measure	Dodging crickets*	Running crickets†	Rats‡
Dodge path×rob path	**0.548**	**0.732**	**0.512**
Dodge velocity§×rob velocity	**0.503**	**0.321**	**0.162**
Dodge velocity×dodge path	**0.418**	**0.336**	**0.451**
Rob velocity×rob path	**0.806**	**0.635**	**0.433**
Distance**×dodge path	**0.701**	**0.488**	**0.540**
Distance×dodge velocity	0.244	0.113	**0.481**
Distance×rob path	0.008	−0.045	−0.083
Distance×rob velocity	0.053	0.019	0.008

Significant results ($P < 0.05$) are shown in bold.
* $N = 56$.
† $N = 84$.
‡ $N = 246$.
§ Maximum instantaneous velocity.
** Interanimal distance.

DISCUSSION

Cybernetic versus Ballistic Movements

Two aspects of the present findings showed that crickets do not behave ballistically when evading robbing attempts by other crickets. First, defender responses, as measured by distance travelled (path length) were variable (Fig. 2). Given that *T. oceanicus* measure roughly 2 cm in length, the measured range of defender path lengths, less than 1 cm to more than 30 cm, translates into a range of movement from 50% to 1500% relative to body length. Second, although one would expect that the robber's path length and the defender's path length should not be correlated if the movements were ballistic (i.e. the movement of the robber should not be influenced by the movement of the defender, or vice versa, after the initial 'stimulus' event), the data show that a strong correlation exists (see Table 3). Moreover, whereas rats showed a strong correlation between dodge velocity and interanimal distance, crickets did not (Table 3), suggesting that the speed of the movement had more of an effect on the outcome of the defending rat's behaviour than it did for defending crickets. If anything, these data indicate that crickets are less, not more, ballistic in their defensive actions than are rats.

Commonalities in the Defensive Behaviour of Crickets and Rats

As was the case in rats, coefficients of variation, $\frac{\sigma}{\mu}$, indicated that interanimal distance is less variable than the any other measure (see Table 2). Crucially, interanimal distance was also not correlated with the movement of the robber (Fig. 3b) together, these findings constitute the test for the controlled variable used in Perceptual Control Theory (PCT), a cybernetic theory of behaviour, which posits that animals move in order to maintain particular perceptions (i.e. controlled variables) constant (Powers 1973). The lack of variability relative to all other measured variables indicates that interanimal distance is controlled by the defender. The lack of a correlation between interanimal distance and the movement of the robber indicates that, despite disturbances (i.e. robbing attempts), the defender is able to compensate behaviourally to defend the state of the interanimal distance variable. This implies that, rather than responding ballistically to robbing attempts by engaging in stereotypical escape strategies, defenders are constantly monitoring the position of the robber and updating their behaviour accordingly.

The pattern of correlations seen between specific variables in the rat system were the same as those seen in the cricket system, even when the crickets used a different evasive strategy as compared to the rats (Table 3). A finding not seemingly consistent with the cybernetic perspective was that defender path length was always strongly correlated with interanimal distance. Indeed, re-examination of the

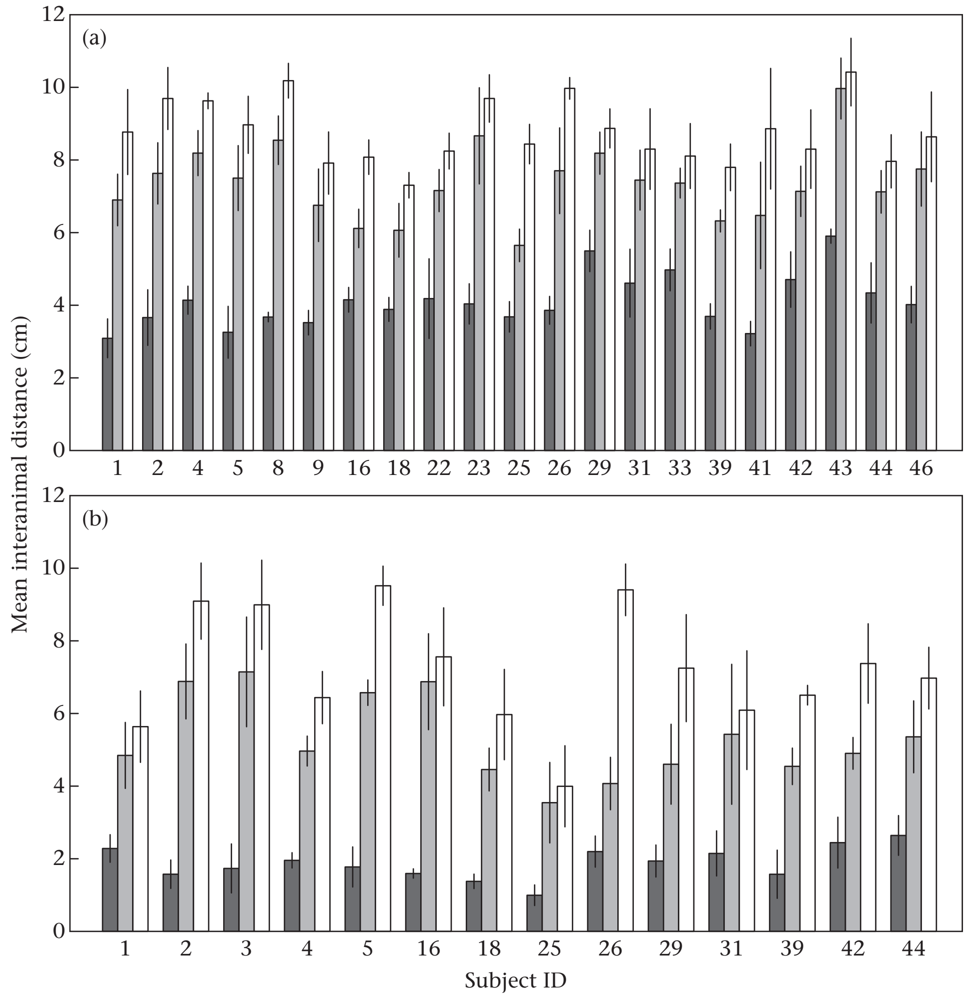

Figure 4. (a) Mean interanimal distance for running crickets at three time points: d_i (■), d_r (■) and d_f (□) (b). Mean interanimal distance for the same three time points as in (a) for dodging crickets.

rat data from Bell & Pellis (2011) showed the same strong correlation in rats as well as crickets (see Table 3). These data indicate that the defender's movement predicts interanimal distance as much as the robber's movement (see Fig. 3). That is, the gained and maintained interanimal distance resulted, in part, from the amount of movement by the defender rather than as movement arising in compensation for the movement by the robber. One way to reconcile these findings is to recognize that the final interanimal distance is composed of two main components: moving to a preferred interanimal distance and moving in response to the approaching movement by the robber. This is reflected in the fact that the defender continues to increase interanimal distance after the robber has ceased its robbing movements (see Fig. 4). Again, this was also found for rats (Bell & Pellis 2011).

The Importance of Orientation

Another possible controlled variable was the final orientation of the robber with respect to the defender. In all but one of the interactions, the defender was facing away from the robber at the end of the encounter, even though encounters were begun in an almost infinite variety of configurations. PCT specifies that controlled variables can be arranged hierarchically; in fact, the hierarchy of controlled variables is that which separates PCT from other cybernetic theories of behaviour, and enables PCT to move beyond explaining isolated components of behaviour to explaining, potentially, most aspects of an organism's behaviour (Powers 1973). That is, controlled variables that are lower in the hierarchy must be controlled before higher-order variables can be controlled. Therefore, the finding that the crickets end their dodges with a specific orientation to the opponent could reflect one of two possible mechanisms. (1) The final orientation and the interanimal distance are controlled simultaneously. That is, they are at the same level on the hierarchy, arranged laterally. (2) The interanimal distance is at a different level on the perceptual hierarchy than the final orientation. That is, the rule for interanimal distance and that for final orientation are fulfiled at different times during the evasion. Indeed,

Table 4
Counts of final defender orientations with respect to robbers

Behaviour	Facing	Side	Away	Total
Run	0	0	192	192
Dodge	0	1	89	90
Total	0	1	281	282

Table 5
Counts of initial robber orientations with respect to defenders

Behaviour	Front	Side	Rear	Total
Run	0	20	172	192
Dodge	67	20	3	90
Total	67	40	175	282

Table 6
Correlations by approach orientation

Measure	Side*	Front†	Rear‡
Defender path×robber path	**0.825**	0.228	**0.586**
Defender path×distance	**0.459**	**0.894**	**0.545**

Significant results ($P < 0.05$) are shown in bold.
* $df = 22$.
† $df = 37$.
‡ $df = 75$.

it is more likely that distance and orientation are at different levels, given that the 'away' orientation is always achieved before the preferred distance. This possibility is supported by the findings in rats, in which the final orientation can be dissociated from the dodging away from the robber (Pellis et al. 1999).

Whereas rats, in most cases, tend to rob from the same approach orientation (Whishaw 1988), crickets will approach from any orientation (see Table 5). Therefore, if the correlation between the defender's movement and interanimal distance reflects the part of the movement required to gain the preferred distance, then different approach orientations should affect the defender's ability to reach that distance, and hence, the amount of movement required. When approached from the front, the defender is most likely to dodge, and when approached from the rear, the defender is most likely to run away (Table 5). In both cases, the defensive action orients the posterior of the abdomen towards the robber, the preferred end orientation for defenders (see Table 4). In addition, these two evasive strategies are also the most efficient means, in each instance, of gaining and maintaining the preferred interanimal distance.

In contrast, when approached from the side, the defender is equally likely to dodge or run (Table 5) to reach the facing-away orientation (Table 4). Conversely, though, from the side approach, the robber is also better placed to counter the movements of the defender. That being the case, the moves and countermoves by robbers and defenders should be most strongly correlated when robbers approach from the side (Table 6). Indeed, the weakest correlation occurs when the robber approaches from the front, as a rapid dodge blocks the robbers approach. Although, in order to gain the preferred interanimal distance, there has to be some degree of correlation between the defender's movement and interanimal distance, given the countermoves afforded the robber from the side approach, this correlation should be strongest for side approaches and weakest for frontal approaches, in which the robber has less capacity to counter the defender's moves, and this is what we found (Table 6).

To gain and maintain the preferred interanimal distance, the defender has to move away from the robber sufficiently to gain that distance and then an additional amount to maintain that distance in compensation for the continued approach of the robber. Therefore, both the correlation between the robber's and defender's movements and the correlation between the defender's movement and interanimal distance are consistent with the defender gaining and maintaining the preferred interanimal distance. These movements contribute to maintaining a constant interanimal distance despite moves and countermoves by the robber (Fig. 3). Thus, all the major facets of the crickets food defence behaviour can be explained in cybernetic terms, with the defender gaining and maintaining a preferred interanimal distance. In this regard, crickets and rats organize their food defence behaviour in the same manner.

As was the case in rats, d_i was not correlated with d_f, but d_r was correlated with d_f. This indicates that the behaviour of the defending cricket at the initiation of an evasion is not dependent on the movement of the robber, but by the time the evasion has ended, the defender is using the movement of the robber to make its decision about when to stop moving. As with the rats, it is likely that, in the absence of information from the robber, the dodging strategy is fairly stereotypical, but that as information from the robber becomes available, the defender will use that information to make decisions. That is, given a particular approach orientation, the defender will use a particular evasive strategy initially, but as the robber continues to move, the defender will compensate for those movements.

The alternative to tracking the robber's movements is to use a ballistic action that is either reflexive, simply respond to the looming stimulus, or some calculated response based on contextual cues (e.g. Whishaw & Gorny 1994). The tests of the predictions support a cybernetic-tracking mechanism (see Table 1). Second, there could be alternative perceptions to track (see e.g. Powers 1973; Marken 1988, 2009; Cziko 2000), and indeed, it seems that there are at least two (distance and orientation) and these combine in ways to increase the variability of the movement performed in evasions.

It is possible that the behaviour seen in the crickets might actually result from two competing motivations that just happen to balance out in our study. The two motivations include eating the catfood and cannibalizing the other cricket. Given that food-deprived female crickets of some species have been known to readily cannibalize conspecifics of similar size (unpublished observations), it is certainly a possibility. However, we think this is unlikely given that, before the food was introduced to the arena, the pairs of crickets were habituated to the enclosure together. During that time, no attempts were observed by any cricket to cannibalize another in any of the trials, nor were any attempts observed during the pretesting we did to determine the appropriate level of food deprivation required to produce robbing and dodging behaviour. That is, not a single incidence of cannnibalism was observed in more than 60 pairs of crickets (including 'pretest' pairs).

Moving Forward with Cybernetics

There is a growing recognition that simple rules can generate complex behaviour (Marken 1988; Alberts 2002; Barrett 2011). Moreover, these simple rules can be modelled using computer simulation techniques like agent-based modelling (Luke et al. 2005), which show that complex outcomes can arise by the agents following simple rules, mimicking the behaviour seen in real animals (e.g. Schank & Alberts 1997; Schank et al. 2004; Muro et al. 2011). Consistent with the present findings is that these simple rules are often in the form of maintaining some perception constant (Bell & Pellis 2011). Therefore, we propose that for any new behaviour to be investigated, the first task is to identify the perception(s) being maintained constant (Cziko 2000). Once that constancy is identified, then the factors contributing to the particular behavioural outcomes can be characterized. For example, in the case of the crickets defending their food, the orientation of the approach of the robber has a major impact both on the particular defensive tactic used and the ease with which the perceptual constancy, in this case interanimal distance, can be maintained. Such an approach can be particularly useful for comparisons across species and contexts, as it provides a firm theoretical and methodological framework within which to identify similarities and differences (e.g. Schleidt & Crawley 1980; Finley et al. 1983; Pellis et al. 2009; Pellis & Bell 2011). That is, different animals may follow the same rules, but differ in the implementation of those rules.

The present results mirror those of another instance in which both mammals and arthropods follow the same simple cybernetic rule. When catching a ball, humans keep the orientation of the ball constant, relative to the horizon, and speed up or slow down their movement accordingly (McBeath et al. 1995). Similarly, when dogs chase and catch frisbees, they use the same rule (Schaffer et al. 2004), as do dragonflies catching prey (Olberg et al. 2000). That is, in all these cases, including crickets and rats protecting a food item, the animals keep a simple perception constant and in maintaining this constancy, variable behaviour is produced (Powers 1973). Although there may be differences in both sensory and motor capabilities that make for subtle differences in being able to detect disturbances and engage compensatory action across species, especially for species spanning different phyla, our work, along with that cited, strongly supports the idea that all organisms use simple cybernetic principles in structuring at least some of their interactions with the world, a point repeatedly converged upon by both physiologists (e.g. von Holst & Mittelstaedt 1950; Bernstein 1967) and ethologists (e.g. von Uexküll 1921; Golani 1976).

Conclusion

Like rats, crickets are able to protect food from being stolen by other crickets by using evasive strategies. The two types of evasion used by crickets (running and dodging) both adhere to the cybernetic 'gain and maintain the preferred interanimal distance' rule that is used by rats, despite the large differences in their body morphology and their mechanics of locomotion. Not only does this show that cybernetic rules can be applied to two different organisms, but also to organisms from vastly different evolutionary lineages, supporting the idea that cybernetic rules may be widely, if not universally applicable (Powers 1973). This possibility has wide-ranging implications, both for understanding the behaviour of organisms and for the development of artificial systems (e.g. robotics).

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