

Catch fast and kill quickly: do tiger beetles use the same strategies when hunting different types of prey? (#25299)

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Catch fast and kill quickly: do tiger beetles use the same strategies when hunting different types of prey?

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Background. Tiger beetles (Coleoptera: Carabidae: Cicindelinae) are fast running predatory insects preying on different small insects and other terrestrial arthropods. Prey is located by sight and captured after short and fast pursuit interspersed with pause-and-look behaviour. At least some tiger beetle species can recognise the size and location of prey using memory, which most probably allows them to achieve greater hunting success.

Material and methods. Two eurytopic tiger beetle species known to occur in different types of habitat were used in the study: *Cicindela hybrida hybrida*, a very common central European beetle found even in artificial habitats such as sandy roads or gravel pits, as well as *Calomera littoralis nemoralis* – a species widely distributed in southern European countries and occurring on sandy sea beaches, in salt marshes, as well as on sandy banks of rivers and lakes. Both species are very similar in terms of their body size. Specimens used in the study were collected in the field and later tested in the laboratory. We checked whether tiger beetles use different hunting strategies when attacking prey of different sizes and abilities to escape as well as whether the sex of the studied species makes a difference in its hunting behaviour.

Results. The hunting strategies of both studied tiger beetle species consist of the following main phases: identification, pursuit (often with stops), attack, and optional release of the prey, and then the secondary attack, abandonment of the prey, or consumption of the prey. Considerable differences were noticed in the course of hunting depending on the type of prey, its movement ability and escape potential. Caterpillars were attacked without pursuit, stabbed mostly in the head or directly behind the head where a concentration of nerves in the insect body as well as the main muscles responsible for walking are located. Effective attacks on beetles were executed in the place where the connection between the thorax and the abdomen is. *Calomera littoralis* strongly preferred slow moving prey, while *Cicindela hybrida* preferred in equal measure slow moving prey and medium-sized fast moving prey. The experiment on the preferred size of prey has indicated small beetles and small caterpillars as favoured by *Calomera littoralis*, while *Cicindela hybrida* preferred medium-sized fast moving prey and large caterpillars. **Discussion.** The hunting behaviour of *Calomera littoralis* and *Cicindela hybrida* is complicated and includes a number of phases allowing to locate, capture and kill the prey. Beetles are able to discriminate between different types of prey and apply different behavioural tactics to hunt it. As the particular strategies are used to increase hunting success, and as a result allow to accumulate energy for future activity of the predator, it can be expected that such a type of hunting behaviour is characteristic also of other tiger beetle species.

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Abstract

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Key words: hunting behaviour, prey-predator interactions, prey selection, Cicindelinae, Coleoptera

Introduction

Tiger beetles (Coleoptera: Cicindelidae) are small to medium-sized predatory beetles hunting for a variety of small, mostly typically epigeic invertebrates. Most species of these fast running predators are characterised by diurnal activity (Pearon & Vogler, 2001). Although they typically use sight as the main tool for locating their fast moving prey (Świecimski, 1956; Gilbert, 1987; Gilbert 1997), it is known that sometimes even day active species can capture prey in complete darkness, which can suggest that other senses, such as chemoreception, hearing or touch, may play an important role in searching for prey in this beetle group (Riggins & Hoback, 2005). A large spectrum of prey, including e.g.: Coleoptera, Hymenoptera, Orthoptera, larvae of Lepidoptera, but also spiders or small crustaceans, makes these beetles a group of opportunistic hunters (Laroche, 1974; Pearson, 1988; Pearon & Vogler, 2001) which can sometimes use also plant material as food (Hori, 1982; Hill & Knisley, 1992; Jaskuła, 2013). Although the diet of tiger beetles as a group is rather well known, little is known about prey preferences and/or hunting strategies of most of tiger beetle species. Generally, a tiger beetle locates its live prey visually and after that starts to pursue it in the course of active running interspersed with pause-and-look behaviour (Gilbert, 1987; Gilbert, 1997) or the beetle waits in a shaded area and attacks the prey when it is approaching (Kaulbars & Freitag, 1993). Pearson and Klisley (1985) have observed that if the attack is successful, the beetle grabs the prey with its mandibles. Before the prey is consumed, the beetle starts to test it in terms of size, hardness, and noxious chemicals. When the prey is too large and/or is inedible because of some chemical substances, it is quickly released. Moreover, Świecimski (1956) has noted that tiger beetles use memory of the shape and location of prey to distinguish small prey located at a shorter distance from large prey placed at a greater distance. Flexibility in terms of hunting strategies usually brings a significant benefit to the predator. Predatory species which use different behavioural tactics can feed on a larger variety of food, and as a consequence, they can often easier survive in changed habitats with a low number of specific prey (= higher adaptation to environmental changes) and/or colonise new areas (= larger dispersal power). Moreover, individuals of such opportunistic species can easier and faster

accumulate energy needed during the reproduction process, which is especially important in the case of females (Curio, 1976).

The aims of this study were: 1/ to check if tiger beetles use different hunting strategies when attacking prey of different sizes and abilities to escape – since tiger beetles encounter different types of prey randomly, it can be expected that they should apply their behavioural strategies flexibly and quickly according to the type of prey encountered; 2/ to verify if sex of the studied species makes a difference in its hunting behaviour – as most Cicindelidae are characterised by a larger body size in females, it can be expected that females would prefer to hunt for larger prey than males. To test our hypotheses, we have chosen two tiger beetle species: 1/ *Calomera littoralis nemoralis* (Olivier, 1790), which is one of the most common Cicindelidae species in the Mediterranean region, having one of the widest habitat ranges among all tiger beetles known from this region (Wiesner, 1992; Jaskuła, 2011; Jaskuła, 2015; Jaskuła & Rewicz, 2015; Jaskuła et al., 2015, Jaskuła et al., 2016), and 2/ *Cicindela hybrida hybrida* Linnaeus, 1758, the most common tiger beetle species known from Central Europe, also recognised as an eurytopic species according to habitat types (Wiesner, 1992; Jaskuła 2003).

Material and methods

Predator

Adult beetles from both species were collected with an entomological net in August 2008. *Cicindela h. hybrida* was collected in Krzywie (51°51'26.49"N, 19°26'48.18"E) in an old gravel pit in Central Poland and *Calomera littoralis nemoralis* in the mouth of the Evros River (40°49'9.29"N, 25°59'28.59"E) on the Greek marine sandy beach. A few dozens of males and females from both species were caught and taken to laboratory conditions. Specimens were kept separately in transparent plastic containers with 2-cm layer of sand at the bottom. The proper humidity was maintained through regular water spraying. The experiment was carried at the stable temperature of 24°C and in the natural photoperiod.

The sampling in Greece was performed during the TB-Quest I Expedition organised by the corresponding author and was financed partially from the internal funds of the University of Lodz.

Prey

Based on earlier personal observations in the field, six taxa of common prey of tiger beetles were chosen for the study. These were: larvae of grasshoppers (Orthoptera: Acrididae), *Bembidion lampros*/*B. properans*, *Calathus melanocephalus*, *C. fuscipes* (Coleoptera: Carabidae), and larvae of Symphyta (Hymenoptera). *Bembidion lampros* and *B. properans* were considered as one type of prey due to their similar weight and size and because of difficulties in correct identification of species when the beetle is alive and fast moving. Caterpillars of Symphyta correspond to the next three stages of their development (Table 1). As different types of prey possess different abilities to escape, we have divided them into three groups: 1/ Orthoptera – possess a high escape potential as they have jumping legs and can jump a long distance away; 2/ ground beetles (Carabidae) – have a medium escape potential as they can run fast and dodge, or turn over, additionally they have the ability to exude a chemical weapon in emergency situations; 3/ caterpillars – are unable to move quickly or dodge and turn over so they are characterised by a small escape potential (Tab 1). Caterpillars and grasshopper larvae were collected in the field by entomological net, and carabids by exhaustor. Different types of prey were collected on the day of experiment or one before, and they were stored individually in a refrigerator in order to reduce their mortality.

Experimental procedure

We conducted experiments in 20-cm diameter plastic buckets with a 2-cm layer of sand at the bottom. Each individual was kept separately. All experiments were conducted between 10:00 and 14:00 hours, during the highest hunting activity of tiger beetles. In each experiment, each specimen was used only once.

Types of experiment

We conducted three experiments.

Prey escape potential

Each specimen (both species, both sexes) got three different types of prey dropped into the experimental bucket at the same time. Preferences of the prey type were noticed after the prey was caught and eaten. Feeding happened in the mornings (10:00) or at noon (12:00), and after two hours the buckets were examined to check which prey was caught and eaten. The types of prey represent different escape potentials: low – medium caterpillar of Symphyta, medium – *Calathus melanocephalus*, high – grasshopper. The number of repetitions differ between species and/or sexes (Table 2) because a different number of species and sexes were collected, and if a

tiger beetle specimen refused to attack the prey three times (three periods of two hours' feeding), it was eliminated from this experiment.

Prey size

Experiment 2 consisted of two parts. First, each specimen (both species, both sexes) got three carabid beetles of different size (Table 2) dropped into the experimental bucket at the same time. ~~Preferences of the prey size were noticed after the prey was caught and eaten. Feeding and checking were conducted under the same conditions as in Experiment 1.~~ There were 48 random individuals in each size of carabid beetles measured and weighted (Table 1). In the second part of the experiment, each specimen (both species, both sexes) got three caterpillars in three different sizes (Table 2) dropped into the experimental bucket at the same time. ~~Preferences of the prey size were noticed after the prey was caught and eaten. Feeding and checking were conducted under same conditions as in Experiment 1. There were 56 random individuals in each size of caterpillar measured and weighted (Table 1).~~

Hunting strategies

In Experiment 3, we checked if tiger beetles use different hunting strategies for different prey types. Specimens (both species, both sexes) were observed separately and every step of their hunting behaviour was noted on special work cards. On the cards, we included each major step of hunting sequences. Types and sizes of prey that were used in this step of the experiment were a result of the two previous experiments and included the most preferred choices of each species and sex of tiger beetle (Table 2).

Data analysis

In Experiment 1 and 2, we counted the number of repetitions and drew diagrams of preferences in terms of type and size of prey. In Experiment 3, the steps of hunting sequences were written down on special experimental cards, and then counted for each species and sex. Several types of specific behaviour were counted for both sexes for each type of prey. Each step of the hunting strategy was checked for significant differences between the sexes. Thus obtained data were used to draw diagrams. The frequency of particular steps of the hunting strategy was calculated as a percentage of such behaviour in relation to all possible behaviours between two successive stages of hunting, and was indicated by the width of the line in the diagram and by the number above the line. The sequence of the hunting strategy was analysed and the frequency of key steps in each species and strategy was calculated.

Preferences regarding the type and size of prey for both sexes and species of tiger beetles as well as key steps of the hunting sequence were analysed using Pearson's chi-squared test.

Results

Prey escape potential

In 91% of cases (n=69), *Calomera littoralis* males chose caterpillars, in 8% (n=6) ground beetles, and in 1% (n=1) a grasshopper. Females in 98% of cases (n=46) preferred caterpillars, and once a ground beetle (2%, n=1) was chosen (Fig. 1). In this case, there is a clear preference for caterpillars as the most common type of prey for both males and females of *Calomera littoralis* (Tab. 2). *Cicindela hybrida* males chose caterpillars in 49% of cases (n=27) and ground beetles in 51% of cases (n=28). Females chose caterpillars in 44% of cases (n=31), ground beetles in 52% of cases (n=36), and grasshoppers in 4% of cases (n=3) (Fig. 1). The total number of repetitions is presented in Table 2. There is no dominant type of prey for males and females of *Cicindela hybrida* ($\chi^2 = 0.260$, $df = 1$, $p = 0.05$).

Preferences of the prey type between *Cicindela hybrida* and *Calomera littoralis* differ significantly ($\chi^2=65.18$, $df=1$, $p=0.05$).

Prey size

Size preferences – carabid beetles

In 91% of cases (n=40) *Calomera littoralis* males chose a small beetle as prey and in 9% cases (n=4) it was a medium beetle. In all the cases, females chose a small beetle (n = 47) (Fig 2A). This species of beetle clearly prefers small prey.

In 30% of cases (n=14) *Cicindela hybrida* males chose small beetles (*Bembidion lampros/properans*), while in 66% of cases they preferred medium beetles (*Calathus melanocephalus*), and in 4% (n=2) large beetles (*C. fuscipes*) were eaten. Females in 57% of cases (n=30) chose small beetles and in 43% of cases (n=23) medium beetles (Fig. 2A). The total number of repetitions is presented in Table 1. The size of the preferred beetle prey was significant between the sexes of *Cicindela hybrida* ($\chi^2=6.830$, $df=1$, $p=0.05$).

Preferences of the beetle prey size between *Cicindela hybrida* and *Calomera littoralis* differ significantly ($\chi^2=54.522$, $df=1$, $p=0.05$).

Size preferences – caterpillars

In 51% of cases (n = 31) *Calomera littoralis* males chose small caterpillars, in 27% of cases (n=16) medium caterpillars, and in 23% of cases (n=13) large ones. Females chose small caterpillars in 52% of cases (n=25), in 25% of cases (n=12) medium ones, and in 23% of cases (n=11) large ones (Fig. 2B). ~~The total number of repetitions is presented in Table 1.~~ There were no significant differences between the sexes of *C. littoralis* and the preferred caterpillar size ($\chi^2=0.047$, $df=2$, $p=0.05$).

In 22% of cases (n=13) *Cicindela hybrida* males chose small caterpillars, in 31% of cases (n=18) medium ones, and in 47% of cases large ones. Females chose small caterpillars in 19% of cases (n=10), medium ones in 34% (n=18) of cases, and large ones in 47% (n=25) of cases (Fig 2B). ~~The total number of repetitions is presented in Table 1.~~ There were no significant differences between the sexes of *C. hybrida* and the preferred caterpillar size ($\chi^2=0.243$, $df=2$, $p=0.05$). Preferences of the caterpillar prey size between *Cicindela hybrida* and *Calomera littoralis* differ significantly ($\chi^2=25.062$, $df=1$, $p=0.05$).

Hunting strategies

We tested if there were differences between sexes of each species in each major step of the hunting scenario. In most cases, we found there were no differences between the sexes, and we decided to simplify the results of Experiment 3 and to summarise repetitions of both sexes of each species.

Scenario of hunting prey with different escape potentials

Regardless of the type of prey, the first steps of the hunting pattern were the perception of the prey, followed by the turning of the hunter toward the prey. Next the tiger beetle freezes for a moment (stops), and starts to chase the prey fast in the case of beetles, or nobble the prey slowly in the case of slow caterpillars. The mandible attacks were conducted against three parts of the prey body: front, middle and back. In the case of beetle prey that meant: the front part - the head; the middle part - the narrow part between the pronotum and the abdomen; the back part - the abdomen. In the case of caterpillar prey, it was more simple: the front part - the head, or the initial sections of the thorax; the middle part - the final sections of the thorax, or the initial sections of the abdomen; the back parts - the abdomen. We can observe that both hunter species prefer to attack caterpillars in the front or middle part of the body, and avoid the back part. Tiger beetles hunting fast moving prey prefer attacking its middle part or - less often - the back part. We noticed only one attack on the front part of a beetle (Fig. 3C). After the attack (stabbing with

the mandibles), the hunters followed two scenarios; either the attack was lethal and immediately after they ate the prey or the prey managed to escape after the first stab. After releasing the prey, the hunters mostly retried the attack (re-attack), even repeatedly to achieve the lethal effect. Less often the hunters abandoned (abandonment of the prey) the dead prey, or finished the attack by leaving the wounded prey (ineffective attack). Sometimes after eating the prey only partially, or after an ineffective attack, they would abandon the prey and start digging the ground with mandibles.

Behavioural prey-type specificity

The beginning of the hunting strategy of *C. hybrida* towards beetles and caterpillars looks similar - after visual prey perception, the hunter turns toward the prey and after a moment of observation chases and stabs the prey. The main difference between the strategies concerns the site of the attack. Almost all attacks towards beetles (96%) were conducted in the middle part of their body, in the case of caterpillars the back part was less preferable (9%), most favourable were the front part (50%) and the middle part (35%) ($\chi^2 = 55.18$, $df = 2$, $p < .001$). (Fig. 3B & D). After the first attack, the prey was released and attacked again. Caterpillars were abandoned more often than beetles (12% to 3% respectively) ($\chi^2 = 4.63$, $df = 1$, $p < .05$). The last stage of the hunting strategy was also different, *C. hybrida* searched the area more often after hunting caterpillars (37% to 17%) ($\chi^2 = 7.14$, $df = 1$, $p < .05$).

The hunting strategy of *C. littoralis* against beetles and caterpillars shows more differences than similarities (Fig. 3A & C). The first clear difference is a lack of chase stage in the case of caterpillars (11% to 88% when attacking beetles) ($\chi^2 = 91.62$, $df = 1$, $p < .05$). The attack against beetles was conducted in 76% in the middle part of the body, and against caterpillars in the front part (39%) and the middle part (57%), which was a significant difference between those types of prey ($\chi^2 = 38.95$, $df = 2$, $p < .00001$). After the first attack, we can observe quite a high level of killed and eaten prey (42% for beetles and 57% for caterpillars), but still there was no significant difference between types of prey. However, killed caterpillars were abandoned more often than beetles (17% to 3 % respectively) ($\chi^2 = 8.95$, $df = 1$, $p < .05$). Altogether it indicates the predator's greater efficiency when hunting beetles (91% killed and eaten prey, compared to 70% killed and eaten caterpillars). *Calomera littoralis* searches the area more often after hunting beetles than caterpillars (46% to 26%) ($\chi^2 = 6.41$, $df = 1$, $p < .05$).

Behavioural hunter-species specificity

The hunting pattern for beetles was quite simple for both hunter species. The main attack sequence was straightforward: prey perception, turn, stop, chase, attack on the middle part of the body, releasing the prey, re-attack, eating the prey. Deviations from this pattern were not abundant. We can observe that tiger beetles clearly prefer attacking the middle part of the prey (*Calomera littoralis* 76%, *Cicindela hybrida* 96%) (Fig. 3C & D), and almost ignore the front and back parts. The difference between tiger beetle species appears after the attack, *C. littoralis* in 58% of cases released the prey after the first stab ($n=44$), and *C. hybrida* in 78% of cases ($n=59$) ($\chi^2 = 6.78$, $df = 1$, $p < .05$). As a consequence, also the re-attack occurred more often in *C. hybrida* than in *C. littoralis* (75% $n=57$ to 51% $n=39$ respectively). *Calomera littoralis* kills faster than *C. hybrida*, we can observe 42% of killed beetles after the first attack, and only 22% in the case of *C. hybrida* ($\chi^2 = 6.78$, $df = 1$, $p < .01$). However, effectiveness of hunting beetles between *C. littoralis* and *C. hybrida* was almost identical with 91% $n=69$ and 89% $n=89$ of respectively killed and eaten prey. One more curious behaviour occurred much more often in the *C. littoralis* pattern. This species searched the area after hunting in 42% of cases, which is significantly different than 14% of such behaviour instances in *C. hybrida* ($\chi^2 = 14.74$, $df = 1$, $p < .001$).

The hunting strategies towards caterpillars were more complicated than towards beetles. We can observe the first difference between hunter species in chasing or approaching the prey after turning towards it. *Cicindela hybrida* uses the same pattern as towards beetles - it freezes for a moment and then chases the prey (94%, $n=64$) (Fig 3B). Surprisingly, *C. littoralis* after freezing approaches slowly (11%, $n=8$, fast chase) the prey before stabbing ($\chi^2 = 100.31$, $df = 1$, $p < .001$). Both hunters stab the caterpillar mostly in the head or the middle part of the body, less than 10% of attacks were carried to the back part. After the first attack, *C. littoralis* released the prey in 43% of cases ($n=33$), and *C. hybrida* significantly more often (76%, $n=52$) ($\chi^2 = 16.21$, $df = 1$, $p < .001$). In consequence, the re-attack occurred only in 24% of cases for *C. littoralis* and in 66% of cases for *C. hybrida* ($\chi^2 = 26.33$, $df = 1$, $p < .05$). *Calomera littoralis* has a higher level of success of the first attack and kill, as it happened in 57% of cases and only in 24% of cases the first stabbing by *C. hybrida* resulted in a killed and eaten caterpillar ($\chi^2 = 16.21$, $df = 1$, $p < .001$). However, overall hunting effectiveness was similar, and both hunting species killed and ate more than 70% of their prey.

Discussion

Both tiger beetle species used in the experiments are known as predators hunting different small arthropods (mainly epigeic insects) but occasionally eating also dead insects (*Cicindela hybrida* – Świecimski, 1956) or even plant material (*Calomera littoralis* – Jaskuła, 2013). That makes both species opportunistic predators hunting for the type of prey which is actually available in the beetle's habitat. Our results clearly confirm the ability of *Cicindela hybrida* and *Calomera littoralis* to catch and kill different types of prey in terms of body size and mobility. On the other hand, we have noted that in the case of prey mobility, a large number of *C. littoralis* (91 or 98% depending on the beetle sex) and almost half of the studied specimens of *Cicindela hybrida* (44 or 49% depending on the beetle sex) preferred caterpillars which cannot escape faster than fast running beetles. Such a strategy can be clearly explained when the energetic cost of such a predatory behaviour is analysed. From the predator's point of view, predation is a very energy-consuming activity as prey needs to be located, which often takes time, caught and killed, which requires additional energy for a potential fight with the prey, and is often dangerous also for the predator as it can be injured. And if the attack is not successful, the predator needs to look for another prey and repeat all the parts of such a behaviour again and again (Bonsall & Hassell, 2007; Creel & Christianson, 2008). Taking this into consideration, hunting for slow moving prey characterised by a small escape potential is much better as it allows the predator to preserve more energy for any future activity. On the other hand, in the case of *C. hybrida*, fast moving beetles were noted as very important prey, too (51 or 52% depending on the beetle sex). This confirms earlier observations by Świecimski (1956), who noted that this species chooses fast moving prey as their faster movement can be probably easier perceived by the predator. On the other hand, ignoring this type of prey by *Calomera littoralis* (if slow moving caterpillars were available as food) can be probably explained by chemical defence regularly used by different ground beetle species, including *Calathus* and *Bembidion* beetles (Moore, 1979), as it is known that tiger beetles often release prey which emits chemicals (Pearson & Knisley, 1985). In the case of habitats where *Cicindela hybrida* occurs, both *Calathus melanocephalus* and *Bembidion lampros/properans* are regularly observed, and the tiger beetle was observed hunting for them (Jaskuła – personal observations), while in the case of habitats occupied by *Calomera littoralis*, these species of ground beetles are rarely encountered or even do not occur at all. As a consequence, we cannot exclude the assumption that a lack of potential contact between the prey and the predator under natural conditions does not play a role in choosing the prey under

laboratory conditions. As experiments were made in small containers with a flat surface of substrate at the bottom, we can exclude the role of target elevation in prey selection by tiger beetles as was suggested by Layne et al. (2006). Also, the role of the temperature, a factor noted as important in tiger beetles hunting in the wild (Dreisig, 1981), can be ignored as all the experiments were made under the same conditions.

The size of prey is the second important parameter playing a crucial role in hunting success of the predator (Alcock, 1993). In the case of the studied tiger beetle species, we have noted that *Calomera littoralis* preferred small prey with a small (caterpillars) and fast (ground beetles) escape potential (51-100% depending on the beetle's sex and type of prey), while the medium-sized prey was chosen only in the case of slow moving caterpillars. A different situation was observed in the case of *Cicindela hybrida*. In this species, medium (43 or 66% depending on the beetle sex) and small-sized prey (43% in the case of females) was chosen only in the case of fast running ground beetles, while in the case of slow caterpillars much bigger individuals were attacked (47% for both beetle sexes). The body length of both studied tiger beetle species is very similar. On the other hand, *Cicindela hybrida* has longer mandibles (up to 10% in females compared with *Calomera littoralis*; Jaskuła, 2005; Jaskuła – unpublished), the elements of mouthparts which play a key-role in catching and cutting the prey. Such a difference in the length of mandibles can explain the preference for bigger prey by *Cicindela hybrida*, especially in females, as it is known that longer mandibles allow them to keep a wider distance between the end parts of these organs when the mandibles are fully opened, and as a result potentially bigger prey can be caught (Pearson & Mury, 1979). As mentioned above, hunting for bigger and easy to catch prey has great evolutionary sense from the predator's point of view, as such a strategy allows to keep energy for future activity of the predator. This seems to be especially important in the case of females which need to accumulate much more energy for the breeding season than males (e.g.: for production of eggs and finding the right place to lay them) (Thornhill & Alcock, 1983).

Both studied tiger beetle species located their prey visually and then tried to catch it after fast active pursuit interspersed by short stops. All these elements of hunting behaviour were earlier noted in *C. hybrida* (Świecinski, 1956) as well as in other tiger beetle species (e.g.: Gilbert, 1986; Gilbert, 1987; Gilbert, 1997) and seem to be very typical for all beetles classified in this group, even if at least some diurnal species can locate and catch prey without sight (Riggins &

Hoback, 2005). Although there are no data about the physiological base of such a pause-and-look behaviour in the case of the species studied by us, it is known that in other tiger beetles such a behaviour plays a very important role in the actualisation of prey position as the signal sent from ommatidia in the beetle's eyes to its central nervous system is slower than the speed of running tiger beetle (Gilbert, 1997). As in the cases of earlier studied tiger beetle species (e.g.: Świecimski, 1956; Pearson & Knisley, 1985; Gilbert, 1987; Lovari et al., 1992; Gilbert, 1997; Zurek et al., 2014), we have noted that *Calomera littoralis* and *Cicindela hybrida* use mandibles to test the size, shape, and probably also noxious chemicals of their prey before it is killed and eaten. The significant difference in the "testing behaviour" observed by us between both species (releasing of prey in 58% cases in *Calomera littoralis* and 78% in *Cicindela hybrida*) is most probably connected with the size of their preferred prey. Smaller prey can be faster and more easily tested than the bigger one, and as a consequence can be killed quicker. Exactly such an observation was noted in the case of *Calomera littoralis* which preferred smaller types of prey. On the other hand, *Cicindela hybrida*, which hunted mainly medium and/or larger prey, was characterised by a much longer "testing behaviour" (prey released in 75-76% of cases after the first attack). Such a behaviour seems to play an important role as the final hunting success was very similar in both species.

Both tiger beetles clearly preferred attacking in the middle (the connection between the thorax and the abdomen in ground beetles) or in the middle or front part of the prey (the head or the thorax in caterpillars), almost ignoring the back parts. The explanation of such a hunting strategy is rather simple as the main muscles responsible for walking are placed in the insect's thorax. Moreover, in the front part of the insect body (the head and partly the thorax), the main part of the insect nervous system is placed (Gilliot, 2005). As a consequence, an attack on these body parts usually allows to immobilise and kill the prey quickly. Although there is only a small number of studies on the hunting behaviour of tiger beetles, and therefore we cannot provide similar results from the literature, single field observations of the second author upon some European (*Cephalota chiloleuca*, *C. circumdata*, *Cicindela campestris*, *C. sylvatica*, *Cylindera germanica*, *Cylindera trisignata*, *Myriochila melancholica*) and North African species (*Grammognatha euphratica*, *Lophyra flexuosa*) suggest that this is a common strategy among tiger beetles. Moreover, the same or very similar strategy can be found in other predatory insects which need to catch prey quickly, such as some diurnal ground beetles (e.g.: Bauer, 1981; Bauer

1985) as well as other terrestrial arthropods, including jumping spiders (e.g.: Jackson & Pollard, 1996; Bartos, 2002; Bartos, 2007; Bartos, 2008; Bartos & Minias, 2016).

Conclusions

The results of the presented study clearly confirm that the hunting behaviour of tiger beetles is complicated and multi-staged. *Calomera littoralis* and *Cicindela hybdrida* are able to discriminate between different types of prey (both according to their size and escape potential) and apply different behavioural tactics to hunt them. Particular strategies are used to increase hunting success and as a result allow to accumulate energy for future activity of the predator. Although there is a lack of similar data for most of other tiger beetle genera, we should expect that this type of behaviour, very logical in the wide evolutionary sense, is characteristic of the entire group. On the other hand, future studies, especially on nocturnal and/or arboreal tiger beetle species which occupy different types of environment or hunt at night, may provide additional facts about hunting strategies of Cicindelinae.

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Figure 1

Number of chosen preys by male and females of *Calomera littoralis* and *Cicindela hybrida* respectively in experiment 1.

Colors of vertical bars are showing respectively: grasshopper - grey, caterpillar - white, beetle - black.

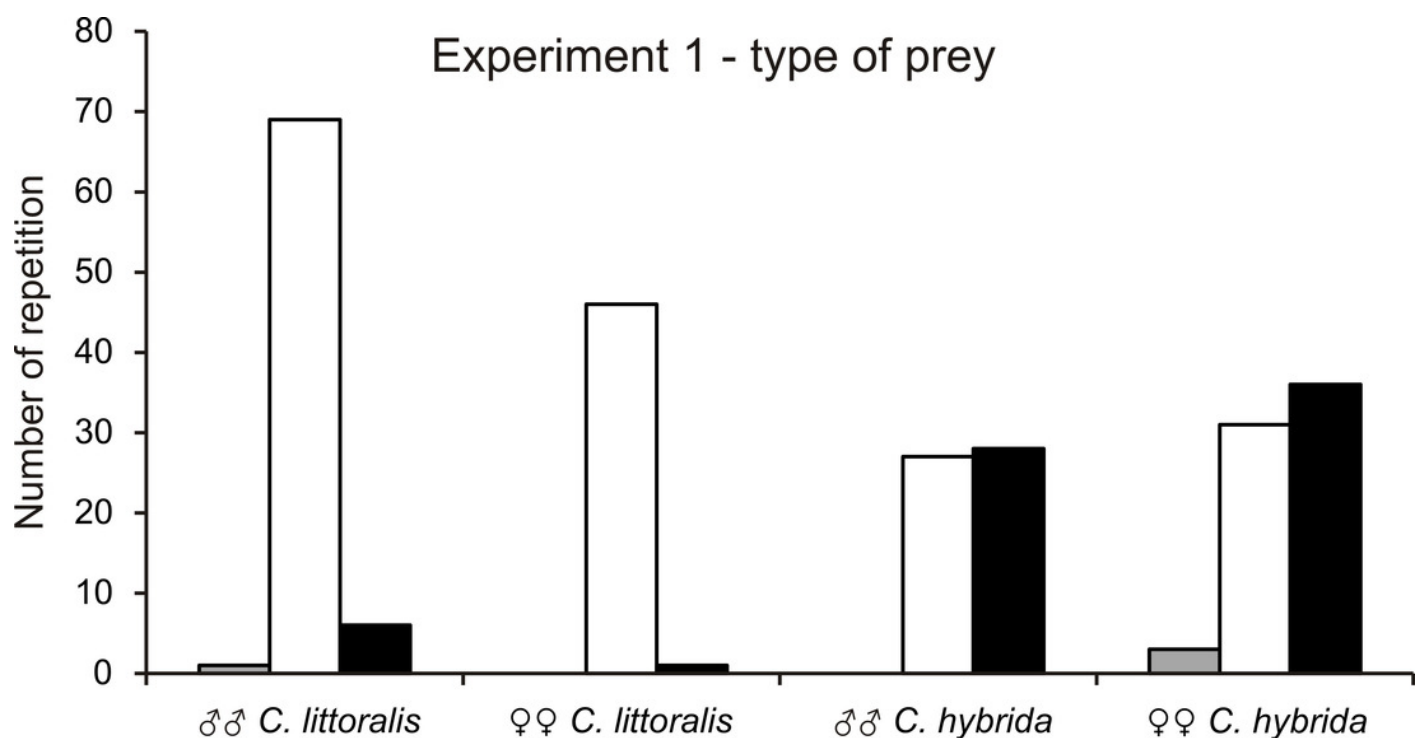


Figure 2

Number of chosen preys by males and females of *Calomera littoralis* and *Cicindela hybrida* in experiment 2 for beetles and caterpillars in part A and B respectively.

In both cases colors correspond to size of the prey in the following pattern: grey - small, white - medium, black - large.

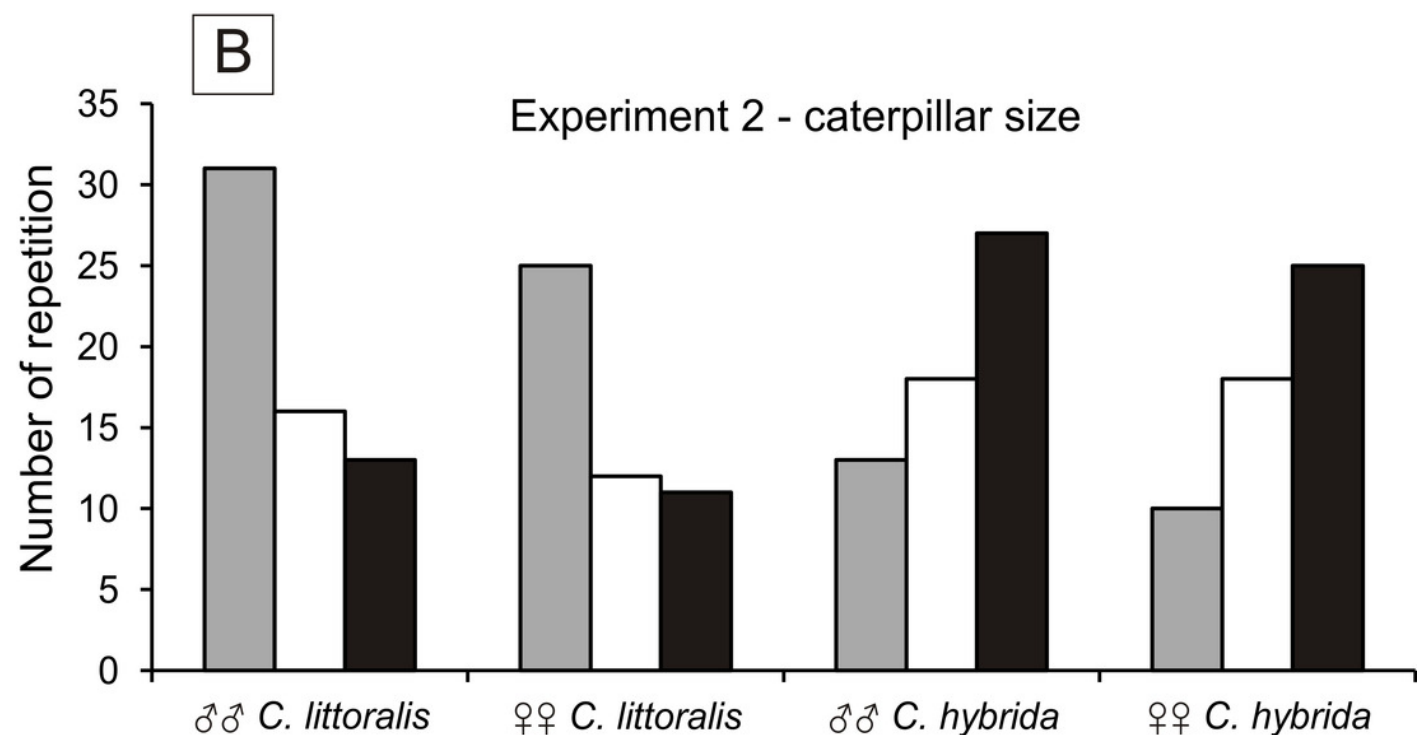
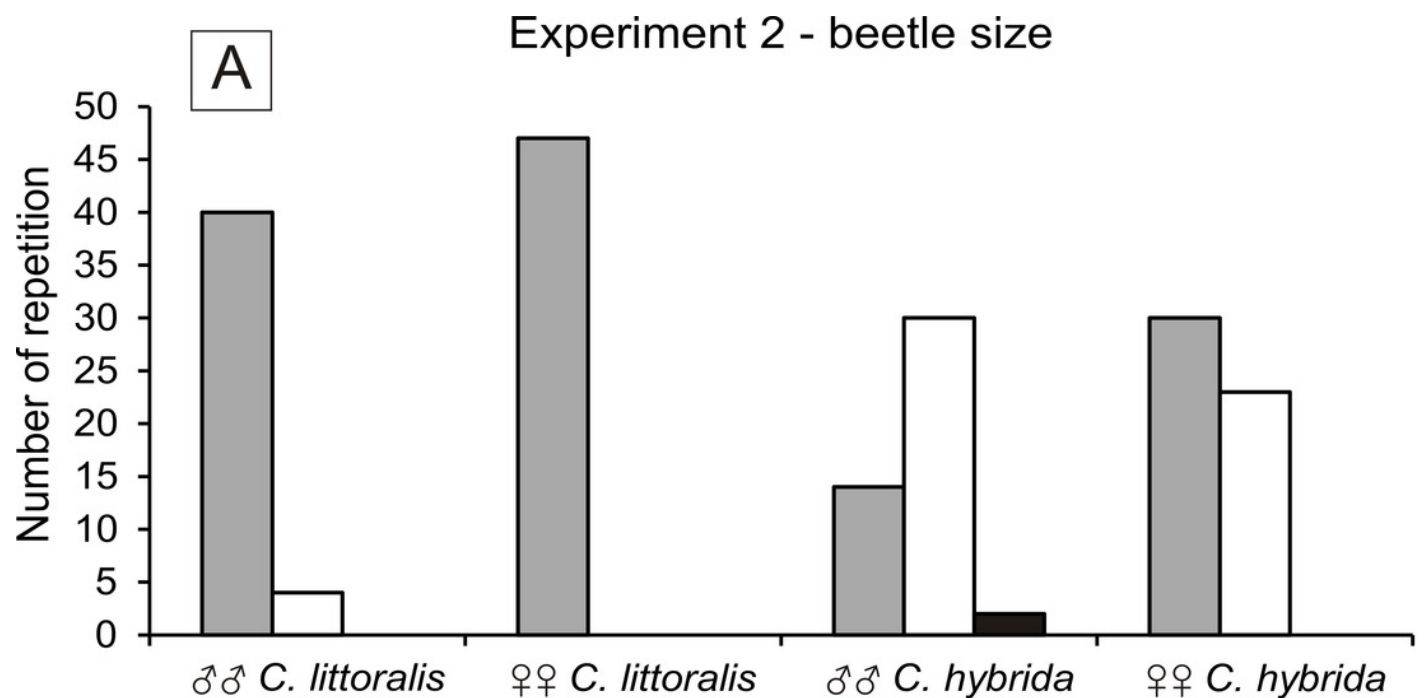
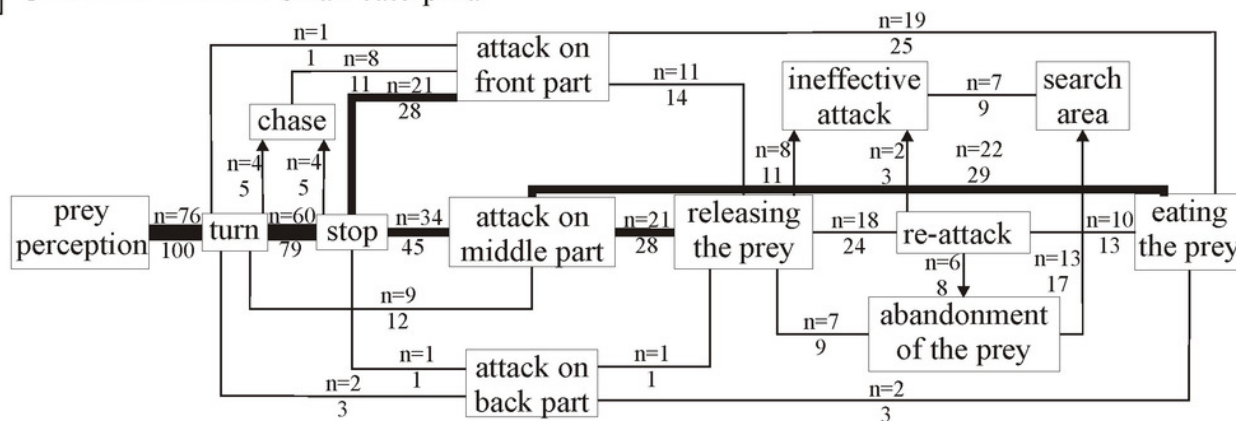


Figure 3

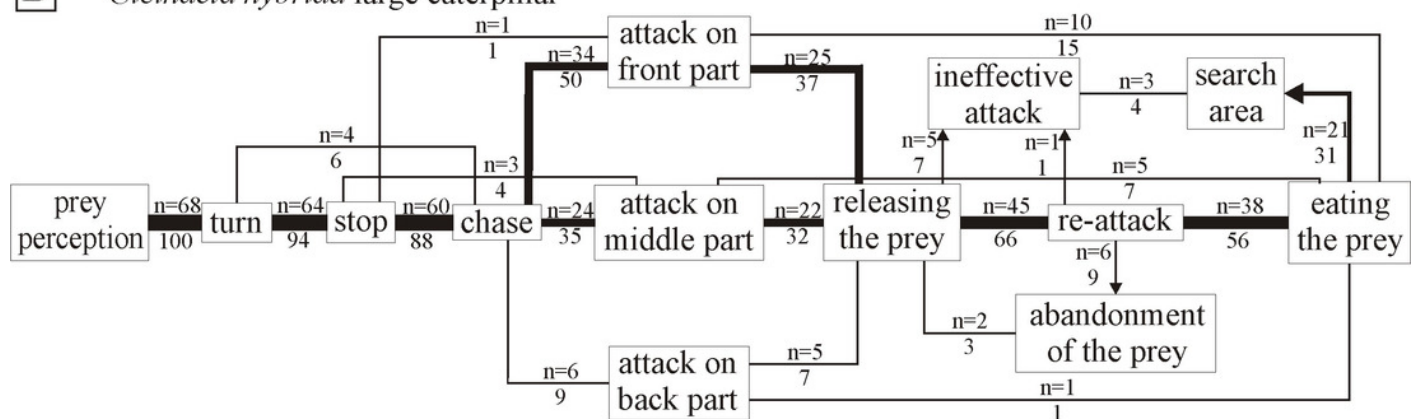
The flow diagrams of *Calomera littoralis* hunting small caterpillar (A), small beetle (C); and *Cicindela hybrida* hunting large caterpillar (B), and medium beetle (D).

The frequency of particular steps of the hunting strategy was calculated as a percentage of such behaviour in relation to all possible behaviours between two successive stages of hunting, and was indicated by the appropriate line width in the diagram and by the number below the repetition number of such behaviour. The sequence should be read from left to right unless indicated by an arrow.

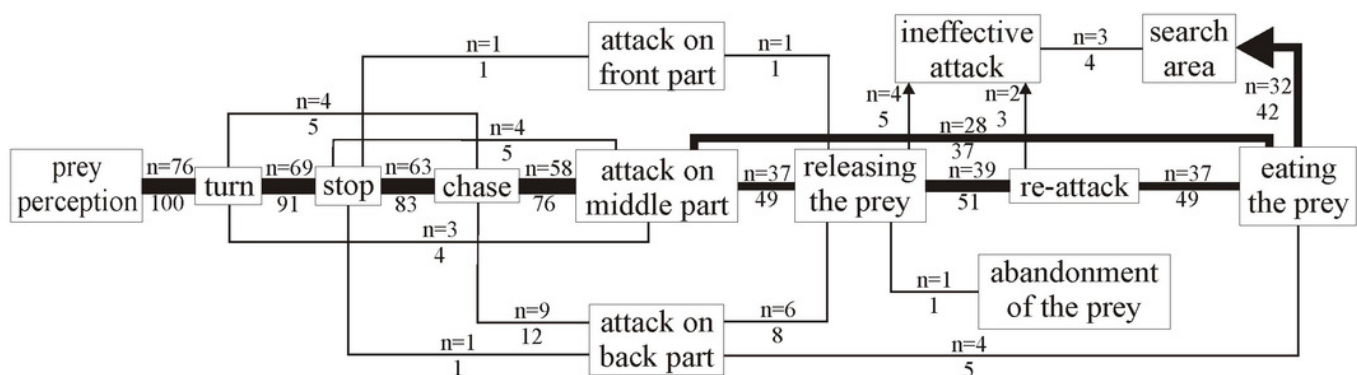
A *Calomera littoralis* small caterpillar



B *Cicindela hybrida* large caterpillar



C *Calomera littoralis* small beetle



D *Cicindela hybrida* medium beetle

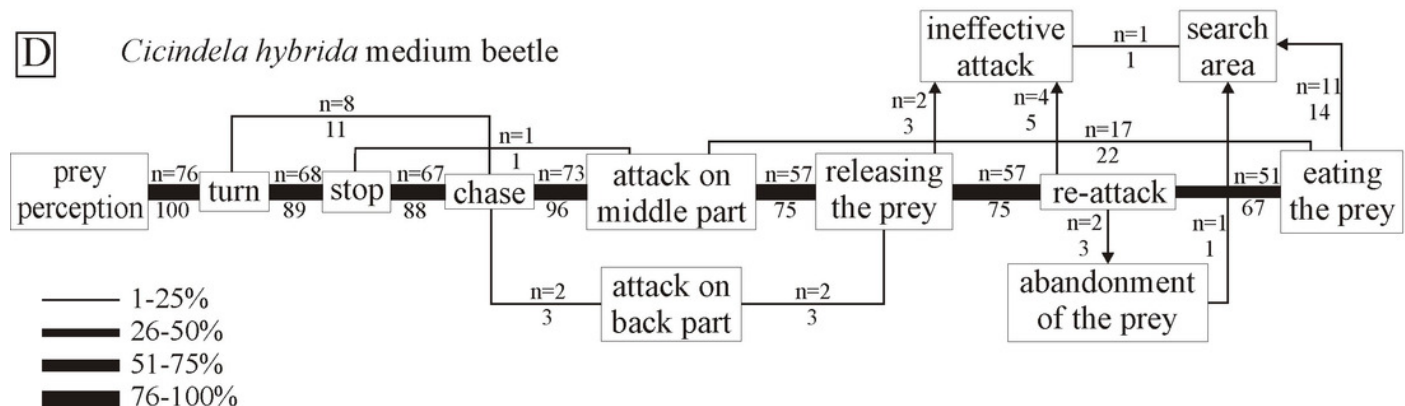


Table 1 (on next page)

Prey taxa used in the experiments.

Prey species	Order/Family	Size type	Ability to escape	Length (mm)	Mean	Weight (g)	Mean
grasshopper	Orthoptera	-	high	-	-	-	-
<i>Metalina lampros/properans</i>	Carabidae	small	medium	3-5	4.0 ± 0.44	2-5	3.8 ± 0.88
<i>Calathus melanocephalus</i>	Carabidae	medium	medium	6-9	7.5 ± 0.68	8-28	16.5 ± 4.12
<i>C. fuscipes</i>	Carabidae	large	medium	9-11	9.9 ± 0.55	36-68	49.4 ± 7.46
Symphyta	Hymenoptera	small	low	8-12	10.4 ± 1.13	17-40	28.2 ± 4.27
Symphyta	Hymenoptera	medium	low	12-15	13.8 ± 0.81	32-63	46.4 ± 8.62
Symphyta	Hymenoptera	large	low	15-21	17.3 ± 1.25	55-97	77.0 ± 11.9

1

2

3

Table 2 (on next page)

Number of repetitions, and types of the prey in each experiment.

N - number of repetition, gra - grasshopper, s bet - small beetle, m bet - medium beetle, l bet - large beetle, s cat - small caterpillar, m cat - medium caterpillar, l cat - large caterpillar.

Species	experiment 1		experiment 2				experiment 3			
	N	type	caterpillar		beetle		caterpillar		beetle	
			N	size	N	size	N	size	N	size
♀♀ <i>Calomera littoralis</i>	47	gra, m bet, m cat	48	s cat, m cat, l cat	47	s bet, m bet, l bet	38	s cat	38	s bet
♂♂ <i>Calomera littoralis</i>	76	gra, m bet, m cat	60	s cat, m cat, l cat	44	s bet, m bet, l bet	38	s cat	38	s bet
♀♀ <i>Cicindela hybrida</i>	70	gra, m bet, m cat	53	s cat, m cat, l cat	53	s bet, m bet, l bet	32	l cat	38	m bet
♂♂ <i>Cicindela hybrida</i>	55	gra, m bet, m cat	58	s cat, m cat, l cat	46	s bet, m bet, l bet	36	l cat	38	m bet

1