

# The Scent of Danger: the Impact of Predator Chemical Cues on Emergence from Refuge and Willingness to Autotomize Limbs in the House Cricket (*Acheta domesticus*)

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**Abstract** Prey can accurately assess predation risk via the detection of chemical cues and take appropriate measures to survive encounters with predators. Research on the chemical ecology of terrestrial invertebrate predator-prey interactions has repeatedly found that direct chemical cues can alter prey organisms' antipredator behavior. However, much of this research has focused on the chemical mediation of avoidance and immobility by cues from lycosid spiders neglecting other prominent invertebrate predators and behavior such as autotomy. In our study, house crickets (*Acheta domesticus*) were exposed to cues from cricket-fed orange-footed centipedes (*Cormocephalus aurantiipes*), red-back spiders (*Latrodectus hasselti*), an odorous (cologne) control, and a non-odorous control to determine whether direct chemical cues had any influence on two types of anti-predatory behavior: the willingness (latency) to emerge from a refuge and to autotomize limbs. Exposure to *C. aurantiipes* cues resulted in a significantly slower emergence from a refuge, but exposure to *L. hasselti* cues did not. Direct chemical cues had no influence on initial autotomy, but exposure to *L. hasselti* cues did significantly decrease the latency to autotomize a second limb. That cues from *L. hasselti* had an influence on a second autotomy, but not initial autotomy may be because crickets that undergo autotomy for a second time may perceive themselves to be already at a higher risk of predation as they were already missing a limb. Variation in responses to cues from different predators demonstrates a need to examine the influence of chemical cues from a wider variety of invertebrate predators on anti-predator behavior.

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## Introduction

Under the selective pressure of predation, prey have evolved a diverse array of behavioral adaptations to avoid the fatal consequences of capture (Kats and Dill 1998; Lima and Dill 1990). Anti-predatory behavior, such as seeking refuge (Cooper 2003; Martín and López 2000), comes with costs to fitness in the form of lost opportunities for other fitness related activities, such as feeding or reproduction (Scherer and Smee 2016). Due to these costs, the threat sensitivity hypothesis predicts that prey should adjust their reactions to potential predation in relation to the level of perceived predation risk (Helfman 1989; Hoefler et al. 2012; Lima and Dill 1990). Through an accurate assessment of predation risk prey can adaptively use such behavior to successfully evade predators, and avoid incurring needless fitness costs from the unnecessary use of them (Dicke and Grostal 2001; Kats and Dill 1998). To do this, prey can make use of a range of different predator cues (e.g., visual, mechanical, or chemical) to evaluate predation risk (Zimmerman and Kight 2016).

A common means of assessing predation risk across taxa is through the detection of chemical cues via chemoreception (Scherer and Smee 2016; Storm and Lima 2008). These cues can be direct cues coming from the excretions and secretions of predators and indirect cues from the pheromones associated with alarmed, injured or deceased conspecifics (Dicke and Grostal 2001; Zimmerman and Kight 2016). Prey can show a generalized awareness response to chemical cues from predators to accurately assess predation risk by providing important insights into the threat posed by a predator (Kats and Dill 1998; Scherer and Smee 2016) and allow them to take appropriate measures in avoiding predation. For example, the wolf spider (Lycosidae) *Pardosa milvina* subjected to predation from another wolf spider, *Hogna helluo*, experienced greater survival rates when exposed to chemical cues from *H. helluo*, as these cues allowed effective risk assessment such that *P. milvina* was able to avoid the predator (Barnes et al. 2002; Bell et al. 2006; Persons and Rypstra 2001; Persons et al. 2001). Responses to predator cues can be heightened by other specific cues; for example, *P. milvina* also demonstrated graded antipredatory responses to cues based on the diet (Persons et al. 2001), size (Persons and Rypstra 2001) and hunger as indicated by cues in the silk and excreta of the *H. helluo* that produced them (Bell et al. 2006).

A substantial body of research has now been conducted on the chemical ecology of predator-prey interactions; however, it remains biased towards certain environments and taxa (Binz et al. 2014; Dicke and Grostal 2001; Storm and Lima 2008). There has been much research on the use of chemical cues for anti-predation behavior by aquatic organisms (reviewed by (Chivers and Mirza 2001; Ferrari et al. 2010; Wisenden 2000), but relatively little research in this area has examined terrestrial organisms, especially invertebrates (Binz et al. 2014; Hoefler et al. 2012). Chemical cues have vital roles in the fitness of terrestrial invertebrates with regard to reproduction (Brodt et al. 2006; Eisner and Meinwald 1995; Ruther et al. 2009) and acquiring food (Dicke and van Loon 2000; Glendinning et al. 2009) and yet have received much less attention for their role in the assessment of predation risk (Binz et al. 2014; Hoefler et al. 2012). What research exists has repeatedly demonstrated that chemical cues can mediate anti-

predator behavior in terrestrial invertebrates, such as immobility and avoidance (Binz et al. 2014; Bucher et al. 2014a; Bucher et al. 2015a, b; Hoefler et al. 2012), and is associated with enhanced survival (Bucher et al. 2014b; Van Maanen et al. 2015). Within the invertebrates, most research has been focused on lycosid spiders, as both a source of cues and as prey, with little or no attention to other prominent invertebrate predators, such as ants, centipedes or other types of spiders (Binz et al. 2014; Hoefler et al. 2012).

Research on chemically mediated anti-predator behavior of invertebrates has generally focused on avoidance and immobility as adaptive responses to predator cues; however, other predation avoidance tactics, such as autotomy, have been poorly explored. Autotomy is the self-amputation or shedding of a limb or other body part as a means of escape when held by a predator (Bateman and Fleming 2005; Cooper and Frederick 2010). This behavior is adaptive as it allows the prey to escape and survive, but often comes with significant costs to future fitness (Cooper and Frederick 2010; Fleming and Bateman 2007; Fleming et al. 2007). In crickets (Gryllidae) for instance, the loss of a hind leg can increase susceptibility to subsequent predation events due to a diminished escape speed, (Bateman and Fleming 2005, 2006a; Cooper and Frederick 2010; Fleming and Bateman 2007), and a decline in mating competence (Bateman and Fleming 2005, 2006b, c). As autotomy is a conscious decision and willingness to autotomize can vary between individuals and predation scenarios, given the influence of chemical cues observed in other anti-predator behaviors of invertebrates it would not be unreasonable to expect that these cues may also have some effect on the latency to autotomize. To the best of our knowledge no research has been conducted on the effect of predatory chemical cues on the use of autotomy in invertebrates.

Here we aimed to determine the impact of direct chemical cues from red-back spiders (*Latrodectus hasseltii*) and orange-footed centipedes (*Cormocephalus aurantiipes*) on anti-predator behavior of the house cricket (*Acheta domesticus*) at two different levels of predatory encounter: specifically latency to emerge from a refuge in the presence or absence of predatory cues, and latency to autotomize a limb (representing a predatory encounter) in the presence or absence of predatory cues. We hypothesized that exposure to chemical cues from predators would increase perceived predation risk such that: a) crickets exposed to such cues would take significantly more time to emerge from a refuge; and b) that crickets exposed to predatory chemical cues would autotomize a hind leg significantly faster than crickets that were exposed to no scent or an odorous control.

## Materials and Methods

### Invertebrate Husbandry

Adult *A. domesticus* were sourced from commercially bred populations (*Bugs “N” Things*, Kwinana, Perth, WA). Crickets were kept in 60 × 25 × 40 cm glass enclosures, with cardboard refuges and ad libitum food (“Clear Pond” fish flakes and pellets) and water. Enclosures were maintained with a density of ~60 crickets each, with a consistent ambient temperature between 25 and 26 °C and a 12:12 light:dark cycle. All crickets were subjected to the experimental procedure within two weeks of their adult

molt. During the experimental procedure crickets were housed in individual 205 mL sealed containers with ad libitum food and water and maintained under the same environmental conditions as those in the glass tanks.

The invertebrate predators used in this experiment, *L. hasselti* and *C. aurantiipes*, were sourced from wild populations around Curtin University, Western Australia, and were housed in individual 15 × 10 × 9 cm plastic containers ( $n = 2$  and  $n = 1$  respectively). *Latrodectus hasselti* were given a quarter of a cardboard egg carton lid as a substrate for their webs and the *C. aurantiipes* containers were provided with a petri dish containing wet paper towel, for humidity control, and a cardboard roll for shelter. These predators were maintained under the same conditions as the crickets (temperature between 25 and 26 °C; 12:12 light:dark cycle) and were fed an ad libitum diet consisting of live *A. domesticus* adults.

## Cue Preparation

We examined the influence of direct chemical cues from *L. hasselti* and *C. aurantiipes* on autotomy and refuge emergence. To eliminate the influence of scents other than those being examined, nitrile gloves were worn whenever handling the crickets and were cleaned, along with all other equipment used, with a 70% ethanol solution in between trials. Cues from *L. hasselti* were prepared by rolling a cotton bud through spider silk and excreta until the bud was covered. To limit variation and improve consistency of cue dosage and quality spiders were given ~48 h to replenish any silk and excreta between cue collections. *C. aurantiipes* cues collected by taking 5 × 2 cm piece of the cardboard roll used to provide *C. aurantiipes* shelter and had been exposed to the centipede for 24 h (adapted from Hoefler et al. 2012, substituting filter paper with thin cardboard). Crickets were exposed to cues by placing them in sealed 205 mL containers lined with a piece of damp filter paper inoculated with a cue by brushing it with two cotton buds or piece of cardboard, that were then left in the container for the duration of the exposure treatment. Control cues were prepared using cotton buds that had only been exposed to distilled water. To determine the impact of these cues on prey behavior, crickets were exposed to cues from either a predator (*C. aurantiipes*,  $n(M) = 20$ ,  $n(F) = 27$ ; spider  $n = 50$ ,  $n(M) = 25$ ,  $n(F) = 25$ ); an odorous control (*Adidas Ice Dive* cologne delivered as a single drop <0.5 ml,  $n(M) = 26$ ,  $n(F) = 24$ ) and a non-odorous control (no scent,  $n(M) = 25$ ,  $n(F) = 25$ ).

## Behavior Trials

### Emergence

To examine the effect of chemical cues on the latency of crickets to emerge from a refuge, a metric of predator avoidance (Hedrick 2000; Bateman and Fleming 2006c), crickets were exposed in the method described above for five minutes. After this exposure an individual cricket was disoriented, to simulate an altercation with a predator and maintain a consistent transfer, by being gently shaken in cupped hands and placed inside a cardboard refuge (12 × 9 × 3.5 cm) which was then placed into a

neutral container. The time taken for the cricket to completely emerge (whole body) from the refuge (latency to emerge) was recorded with a stopwatch ( $\pm 0.1$  s). Crickets that took longer than two minutes were removed from the refuge and were recorded as taking one hundred and twenty seconds.

### *Autotomy and Second Autotomy*

After the completion of an emergence trial crickets were returned to the sealed container and exposed to the same scent for a period of 10 min. After this second exposure the crickets were placed and given purchase on a piece of rough cardboard (egg carton lid). Crickets were then held with a pair of curved forceps by the femur near the joint connected to the tibia until the limb was autotomized. The time take to autotomize the leg was recorded with a stopwatch. Autotomy trials were terminated if the crickets took more than one hundred and twenty seconds to autotomize the limb. The hind leg was chosen in this experiment as they are considered, due to their size, to be more likely to be seized by a predator and have been found to be the most commonly lost limbs in other gryllid crickets (Bateman and Fleming 2005).

Once autotomy had been induced crickets were returned to their individual housing containers for a minimum of 24 h and no more than 25 h. After this period the crickets were subjected to the autotomy procedure again with the remaining hind leg. In other gryllid crickets autotomizing a second leg has been found to take significantly longer compared to the first (Bateman and Fleming 2005). This reluctance is thought to be a response to the cumulative costs to fitness resulting from the loss of limbs (Bateman and Fleming 2005; Bateman and Fleming 2006a). We predicted that although a second autotomy would take significantly longer than the initial autotomy, crickets exposed to the predator chemical cues would autotomize a second limb significantly faster than those exposed to controls.

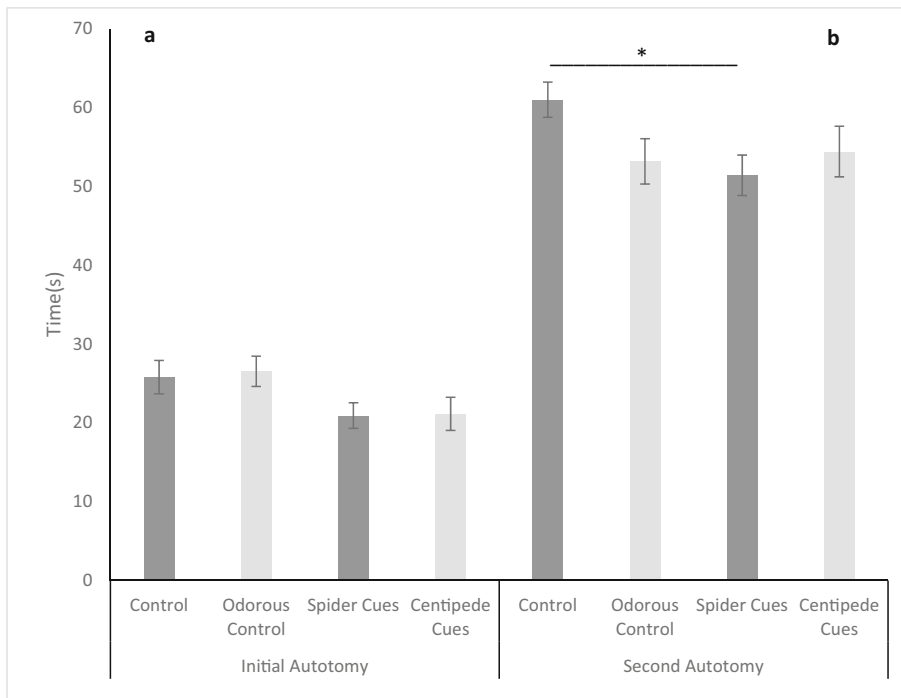
### *Data Analysis*

All data analyses were performed using R (3.4.2, R Core Team 2017). As the data were not normally distributed, despite attempted transformations, separate Kruskal-Wallis tests by ranks and Dunn tests of multiple comparisons were performed to determine whether latency to emerge, initial autotomy or a second autotomy significantly differed between chemical cue treatments. An analysis of covariance (ANCOVA) was used to determine whether there was a significant difference in the emergence and autotomy times between the different treatment groups. Previous studies have shown that both body size and sex may influence the use of autotomy (Bateman and Fleming 2006b, 2008) thus, we included both sex and mass as covariates in this analysis. A two tailed paired t-test was also performed to determine if there was a significant difference between the overall times taken to autotomize a limb and a second limb. This test was used despite the fact that the data were not normally distributed as t-tests are robust to violations of assumed normal distribution and can accurately analyze data such as this (Lumley et al. 2002).

## Results

### Latency to Emerge

There was significant variation in time taken to emerge from a refuge for crickets exposed to different chemical cues (Kruskal-Wallis:  $\alpha = 0.05$ ;  $\chi^2 = 8.0287$ ;  $p = 0.04542$ ; see Fig. 1a). Crickets exposed to *C. aurantiipes* cues took significantly more time on to emerge from a refuge ( $10.6 \text{ s} \pm 4.1$ ) than those that weren't exposed to the no scent control ( $6.3 \text{ s} \pm 1.5$ ) ( $p = 0.0372$ ). Crickets exposed to spider cues took longer on average to emerge from a refuge ( $9.8 \text{ s} \pm 2.8$ ) than those exposed to a no scent control; however, no significant difference in latency to emerge was found between those exposed to spider cues and to an odorous control ( $p = 0.2682$ ). Emergence times of crickets exposed to control and predator treatments did not significantly differ from those exposed to an odorous control, despite taking the least amount of time on average to emerge from a refuge ( $3.4 \text{ s} \pm 0.7$ ).



**Fig. 1 a** Mean latency to emerge (s) ± SE of crickets exposed to different chemical cues. Control ( $6.31 \text{ s} \pm 1.521$ ); Odorous Control ( $3.44 \text{ s} \pm 0.72$ ); Spider Cues ( $9.84 \text{ s} \pm 2.81$ ); & Centipede Cues ( $10.57 \text{ s} \pm 4.10$ ). A significant difference (marked by \*) was found between the centipede and control treatments ( $p = 0.0372$ ). No other significant differences were found between these treatments. **b** Mean times (s) ± SE taken by crickets to autotomize a hind leg. Control ( $25.79 \text{ s} \pm 2.12$ ); Odorous Control ( $26.52 \text{ s} \pm 1.92$ ); Spider Cues ( $20.91 \text{ s} \pm 1.62$ ); Centipede Cues ( $21.12 \text{ s} \pm 2.10$ ). No significant difference was found between the times of these treatments ( $\chi^2 = 6.4045$ ;  $p = 0.0935$ )

## Initial Autotomy

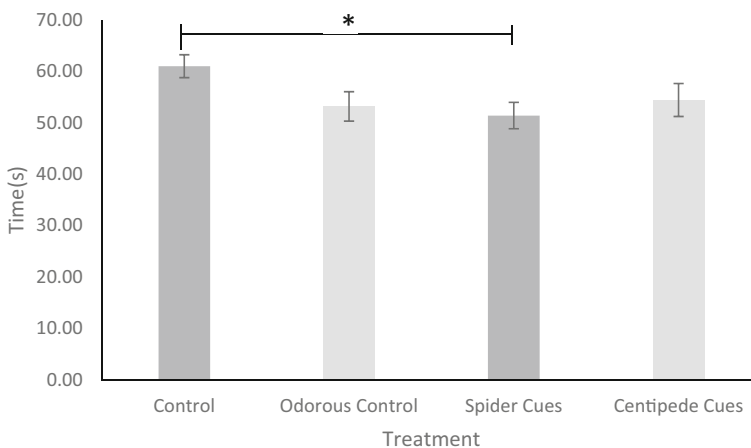
Crickets, exposed to cues from *C. aurantiipes* and spiders, autotomized a hind leg in less time on average than did those exposed to an odorous control or a control (*C. aurantiipes* cues: 21.1 s  $\pm$ 2.1; spider cues: 20.9 s  $\pm$ 1.6; Fig. 1b). However, no significant difference was found in the latency to autotomize a hind leg between crickets exposed to these different chemical cues (Kruskal-Wallis:  $\chi^2 = 6.4045$ ;  $p = 0.0935$ ).

## Second Autotomy

A significant difference was found between the times taken by crickets to autotomize a second hind leg when exposed to different chemical cues ( $\chi^2 = 7.8776$ ;  $p = 0.04861$ ). Crickets exposed to cues from spiders underwent a second autotomy significantly faster than did than crickets exposed to no scent ( $p = 0.0384$ ) (Fig. 2). No significant difference was found between the latency to autotomize with any of the other treatments (Fig. 2). A significant difference was also observed between the time taken to autotomize a hind leg and undergo a second autotomy. Crickets took significantly more time to undergo a second autotomy (55.0 s  $\pm$ 1.4) compared to that taken in the initial autotomy (23.6 s  $\pm$ 1.0) ( $t = -19.386$ ;  $df = 196$ ;  $p < 0.001$ ).

## Sex and Mass

An ANCOVA was performed to examine the effect of olfactory cues on the times taken to emerge from a refuge and autotomize a limb in *A. domesticus* while controlling for the effects of mass and sex. There was no evidence to suggest that either sex or mass significantly influenced latency to emerge (ANCOVA: mass:  $F = 0.684$ ;  $p = 0.409$ ; sex:  $F = 0.254$ ;  $p = 0.615$ ), latency of initial autotomy (ANCOVA: mass:  $F = 1.372$ ;



**Fig. 2** Mean times (s) taken to autotomize a second hind leg by crickets exposed to no scent (control) (60.99 s  $\pm$ 2.23), an odorous control (53.18 s  $\pm$ 2.88), spider cues (51.40s  $\pm$ 2.57), and centipede cues (54.42 s  $\pm$ 3.21). A significant difference (marked by \*) was found between crickets exposed to spider cues and no scent ( $p = 0.0384$ ). No significant difference was found between the times of any other treatments

$p = 0.243$ ; sex:  $F = 0.272$ ;  $p = 0.603$ ) or latency of second autotomy (ANCOVA: mass:  $F = 0.095$ ;  $p = 0.758$ ; sex:  $F = 0.755$ ;  $p = 0.386$ ).

## Discussion

Direct chemical cues from *Latrodectus hasselti* did not impact the crickets' latency to emerge; however, exposure to cues from *Cormocephalus aurantiipes* did result in a significant reluctance to emerge from a refuge indicating that risk assessment by crickets differed for the two predators. Our hypotheses were weakly supported in that these data document the first evidence of direct chemical cues influencing willingness to autotomize a limb, though not as expected (Fig. 2). Exposure to direct chemical cues derived from *L. hasselti* resulted in a significantly faster second autotomy, but, contrary to our hypothesis, had no impact on the initial autotomy. This result may be due to the heightened sense of risk resulting from exposure to said cues and the compounding fitness costs of the initial autotomy.

### Response to Odorous Control

As there was no evidence to suggest that there was a difference in response to the control and odorous control treatments in any of the experiments conducted we can dismiss the notion that variances in latency in emergence or autotomy are merely a response to an unfamiliar odor. Therefore responses to chemical cues from predators can be assumed to be a result of the perceived predation risk determined by the detection of these cues.

### Latency to Emerge

In accordance with our hypothesis, crickets exposed to cues from *C. aurantiipes* were found to take significantly more time to emerge compared to those exposed to no scent (Fig. 1b). This reluctance to emerge from a refuge may, in concordance with the threat sensitivity hypothesis (Helfman 1989), be an adaptive response to the perceived increase in predation risk, resulting from exposure to predator cues. Similar results have been observed in *A. domesticus* with regard to refuge choice as crickets have been found to avoid refuges marked with indirect chemical cues (conspecific necromones) due to a higher perceived risk (Aksenov and Rollo 2017). These findings are also similar to the only other examination of the effect of direct *C. aurantiipes* chemical cues on invertebrate prey behavior. Chemical cues derived from another scolopendrid centipede, *Scolopocryptops sexspinosus*, were found to mediate avoidance behavior in *A. domesticus* (Hoefler et al. 2012). As with the centipedes used in the present study, these *S. sexspinosus* were also fed on a diet of *A. domesticus* adults. The reluctance of crickets exposed to *C. aurantiipes* cues to emerge from a refuge in this study may be another example of centipede cues mediating avoidance behavior in *A. domesticus*. The adaptive benefit of this reluctance to leave a refuge may be related to the hunting mode of the predator whose scent elicited the response. Centipedes such as *C. aurantiipes* are



generalist predators that actively hunt a diverse range of prey (Koch 1983; Lewis 2006); therefore, the crickets' response could potentially be adaptive, as remaining hidden in a refuge, even for a very short time, may be a beneficial means of avoiding an active hunter such as *C. aurantiipes*. The hunting modes of different spider species has already been found to have significant influence over anti-predator in another orthopteran, *Melanoplus femurrubrum*, (Miller et al. 2014; Schmitz and Suttle 2001) which may have been guided by chemical cues (Miller et al. 2014).

Exposure to *L. hasselti* cues resulted in a mean emergence latency that was greater than that of both the control and odorous control treatments (Fig. 1a); however, these differences were not statistically significant. Although these results are contrary to what we hypothesized, they are consistent with the results of the only other research to examine the influence of theridiid spider chemical cues on invertebrate prey behavior. Research conducted on another gryllid cricket, *Nemobius sylvestris*, found that when these crickets were exposed to cues from candy-striped spiders (*Enoplognatha ovata*) they did not exhibit statistically significant increases in avoidance behavior compared to a control (Binz et al. 2014). This was thought to be due to the rarity of *E. ovata* as a predator of *N. sylvestris*. A notable difference between these spiders and those used in the present study is that the *E. ovata* were maintained on diet of fruit flies. While predator diet is known to influence prey response to direct chemical cues (Hoeffler et al. 2012; Kortet and Hedrick 2004; Persons et al. 2001), other gryllid crickets, including *N. sylvestris*, (Binz et al. 2014; Bucher et al. 2014b; Bucher et al. 2015a) have been found to exhibit anti-predator behavior, i.e. avoidance, in response to cues from spiders that were not fed conspecifics. As *N. sylvestris* has been found to exhibit anti-predator behavior in response to cues from spiders, other than *E. ovata*, fed on fruit flies these findings may be considered consistent with those of the present study.

### Autotomy and Direct Chemical Cues

Although crickets exposed to the cues of predators did autotomize a hind leg in less time than crickets in both the control and odorous control treatments (Fig. 1b), these differences were not statistically significant. In contrast, crickets exposed to *L. hasselti* cues took significantly less time to autotomize a second hind limb compared to a control (Fig. 2). The costs associated with autotomy (Bateman and Fleming 2005, 2006a; Fleming and Bateman 2007) that accompanied the loss of the first limb may explain why the predatory chemical cues of *L. hasselti* influenced the latency to autotomize during the second autotomy, but not the first. An increased predation risk assessment, resulting from exposure to direct chemical cues alone, may not be enough to elicit a faster initial autotomy; however, an increased risk assessment resulting from both exposure to predator cues and an increased vulnerability due to the initial autotomy may be enough to trigger a faster second autotomy. This may represent an adaptive response to a greater perceived predation risk that has resulted from the exposure to direct chemical cues and to the fitness costs of an initial autotomy. Other gryllid crickets, *G. bimaculatus*, have been found to adaptively alter their refuge use and latency to sing after the loss of a single leg (Bateman and Fleming 2006c) potentially due to a consequential increase in predation risk (Bateman and Fleming 2005, 2006a).

## Longer Second Autotomy

Congruent with our hypothesis, a second autotomy was found to take significantly more time to occur than the initial autotomy. Similar results regarding a second autotomy have been found in another gryllid cricket, *Gryllus bimaculatus* (Bateman and Fleming 2005). This apparent reluctance to sever another limb is thought to be a response to the cumulative fitness costs that come with the loss of limbs. Both *G. bimaculatus* and *A. domesticus* suffer an 18 to 31% decrease in escape speed with the loss of a single hind leg and a 43 to 61% decrease with the loss of two legs (Bateman and Fleming 2005; Bateman and Fleming 2006a). Both species pay a cost of limb loss through increased vulnerability to predation and to mating competence (Bateman and Fleming 2006a; Bateman and Fleming 2005).

In conclusion, our findings indicate that direct chemical cues can influence the latency of a second autotomy and latency of emergence in *A. domesticus*. To our knowledge this is the first time that the impact of chemical cues on autotomy has been examined, and only the second to examine the effect of either centipede or theridiid spider cues on invertebrate prey behavior. These findings suggest there is merit in further investigation into the impact of chemical cues from a broader range of invertebrate predators on autotomy and other anti-predatory behaviors.

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