

Escape performance decreases during ontogeny in wild crickets

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Summary

Increasing the ecological relevance of studies relating to the performance of organisms has been a central issue for functional biologists over the last few years. Of particular concern are changes in performance throughout the life cycle as selective forces act differently on various life stages. We addressed this issue experimentally by following ontogenic variations in the escape performance of crickets threatened by artificial predatory signals. We measured their performance under natural settings, which is a necessary approach yet one that is undocumented in insects. We analysed numeric film sequences obtained using a high-speed video camera at 1000 frames s⁻¹ to quantify wild cricket performance and behaviour in the

field. We detected significant differences in cricket escape performance throughout ontogeny. Escape performances were higher in juvenile crickets than older instars. Complementary behavioural measurements for escaping crickets suggest that these variations may be related to the lower predatory risk perceived by large adults than by juveniles. We expect that our analysis of size-refuge will also improve our understanding in the development of performance, given its importance in community and population ecology theories.

Key words: ontogeny, field experiment, crickets, antipredator behaviour, cercal system.

Introduction

Increasing the ecological relevance of studies on the performance of organisms has been a central issue for functional biologists over the last few years (Schmalhofer and Casey, 1999; Irschick, 2003; Vanhooydonck and Van Damme, 2003; Irschick et al., 2005). Factors related to the performance of organisms operate within an ecological context and are subject to complex interactions with other intrinsic (e.g. age, experience, learning) and extrinsic variables (e.g. predator type, habitat characteristics). Among them ontogeny is a major factor that can influence the level of ecological performance within natural populations as it affects a broad range of ecological, physiological and behavioural characteristics (see Roth and Johnson, 2004). However, studies investigating changes in the performance of animal function with ontogeny are restricted to relatively few groups of organisms, mainly vertebrates, and few traits, such as locomotor and feeding systems. Little consideration is generally given to the ecological context in which these traits take place and are selected (Irschick, 2003; Herrel and Gibb, 2006). Of particular ecological and evolutionary relevance are traits related to escape performance, as they are directly related to the survival and, therefore, the fitness of organisms (O'Steen et al., 2002; Walker et al., 2005). Most studies have focused on the kinematics of various locomotor behaviours displayed during escape, for example sprinting and jumping (Thompson and Kier, 2002). However, from an evolutionary perspective, organisms are likely to adapt to predation risks at an earlier detection stage of the predation

sequence, as it confers substantial selective advantages for prey (Endler, 1991; Fox et al., 2001).

Arthropods (e.g. insects and spiders) are good models of evolved high performance detection systems; they have hundreds of mechanoreceptive cuticular hairs, which are sensitive to touch (filiform hairs) or wind currents (trichoid hairs) generated by approaching predators (Tautz and Markl, 1978; Gnatzy, 1996; Suter, 2003). The sensing performance of animals greatly influences their ability to detect and escape predators. Prey with high performance levels of detection may achieve greater fitness levels in nature, up to a certain point. Given that juveniles generally suffer higher rates of predation than adults, selection for mechanisms that improve juvenile escape performance is likely to be strong. This is observed in wood crickets (*Nemobius sylvestris* Bosc), a widespread detritivorous insect, foraging on leaf litter of deciduous European forests. Wood crickets suffer high rates of predation by wolf spiders (*Pardosa* sp.), especially during juvenile instars (Dangles et al., 2006a). Crickets have evolved one of the highest performance anti-predatory sensory systems (Shimozawa et al., 2003) and because the structure of their mechano-sensory system varies throughout development (Dangles et al., 2006c), we expect there to be strong selective forces acting on their escape performance during ontogeny.

The relationship between performance and body size of organisms remains controversial. Many studies have reported that as animals get larger performance levels increase or remain constant (Irschick, 2000; Trillmich et al., 2003). Recently, there

have been reports describing a decrease in performance throughout ontogeny (Gibb et al., 2006). Previous research on performance remains dominated by studies relating to vertebrates and nothing is known about the ontogenic changes relating to invertebrate performance. We measured ontogenic changes and their effects on performance (measured as the escape distance) in wild wood crickets behaving freely under natural conditions. We devised a portable actuator that mimicked the attack dynamics of natural predators on crickets, for example wolf spiders. We quantified the cricket escape performance and behaviour by analysing numeric film sequences obtained with a high-speed video camera.

Materials and methods

Experimental subjects

We examined the escape performance in 30 wood crickets *Nemobius sylvestris* Bosc in three age classes: two juveniles and one adult. Juveniles (instars II–III, named juveniles I) had tibia II lengths between 1.8 and 2.1 mm, and a mean body length of 0.57 ± 0.02 cm. Intermediate crickets (instar IV–V, named juveniles II) had tibia II lengths between 2.6 and 2.9 mm, and a mean body length of 0.69 ± 0.03 cm. Adults had tibia lengths between 5.4 and 5.6 mm and a mean body length of 0.89 ± 0.03 cm. The morphological characteristics of wood cricket cerci throughout ontogeny have been described (Dangles et al., 2006c). Mean cercus lengths were varied: 1.1 mm in juveniles I, 1.9 mm in juveniles II, and 4.5 mm in adults. Only young adults displaying a high level of foraging activity were selected to exclude senescent individuals. All crickets were collected from an oak forest in the vicinity of Tours, France ($47^{\circ}17'06''\text{N}$, $00^{\circ}47'13''\text{E}$) the day before the experiment. The crickets were housed in plastic boxes filled with layer of leaves

after capture, fed with dry cat food, and watered using wet cotton swabs.

Design of a field device to measure cricket escape performance

Measuring the escape performance of freely behaving crickets in the field requires portable equipment, including an attack simulator and a video recording system (Fig. 1). To simulate a spider attack, a 'spider operator' used an original device based on the controlled displacement of an actuator-triggered 'piston'. The piston measured 0.8 cm in diameter (Fig. 1A; A) (LAL35 actuator/LAC1 controller, Cedrat Technologies, Meylan, France), and has been previously tested and used (Dangles et al., 2006b). The acceleration and velocity of the piston displacement was driven easily and with high precision ($\pm 4\%$) using specific macro commands *via* hyperterminal software and the rs232 port of a laptop (Fig. 1A; B). This allowed us to control and set it to mimic a spider attack. We had previously validated this device using particle image velocimetry (PIV) analyses of the air-flow in front of the moving piston (see Dangles et al., 2006b). The piston displacement produces a flow pattern very similar to that produced in front of a running spider. Initially, the piston was fixed to an actuator, which could not be easily moved under field conditions to follow wandering crickets. Therefore, we added a 1.5 m wire between the actuator and the tip of the piston to facilitate its use (Fig. 1A; A,C).

Cricket behaviour was recorded using a lightning RDT1 high-speed (HS) digital video camera (Fig. 1A; D) (DRS Data & Imaging Systems, Inc., Oakland, NJ, USA) with a frame rate of $1000 \text{ frames s}^{-1}$ and resolution of 1280×512 pixels. The escape response for freely behaving animals was recorded by following a cricket with the camera after its initial release until

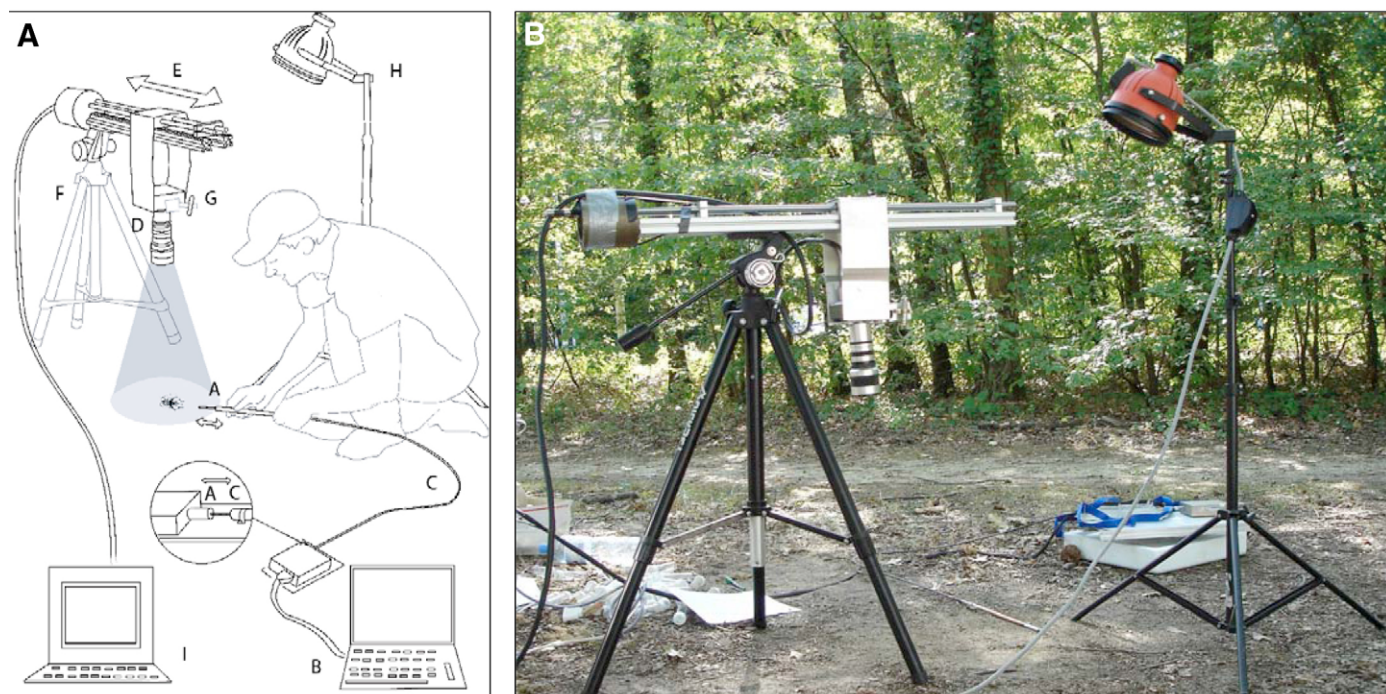


Fig. 1. (A) Detailed drawing and (B) picture of the portable design used to simulate and record cricket escape responses under field conditions. See the text for further explanation and references to letters in A.

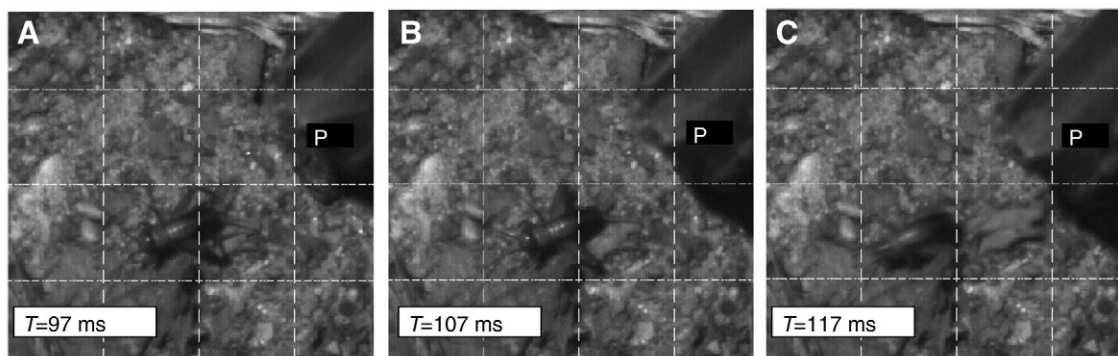


Fig. 2. High-speed videographic sequence of an air-evoked escape response performed by a juvenile wood cricket (*N. sylvestris*) after being subjected to the predatory strike simulator (piston, P). Time (T ; ms) from the start of the piston is shown in each frame. (A) A cricket in its resting position as the piston is approaching from the rear. (B) The cricket enhances its escape behaviour by a flexion of its hind legs. (C) The cricket starts jumping (some sand is moved away by the action of hind legs).

it stopped moving. The camera was mounted on a ramp (Fig. 1A; E) fixed on the rotating head of a stable tripod 0.5 m above the ground (Fig. 1A; F). This system allowed us to follow cricket displacements within a 2.5 m diameter. The size of the image on the camera was only about twice the size of the cricket, providing sufficient detail for measuring escape distances, but making it difficult to keep the moving cricket centred on the camera screen. We overcame this problem by fixing a red laser pointer (Fig. 1A; G) to the camera support in such a manner that pointing the laser on the cricket body ensured that the cricket was well-centred on the camera. The ground was illuminated by a halogen lamp (Fig. 1A; H) located 1 m above the ground surface. The video acquisition was controlled using a laptop (Fig. 1A; I) equipped with a DA170M data acquisition board (4 Gb of memory) and MIDAS 2.0 software (Xcitex Inc, Cambridge, USA).

Simulated attacks on crickets in the field

The escape response of crickets to predatory signals produced by the piston was recorded on the ground litter of a beechwood tree at the University of Tours, where wood crickets and wolf spiders can be found. The experiment duration was a single summer day (ground temperature illuminated by the lamp: 30°C). Crickets were individually placed on the ground and followed by our tripod-ramp-HS camera system as they started to walk freely. We waited for the crickets to stop moving before launching the piston because cricket behaviour (such as walking, running) at the time of simulation influences their behavioural latency [as reported for cockroaches (Camhi et al., 1978)]. Once the cricket was motionless, the piston was placed rear-on 4.5 cm from the cricket: this is the median distance at which spiders attack wood crickets (Dangles et al., 2006b). The piston was positioned at the height of a spider, 0.2 cm above ground. The piston was launched at an attack angle of $\pm 20^\circ$ from the rear of the cricket, to make sure that crickets relied only on their cercal system for detection. The piston travelled far enough to touch the cricket. The cricket escape behaviour was recorded by the HS camera (Fig. 2).

The kinematics of the spider run is composed of a short initial acceleration over 1 cm followed by a phase of relatively constant velocity up to prey (Dangles et al., 2006b). Piston kinematic was set up to mimic these properties. Moreover, we

simulated various piston velocities because wolf spiders modulate their attack velocity when preying on crickets (see Dangles et al., 2006b), thus increasing the ecological relevance of our biological test. We chose three attack velocities within the range of those recorded for spider attacks (see Dangles et al., 2006b): slow (40 mm s^{-1}), intermediate (150 mm s^{-1}) and fast (300 mm s^{-1}) attack. In total, 90 individuals (10 replicates \times 3 instars \times 3 velocities) were tested in a randomised set-up to avoid any of them adapting to the piston velocity.

Behavioural measurements

Crickets regularly respond to a wind stimulus by first turning their bodies consistently away from the danger source (by e.g. $60\text{--}90^\circ$) with a short latency and then by walking/running or jumping (Stabel et al., 1985; Tauber and Camhi, 1995). Pivoting is time-consuming, but this strategy appears to be adaptive in escaping from natural predators [as suggested for cockroaches (Camhi et al., 1978)]. In the present study, we determined two variables for each HS video recording: (1) the type of escape (walking or jumping) and (2) the escape angle, i.e. the body angle of the cricket at the moment of escape relative to the direction of the piston.

Performance measurements

The escape performance by evading crickets was expressed as a function of their escape distance, i.e. the distance between

Table 1. Details of the behavioural elements of the escape response by wood crickets (*N. sylvestris*) of different instars to simulated attacks in the field

Instars	Juvenile I	Juvenile II	Adult
Number of escapes ($N=30$ attacks)			
Total	28	30	27
Before contact (air-evoked)	9	10	5
After contact (touch-evoked)	19	20	22
Escape behavior			
Walk response	0	2	7
Jump response	28	28	20
Escape angle			
0– 30°	18	20	18
30– 60°	7	9	7
60– 90°	3	1	2

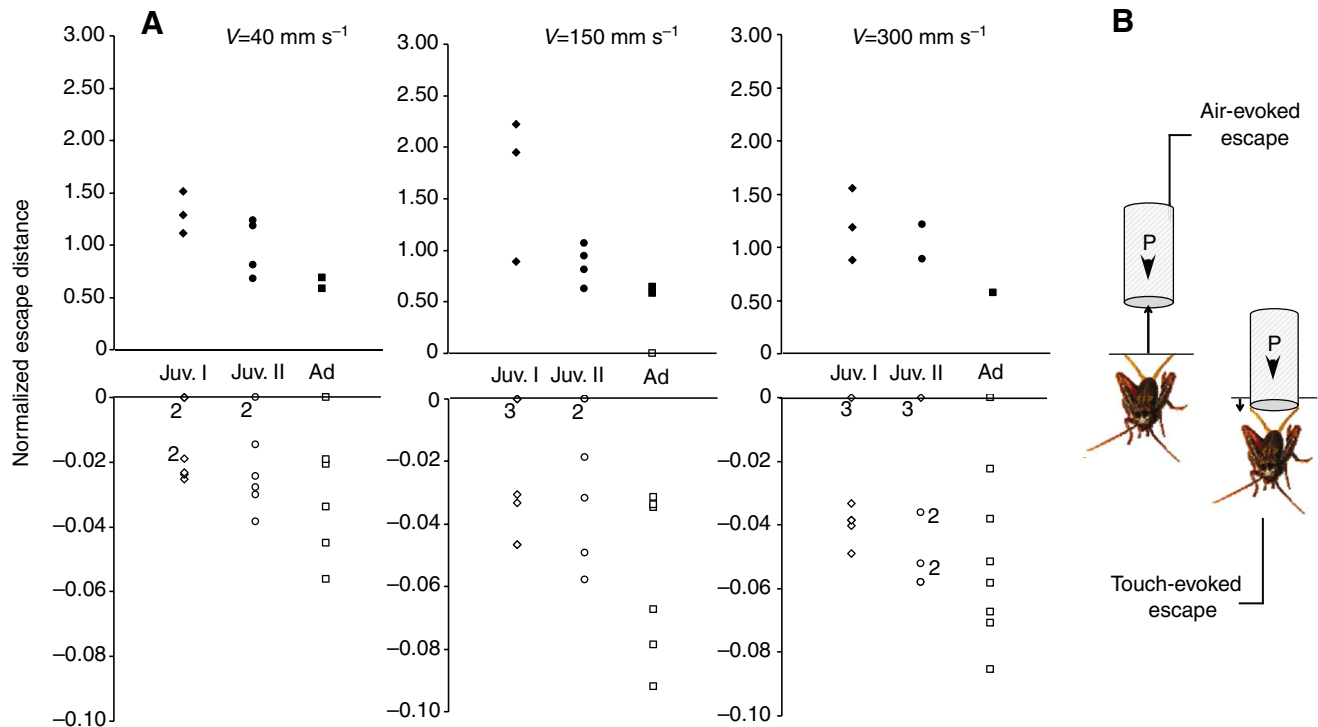


Fig. 3. (A) Escape distances normalised to total body length of wood crickets (*N. sylvestris*) for three different instars: juvenile I (Juv. 1), juvenile II (Juv. 2) and adults (Ad.) at three piston velocities (40 mm s^{-1} , 150 mm s^{-1} and 300 mm s^{-1}). Numbers indicate two or three crickets escaping at similar distance values. As shown on the drawing (B), the tip of the cerci lines up with the x -axis. An escape distance of zero corresponds to the tip of the cerci being touched by the piston (P). Bold arrows represent the direction of piston movement. Positive and negative values of escape distances correspond to air- and touch-evoked responses, respectively. Note that the y -axis in the touch-evoked graphs is more than an order of magnitude less than in the air-evoked graphs.

the cricket and the piston at the time the cricket initiates its escape. The escape performance was divided into two categories, depending on whether the cricket escaped before or after being touched by the piston. (1) The escape distance before contact between the cricket and the piston; this was the straight-line distance between the tip of the cercus and the tip of the piston in the frame prior to cricket-leg flexion, either to turn (most cases) or directly jump/walk (few cases). This measured the air-evoked escape performance of the cricket. (2) The escape distance after contact between the piston and the cricket; this was the distance between the location of the tip of the piston in the frame of contact and its location in the frame prior to cricket-

leg flexion. This is an inverse measurement for touch-evoked escape performances in crickets. Therefore, an escape distance of zero corresponded to the tip of the cerci being touched by the piston. Positive and negative values for escape distances corresponded to air- and touch-evoked responses, respectively. We normalised escape distances to the total body length of the cricket to provide a more ecologically relevant measure of cricket escape performance. This measurement indicates how many cricket body lengths remain between the cricket and the mimicked spider before the cricket escapes (Fig. 3). All image analyses were performed using R (R development core team 2004).

Table 2. Results of the two-way ANOVA analysis on cricket (*N. sylvestris*) escape distance to simulated attacks in the field for touch-evoked and air-evoked escape responses

	d.f.	Sum of squares	Mean of squares	<i>F</i> value	<i>P</i> value
Touch-evoked response					
Instar	2	0.0011	0.0006	5.996	0.0047*
Velocity	2	0.0006	0.0003	2.990	0.0593
Instar \times velocity	4	0.0002	0.0001	0.567	0.6879
Residuals	55	0.0048	0.0001		
Air-evoked response					
Instar	2	0.3087	0.1493	11.8976	0.0001*
Velocity	2	0.0002	0.0001	0.0169	0.9833
Instar \times velocity	4	0.0206	0.0051	0.6687	0.6220
Residuals	16	0.1389	0.0077		

$N=85$ for the two types of response (a) touch-evoked escape, (b) air-evoked escape.

* $P<0.005$.

Statistical analyses

Log-transformed proportions of various types of escape behaviours (Table 1) were analysed using a Tukey-type multiple comparison test (Zar, 1998). Log-transformed escape distance data (Table 2) were analysed using two-way repeated-measures ANOVA, in which 'instar' and 'attack velocity' were the first and second factors. In cases of statistically significant changes, data were further analysed using a *post hoc* Fisher's least significant difference (LSD) test. Data were considered significant for *P* values less than 0.05. All statistical and image analyses were performed using R.

Results

Cricket escape behaviour in response to simulated attacks

In 90 trials, only five crickets (two juveniles and three adults) did not respond to attacks simulated by the piston, i.e. they remained motionless. We observed a significantly higher proportion of air-evoked escapes in juvenile I and II (32.1% and 33.3%, respectively) than in adults (18.5%) (Table 1, Tukey test: $P=0.030$ and $P=0.027$, respectively); this was not the case between juveniles I and II (Tukey test, $P=0.56$). We also observed ontogenic differences in cricket escape behaviour: juveniles almost always (96.5%) responded to predatory stimuli by jumping, whereas a substantial proportion of adults (25.9%) escaped by walking. Most (64.3–66.6%) instar escape turn angles were between 0° and 30° . Only six crickets in total escaped with a turn angle greater than 60° . No difference was observed for the frequency or magnitude of turns between walking and jumping responses.

Cricket escape distance

We detected significant differences in normalised cricket escape distance among instars for all three piston velocities in both air- and touch-evoked escapes (Fig. 3, Table 2). *Post-hoc* comparisons revealed that adults had lower air- and touch-evoked escape distances than juveniles (I and II), for all attack velocities. Interestingly, we observed an increase in inter-individual variability of escape distance with cricket development: few adult crickets can react as quickly as juveniles after being touched by the piston and most adults have a two- to fivefold increase in normalised escape distances. This ontogenic difference in escape distance was more pronounced for air-evoked escapes: the greatest escape distances to wind signal (up to 2.3 times the cricket body length) were always observed in juveniles for all three piston velocities (Fig. 3). However, this result was a consequence of the normalisation of escape distances to cricket body length. When applied to absolute escape distance, the wind-evoked response was the same among age classes (ANOVA, $F=1.9361$, $P=0.1766$, data not shown). No effects of piston velocity on the escape distance of crickets for any type of response were detected (Table 2).

Discussion

Role of touch-sensing for escape from predators

The use of air cues by crickets and cockroaches to escape their predators is well documented (Camhi, 1984; Gnatzy, 1996). However, our field study further describes various types of predator signals. We observed that most crickets escaped running predator signals only after physical contact and not by

using their air-detection system, as it is generally assumed. This result was observed for all tested piston velocities and suggests a crucial, but previously disregarded, role for cercal touch perception in cricket escape performance. Crickets can rely on powerful legs to escape predators and this may explain why they wait until the last moment to initiate a jump. This late reaction may explain why most crickets do not consistently achieve escape angles between 60° and 90° from the source of danger (e.g. $60\text{--}90^\circ$) (see Tauber and Camhi, 1995) before jumping. The prominent role of touch-sensing for escaping from predators may have been reinforced by the field conditions of the experiment. Air signals from a predator may be barely detectable and poorly reliable in the presence of background noise created by wind turbulence, a feature that has been observed in foraging bats (Jones and Rydell, 1994). Moreover, touch-sensing may be more efficient than air-sensing in detecting predators (such as spiders) at close range in leaf litter.

Ontogeny of escape performance in an evolutionary ecological context

Most studies on the development of performance of traits related to escape behaviour have focused on locomotion, generally reporting that adults have higher or similar absolute capacities than juveniles [e.g. lizard speed (Irschick, 2000), mammal speed (Trillmich et al., 2003)]. However, Gibb et al. (Gibb et al., 2006) proposed that the development of the escape response in Teleost fish would decrease as juveniles become larger, as a result of biomechanical constraints in body shape. Measurements of the escape distance in crickets lead us to similar conclusions: escape performances in juveniles were higher than those in older instars. This increase in the escape distance for juveniles was in most cases related to a lower reaction distance after being touched by the piston: they respond faster than adults to an immediate danger. The decline in the escape performance for all tested speeds and for both escape types, despite strong differences in stimulus transmission to the sensory structures, is striking and calls for further interpretation in terms of neural control processes related to the age of the animal.

The negative relationship between body size and escape performance may have important implications in an evolutionary and ecological context. For instance, optimality theory suggests that the behavioural response of an individual in response to a predator is influenced by the risk of predation (Ydenberg and Dill, 1986). Although juvenile crickets forage in the same environment as adults and are faced with the same predators, they suffer higher rates of mortality, partly because their smaller size makes them more vulnerable to predators (Dangles et al., 2006a). An increase in absolute size allows crickets to reach a size-refuge, the size at which they become too big to be caught by most wandering predators. This hypothesis is supported by the greater proportion of walking responses in adults than juveniles; it is also supported by a previous experiment reporting more frequent hiding behaviour in juvenile crickets than in adults exposed to predators (Dangles et al., 2006a). A broad range of morphological, physiological, behavioural and ecological changes through ontogeny affect performance (Irschick, 2003); however, the specific concept of size-refuge has seldom been considered by functional ecologists

[for an exception, see Wainwright (Wainwright, 1996)]. We expect that the concept of size-refuge would improve our understanding in the development of performance, given its importance in community and population ecology theories [see Aljetlawi et al. (Aljetlawi et al., 2004) and references therein]. This is another reason to move swiftly towards more field experiments carried out in ecologically relevant settings.

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References

- Aljetlawi, A. A., Sparrevik, E. and Leonardsson, K. (2004). Prey-predator size-dependent functional response: derivation and rescaling to the real world. *J. Anim. Ecol.* **73**, 239-252.
- Camhi, J. M. (1984). A case study in neuroethology: the escape system of the cockroach. In *Neuroethology: Nerve Cells and the Natural Behaviour of Animals* (ed. J. M. Camhi), pp. 79-105. Sunderland: Sinauer Associates.
- Camhi, J. M., Tom, W. and Volman, S. (1978). The escape behavior of the cockroach *Periplaneta Americana* II. Detection of natural predators by air displacement. *J. Comp. Physiol. A* **128**, 203-212.
- Dangles, O., Casas, J. and Coolen, I. (2006a). Textbook cricket goes to the field: the ecological scene of the neuroethological play. *J. Exp. Biol.* **209**, 393-398.
- Dangles, O., Ory, O., Steinmann, T., Christides, J.-P. and Casas, J. (2006b). Spider's attack vs. cricket's escape: velocity modes determine success. *Anim. Behav.* **72**, 603-610.
- Dangles, O., Pierre, D., Magal, C., Vannier, F. and Casas, J. (2006c). Ontogeny of air-motion sensing in cricket. *J. Exp. Biol.* **209**, 4363-4370.
- Endler, J. A. (1991). Interactions between predators and prey. In *Behavioural Ecology: An Evolutionary Approach* (ed. J. R. Krebs and N. B. Davies), pp. 169-196. London: Blackwell Scientific.
- Fox, C. W., Roff, D. A. and Fairbain, D. J. (2001). *Evolutionary Ecology: Concepts and Case Studies*. Oxford: Oxford University Press.
- Gibb, A. C., Swanson, B. O., Wesp, H., Landels, C. and Liu, C. (2006). Development of the escape response in teleost fishes: do ontogenetic changes enable improved performance? *Physiol. Biochem. Zool.* **79**, 7-19.
- Gnatzy, W. (1996). Digger wasp vs. cricket: neuroethology of a predator-prey interaction. *Inf. Process. Anim.* **10**, 1-92.
- Herrel, A. and Gibb, A. C. (2006). Ontogeny of performance in vertebrates. *Physiol. Biochem. Zool.* **79**, 1-6.
- Irschick, D. J. (2000). Effects of behaviour and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. *Funct. Ecol.* **14**, 438-444.
- Irschick, D. J. (2003). Measuring performance in Nature: implications for studies of fitness within populations. *Integr. Comp. Biol.* **43**, 396-407.
- Irschick, D. J., Herrel, A., Vanhooydonck, B., Huyghe, K. and Van Damme, R. (2005). Locomotor compensation creates a mismatch between laboratory and field estimates of escape speed in lizards: a cautionary tale for performance to fitness studies. *Evolution* **59**, 1579-1587.
- Jones, G. and Rydell, J. (1994). Foraging strategy and predation risk as factor influencing emergence time in echolocating bats. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **346**, 445-455.
- O'Steen, S., Cullum, A. J. and Bennet, A. F. (2002). Rapid evolution of escape ability in Trinidadian guppies. *Evolution* **56**, 776-784.
- Roth, E. D. and Johnson, J. A. (2004). Size-based variation in antipredator behaviour within a snake (*Agkistrodon piscivorus*) population. *Behav. Ecol.* **15**, 365-370.
- Schmalhofer, A. and Casey, J. (1999). Crab spider hunting performance is temperature insensitive. *Ecol. Entomol.* **24**, 345-353.
- Shimozawa, T., Murakami, J. and Kumagai, T. (2003). Cricket wind receptors: thermal noise for the highest sensitivity known. In *Sensors and Sensing in Biology and Engineering* (ed. F. G. Barth, J. A. C. Humphrey and T. Secomb), pp. 145-157. Berlin: Springer Verlag.
- Stabel, J., Wedler, G. and Scharstein, H. (1985). The escape reaction of *Acheta domestica* under open-loop conditions. In *Insect Locomotion* (ed. G. Wendler), pp. 79-85. Berlin, Hamburg: Paul Parey.
- Suter, R. B. (2003). Trichobothrial mediation of an aquatic escape response: directional jumps by the fishing spider, *Dolomedes triton*, foil frog attack. *J. Insect Sci.* **3**, 19.
- Tauber, E. and Camhi, J. M. (1995). The wind evoked escape behaviour of the cricket *Gryllus bimaculatus*: integration of behavioural elements. *J. Exp. Biol.* **198**, 1895-1907.
- Tautz, J. and Markl, H. (1978). Caterpillars detect flying wasps by hairs sensitive to airborne vibration. *Behav. Ecol. Sociobiol.* **4**, 101-110.
- Thompson, J. T. and Kier, W. M. (2002). Ontogeny of squid mantle function: changes in the mechanics of escape-jet locomotion in the oval squid, *Sepioteuthis lessoniana Lesson*, 1830. *Biol. Bull.* **203**, 14-26.
- Trillmich, F., Bieneck, M., Geissler, E. and Bischof, H.-J. (2003). Ontogeny of running performance in the wild guinea pig (*Cavia apereia*). *Mamm. Biol.* **68**, 214-223.
- Vanhooydonck, B. and Van Damme, R. (2003). Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards. *Funct. Ecol.* **17**, 160-169.
- Wainwright, P. C. (1996). Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* **77**, 1336-1343.
- Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D. and Reznick, D. N. (2005). Do faster starts increase the probability of evading predators? *Funct. Ecol.* **19**, 808-815.
- Ydenberg, R. C. and Dill, L. M. (1986). The economics of fleeing from predators. *Adv. Stud. Behav.* **16**, 229-249.
- Zar, J. H. (1998). *Biostatistical Analysis* (4th edn). Upper Saddle River: Prentice Hall.