Large size as an antipredator defense in an insect

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Abstract

Although large size is considered an evolved antipredator defense for some vertebrates and shellfish, large size is generally not considered an adaptive defensive trait in insects. Here we propose that large size in chemically defended grasshoppers has evolved as a beneficial antipredator trait. The lubber grasshoppers Romalea microptera and Taeniopoda eques are the largest grasshoppers in North America north of Mexico. These closely related species escape most vertebrate predation by possessing powerful predator-deterrent toxins and by nocturnal roosting. We hypothesize that escape from vertebrate predation allowed lubbers to evolve a larger body size, increased fecundity and provided many other benefits, including defense against invertebrate predators. To test the hypotheses that large lubber size reduces predation, we conducted feeding trials with wolf spiders (Hogna carolinensis), assassin bugs (Arilus cristatus), praying mantids (Tenodera aridifolia), fire ants (Solenopsis invicta), frogs (Rana pipiens), and birds (Sturnus vulgaris and Paser domesticus). Our results show that larger lubber instars enjoyed a highly significant advantage vis-à-vis predators, demonstrating the adaptive value of large size against both vertebrate and invertebrate predators. Adult lubbers were generally immune from predation. It appears that lubbers have evolved to occupy a relatively predator-free ecological space: they are too large to be attacked by most invertebrate predators and too toxic for most vertebrate predators. We propose an evolutionary scenario whereby a change in feeding behavior toward vertebrate-toxic plants served as an evolutionary breakthrough, setting in motion the subsequent evolution of increased chemical defense and large body size in lubbers. To determine if large size is associated with chemical defense in grasshoppers in general, we compared body sizes of ~40 toxic vs ~3,000 nontoxic grasshopper species. Our results show that chemically defended species tend to be larger than nondefended grasshoppers, supporting an association between chemical defense and large size in insects. Large size may be favored in insects when vertebrate predation is removed as a strong selective factor.

Key words

antipredator defense, body size, size refuge, predator-free space, defense mechanism, chemical defense, allomone, grasshopper, lubber, Acrididae, Romaleidae, Romalea microptera, Taeniopoda eques

Introduction

Insects have evolved an impressive arsenal of antipredator defenses, including, rapid escape, crypsis, anachoretes (hiding in holes), mechanical and chemical defenses, startle and threat behaviors, hard exoskeletons, mimicry, deimatic behavior, shelter-building, group and symbiotic defenses, and rapid reproduction, which outpaces that of associated predators (Edmunds 1974, Blum 1981, Evans & Schmidt 1990, Salazar & Whitman 2001). Small size is a key component of many of these defensive strategies. Small insect prey are less conspicuous to vertebrate predators than large prey and are often more difficult to catch. Small insects generally have faster population growth rates than larger insects, and vertebrate predators generally prefer larger insect prey over smaller. In fact, size-selective vertebrate predation may be one evolutionary factor that explains why insects as a group remain small in body size.

In contrast to the idea that small size aids insect defense, there has been little discussion of the possibility of large size serving an antipredator function in insects. For example, neither Edmunds (1974), Harvey & Greenwood (1978), Cloudsley-Thompson (1980), Hermann (1984), Endler (1986, 1991), Evans & Schmidt (1990), New (1991) nor Ruxton et al. (2004), discuss large size as an evolved antipredator mechanism in insects. However, we believe that under certain circumstances, large body size can greatly enhance insect survival against both invertebrate and vertebrate predators, and therefore may be under positive directional selection.

In this paper, we argue that large size serves as an antipredator defense in two species of lubber grasshopper (Romalea microptera (Beauvois) and Taeniopoda eques (Burmeister), family Romaleidae). We provide evidence to support five points: 1) Vertebrate predation typically selects against large size in insects. 2) Lubber grasshoppers are chemically and behaviorally defended against most vertebrate predators. 3) Escape from vertebrate predation has released lubbers from predatory small-size selection, allowing them to evolve a larger size. 4) Large size is highly beneficial to lubber grasshoppers vis-à-vis both invertebrate and vertebrate predators, and as such, is evolutionarily favored as an adaptive antipredator trait. 5) This syndrome is common among chemically defended grasshoppers, which tend to be larger than palatable grasshoppers.

Results and Discussion

1) Vertebrate predation selects against large size in insects.—Insect predator-prey interactions are extremely diverse and complicated (Evans & Schmidt 1990, New 1991, Woodward et al. 2005), and nearly all types of interactions are possible. However in general, larger arthropod prey are more conspicuous to vertebrate predators than are smaller arthropod prey (Curio 1976, Winfield & Townsend 1983, Schüelt & Dicke 2002, Shane & Thomas 2005). This is partly because the probability of encountering/detecting a prey item increases as prey size increases (Maly 1970, Ware 1972, Curio 1976, Maiorana 1981, Bell 1990, Goerlitz & Siemers 2007, Troost et al.). In addition, small insects can more easily hide behind small objects or enter small cavities inaccessible to large predators, such as under bark or rocks, or between tight-fitting plant parts (Edmunds 1974). Although maximum running and flying speeds in insects scale positively with...

We will refer to R. microptera and T. eques as “lubbers,” although that term is often applied to all members of the family Romaleidae.
body size (Dudley 2000, 2002; Bonner 2006), flying insects usually escape flying predators not by speed, but by maneuverability (Cloudsley-Thompson 1980) and acceleration, both of which are inversely proportional to body size (Dudley 2000, 2002) (e.g., syrphid flies vs large beetles, dobsonflies, mantids, etc.: McLachlan et al. 2003). Likewise, small insect species typically exhibit greater burst-acceleration during escape-jumping than large species (e.g., fleas, flea beetles, and leaf hoppers vs crickets) (see Alexander 1985), and smaller individuals are theoretically more maneuverable than larger ones when running (Full et al. 2002). These size-relationships imply that larger insects may be under greater threat than small insects from vertebrate predators.

Both optimal foraging theory (Stephens & Krebs 1986) and empirical evidence (Prop 1960, Tinbergen 1960, Mattson et al. 1968, Curio 1976, Churchfield et al. 1991, Schulert & Dicke 2002), suggest that when all other things are equal, vertebrate predators prefer larger over smaller insect prey items, because large insect prey are energetically more nutritious and are often easier to capture (O’Brien et al. 1976, Morin 1984, Chen et al. 2004, McCracken et al. 2004; but see Shine & Thomas 2005). For example, broad-headed skinks, Eumeces laticeps, selected large crickets and ignored small crickets when offered both simultaneously (Cooper et al. 2007), and all of six species of insectivorous mammals tested by Dickman (1988) preferred large vs small cockroaches. Field studies show that large insects are more susceptible to vertebrate predation than small insects (Exnerova et al. 2003). For example, larger insects comprised only 2% of available prey, but 28% of all prey items fed by water pipits, Anthus spinolletta, to nestlings (Brodmann & Reyer 1999). Likewise, sphingid caterpillars represent 70% of the biomass fed by trogons, Trogon elegans, to their nestlings, and 98% of the sphingid prey were the last (largest) instar (Janzen 1993). Finally, many field studies show that birds, which in some communities consume enormous numbers of grasshoppers (Bryant 1912; Smith & Popov 1953; Greethead 1966; Joern 1986, 1992; Johnson et al. 1987; Fowler et al. 1991; Bock et al. 1992; Ji et al. 2008), prefer large, over small grasshoppers (Stower & Greathead 1969, Belovsky 1990, Belovsky et al. 1990, Belovsky & Slade 1993, Gardner & Thompson 1998).

On a community scale, each vertebrate predator species restricts itself to a specific range of prey sizes (Sinclair et al. 2003, Radloff & Du Toit 2004, Churchfield & Rychlik 2006, Montoya & Burns 2007, Whiting et al. 2007, Owen-Smith & Mills 2008). This range very often exceeds the largest, but not the smallest insect size – i.e., many vertebrate predators can take prey several orders of magnitude larger than the largest insects, but cannot successfully prey on the smallest insects (Wilson 1975, Sinclair et al. 2003). This is seen with large alligators (pers. obs.), owls (Craighead & Craighead 1956, Salvati et al. 2001), hawks (Craighead & Craighead 1956, Johnson et al. 1987), storks (Smith & Popov 1953, Falk et al. 2006), fox (Aranda 1995), coyotes (Fichter et al. 1955, Ortega 1987), hyenas (Kingdom 1997), bears (Chapman & Feldhamer 1982) and African leopards (Ray & Sunquist 2001), all of which take both insects and much larger vertebrate prey.

In contrast, some very large insects can escape predation by the smallest vertebrates (salamanders, tiny frogs, small birds); however, many small vertebrates can handle large insect prey by ingesting them in pieces (birds, mice, some lizards) (Kaspari 1990) or by having exceptionally large mouths or expandable gullets (Emerson et al. 1994). In addition, even if an insect species did gain protection against small vertebrates by evolving a larger size, that would presumably make that insect prey even more conspicuous and attractive to the numerous larger vertebrate predators in that same community (e.g., Pearson 1985). As such, insects generally cannot escape vertebrate predation by evolving a larger body size.

In contrast, insects can escape vertebrate predation by evolving smaller size. Arthropod size decreases by an order of magnitude below the small-size limit for acceptance by most vertebrate predators (except small fish and larval amphibians). Indeed, mites, Colembola, thrips, Psocoptera, Zoraptera, aphids, whiteflies, lice, fleas, and many scale insects, beetles, Diptera, Hymenoptera, and early instars of many insects are simply below the acceptable prey-size range of most vertebrate predators. Hence, vertebrates are a strong selective force against large insect size, but not against small insect body size (Nylin & Gotthard 1998).

2) Lubber grasshoppers are chemically and behaviorally defended against most vertebrate predators. — The lubber grasshoppers Romalea microptera and Taeniopoda eques are closely-related species from North America. R. microptera inhabits the southeastern portion of the USA, whereas T. eques survives primarily in the Chihuahuan Desert of the southwestern USA and northern Mexico (Rehn & Grant 1959, 1961). Their morphologies, behaviors and antipredator defenses are similar to each other, and different from all other North American grasshoppers (Stuaffer & Whitman 2007). These two species are so closely-related that they can interbreed and produce fertile offspring in the laboratory (Whitman unpub.). Because of their close related-
ness and similarity in defense traits, we will combine the results from both species, in this paper.

These two grasshopper species are chemically defended by two, nearly identical, two-component antipredator mechanisms. The first mechanism is a secretory defense derived from the respiratory system, and unique among arthropods. In both species, the spiracular tracheal trunks of the metathorax produce and store an odorous, noxious secretion that is sprayed out at attacking predators. This defensive secretion emerges from the metathoracic spiracles first as a dispersive spray, and then as an adherent froth (Fig. 1) (Whitman et al. 1991, 1992). It contains a witches' brew of low-weight phenolics, quinones, aldehydes, ketones, alcohols, organic acids, terpenoids, and miscellaneous other substances (Jones et al. 1988, Polanowski et al. 1997).

Some of the secretion components are synthesized by the insect itself, whereas others are derived from its diet. Lubbers are poison-plant generalists, and they sequester many plant toxins into their tracheal defense glands. For example, lubbers that feed on onion or garlic secrete a variety of plant-derived sulfur compounds characteristic of those plants (Jones et al. 1987, 1988, 1989). Lubbers that feed on catnip sequester and secrete terpenoid lactones (Blum et al. 1990), and those that feed on diets high in catechol or hydroquinone, sequester and release large amounts of these substances (Snook et al. 1993). As such, this unique defense gland serves as a toxic waste dump for potentially harmful, plant secondary compounds. When ejected, these low-weight substances quickly volatize, enveloping the grasshopper in a noxious chemical cloud, deterrent to many vertebrate predators (Fig. 2). We have observed naïve lizards and birds violently flinging lubbers from their mouths after secretion ejection. Some predators gagged or wiped their mouths or snouts on the substrate after encountering this pungent and irritating exudate (Fig. 3) (Whitman et al. 1985, Yosef & Whitman 1992).

The second mechanism of the chemical defense system of lubbers is an internal toxin, apparently synthesized by, and present in, all lubber instars (Whitman 1990). It is relatively potent, and consumption of a single 2nd instar lubber can induce vomiting in an inexperienced bird or lizard (Fig. 4). Often a naïve vertebrate predator will attack the first few lubbers it encounters, then after experiencing the negative effects (Figs 3-5), will refuse to attack subsequent offerings. Such food-aversion conditioning is probably highly adaptive to predators, because consumption of lubbers can be lethal (Whitman unpub.). The internal toxin has not been chemically identified, but is present even in first-instar nymphs fed lettuce (Whitman & Orsak 1985).

Dual-mechanism chemical defenses are common in insects, where a volatile secretion often serves both a rapid warning or alerting function for naïve predators, and a memory-eliciting function for experienced predators (Whitman et al. 1985, 1986, 1990, 1991). A second substance, held in the blood or body tissues, then poisons the predator, inducing food-aversion conditioning and a lasting learned association to the first defense (Whitman et al. 1990).

In lubbers, these two defenses have different effects on predators. The secretion alone can deter some invertebrate and vertebrate predators outright (Eisner et al. 1971, Jones et al. 1989, Blum et al. 1990), but seems to have less effect against others, such as preying mantids, wheel bugs, large spiders, centipedes, toads, and some mammals. By contrast, the internal defense is highly toxic to birds and lizards, partially toxic to toads and mammals, and only mildly

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2To understand lubber defense ecology, we tested lubbers against 112 species of various predator taxa. Given the two separate defense mechanisms and the great physiological, morphological, and behavioral diversity among grasshopper predators, it is not surprising that we observed virtually every type of predator response against lubbers. The results of these trials will be published elsewhere.
deterrent to invertebrate predators (see below).

Strong chemical defenses explain why lubbers can afford to be flightless, lumbering, brightly colored, large, gregarious, and often extremely abundant in nature: we have recorded > 900 individuals per 100 m² (Lamb et al. 1999). Despite their abundance, conspicuous appearance and sluggish nature, lubbers seem to suffer little vertebrate predation. Indeed, during 38 h of field observations of large and dense populations of active and conspicuous lubber grasshoppers inhabiting natural and old-field habitats, we recorded 102 individual insectivorous birds from 17 species foraging among the grasshoppers, and only observed one bird attack a lubber, despite observing constant bird attacks on other insect species (Whitman, unpubl.).

Although some mammals (mice, rats, raccoons, opossums) and toads will occasionally consume a few lubbers, these predators are generally not a threat because they hunt at night, and lubbers roost at the tops of vegetation from dusk to dawn (Whitman 1987). In summary, lubbers are generally immune to vertebrate predation, due to a combination of toxins and nocturnal roosting.

3) Escape from vertebrate predation releases lubbers from small-size selection, allowing them to evolve large size.— Most organismal traits are thought to be under conflicting selection pressures (Mayr 1956, Slatkin 1984, Schluter et al. 1991, Mayhew 2006). This is certainly the case for body size (Roff 1981, 2002; Nylin & Gotthard 1998; Blankenhorn 2005; Lomolino 2005; Mänd et al. 2007), where any number of factors could select for large size (e.g., fecundity, sexual selection, surface-volume relationships, desiccation resistance, thermal inertia, lowered mass-specific metabolic rates, increased strength, ability to consume tough food, locomotion, and increased food and water reserves, etc.) (Peters 1983, Schmidt-Nielsen 1984, Honěk 1993, Roff 2002, Chown & Nicolson 2004, Makarieva et al. 2005, Vincent 2006, Vincent & Herrel 2007, Whitman 2008). Likewise, any number of factors might select for small size, the most important being viability selection from either time constraints or predative pressures (Stearns 1992, Blanckenhorn 2000, Roff 2002). As previously discussed, vertebrate predation may select for small size in insect prey, and this may be a contributing reason to why most grasshoppers and most insects are relatively small in comparison to vertebrates.

Hence, for most species, there are probably manifold environmental factors selecting for both large and small body size, during each generation; and for many populations, body-size evolution may have already reached relative equilibrium under a balance of conflicting selective pressures (Thompson & Fincke 2002). However, when specific selective factors change in strength, we would expect natural selection to alter mean population trait values, given additive genetic variance and heritability in these traits. We suggest that this occurred in lubber grasshoppers.

We hypothesize that the ancestors of lubber grasshoppers began feeding on vertebrate-toxic plants, which imbued them with chemi-

Except in certain cases (such as in social or trapping predators — e.g., Enders 1975, Hölldobler & Wilson 1990, Kim et al. 2005, Souza et al. 2007), the vast majority of predaceous arthropods will not, or cannot, successfully attack prey much larger than themselves (Shelly & Pearson 1980, Lentwig & Wissel 1986, Wheeler 1988, Sabelis 1992, Cohen et al. 1993, Montllor & Bernays 1993, Matlock 2005, Olberg et al. 2005). As Warren & Lawton (1978) suggest, “Invertebrate predators usually eat prey of about their own size or smaller . . . . Those that occasionally attempt to capture large prey usually fail (Dixon & Russell 1972, New 1991), such as when ants attack large vertebrates, which simply move away. One might expect predaceous arthropods to evolve larger sizes to make use of large prey; however, arthropod predators are under the same vertebrate predator-enforced small-size selection as other arthropods.

The inability of predaceous arthropods to take large prey is a weakness that can be exploited by any invertebrate prey species that can evolve large body size. Insects are normally constrained from evolving large size, in part by increased liability to vertebrate predators. However, insect prey with effective antivertebrate predator defenses are released from this constraint, allowing them to evolve larger body size, which then reduces invertebrate predation.

We tested the hypothesis that large size is an advantageous antipredator trait in lubber grasshoppers. A full accounting of these experiments will be presented elsewhere, but we will provide a brief description of the methods and results here. We tested wild ants and birds in the field. For spiders, preying mantids, wheel bugs, and frogs, we used naive predators collected from the wild, and then acclimated to laboratory conditions for several days. Trials
began only after the predator routinely attacked and ate edible prey (Acheta domestica crickets, Tenebrio molitor mealworms, Galleria mellonella wax-moth caterpillars, Musca domestica house flies, etc.) that were offered. In each laboratory trial, a single predator individual was allowed to acclimate to a single cage or arena. We then gently introduced a single R. microptera grasshopper of a specific size, and recorded if the grasshopper was or was not attacked. Table 1 shows size and mass for various R. microptera instars.

We collected 42 wolf spiders, Hogna carolinensis (Lycosidae), by headlamps at night near Tifton, Georgia, and divided them into six treatment groups, each balanced for body mass, which ranged from 0.30 to 1.72 g. Spiders were maintained in individual 1-L plastic containers and given an adult cricket on the day of capture, and water thereafter. Four days later, we introduced a single R. microptera grasshopper into the container and recorded if the spider did or did not attack the grasshopper during the next 15 min. Here, attack is defined as lunging at and covering prey with the fore-legs and anterior body. Each spider was tested once. Table 2 shows that the spiders refused to attack large, late-instar grasshoppers. In fact, spiders often fled from 5th-instar and adult grasshoppers. The results show that the mantids attacked significantly more of the small grasshopper size classes than the large size classes (Table 3), and that larger mantids attacked larger lubbers (Spearman’s rho = 0.675, df = 21, p < 0.001; Fig. 6). Male and female mantids differed in the mean size of prey taken. Female mantids are larger (mean ± SD: mass = 2.14 ± 0.35 g; body length = 8.95 ± 0.56 cm, n=11) than males (mass = 1.38 ± 0.19 g; body length 7.95 ± 0.32 cm, n=10), and attacked larger prey than males (Mann Whitney U = 26.5, df = 20, p < 0.05). Male mantids refused to attack adult lubbers, whereas female mantids attacked four lubber adults (Table 3). Some mantids exhibited threat or defensive behavior, but only against large grasshoppers.

Table 2. Attack rate of Hogna carolinensis wolf spiders on R. microptera grasshoppers of different sizes and instars. Seven different spiders tested for each grasshopper size class; each spider tested once.

<table>
<thead>
<tr>
<th>Grasshopper instar</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>N attacked</td>
<td>5</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Attack rate by adult male and female T. aridifolia preying mantids against various sizes and stages of R. microptera grasshoppers.

<table>
<thead>
<tr>
<th>Grasshopper instar</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. prey attacked</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male mantids (N=10)</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Female mantids (N=11)</td>
<td>10</td>
<td>10</td>
<td>11</td>
<td>10</td>
<td>8</td>
<td>2</td>
</tr>
</tbody>
</table>

Fig. 5. Left: A naive Didelphis marsupialis opossum eating a toxic R. microptera grasshopper. This predator refused all subsequent lubbers offered. Photos by Larry Orsak. See Plate VIII. Right: Same opossum vomiting after consuming several R. microptera grasshoppers. This predator refused all subsequent lubbers offered.
across the face of the mantid. The same result occurred with an adult female mantid and an adult male lubber. Interestingly, only two of the four attacks by female mantids on adult lubbers resulted in capture; in two cases, the female’s raptorial legs bounced off of the hard cuticle of the grasshopper’s prothoacic shield. In other unpublished tests, we have observed large captured lubbers struggle wildly, pulling, pushing, twisting, or kicking themselves free of a mantid grasp. In such cases, the mantid did not re-attack.

We tested 23 adult wheel bugs, Arilus cristatus, against three lubber size classes. Bugs (mean ± SD body length and mass, female: 3.1 ± 0.14 cm, 0.83 ± 0.16 g; male: 2.7 ± 0.10 cm, 0.36 ± 0.033 g) were captured in McLean Co., Illinois, and thereafter maintained in clear 500-ml ventilated plastic containers and fed a variety of palatable insects. Each bug was tested against three lubber instars: 1st, 3rd, and 5th at three- to six-day intervals in a balanced presentation. Bugs consumed significantly more of the smaller sized grasshoppers (1st and 3rd instars) than the larger, 5th instars ($\chi^2 = 19.7, df = 2, p < 0.001$).

Table 4. Predation by 23 adult Arilus cristatus wheel bugs (Reduviidae) on R. microptera grasshoppers. Each bug was offered a 1st, 3rd, and a 5th-instar grasshopper, at 3 to 6-d intervals, in a balanced presentation. Bugs consumed significantly more of the smaller sized grasshoppers (1st and 3rd instars) than the larger, 5th instars ($\chi^2 = 19.7, df = 2, p < 0.001$).

<table>
<thead>
<tr>
<th>Grasshopper instar</th>
<th>1</th>
<th>3</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. prey consumed</td>
<td>18</td>
<td>12</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 5. Ability of R. microptera grasshoppers of different sizes to escape from disturbed fire ant (Solenopsis invicta) mounds. Ten grasshoppers tested for each instar.

<table>
<thead>
<tr>
<th>Instar</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Adult male</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. escape</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td>8</td>
<td>10</td>
<td>10</td>
</tr>
</tbody>
</table>

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We tested 22 northern leopard frogs, Rana pipiens, obtained from a biological supply company, against various R. microptera instars and sizes. Frogs were maintained in individual 4-L plastic jars with water, during which they were fed crickets, then starved for two days prior to testing. Trials ran for 10 d. Each frog was offered a single R. microptera grasshopper on odd days and an adult cricket on even days. Each frog received a different size-sequence of grasshoppers, such that the presentation sequence of lubbers of various sizes was balanced. Previous work suggests that frogs do not readily develop food-aversion conditioning to lubbers (Hatle & Faragher 1998), and indeed, attack rates did not decline between...
the 1st and the last days of testing. The results (Table 6) show that, against frog predators, large lubbers enjoyed a significant survival advantage over small lubbers. Over half of the 22 frogs attacked 1st instar lubbers, but no frogs attacked adult lubbers and only two frogs attacked 5th instar lubbers.

We tested wild, naive starlings, *Sturnus vulgaris*, and house sparrows, *Passer domesticus* against *R. microptera* grasshoppers in Normal, Illinois. We first trained these birds to feed at a feeder on frozen-then-thawed crickets, wax-moth larvae and mealworms, and 0.5-g pieces of moist cat food. After two or three days, when the birds repeatedly and aggressively fed at the feeder, we placed out three feeders, each separated by ~60 cm. One feeder contained one each of a living 1st, 2nd and 3rd-instar *R. microptera*, tied to the feeder by thin strings. The 2nd feeder contained a live 4th and a live 5th-instar grasshopper, and the 3rd feeder contained a live-tethered adult male and adult female grasshopper. We separated the lubber size classes onto different feeders because trials a year earlier showed that the birds were hesitant to approach the feeders containing adult grasshoppers. Wariness in birds increases with prey size (Gamberale & Tullberg 1998). The feeders were placed out at dawn and inspected and removed as soon as feeding had occurred (13 min to 2.2 h). Overall, we tested at four locations, each at least 1.2 km from the others. We assume that each test involved a different flock of birds. We tested at each site only once. In some cases we do not know which species of bird ate or attacked lubbers, and so we have combined the response for the two bird species.

Table 7 gives the number of grasshoppers attacked (defined as wounded, missing body parts, gone from the feeder, or observed to be taken by a bird). The results show that large lubbers were not attacked. Indeed, not a single 5th instar, adult male, or adult female *R. microptera* was damaged. In contrast, nearly all small individuals were damaged, killed, or missing from the feeders during each of the four tests. These wild birds had probably never encountered these grasshoppers, because lubbers do not exist in the midwest of the USA. These, presumably naive, birds sampled lubbers, even though this prey is warningly colored and chemically defended.

In all of our experiments, testing seven different predator species from different taxa (spider, preying mantid, wheel bug, ant, frog, starling and sparrow), large lubber instars enjoyed a highly significant advantage against predation: predators tended to attack or overcome smaller size classes of lubber grasshoppers, but refused to attack or failed to overcome large-sized lubbers. These data demonstrate a strong advantage for large body size for lubber grasshoppers against...
predators. Most surprising is that larger lubber body size decreased both invertebrate and vertebrate predation. As such, our results suggest that large size in an insect can be an antipredator defense, against both vertebrate and invertebrate predators (Fig. 7).

5) Chemically defended grasshoppers are generally larger than their non-chemically defended relatives.—We wanted to know if large body size was associated with chemical defense in other grasshopper species, and therefore we compared body sizes of chemically defended grasshoppers to those of grasshopper species that lack chemical defenses. We obtained body-size data for female grasshoppers from various faunal monographs and field guides, and present the data here as geographic or taxonomic summaries (Figs 8-10, Table 8).

We also list all the grasshopper species known or suspected by us to be chemically defended (see Whitman 1990), and provide size and mass data when available (Table 9).[^4]

Among the ~13,000 species of grasshopper (Orthoptera Species File), adult body mass ranges across three orders of magnitude, length by 1.5 orders of magnitude: from ~ 15 mg and 5 mm for tiny adult male *Illapelia penai* from South America (Carbonell & Mesa 1972), to 30,000 mg and ~ 120 mm (head to tip of abdomen, and 145 mm (to wing tip) for the largest female individuals of *Tropidacris cristata* from Central and South America (Uvarov 1966, 1968).

[^4]: We tabulated “body length” from various sources. However, different authors recorded body length in different ways (i.e., fastigium to tip of abdomen or fastigium to wing tip), and it is not always clear which method they used. Most measurements are probably based on dried museum specimens, which are shorter than live specimens. In addition, grasshopper masses and lengths vary widely geographically, annually, seasonally, with local environmental conditions, and in females, during the gonotrophic cycle. Also, nomenclature changes over time, and the taxonomic designation for many of the early descriptions for size or chemical defense are questionable. Hence, our data can only be considered as the best current estimate of the situation.
In general, grasshopper mass, shape, and length vary with family, latitude, and life form, with the largest species usually inhabiting warmer climates (Uvarov 1966, 1977). Ground-dwelling, "terricolis" grasshoppers tend to be robust and heavy, and grass-mimicking species (e.g., *Acrida*, *Achurum*) tend to be long, thin and light.

However, even with such wide background variability in size, shape, and mass among grasshoppers, there are striking trends related to chemical defense. First is that the majority of females of all grasshopper species are under 1 g and 4 cm (Table 8, Figs 8-10). By comparison, the females of most of the ~ 40 known chemically defended species of grasshopper (from among seven subfamilies) are heavier than 2 g and longer than 4 cm (Fig. 9, Table 9). Figure 9 gives female body sizes for some pyrgomorphids from Africa and Thailand, and also for USA Melanoplinae; chemically defended species are designated in grey. Note that in each case, the chemically defended species sort to the larger-sized classes. Thus, chemically defended grasshoppers tend to be larger than nonchemically defended grasshoppers.

A problem in our analysis is that many palatable grass-mimicking grasshoppers are very long, thus weakening the correlation between chemical defense and body length. However, such grasshoppers weigh substantially less than chemically defended grasshoppers, which tend to be robust and heavy. Mass is a better metric than length for predicting ecological interactions, in part because mass scales as the cube of length for isometric bodies (Peters 1983, Calder 1996). Hence, a doubling of body length would increase volume and mass by eight times, for individuals with the same relative dimensions. Although chemically defended grasshoppers may be only somewhat larger than palatable grasshoppers, they are substantially heavier. Unfortunately, grasshopper fresh-body masses are difficult to come by. However, Pfadt (1994) gives fresh adult mass for 30 common Western USA species (Fig. 10). Of these, the greatest mean female mass was 1.65 g, and females of only three species exceeded 1.0 g. In comparison, median wet masses for females of chemically defended grasshoppers center around 4 to 5 g (Table 9).

Another problem is our incomplete knowledge of chemical defenses among grasshoppers. Many chemically defended species are yet to be discovered, and in many cases we only have strong, not conclusive, evidence for chemical defense. For example, the largest grasshopper known, *T. cristata* (see above), is probably chemically defended, as they (and some other Romaleinae – including *Tropidacris*, *Chromacris*, and *Taeniopoda*; see Table 9) possess many of the traits characteristic of the chemical defense syndrome (Whitman *et al.* 1985): they feed on toxic plants, and the nymphs aggregate and flaunt bright (presumably warning) colors (Rowell 1983, Carbonell 1986, Whitman unpub.). Locust species, two of which have been found to be chemically defended when in the gregarious, swarming phase (Sword 1999, Despland & Simpson 2005, Simpson & Sword 2009), also tend to be large and heavy (Uvarov 1966, 1977). Some larger-bodied locust species, Proscopiidae, Pyrgomorphidae, Pamphagidae and Romaleinae may likewise be chemically defended (Schultz 1981, López *et al.* 2007), but we will not know until careful predator-feeding trials are completed.

In summary, large size appears to be correlated with chemical defense in grasshoppers. And, as our results demonstrate, large size in an insect can deter invertebrate predation. This supports the hypotheses that large size is beneficial for chemically defended

### Table 8. Percentage of grasshopper species with females under 4-cm body length for different geographic regions.

<table>
<thead>
<tr>
<th>Location</th>
<th>N</th>
<th>Percentage of females &lt; 4.0 cm</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Europe</td>
<td>332</td>
<td>90</td>
<td>Harz 1975</td>
</tr>
<tr>
<td>USA &amp; Canada</td>
<td>233</td>
<td>88</td>
<td>Capinera <em>et al.</em> 2004, Vickery &amp; Kevan 1985</td>
</tr>
<tr>
<td>New Zealand</td>
<td>15</td>
<td>87</td>
<td>Bigelow 1967</td>
</tr>
<tr>
<td>USSR &amp; adjacent areas</td>
<td>977</td>
<td>85</td>
<td>Bei-Bienko &amp; Mishchenko 1963, 1964</td>
</tr>
<tr>
<td>Japan</td>
<td>119</td>
<td>84</td>
<td>Ichikawa <em>et al.</em> 2006</td>
</tr>
<tr>
<td>North Africa</td>
<td>205</td>
<td>75</td>
<td>Chopard 1943</td>
</tr>
<tr>
<td>Thailand</td>
<td>56</td>
<td>71</td>
<td>Roffey 1979</td>
</tr>
</tbody>
</table>
grasshoppers and that escape from vertebrate predation (via chemical defense) allows some grasshoppers to evolve large size.

**General discussion**

Copious evidence suggests that predation can be a strong selective force on prey morphology (Kittlewell 1973, Swain 1992, Heinrich 1993). Although large size is perhaps the most successful defence in vertebrates (e.g., elephants and rhinos), large body size has seldom been considered as an antipredator defense in insects. However, our results show that large lubber size is highly beneficial against both invertebrate and vertebrate predators, and thus serves as a defensive trait.

In our trials, the largest lubber grasshoppers were relatively immune to predation. Note that we selected as test predators, the largest wolf spider (*Honga carolinensis*), largest mantid (*Tenodera aridifolia*), and the largest reduviid species (*Arilus cristatus*) in the USA, as well as a very aggressive ant species (*Solenopsis invicta*). Presumably, lubbers would enjoy even greater protection against the more common smaller and less aggressive invertebrate predators that share their habitats. In addition to size-escape from invertebrate predation, our results show that large lubber size can deter vertebrate predators as well (Tables 6, 7). As such, lubbers have come to occupy a relatively predator-free niche.

We suggest that large size in lubber grasshoppers evolved as a direct consequence of chemical defense against vertebrate predators.

We further propose that large size is a common antipredator trait among chemically defended insects. Chemically defended insects often possess a suite of characteristics that are diametrically opposite to those of nonchemically defended insects (Salazar & Whitman 2001). This ensemble of traits has been named the Chemical Defense Syndrome (CDS), and includes chemical defense, visual, chemical, and/or mechanical (tactile or auditory) warning signals (aposematism) and threat displays, aggregation, exposed diurnal behavior, flightlessness, sluggishness, and large size (Whitman *et al.* 1985, Yosef & Whitman 1992, Salazar & Whitman 2001). Not all chemically defended insects exhibit all of these traits, but enough do to validate the principle.

Various components of the CDS have been thoroughly examined (Ruxton *et al.*, 2004), such as chemical defense (Blum 1981, Whitman *et al.* 1990, Eisner *et al.* 2005), aposematism (Guilford 1990, Prudic *et al.* 2007), aggregation (Vulinec 1990, Costa 2006), and sluggishness (Hatle & Whitman 2001, Hatle *et al.* 2002). However, large size as a component of the CDS has received little attention, despite its apparent common association with chemical defense across numerous insect orders (Pasteels *et al.* 1983), and the fact that the efficacy of warning coloration increases with body size (Nilsson & Forsman 2003).

The consequences of this association are not trivial: the presence or absence of chemical defense may be an important factor in body size evolution in insect prey (Forsman & Merilaita 1999). In fact, just the presumption of chemical defense may be enough to influence body-size evolution, such as in those Batesian mimics that lack chemical defenses, but mimic large insects that do. An example may be seen in the barklice (*Pscooptera*), nearly all of which are cryptic and ≤ 5 mm long (Mockford 1993), except for a group of giant-bodied (up to 11.5-mm long) *Pscooptera* from Central America that apparently mimic assassin bugs and wasps (Mockford 1992). Whether these giant barklice are actually chemically defended or are only mimics is unknown. However, the important ecological and evolutionary reality is that they appear to be defended, and as a result presumably suffer less predation and less selection for small size.

Another feature of many species of chemically defended grasshoppers is that (like lubbers), their chemical defenses often work better against vertebrate predators than invertebrate predators (Whitman 1990). For example, both birds (Descamps & Wintrebert 1966) and humans (Steyn 1962) have died after eating toxic *Phymateus* grasshoppers. Euw and coworkers (1967) calculated that a single *Poekilocerus bufonius* contained enough cardenolide to kill a cat. Greg Sword experienced golf-ball sized lymph nodes after consuming a single *Schistocerca emarginata* grasshopper (Sword 2000), and we thank him for his personal commitment to understanding the dynamics of chemical defense in Orthoptera.

Of course, there is great variability among the interactions of the ~40 known chemically defended grasshopper species and their >200,000 species of potential predators. However, for those protected species that have been thoroughly studied, there are usually several species of invertebrate predator that are not deterred by the chemical defenses of the grasshopper (Whitman 1990, Sword 2000). Insect chemical defenses may have evolved primarily against birds (Pasteels *et al.* 1983, Brower 1984, Rothschild 1985), and chemical defense in grasshoppers may have evolved primarily against vertebrate predation.

Our results suggest a broader evolutionary theme. The evolutionary path of a species is guided by phylogenetic and ecological constraints. Major evolutionary changes and rapid speciation and
Table 9. Body sizes of chemically defended grasshoppers. Note that females of most species >2g and 4 cm. * no sex specified.

<table>
<thead>
<tr>
<th>SUPERFAMILY</th>
<th>Family</th>
<th>Body mass (g)</th>
<th>Body length (mm)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>male</td>
<td>female</td>
<td>male</td>
</tr>
<tr>
<td>Subfamily:</td>
<td>PAMPHAGOIDEA</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Orthacridinae</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Colemania sphenarioides</td>
<td>–</td>
<td>–</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>Pyrgomorphinae</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Attractomorpha crunulata</td>
<td>–</td>
<td>–</td>
<td>16-19</td>
</tr>
<tr>
<td></td>
<td>Aularches milliaris (=punctus, scabiosus)</td>
<td>–</td>
<td>–</td>
<td>37-55</td>
</tr>
<tr>
<td></td>
<td>Dicyophorus spumans</td>
<td>–</td>
<td>–</td>
<td>47-49</td>
</tr>
<tr>
<td></td>
<td>Maura rubroornata (=rugulosa)</td>
<td>–</td>
<td>–</td>
<td>22-24</td>
</tr>
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<td></td>
<td>Monistria discrepans</td>
<td>–</td>
<td>–</td>
<td>&lt;28</td>
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<td></td>
<td>Monistria pustulifera</td>
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<td>–</td>
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<td>Petasida ephippigera</td>
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<td>–</td>
<td>&lt;53</td>
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<td></td>
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<td>–</td>
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<td></td>
<td>Phymateus viridipes</td>
<td>–</td>
<td>–</td>
<td>42-46</td>
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<td>Phymateus aegrotus (=hildebrandti)</td>
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<td>–</td>
<td>–</td>
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<tr>
<td></td>
<td>Phymateus leprosus</td>
<td>–</td>
<td>–</td>
<td>70*</td>
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<tr>
<td></td>
<td>Phymateus madagassus</td>
<td>–</td>
<td>–</td>
<td>43-51</td>
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<tr>
<td></td>
<td>Phymateus morbillosus</td>
<td>3.6</td>
<td>12.3</td>
<td>55</td>
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<tr>
<td></td>
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<td>Phymateus viridipes</td>
<td>–</td>
<td>–</td>
<td>50-61</td>
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<td>Phymateus seroticus</td>
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<td>Phyteumas (Phymateus) purpurascens</td>
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<td>Poekilocerus bufonius</td>
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<td>Poekilocerus hieroglyphicus</td>
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<td>4.1</td>
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<td>–</td>
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<td>Taphronota calliparea (=cincta)</td>
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<td>–</td>
<td>23-40</td>
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<td></td>
<td>Taphronota occidentalis</td>
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<td>–</td>
<td>–</td>
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<td>Zonocerus variegatus</td>
<td>1.0</td>
<td>1.8</td>
<td>28-37</td>
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<td>Pamphaginae</td>
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<tr>
<td></td>
<td>Romaleidae</td>
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<td></td>
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<tr>
<td></td>
<td>Romaleini</td>
<td></td>
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<tr>
<td></td>
<td>Chromacris colorata</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Chromacris pedes</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Romalea microptera</td>
<td>1.5-6.9</td>
<td>2.1-18.5</td>
<td>41-70</td>
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<tr>
<td></td>
<td>Taeniopoda eques</td>
<td>0.8-2.8</td>
<td>2.3-8.3</td>
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<td></td>
<td>Taeniopoda reticulata</td>
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<td>–</td>
<td>43-52</td>
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<td></td>
<td>Tropadacris cristata</td>
<td>≤30.0*</td>
<td>–</td>
<td>60</td>
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<td></td>
<td>Tropadacris collaris (=grandis)</td>
<td>–</td>
<td>–</td>
<td>72</td>
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<tr>
<td>Family:</td>
<td>Acrididae</td>
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<td>Catantopinae</td>
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<td>Melanoplinae</td>
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<tr>
<td></td>
<td>Dactylotum bicolor</td>
<td>–</td>
<td>–</td>
<td>21</td>
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<tr>
<td></td>
<td>Dactylotum variegatum</td>
<td>–</td>
<td>–</td>
<td>22</td>
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<td></td>
<td>Cyrtacanthacridinae</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Schistocerca emarginata (=lineate)</td>
<td>–</td>
<td>–</td>
<td>23-35</td>
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<td>Schistocerca gregaria</td>
<td>1.5-2.3</td>
<td>1.9-3.6</td>
<td>42-50</td>
</tr>
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diversification follow those rare breakthroughs when a taxon eliminates a constraint. Body size, as all organismal traits, is under conflicting selection pressures, with some factors selecting for small and others for large size. A change in strength or direction in any one factor can alter the overall balance between these competing selective forces, pushing (or allowing) the population to evolve until a new equilibrium body size is reached. Such a process might explain some cases of island gigantism (Evenhuis & Eldredge 2004, Lomolino 2005, Bell et al. 2007), the loss of pigment and eyes in cave-dwelling species (Culver 1982), the loss of flight and defensive behavior in island-dwelling birds (MacArthur & Wilson 1967) and the correlation of defense mechanisms with predator sympathy, but not allopatri (Jones et al. 1978, Endler 1985).

In some cases, ecological or behavioral change stimulates a beneficial evolutionary breakthrough, which then alters overall selection dynamics, releasing a cascade of new evolutionary events. Such an “accidental” or serendipitous evolutionary breakthrough may lead to rapid increases in population density and range, speciation and radiation. Examples might include the evolution of lungs, flight, sociality, or chemical defense – all presumably beneficial traits that dramatically alter overall selection dynamics, leading to multiple changes in numerous other traits (e.g., Schmidt 1990). For example, chemical defense may be a prerequisite for the evolution of insect sociality (Starr 1985, Kukuk et al. 1989), or the many components of the CDS.

Perhaps the evolution of chemical defense in lubber grasshoppers was a breakthrough adaptation that sent them down a different evolutionary pathway, and set in motion a series of subsequent evolutionary events that profoundly altered their physiology, morphology, behavior, life-history, and ecology. This could have started when their cryptic and palatable ancestors encountered and fed on euglena containing defensive compounds, releasing the insect’s gut and oral and anal discharges with deterrent substances, causing reduced predation on that population (e.g., Jones et al. 1988, Sword 2001, Calcagno et al. 2004). Continued directional selection by predators could have then selected for specialization on toxin-providing food plants, and greater defensive capabilities (e.g., Jones et al. 1988, Dopman 2002), including all the traits of the Chemical Defense Syndrome (Whitman et al. 1985), such as aposematism, threat displays, gregariousness, flightlessness, sluggishness, and large size. Similar arguments have been made for other chemically defended groups (e.g., Schmidt 1990 for Hymenoptera).

Hence, the key evolutionary event for lubber grasshoppers may have been feeding on toxic plants, which increased defense against vertebrate predators, thus favoring the evolution of stronger chemical defenses. Escape from vertebrate predation (via toxins), released lubbers to evolve large body size, which then allowed them to escape from invertebrate predation via mechanical defense (large size). As such, the size difference between chemically defended lubber grasshoppers and their palatable relatives, represents the magnitude of the evolutionary force of vertebrate predation on grasshopper body size.

Of course large size has many benefits, including perhaps greater mating success, fecundity, homeostasis, an ability to consume tough food, dominate intraspecific competitors, and for grasshoppers, to lay egg pods deeper to thwart egg predators and parasitoids (Peters 1983, Andersson 1994, Calder 1996, Vincent 2006, Stauffer & Whitman 2007, Whitman 2008). Another reason large body size may be advantageous as an antipredator mechanism in insects is because it strongly covaries with the strength of mechanical defenses such as biting or kicking (Norman 1995, Burrows & Morris 2003, Vincent 2006, Vincent & Lailvaux 2008). Whereas small insects must rely on crypsis or rapid-escape behaviors to avoid predation (Dangles et al. 2007), larger species or instars can often generate strong forces during defensive kicking or biting behaviors. For example, another large bodied lubber grasshopper, Brachystola magna, can bite through human skin, and can employ its spiked hindlegs during defensive kicking bouts to generate upwards of 25 Newtons of force, enough to pierce the integument of some vertebrate and invertebrate predators (Vincent, pers. obs.). All of these features should select for larger insect size. However, the fact that insects as a group remain small (Blankenhorn 2000, Whitman 2008) suggests that the disadvantages of increasing size generally outweigh the advantages.

In this paper we propose that lubber grasshoppers evolved chemical defense prior to large size. However there are other scenarios for the evolution of size and defense in lubbers. Perhaps lubbers evolved large size first, which exposed them to increasing predation from vertebrates and placed them under strong selection to develop antinvertebrate chemical defense. Hence, maybe chemical defense is a result of large size and not vice-versa.

Our results also confirm that predator threat changes with prey ontogeny, as in other insects (Dempster 1967, Stortenbecker 1967, Feeny et al. 1985, Dixon & Baker 1988, Belovsky et al. 1990, Medina & Barbosa 2002). For many insect prey, invertebrate predators attacked the smallest instars or species, and vertebrate predators the larger instars or species (Watanabe 1976, 1981, Montllor & Bernays 1993). This is well documented in grasshoppers (Stower & Greathead 1969, Chapman & Page 1979, Belovsky et al 1990, Belovsky & Slade 1993), where smaller instars usually suffer higher rates of predative mortality than larger (larger) instars (Stortenbecker 1967, Belovsky et al. 1990; Danner & Joern 2003). In lubbers, if the smaller, earlier instars suffer higher predation rates than the larger, later instars, then we might expect selection for large egg size and rapid growth (Paine 1976, Arendt 1997) of the small early stages. This may be the case for lubbers, which have one of the largest egg sizes known for grasshoppers (1 cm long and up to 43 mg fresh mass), and which are black as nymphs, which aids solar heating, growth, and development (Whitman 1987, 1988).

Lastly, we previously mentioned that predator-prey interactions are exceedingly complex. Because of such complexity, there are exceptions to nearly every generality that we have discussed. Hence, some small invertebrate prey are more conspicuous, more nutritious, and less agile than some large invertebrate prey species. Some vertebrates prefer smaller invertebrate prey, some invertebrate predators can capture large prey (Lorenz 2007), some chemically defended prey are quite small (Pasteeles et al. 1983), and some palatable insect prey are large. Furthermore, previous authors have anecdotally noted the defensive benefits of large body size in invertebrates, such as shellfish (Roff 2002), or documented the association between chemical defense and large size in insects (Pasteeles et al. 1983). However, we believe that overall, the generalities and principles proposed here are valid.

Acknowledgements

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