Variation in body size among populations of the bushcricket Poecilimon thessalicus (Orthoptera: Phaneropteridae): an ecological adaptation

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Variation in body size among populations of the bushcricket *Poecilimon thessalicus* (Orthoptera: Phaneropteridae): an ecological adaptation?

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Abstract

We analyzed geographical variation in body size in males and females of nine Greek populations of the bushcricket *Poecilimon thessalicus* Brunner von Wattenwyl, 1891. We found significant geographic variability in *P. thessalicus*, with all three morphometric body-size characters (hind femur, front tibia, and pronotum) highly correlated within populations. Populations differed in mean size between three mountain ranges, and were larger on moist eastern, than on dry western slopes. We suggest that the observed smaller size of the bushcrickets on western slopes is mainly the consequence of a shorter growing season due to summer drying on western slopes. Sex-specific growth rates might contribute to the observed smaller body size in males in all populations. Rensch's rule that sexual size dimorphism (SSD) decreases as body size increases is supported, with males growing relatively larger compared to females in populations with larger body sizes. This pattern might be sexually selected, as males that produce larger nuptial gifts are favored as mates in *Poecilimon* bushcrickets.

Key words

geographic variation, protandry, Rensch's rule, spermatophore

Introduction

Body size in animals influences many traits, such as competitiveness, dispersal ability, number and size of offspring and longevity. This is why fitness is often highly correlated with body size (Peters 1983, Stearns 1992, Honek 1999, Roff 2002). Geographic variation in size is common in animals, with conspecific populations often showing considerable differences in adult body size (Atkinson 1994). Explanations for this variation include both proximal (developmental) and ultimate (evolutionary) reasons, including differences in climate, resource quality and availability, size-specific predation, social factors such as population density and competition, character displacement, sexual selection and clinal variation in development rate (Berven & Gill 1983, Peters 1983, Petraitis *et al.* 2001, Sandland & Minchella 2004).

During development, body size is affected by any number of environmental factors, including disease, parasites, toxins, and nutrition (Ikeya *et al.* 2002, Davidowitz *et al.* 2004), with dietary restrictions generally causing smaller body size. Temperature also affects body size, and higher temperatures generally result in the development of smaller animals (Atkinson & Sibly 1997, Davidowitz & Nijhout 2004).

On an evolutionary scale, populations can respond to local selection on body size. One commonly observed intraspecific clinal pattern in body size for mammals is an increase in size with latitude, known as Bergmann's rule. However, many invertebrates show trends consistent with the converse of Bergmann's rule, whereby body size is smaller in populations at higher latitudes and altitudes (Masaki 1967, Mousseau & Roff 1989, Blanckenhorn & Fairbairn 1995, Blanckenhorn & Hellriegel 2002). Nevertheless, patterns consistent or inconsistent with Bergmann's rule are not mutually exclusive since they can be affected by different environmental causes (temperature and season length, respectively) and have different underlying mechanisms (Blanckenhorn & Demont 2004).

The optimal size (and age) at maturity is a frequently studied topic in life history theory and it is based on the assumption of a fundamental trade-off between the benefits of a large body size and the costs of a consequently long juvenile period (Stearns 1992, Roff 2002, Kingsolver *et al.* 2004). Presumably, individuals can become larger (and thus increase fecundity) by lengthening the growth period. However, such individuals suffer a cost in that they may die before reproducing. In contrast, an individual can rush through its development in order to rapidly reach adulthood and reproduce, but at a lower body size and fecundity. Which of these strategies evolves should depend on daily mortality rates and length of growing season (Masaki 1967; Roff 1980; Gotthard 2001, 2004; Blanckenhorn & Demont 2004). We would expect rapid development and small adult size under short growing seasons and high daily mortality rates. Thus, characterizing lengths of growing seasons is an important factor when explaining size variation among animal populations.

In addition to natural selection on body size, there can also be sexual selection on size. This selection can be sex specific, and result in different sizes in males *vs* females: sexual size dimorphism (SSD). For example, when the earliest maturing males fertilize more eggs, then there should be selection for fast development in males (protandry), possibly resulting in smaller male size. When males fight for possession of females, then there should be strong selection for large male size. In contrast, when males choose females based on large size, then large females should be selected. In orthopterans, male and female size often varies differently among geographic populations, in acridids (Roff & Mousseau 2005, Berner & Blanckenhorn 2006, Bidau & Martí 2007), gryllids (Masaki 1967, Mousseau & Roff 1989, 1995) and bushcrickets (katydids) (Landman *et al.* 1989). This variability in SSD may be a consequence of differential natural and sexual selection on the two sexes. Rensch's rule states that SSD should decrease as overall body size increases, and is a macroecological pattern that has been observed in a wide range of species (Fairbairn 1997, Blanckenhorn *et al.* 2007).

The *Poecilimon propinquus* group (Lehmann AW 1998, Lehmann AW *et al.* 2006) of bushcrickets (katydids) form an interesting clade, because they exhibit interspecific, intraspecific, and sexual size variation, and have served as model organisms in various evolutionary studies (*e.g.*, Heller 1997, Lehmann AW 1998, Lehmann GUC 1998).

Table 1. Geographic data for the nine populations of *P. thessalicus* used for body-size analysis.

Population	Mountain range	Altitude m [a.s.l.]	Latitude N	Longitude E	n males	n females
Rizómata	Piería	950	22 23′	40 29′	7	
Elatohóri 2km W	Piería	800	22 24′	40 32′	96	30
Elatohóri 3km W	Piería	850	22 23′	40 30′	10	
Katafígi	Piería	1000	22 14′	40 24′	25	25
Litóhoro 13.6km W	Olymp	1000	22 45′	40 10′	8	5
Sparmoú 4km N	Olymp	1800	22 31′	40 03′	25	20
Melívia 1km E	Ossa		22 81′	39 74′	7	5
Dimitra SE	Ossa	400	22 65′	39 68′	8	8
Skíti 1km NW	Ossa		22 82′	39 68′	15	5
				Total n	201	98

Phenologically, all *Poecilimon* are typical spring species, with a remarkable earlier appearance than most other bushcrickets, and an adult season lasting for around four weeks (*e.g.*, Lehmann & Lehmann 2006). All members of the *P. propinquus* group are nocturnal (Heller & von Helversen 1993). In *Poecilimon veluchianus*, the discovery of remarkably smaller-sized individuals in some populations led to the description of a separate subspecies (Heller & Reinhold 1993). Subspecies crossing revealed a genetic basis for body size parameters and male fertility (Reinhold 1994), leading to differences in the mating effort of males (Heller & Reinhold 1994). In contrast to *P. veluchianus*, body- size variation has been little studied in *Poecilimon thessalicus* Brunner von Wattenwyl, 1891 (Orthoptera: Phaneropteridae), a medium-sized flightless bushcricket approximately two centimeters in length (Lehmann *et al.* 2001). This univoltine species has an obligatory egg diapause and six nymphal stages in both sexes (unpub. data).

The present study addresses the geographic distribution of body size in populations of *P. thessalicus*. This species is distributed nearly continuously over the mountain ranges in the eastern mainland of Greece (Lehmann AW 1998), and shows extensive size variation between populations. We propose a correlation between body size and ecological parameters in these populations. Specifically, we hypothesize that smaller-sized individuals will exist in areas with shorter growing seasons, because a shorter growing season should select for earlier maturation and smaller body size. We also hypothesize that this species will follow Rensch's rule, which predicts lowered SSD in populations with larger overall body size.

Methods

We collected adult male and female *P. thessalicus* bushcrickets (katydids) from nine localities throughout the species' geographic range in three mountain ranges: Piería, Olymp and Ossa, in eastern Greece (Table 1). We used Mitutoyo calipers (accuracy 0.01 mm) to measure three morphometric external characters in live individuals: the length of the right hind femur, length of the right front tibia and the mid-dorsal length of the pronotum.

Results

Body size varied widely between populations of *P. thessalicus* (Table 2). The smallest and largest female individuals showed hind-femur lengths of 15.0 mm and 18.3 mm, respectively, while hind-femur length for individual males ranged from 13.0 mm to 17.7 mm. We found a significant difference between populations for mean hind-femur length (two-way ANOVA: factor population: $F_{6,266}= 32.28$, $P<0.001$), pronotum ($F_{6,218}= 12.54$, $P<0.001$) and front tibia ($F_{6,218}= 35.69$, $P<0.001$). Additionally, a strong positive correlation between the three body parameters was apparent (pronotum *vs* femur length: $y_{pron} = 0.25x_{fem} + 2.01$, $R^2 = 0.66$, n= 230, $P<0.001$; tibia *vs* femur length: $y_{tib} = 0.34x_{fem} + 1.22$, $R^2 = 0.80$, n=230, $P<0.001$), and pronotum *vs* tibia length: $y_{pron} = 0.63_{tib} + 1.73$, $R^2 = 0.62$, n= 232, $P<0.001$). Females were larger than males in all three body parameters (two-way ANOVA: factor sex: $F_{1,266;218;218}$=333.72; 44.67; 69.71, $P<0.001$).

Table 2. Means and standard errors of three morphometric characters in nine populations of *P. thessalicus*. We measured the length of the hind femur, the front tibia, and the pronotum, in mm, for live males and females separately. The data are sorted geographically from North to South.

		males						females					
	Population	Meta femur	n=	Pro tibia	n=	Pronotum	n=	Meta femur	n=	Pro tibia	n=	Pronotum	n=
1	Rizómata	14.53 ± 0.36	7	6.40 ± 0.34	7	5.46 ± 0.13	7						
2	Elatohóri 3	14.90 ± 0.71	9	6.41 ± 0.28	10	5.81 ± 0.26	10						
3	Elatohóri 2	14.98 ± 0.71	96	6.55 ± 0.36	46	5.84 ± 0.32	46	16.87 ± 0.71	30	6.92 ± 0.28	30	6.14 ± 0.35	30
4	Katafígi	14.20 ± 0.59	24	6.09 ± 0.22	25	5.48 ± 0.19	25	16.27 ± 0.66	25	6.71 ± 0.26	25	5.94 ± 0.24	25
5	Litóhoro	16.78 ± 0.61	8	7.17 ± 0.31	8	6.21 ± 0.37	8	17.52 ± 0.26	5	7.21 ± 0.22	5	6.25 ± 0.23	5
6	Sparmoú	14.13 ± 0.45	25	6.06 ± 0.30	25	5.55 ± 0.26	25	15.77 ± 0.34	20	6.54 ± 0.22	20	5.90 ± 0.26	20
7	Melívia	15.73 ± 0.69	6	6.91 ± 0.47	7	5.96 ± 0.43	7	16.83 ± 1.24	5	7.11 ± 0.50	5	6.20 ± 0.29	5
8	Dimitra	14.94 ± 0.66	8	6.56 ± 0.32	8	5.96 ± 0.30	8	15.94 ± 0.52	8	6.77 ± 0.24	8	6.13 ± 0.26	8
9	Skíti	16.29 ± 0.83	15	7.07 ± 0.34	15	6.10 ± 0.30	15	17.26 ± 0.86	5	7.37 ± 0.23	5	6.26 ± 0.37	5
			198		151		151		98		98		98

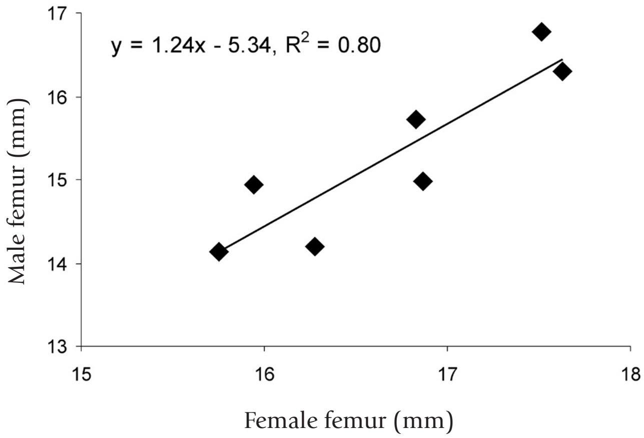

Fig. 1. Correlation between population means of male and female hind-femur lengths, for nine populations of *P. thessalicus* from eastern Greece.

Male and female femur sizes correlated strongly within populations ($y_{mfl} = 1.24x_{ffl} - 5.34$, $R^2 = 0.80$, $P < 0.001$) (Fig. 1). An allometric analysis on log-transformed data confirmed a relative increase in male, compared to female, femur length, with an allometric slope of b = 1.34, indicating that in populations with larger individuals, sexual size dimorphism is less pronounced.

Geographical location had a significant influence on body size (Fig. 2). A two-way analysis of variance revealed that males from the Piería mountain range were smaller than those from the Olymp or the Ossa mountain range ($F_{2,192} = 27.53$, $P < 0.001$). In addition, males on the western side of all the mountains were smaller than those on the eastern sides ($F_{2,192} = 27.53$, $P < 0.001$, see black symbols in Fig. 2). Body-size differences between western and eastern populations were greatest in the Olymp, and smallest in the Piería, mountain range.

Discussion

P. thessalicus exhibited reasonably large body-size variation between populations (Fig. 2). In ectothermic species several geographic body-size patterns have been found. In many species these patterns follow altitudinal or latitudinal clines (Blanckenhorn & Demont 2004, Chown & Klok 2003). This is also true for orthopterans, where several studies reported a reduction of body size with altitude (Berner & Blanckenhorn 2006, Landman *et al.* 1989), latitude (Bidau & Martí 2007, Masaki 1967, Mousseau & Roff 1989) or both (Roff & Mousseau 2005). However, the generality of this clinal rule has been questioned. Blanckenhorn & Demont (2004) list 46 insect species belonging to 11 orders and found 37% followed Bergmann's rule (with larger individuals occurring in cooler climates), while 63% exhibited the converse pattern. They suggested that these two clinal patterns might be part of a continuum of adaptive responses to ambient temperature or length of growing season. These different effects might be jointly operating to produce a variety of clines (Blanckenhorn & Demont 2004). Any change in temperature, nutrition, or pathogens with geography might itself be the agent causing variation, because these factors can strongly influence growth patterns and ultimate body size (Atkinson 1994, Angilletta & Dunham 2003).

In *P. thessalicus*, geography is likely to be an indicator variable of some other factor that directly exerts a selective pressure on the populations. The only obvious geographic pattern we found to have a significant influence on body size between populations was whether the populations lived on the western or eastern slopes of the three mountain ranges. It is possible that there are climate differences between western and eastern slopes, especially in terms of precipitation and length of growing season.

Seasonality can also be a determinant of body-size variation (Chown & Gaston 1999, Chown & Klok 2003). In univoltine insects,

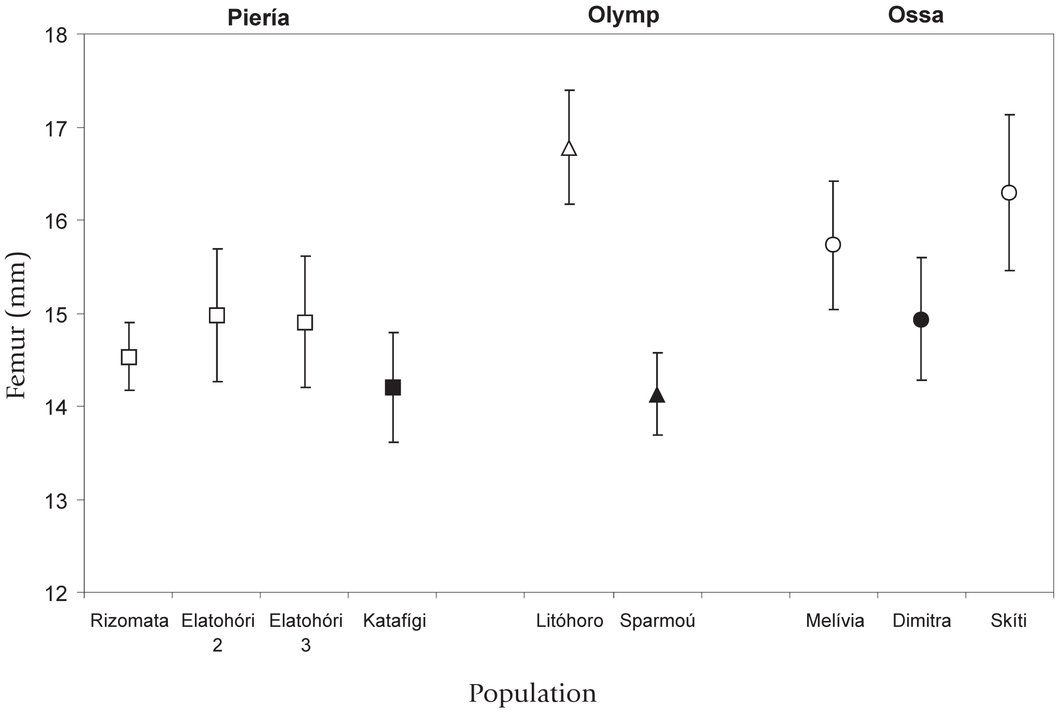

Fig. 2. Population means (± SD) of male hind femur length, sorted from north to south. Black symbols represent populations on the western slopes of the three mountain ranges.

such as *P. thessalicus*, the length of the growing season represents a powerful limiting factor (Masaki 1967, Roff 1980). Short-season climates can constrain growth and development (Chown & Klok 2003) and so produce smaller body sizes. The length of the insect growing season is generally thought to correlate with ambient temperatures, with longer seasons at lower altitudes and latitudes (Masaki 1967).

Greece has a Mediterranean climate, whereby lack of summer rain turns the vegetation dry and brown in mid to late summer. Observed body-size variation in *P. thessalicus* may, therefore, result from climatic selection on the duration of the nymphal stages. Larger adults would develop in more suitable habitats where there is, for instance, longer-lasting nutritious vegetation (Masaki 1967, 1978; Roff 1980; Blanckenhorn & Demont 2004). Phenotypic differences among populations presumably have a strong genetic component (Masaki 1967, 1978; Roff 1980; Blanckenhorn & Fairbairn 1995; Blanckenhorn & Demont 2004). Indeed, in *P. veluchianus*, crossings between populations with distinct body sizes clearly revealed the genetic base for body-size differences (Reinhold 1994).

Sexual size dimorphism.—Male and female animals are rarely the same size, and the selective processes that create sexual size dimorphism (SSD) are controversial (Andersson 1994). Sexual selection often favors males with larger body size (Blanckenhorn *et al.* 1999, Fairbain & Preziosi 1994, Kraushaar & Blanckenhorn 2002). The difference in size between the sexes of a given species will then be a result of differential selection on the sexes, and the balance between selection pressures and constraints. Male bushcrickets transfer very large nuptial gifts during mating. Such gifts can account for around 30 percent of male body weight in *P. thessalicus* (McCartney *et al.* this issue, p. 231). Females of *P. zimmeri* preferentially mate with heavier males (Lehmann & Lehmann 2008), and these males produce heavier spermatophores (Lehmann & Lehmann in press), suggesting that sexual selection has a strong influence in this species.

Females of *P. thessalicus* are larger than males in all populations studied, but SSD decreases as female body size in *P. thessalicus* increases, following Rensch's rule. SSD could be explained — either by equal growth rates but different ages of maturation between males and females — or as the result of differences in growth rates between the sexes. However, Blanckenhorn and coworkers (2007) found only a weak positive relationship between SSD and developmental time for arthropods in general. They suggest that growth-rate differences between the sexes are more important than development-time differences in a wide range of arthropod taxa. Assuming equal growth rates of males and females, SSD would be mediated by sexual differences in development times, with the larger sex developing for a proportionately longer time. Males develop faster than females in a wide range of arthropods, including butterflies (Wicklund & Fagerström 1977, Wicklund & Forsberg 1991), spiders (Maklakov *et al.* 2004, Uhl *et al.* 2004), acridids (Berner & Blanckenhorn 2006) and bushcrickets (Wedell 1992, Simmons *et al.* 1994). Indeed, protandry is common in members of the *P. propinquus*-group, including *P. thessalicus*, in both the lab and the field, with males generally maturing three days before females (unpub. data).

In conclusion, we found significant variation in body size among populations of *P. thessalicus*. We speculate that this represents an ecologically selected growth adaptation, whereby smaller body size is selected for by the need for rapid development in a highly seasonal Mediterranean climate, which can produce poor food conditions because of summer drying of food plants. Additionally, *P. thessalicus* follows Rensch's rule, with males growing relatively larger compared to females in populations with larger body sizes.

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