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SEXUAL SIZE DIMORPHISM IN BURROWING WOLF SPIDERS (ARANEAE: LYCOSIDAE)

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ABSTRACT

This paper presents an overview of various aspects of sexual size dimorphism (SSD) in the Lycosidae, with particular emphasis on burrowing wolf spiders. Three species of the genus *Zyuzicosa* Logunov, 2010 exhibit pronounced SSD, having typical dwarf males that are half or less than half the size of females. It is argued that although the reported case of extreme SSD could reasonably be explained by the differential mortality model, understanding the evolutionary origin of extreme SSD in wolf spiders is better elucidated by examining life-history theory integrated with aspects of whole organism ontogeny.

Key Words: Araneae, extreme sexual size dimorphism, Lycosidae, wolf spiders

ПОЛОВОЙ РАЗМЕРНЫЙ ДИМОРФИЗМ У НОРНЫХ ПАУКОВ-ВОЛКОВ (ARANEAE: LYCOSIDAE)

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РЕЗЮМЕ

Данная статья представляет собой обзор различных аспектов полового размерного диморфизма (ПРД) в семействе Lycosidae, но особое внимание уделено норным паукам-волкам. У трех видов рода *Zyuzicosa* Logunov, 2010 обнаружен сильно выраженный ПРД, при котором размер карликовых самцов составляет половину (или менее) размера самок. Утверждается, что хотя отмеченный случай ПРД приемлемо объясним с помощью модели избирательной смертности, но общее понимание эволюционного происхождения экстремального ПРД следует базировать на основе изучения жизненных циклов организмов в совокупности с особенностями их онтогенеза.

Key Words: Araneae, экстремальный половой размерный диморфизм, Lycosidae, пауки-волки

INTRODUCTION

Sexual body size dimorphism (SSD) is common in spiders. It has been studied extensively, particularly regarding the extreme sexual size dimorphism in orb-weavers (Araneidae and Nephilidae), comb-footed spiders (Theridiidae) and crab spiders (Thomisidae) (see Vollrath and Parker 1992; Mikhailov 1995; Voll-

rath 1998; Hormiga et al. 2000; Huber 2005; Foellmer and Moya-Laraño 2007; Mas et al. 2009; etc.). Both 'male dwarfism' and 'female gigantism' have been documented. It was suggested that the extreme SSD should have evolved repeatedly even within the same taxonomic group, e.g., the Orbiculariae (Hormiga et al. 2000). Yet, the underlying evolutionary mechanisms of SSD remain poorly understood, especially

as body size is usually subject to several selection pressures operating simultaneously, some of which may differ between males and females (Hedrick and Temeles 1989; Andersson 1994). At least seven major hypotheses have been proposed to explain these mechanisms in spiders (reviewed by Foellmer and Moya-Laraño 2007). It is agreed that no single hypothesis can fully explain the phenomenon of SSD in spiders, which thus requires case-by-case explanation.

The starting point of the following discussion was the discovery of extreme SSD in three species of burrowing wolf spiders of the central Asian genus *Zyuzicosa* Logunov, 2010 (Logunov 2010; see Figs 1–3). The body length of the males in these species is 37–49% of that of corresponding females (Table 1). The males appear dwarfish even when compared to a ‘normal-sized’ male of *Z. gigantea* Logunov, 2010 (Fig. 4). It is the only case of extreme SSD reported for Lycosidae. Although all *Zyuzicosa* species possess a number of specific morphological adaptations to burrowing (such as, a black ventral colour pattern on the sternum, coxae and abdomen, the fur-like pubescence on the carapace and a cluster of rigid and straight bristles on the cymbial tips in males; see Logunov 2010), nothing is known about their life history, apart from field and lab observations by one of their collectors (A. Zyuzin pers. comm.) that females and juveniles do make burrows.

Overall, there is an extreme paucity of good biological information for most lycosids from areas other than Europe or North America. This is why

the discovery of extreme SSD in the genus *Zyuzicosa* seems to present a particular challenge for evolutionary biologists. The aim of this paper is to review the occurrence of SSD in wolf spiders. The following discussion is not intended as a comprehensive synopsis of SSD in spiders but rather as an overview of various aspects of SSD relevant to burrowing Lycosidae.

DISCUSSION

Low SSD in wolf spiders

Vagrant hunting spiders, including the Lycosidae, generally display moderate to low SSD, with males being about 10–20% smaller than females but having comparatively longer legs (Vollrath 1998; Walker and Rypstra 2001; Head 1995; etc.); but see Jocqué (1983), Alderweireldt and Jocqué (1991a), Gagnier et al. (2002), Huber (2005) and Aisenberg et al. (2007), for examples of reversed SSD. Usually males also have a shorter life cycle (reviewed by Mikhailov 1995). As the theory suggests (reviewed by Fairbairn 1997; Blanckenhorn 2000, 2005), each sex should be at its optimal size, and thus SSD should be adaptive (viability selection). The low SSD in wolf spiders has been discussed by a number of authors.

Framenau (2005) argued that the smaller size of male wolf spiders is related to the male mate-searching behaviour and could be explained by sexual selection through indirect male-male competition favouring comparatively longer legs and smaller size

Table 1. Range of carapace length/width and body length of three *Zyuzicosa* species: mean \pm SD (min–max).

Taxon and n	Carapace length	Carapace width	Body length
<i>Z. baisunica</i> Logunov, 2010			
female (n=2)	13.0, 15.3	9.0, 10.8	24.0, 28.8
male (n=12)	5.25 \pm 0.50 (4.5–6.2)	3.85 \pm 0.33 (3.3–4.5)	9.83 \pm 0.86 (8.5–11.5)
<i>Z. fulviventris</i> (Kroneberg, 1875)*			
female (n=3)	12.07 \pm 0.70 (11.4–12.8)	8.43 \pm 1.01 (7.5–8.3)	22.83 \pm 1.12 (22.0–24.1)
male (n=5)	5.80 \pm 0.26 (5.5–6.2)	4.12 \pm 0.23 (3.9–4.5)	11.18 \pm 0.42 (10.8–11.9)
<i>Z. turlanica</i> Logunov, 2010			
female (n=3)	13.73 \pm 1.50 (12.0–14.7)	9.53 \pm 1.16 (8.2–10.3)	28.07 \pm 1.21 (26.7–29.0)
male (n=3)	6.77 \pm 0.55 (6.2–7.3)	4.97 \pm 0.42 (4.5–5.3)	13.13 \pm 1.01 (12.5–14.3)

* – Numerous newly collected material of this species allowed the author to reveal a strong intra-specific variation of its female copulatory organs, of which the female of *Z. zeraevshanica* Logunov, 2010 and the female holotype of *Z. fulviventris* just represent extreme variants (cf. figs 72–73 and 76–77 in Logunov 2010). Therefore, the case of extreme SSD reported by Logunov (2010) for *Z. zeraevshanica* should actually be referred to *Z. fulviventris*. Yet, both names are to be synonymized (Logunov in preparation).



Figs 1–4. Extreme sexual size dimorphism in *Zyuzicosa* species (Lycosidae): 1, *Z. baisunica* Logunov, 2010 (female – left, male – right); 2, *Z. turlanica* Logunov, 2010 (female – left, male – right); 3, *Z. fulviventris* (Kroneberg, 1875) (female – left, male – right); 4, males of *Z. gigantea* Logunov, 2010 (on the left) and *Z. baisunica* Logunov, 2010 (on the right). Scale bars = 10 mm.

in males. Indeed, mate-searching males of some burrowing lycosids, e.g., *Hogna angusta* (Tullgren, 1901) from south-eastern USA, proved to have home ranges about four times larger than conspecific females (see Kuenzler 1958). Overall, direct male-male competition (and female choice) usually results in escalation of large male size, which is largely a vertebrate peculiarity (Andersson 1994; Fairbairn 1997; but see Huber 2005, for examples in arthropods). Framenau (2005) speculated that smaller and longer-legged males are more agile and this potentially increases their encounter rates with females. This idea is in agreement with the general conception that reduced size increases the agility of males and raises their search efficiency; i.e., the male puts 'its energy into locomotion rather than growth' (Ghiselin 1974: p. 192; see also Andersson 1994). Yet, experimental evidence of the latter conception are lacking and, as noticed by Blanckenhorn (2005), this hypothesis requires demonstration that the agility of males affects their mating success.

According to Walker and Rypstra (2001, 2002), selective forces acting on adult males and females of wolf spiders arise from a difference in their reproductive strategies. Females require more energy for reproduction than males and therefore there is likely strong selection on females to maximize their energy intake (Walker and Rypstra 2001, 2002). If food supply drops below a certain critical level, reproduction is suspended rather than clutch-size being reduced (Jocqué 1983; but see Anderson 1974, for contrary evidence). Females capture larger and a wider variety of prey than males, for they have larger chelicerae, fangs and venom glands. At the same time, males should minimize time and resources spent foraging and maximize their encounter rate with females. In wolf spiders, adult males consume considerably less prey than females or do not eat at all (Marikovski 1956; Walker and Rypstra 2001).

With regards to the obligate burrowing *Allocosa fasciiventris*¹, which exhibits low SSD, it was speculated (Foellmer and Moya-Laraño 2007;

Fernández-Montraveta and Moya-Laraño 2007) that selection acts differently on males and females. A larger carapace increases the mating success in both sexes, whereas a smaller carapace in females favours them in fights over burrows and territories (see Fernández-Montraveta et al. 1991). Thus, the authors argued that body size of *A. fasciiventris* seems to be under directional selection in males but under net stabilizing selection in females. However, as discussed earlier, males should maximize their encounter rate with females, and smaller body size and longer legs are likely to aid in this (Walker and Rypstra 2001, 2002; Framenau 2005). If so, both males and females of *A. fasciiventris* seem to be under stabilizing selection.

Surprisingly, only a few authors (e.g., Prenter et al. 1999) have related the occurrence of low SSD in wolf spiders with the fact that females of all species actively transport the egg sac on their spinnerets and then young spiderlings on the mother's abdomen. This behavioural trait is considered one of the three main synapomorphies of Lycosidae (see Dondale 1986). In such parental care, larger size should be an advantage (viz., better parental care) and selection pressures would favour larger females. As Prenter et al. (1999) put it, clutch size may impose constraint on female size, so that the weight of a large clutch will necessitate more powerful legs and a stronger carapace. However, before accepting this interpretation, differential survival and reproduction of females of different sizes should be investigated. Yet, there are plenty of data demonstrating that larger females confer greater fecundity: viz., clutch size increases with body size in many spiders (e.g., Jocqué 1983; Vollrath 1987; Marshall and Gittleman 1994; Head 1995; etc.), including the burrowing wolf spiders (e.g., McQueen 1978), which may indicate a selection for increasing of body size in females. It is worth mentioning that larger females may be better at overcoming competitors but be less preferred by males, as shown by Fernández-Montraveta and Moya-Laraño (2007) for the burrowing *A. fasciiventris*.

¹Fernández-Montraveta and co-authors have published a series of works devoted to various aspects of natural history of the burrowing wolf spider from central Spain. In some works this species was named *Lycosa tarantula* (Fernández-Montraveta and Cuadrado 2003; Foellmer and Moya-Laraño 2007; etc.), in others *Lycosa tarantula fasciiventris* (Fernández-Montraveta et al. 1991; Fernández-Montraveta and Ortega 1993; etc.). I suspect that these authors have reported on the same species, which in the current discussion is referred to as *Allocosa fasciiventris*, following the catalogue by Platnick (2011). According to Barrientos (1981), *Lycosa tarantula* is an east-Mediterranean species not occurring in Spain. The only taxonomic discrimination of both species known to me is that by Simon (1876); yet their taxonomy requires further study.

Reversed SSD in the Lycosidae

There are only a few examples of reversed SSD in burrowing wolf spiders. A striking example of sexual dimorphism was described for *Donacosa merlini* Alderweireldt et Jocqué, 1991, an obligate burrowing lycosid from SW Spain (Alderweireldt and Jocqué 1991a, b). In this species, males are slightly bigger (regarding both carapace and body lengths) than females, are brighter coloured and have a flat carapace (as in non-burrowing species; see Zyuzin 1990) compared to the sloping carapace in females. Another impressive example was given by Aisenberg et al. (2007, 2010a, b), who reported on reverse sexual size dimorphism in the sand-dwelling Uruguayan wolf spiders *Allocosa brasiliensis* (Petrunkevitch, 1910) and *A. alticeps* (Mello-Leitão, 1944). In both species females are the mobile sex. They are attracted by male volatile pheromones and initiate courtship, whereas males dig deep burrows, in which copulation takes place, and then donate them to the females after copulation (a kind of nuptial gift). Thus, large male size, as well as some other morphological traits (e.g., stronger chelicerae and sclerotized palpal claws; see Aisenberg et al. 2010a), could be explained as an adaptation to constructing burrows.

Are all burrowing wolf spiders large?

Burrowing behaviour of the Lycosidae includes making both permanent burrows (open, with trap-door or with turret) and temporary broodcare burrows. Burrowing behaviour is not restricted to a single taxon (tribe or subfamily) of the Lycosidae and is likely to have evolved several times (Alderweireldt and Jocqué 1991a; Murphy et al. 2006). Nevertheless, the majority of burrowing (both permanent and temporary) lycosids belong to the traditional Lycosinae (*Allocosa* spp, *Allohogna* spp, *Alopecosa* spp, *Geolycosa* spp, *Hogna* spp., *Lycosa* spp, etc.) (see Murphy et al. 2006). Other examples include the Australian genus *Tetrallycosa* Roewer, 1960 of uncertain placement (Framenau et al. 2006) and the Palaeartic genus *Xerolycosa* Dahl, 1908 of either the Evippinae (Zyuzin 1985; Marusik et al. 2011) or of the Venoniinae (Murphy et al. 2006).

Burrowing wolf spiders are not truly fossorial because they are not specifically adapted to digging and life underground. For instance, burrowing lycosids are not equipped with special morphological

structures, such as the rastellum of some Mygalomorphae, to dig burrows, although some groups (e.g., south American *Allocosa* species; see Aisenberg et al. 2010a) may possess heavily sclerotized and thickened palpal claws. Burrowing lycosids are not completely sedentary, as at night spiders can vacate their retreat and forage over a defined territory, usually near the burrow entrance (Kuenzler 1958; Shook 1978; Miller and Miller 1984; Conley 1985). Following disturbance (e.g., flooding or cultivation) many of the burrowing lycosids can relocate their burrows (Wagner 1868; Marikovski 1956; Main 1984; but see Marshall 1995). Usually, when the spiderlings emerge from the egg cocoon they move onto the mother's back; then the female abandons its burrow and spreads out the broods over a relatively small range: e.g., up to 30m² in *Allohogna singoriensis* (Laxmann, 1770) (see Marikovski 1956). Mature males do not live in burrows and are typical cursorial spiders, as with the majority of Lycosidae. During daytime males of many species, for instance of *A. fasciiventris*, can occupy empty burrows (see Fernández-Montraveta and Cuadrado 2001). Finally, females of some burrowing species, such as *Geolycosa vultuosa* (C.L. Koch, 1838), which normally make deep (16–20 cm) burrows (see Fuhn and Niculescu-Burlacu 1971), in stony areas can make shallow hollows under stones (M. Kovblyuk, personal observations in the Crimea).

It has been known that desert burrow-inhabiting spiders, whether Mygalomorphae or Araneomorphae, are usually large, with relatively big bodies and thick-set legs. The obligatory burrowing lycosids are usually larger (in both sexes) than their vagrant counterparts; examples were given by Main (1984), Dondale and Redner (1990), Zyuzin (1993), etc. Cloudsley-Thompson (1983: p. 308) suggested that the surface-to-volume ratio is lower in larger than in smaller animals so that they have a comparatively smaller area through which evaporative water loss can occur. However, Humphreys (1975) demonstrated that in *Lycosa godeffroyi* (L. Koch, 1865) there is no direct relation between water loss and either the weight or surface area of the spiders.

Marikovski (1956) argued that the burrow provides more favourable hunting conditions for a spider, as it can capture prey without leaving its burrow. Therefore, the sit-and-wait lifestyle of burrowing lycosids should lead to a relative reduction in expenditure of energy and result in a lower basal metabolic rate, unless a relocation of the burrow is

required (Marshall 1995; cf. also Culik and McQueen 1984). Furthermore, Marikovski (1956: p. 89) speculated that a low rate of metabolism of burrowing wolf spiders combined with more favourable conditions for their nourishment could be a selective factor favouring increase in their body size. Whether it is so, or not, remains to be further studied, but Walker and Irwin (2006) failed to reveal gender-related differences in the metabolic rate of the sexually dimorphic, sedentary *Hogna helluo* (Walckenaer, 1837), though such differences were found in the vagrant *Pardosa milvina* (Hentz, 1844) (e.g., males have higher mass-metabolic rate than females; see also Kotiaho 1998, for other examples).

H. helluo had a lower metabolic rate than *P. milvina* but was more active when exposed to food deprivation (Walker et al. 1999). These data may suggest that *H. helluo* is better adapted to uncertain food supply and that its low metabolic rate is associated with a sit-and-wait lifestyle (Walker and Irwin 2006; but see Culik and McQueen 1984). This may hold true for all burrowing wolf spiders. However, as shown by Moeur and Eriksen (1974; cited in Cloudsley-Thompson 1983: p. 311) for *Hogna carolinensis* (Walckenaer, 1805), the reduction in metabolic rate can also be a physiological compensation at high temperature. Yet, the low basal metabolic rate and large size of burrow-dwelling lycosids could also result in a greater resistance to starvation, which is a common feature of desert arthropods (see Punzo 2000). However, I am unaware of any comparative study considering starvation survival rates between burrowing and wandering lifestyles in wolf spiders (but see Anderson 1974; Conley 1985). For instance, Anderson (1974) showed that the females of *Hogna lenta* (Hentz, 1844) could produce egg sacs even when starving (contra Jocqué 1983), and Walker et al. (1999) discovered that *H. helluo* is more tolerant of starvation than active-foraging *P. milvina*. A useful general discussion of the problem of starvation in spiders was provided by Wise (1995), who speculated that 'the sit-and-wait strategy of many spiders is an adaptation to a shortage of prey'.

It is interesting to note that there are small-sized burrowing lycosids as well. For example, the European *Alopecosa fabrilis* (Clerck, 1757) and *Arctosa cinerea* (Fabricius, 1777) make rather deep silk-lined burrows in sandy soil (Nielsen 1932: figs 199 and 204–205; sub. *Tarentula f.* and *Trochosa c.*); their females are 13.3 ± 0.9 and 13.3 ± 2.2 mm

long respectively (see Almquist 2005). Doleš et al. (2008: fig. 1) recently described the rather primitive, unlined burrow of '*Arctosa*' *lutetiana* (Simon, 1876) in which females are less than 9 mm long (Almquist 2005). But the smallest burrowing wolf spider known to date seems to be *Xerolycosa mongolica* (Schenkel, 1963) from Tuva, the mountains of South Siberia. The total length of its burrowing females is 5.7–6.6 mm (see Marusik et al. 2011) and it makes relatively deep vertical burrows, 7–10.5 cm deep and 4–6 mm in diameter. What all burrowing lycosids have in common is their open xerothermic habitats with sparse/no vegetation such as sandy seashores, dune heaths, limestone areas and desert nanophanerophyte steppe (Almquist 2005; Marusik et al. 2000), in which it is difficult or impossible to hide other than by digging.

Could it also be that, having reached a 'critical' body size, a wolf spider has to adopt a fossorial lifestyle in order to survive? Overall, larger body size is positively correlated with fitness, especially in desert habitats (see Punzo 2000, for full discussion). For instance, a spider can generate more mechanical strength for burrowing and resisting other predators. Thus, it seems that the right question is not just why the majority of obligatory burrowing lycosids are large but rather why large wolf spiders should adopt the burrowing life-style? Possible reasons include lack of retreats to hide from predators/parasites and/or the need to cope with harsh climatic regimes such as extreme daytime/summer temperatures, xeric conditions, etc. Shook (1978) argued that the burrows of *H. carolinensis* of the Sonoran Desert serve as retreats from heat, desiccation and some predators. Furthermore, Humphreys (1975, 1978) clearly demonstrated that *L. godeffroyi* from Australia uses its burrow as a means to regulate/maintain the temperature of its body and even as a source of free water (via the use of heat differentials).

Visually oriented predators (e.g., birds) can also play an important role in determining the burrowing lifestyle of larger wolf spiders. Indirect evidence comes from the field experiments on desert darkling beetles (Tenebrionidae) by Groner and Ayal (2001), who argued that these beetles exhibit size-related habitat segregation according to their vulnerability to bird predation, with larger species found in protected habitats only. Overall, of the ectothermic arachnid predators such as spiders or scorpions, in the areas with sparse/no vegetation only burrowers can sur-

vive (see Ayal 2007, for a review). Therefore, as burrows represent efficient refugia reducing predation and providing suitable microclimatic environment (see above), burrowing wolf spiders can be large. Yet, I am unaware of any experimental works considering an effect of bird/mammal predation on body size or size-related habitat preferences in spiders.

It is worth mentioning an interesting detail of the life-history of *A. singoriensis*, the only thoroughly studied species of central Asian burrowing lycosid (Marikovski 1956). In Central Asia, the population of this species exists in three body-size classes (morphs; the latter author called them 'races'): large-sized, intermediate and small-sized. Females of the large-sized morph of *A. singoriensis* usually have a three-year life cycle. Upon maturing, females may relocate their burrow several times. As the spiders use their chelicerae for digging, the fangs get quickly worn down and the venom ducts completely clogged by haemolymph thrombus. Thus, the spiders become as if 'non-poisonous' animals, relying mostly/only on their large size and strength for prey capture or for protecting themselves. In such circumstances, possible selective pressure(s) would also favour larger females.

Ontogeny and the evolution of SSD

Studies of SSD rarely consider the developmental aspects of the evolution of SSD. Yet, it is known that, in order to comprehend the ultimate mechanisms underlying SSD evolution, understanding of the details of ontogeny and selection factors during the growth is essential. In vertebrates, SSD of adults is produced primarily by sex-specific differences in growth rate and longevity, and it is sex-specific sensibility to environmental conditions during ontogeny that is responsible for population divergence in SSD; see Badyaev (2002) for full discussion and numerous empirical examples of rapid evolutionary change in SSD.

The relationship between SSD and sex-specific growth patterns in arthropods was recently reviewed by Blanckenhorn et al. (2007) who argued that in the investigated groups, growth rate differences between the sexes are more important than growth duration. By contrast, in spiders, SSD is mediated largely by growth longevity differences (Levy 1970; Higgins and Rankin 1996; Li and Jackson 1996; etc.). For example, males of *Thomisus onustus* Walckenaer, 1805

(Thomisidae) mature after 3–5 moults and females after 6–9 moults (Levy 1970) resulting in extreme SSD and hence in nature siblings are excluded from mating with each other. Phenotypic plasticity regarding developmental rate, juvenile survival, number of moults, adult size and fecundity is common in spiders (Stratton 1984). This plasticity is induced by growth temperature (see Li and Jackson 1996, and references herein) and allows individuals to respond successfully to specific seasonal cues, e.g. the end of a specific season (Higgins and Rankin 1996).

Of the factors affecting growth longevity, temperature and feeding regime have been studied most extensively (e.g., Li and Jackson 1996). In the Lycosidae, growth duration was shown to be mediated by temperature, humidity and photoperiod (Stratton 1984; Vollrath 1987; Francescoli and Costa 1991; etc.), and by feeding rate and nutrient composition of diet (Uetz et al. 1992; Mayntz and Toft 2001; etc.). What is interesting is that growth duration and maturation rates are not directly correlated with the number of moults but are temperature-dependent (Li and Jackson 1996). They can also be affected by the abundance of food (Schaefer 1987). For instance, in *Pardosa astrigera* L. Koch, 1878, the number of instars and its variation increased with decreased food supply (Miyashita 1968; sub *Lycosa t-insignita*; cited after Schaefer 1987; but see Jespersen and Toft 2003).

As shown for *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae), food shortage only significantly prolonged growth duration in males (Uhl et al. 2004) and also caused decreased male size and mass, whereas females' body mass did not differ under both limited and unlimited food regimes. The latter observation is in close agreement with that of Fernández-Montraveta and Moya-Laraño (2007) who demonstrated that in *A. fasciiventris* feeding regime affected male but not female maturation size. Only males reared under nutritional stress showed a significant SSD (females were 1.1 times larger) whereas well-fed males were roughly of the same size. These data invoke the hypothesis of Jocqué (1983), who argued that small males could be selected in marginal habitats where food resources are less than optimal. Usually, maturation time of males depends on a feeding regime, with less food causing an earlier maturation of males at a smaller size.

Very interesting phenological data on three species of the *Pardosa pullata* species group were pub-

lished by den Hollander (1971), who demonstrated that the degree of synchronization of the final moult is related to the stability of microclimatic conditions (see also Høye et al. 2009). A highly synchronized moult was recorded in sub-populations living under relatively stable microclimate, and far less synchronized moult in sub-populations from a relatively unstable microclimate. These data and observations, as well as those mentioned in the previous paragraph, suggest that SSD in spiders, including the Lycosidae, may result from sex-specific phenotypic plasticity which is known to be influenced by environmental factors, for instance, by the rate of food supply (see Schaefer 1987; Uhl et al. 2004; etc.) or by earlier snow-melt (Høye et al. 2009).

Another very interesting observation comes from the breeding experiments on two west African wolf spiders (*Pardosa injucunda* O. Pickard-Cambridge, 1876 and *Brevilabus gillnorum* Cornic, 1980) by M.-L. Célérier (cited in Jocqué 2002), who showed that spiderlings from the same egg cocoon can grow at a different rate under identical circumstances, which result in forming two separated cohorts. For instance, *P. injucunda* can reach adulthood either in 50 days for the fast cohort and in 100 days for the slow one. The fast development was assumed to be an adaptation to marginal habitats or unfavourable seasonal circumstances (shorter rainy season).

Overall, phenotypic plasticity in arthropods is determined genetically (Higgins and Rankin 1996), while the expression of genetic variation can increase under stress and poor growing conditions in seasonal environments (reviewed by Hoffmann and Merilä 1999). For instance, in marginal habitats (see Jocqué 1983, 2002; Main 1990; Høye et al. 2009) SSD is the end result of a complex interplay of various selective pressures. In spiders, the size achieved at sexual maturity usually depends on the number of juvenile instars (Levy 1970; etc.), whereas plasticity in maturation size and number of moults can be environmentally induced (Higgins and Rankin 1996). Yet, physiological mechanisms responsible for the number of moults in spiders remain poorly understood (briefly discussed by Foelix 2011 and Punzo 2007). Studies on spiders analyzing causative factors of SSD, such as sex-specific developmental regulators and modifiers, combined with natural history data and/or related to environmental conditions are lacking (see Badyaev 2002, for examples on vertebrates).

Extreme SSD in burrowing wolf spiders

As already mentioned in the introduction, three of the eight described species of *Zyuzicosa* display extreme SSD (Figs 1–3; Table 1); see also Logunov (2010). It would seem that this case of SSD reasonably conforms to the differential mortality model (DMM) based on low population densities and sedentary females, with dwarf males appearing as a side-effect of earlier maturation (i.e., selection for protandry) (Vollrath and Parker 1992, 1997; Vollrath 1998; Blanckenhorn 2005; Huber 2005; Mas et al. 2009).

The DMM states that in species with sedentary females males suffer adult pre-mating mortality, a selection parameter that favours reduced growth and earlier maturation in males (protandry), resulted in a skewed female-biased sex ratio and the evolution of minute males. Vollrath and Parker (1997) clarified that their model does not generally predict an absolute selection for the reduction of male size but for the relative size of the two sexes. Yet high mortality of searching mature males is seen as a possible mechanism of reducing male-male competition, resulting in the selection for male dwarfism (Vollrath and Parker 1992; Mas et al. 2009). In the Lycosidae, this statement has been confirmed by observations on the burrowing of *A. fasciiventris* from Spain, in which males hardly compete, even over females. Virgin females of this species are receptive to almost every male and also show sequential polyandry. Thus, according to Fernández-Montraveta and Ortega (1993), male-male competition would be better solved by earlier male emergence than by direct combat. However, *A. fasciiventris* exhibits low SSD only (see Simon 1876, for carapace measurements).

The latter observation is in disagreement with the common view (Blanckenhorn et al. 2007: p. 254) that protandry is 'an adaptation to low female promiscuity' so that 'securing copulations with virgin females is pivotal to male reproductive success'. Under these conditions, earlier maturation must come at a cost of smaller size in males and result in female-biased SSD. This idea has been supported by the observations of Maklakov et al. (2004) on *Stegodyphus lineatus* (Latreille, 1817) (Eresidae) from Israel. In this species, female mating behaviour (viz., loss of receptivity of mated females) was argued to be the crucial selective factor for smaller male size. In other words, the protandry was sexually selected rather than an incident-

Table 2. Brief characteristics of the habitats of *Zyuzicosa* species (after Afanasiev and Gubanov 1988; Babaev et al. 1986; Zufarov 1981).

Species	Landscape	Vegetation	Annual precipitation	Average t°	
				winter	summer
<i>Z. turlanica</i> Logunov, 2010	Mountain-xerophytic	Grass-wormwood communities	350–400 mm	–5 °C	+26 °C
<i>Z. fulviventris</i> (Kroneberg, 1875)	Loess-clayey desert	Sedge-bluegrass (<i>Carex pachystylis</i> , <i>Poa bulbosa</i>) ephemeral communities	300–400 mm	–1.5 °C	+26 °C
<i>Z. baisunica</i> Logunov, 2010 <i>Z. gigantea</i> Logunov, 2010 <i>Z. uzbekistanica</i> Logunov, 2010	Loess-clayey desert	Sedge-bluegrass (<i>Carex pachystylis</i> , <i>Poa bulbosa</i>) ephemeral communities	200–300 mm	+2 °C	+29 °C

tal result of natural selection (cf. Vollrath and Parker 1992, 1997).

Besides, despite the lack of gender-specific metabolic differences in the sedentary *H. helluo* (see above), which exhibits low SSD, its males are more active than females but demonstrate the same rate of mortality (see Walker and Rypstra 2003). Whether the latter observation is true for all burrowing wolf spiders remains to be studied, but it is clearly in disagreement with the DMM (but see Mas et al. 2009, for further discussion).

The DMM has been criticized by a number of authors (e.g., Coddington et al. 1997; Hormiga et al. 2000; etc.). Prenter et al. (1997, 1999) even argued that fecundity selection is the only general explanation for the evolution of SSD in spiders (but see Shine 1988; Maklakov et al. 2004; Mas et al. 2009). Even if the DMM of Vollrath and Parker is not fully applicable to certain groups of orb-weavers, it still retains its explanatory power, particularly in the light of extreme SSD in burrowing wolf spiders presented in this paper.

The extreme SSD observed in *Zyuzicosa* is likely to have resulted from selection acting on small male size, in a similar way to that hypothesized for sexually dimorphic mygalomorphs (Main 1990; Vollrath and Parker 1997; Vollrath 1998). Main (1990) postulated that the reduced size in males of certain Mygalomorphae is advantageous in hazardous habitats (characterized by high seasonal aridity or periodic flooding of the ground) in which the species occur. Small males can avoid hostile conditions more easily. In such environments, the females are safe in their burrows and less at risk than the roving males, which are subject to higher adult mortality (Vollrath

and Parker 1997). According to Vollrath (1998), the dwarfing could be one of the major adjustments in adapting to such high-risk habitats. As the majority of burrowing wolf spiders exhibit low SSD, it is safe to conclude that in the case of *Zyuzicosa* species the selection has favoured the evolution of small males rather than of giant females. The male dwarfism is obviously a derived character in the Lycosidae.

Seasonal time constrains requiring brief and synchronized mating season have been seen as one of the prerequisites for protandry (Blanckenhorn et al. 2007). Yet, seasonality is a characteristic feature for all desert burrowing wolf spiders, including *Zyuzicosa* species. Some details of the natural environment of *Zyuzicosa* species are given in Table 2. It is important that all three sites lie in areas characterized by a dry temperate/subtropical continental climate (Afanasiev and Gubanov 1988; Babaev et al. 1986; Zufarov 1981). This results in (1) extreme daily and seasonal changes of temperature; (2) high surface and air temperatures during the summer daytime; (3) very low values of annual precipitation, during the period December–May, often as heavy showers; and (4) low/no snow cover during the winter (i.e., possible exposure to cold temperature stress). Thus seasonal drought and extreme summer temperatures are the main hazards in *Zyuzicosa* habitats. Nothing is known about the density of populations of *Zyuzicosa* species in nature. Based on a low number of collected specimens and the characteristics of the habitats, it is reasonable to assume that the *Zyuzicosa* species are likely to live at low densities, as described for *A. fasciiventris* in which burrows of juveniles tended to be gregarious but those of adult females were spaced far apart, reflecting the minimal distance needed to

reduce cannibalism (Fernández-Montraveta et al. 1991; Fernández-Montraveta and Ortega 1993). Another example comes from Shook (1978) who showed that the large space between burrows of *H. carolinensis* was necessary to avoid overlapping of home ranges of each individual and hence cannibalism. However, the possibility that *Zyuzicosa* species may live in small, localized colonies (=clusters), as in those described for several *Geolycosa* species (see McCrone 1963; Zyuzin and Logunov 2000; etc.) cannot be ruled out.

Nothing is known about the sex ratio of *Zyuzicosa* species in the wild. From the literature, it is known that in some species of burrowing lycosids, e.g. in *Geolycosa domifex* (Hancock, 1899) from southern Ontario, the sex ratio in the wild could be 5:1 in favour of the females (see McQueen 1978), as the DMM predicts (Vollrath and Parker 1992; Vollrath 1998). Yet, this species exhibits low SSD (see Dondale and Redner 1990, for the body measurements). In other species, e.g. *A. fasciventris* from central Spain, the operational sex ratio in nature was shown to be 1:1 (Fernández-Montraveta and Cuadrado 2003).

The extreme SSD in *Zyuzicosa* also means that dwarf males should experience accelerated development compared to females. Thus, it is highly unlikely that the dwarf males of *Zyuzicosa* can mate with the females of their own cohort, but should rather mate with those of the previous generation. There is empirical evidence that this can occur in burrowing wolf spiders. As mentioned above, populations of *A. singoriensis* in Central Asia consists of three body-size classes (Marikovski 1956). Males of the large-sized morph regularly mate with the females of small-sized morph of the same cohort and with the females of large-sized morph from the previous cohort, as these females take two years to mature. Conley (1985) reported that some males of *Geolycosa rafaellana* (Chamberlin, 1928) from desert areas of south-western USA can mate with females of the previous cohort, because males display a three year life-span while females may live four years. Shook (1978) showed that the females of *H. carolinensis* do not reproduce until their third summer, whereas males die over their second year when they mature and reproduce; thus, it is very likely that they mate with females of the previous cohort. None of these three species exhibit extreme SSD.

It is worth noting that quite the opposite situation was described for *G. domifex*, in which the popu-

lation comprised three cohorts which were reproductively separated, with limited (<1%) gene flow between them (see McQueen 1978). Males of this species do not even mature until after reproduction has occurred in the previous cohort. Similar examples of reproductively isolated cohorts were described in Salticidae and Araneidae (Bartos 2005; and references therein). However, in the case of *Zyuzicosa*, dwarf males are most likely to only mate with the giant females from the previous cohort rather than with their own siblings. Examples of other spider groups, in which siblings could not mate (e.g., *Latrodectus* spp.; *T. onustus*; *Nephila* spp.), all of which exhibit extreme SSD, were given by Levy (1970).

Whether mating with the previous cohort in *Zyuzicosa* could be considered a potential cause of gene flow between successive cohorts, as described for some crab spiders (i.e., *T. onustus*; see Levy (1970)), is yet to be studied. But certain groups of sub-social desert spiders, such as *Stegodyphus dumicola* Pocock, 1898 (Eresidae) from Namibia, which show limited migration, intra-colony mating and inbreeding, exist in inbred colonies lasting for many generations (see Lubin et al. 2009). It is known that many obligate burrowing wolf spiders (e.g., *Allohogna* spp., *Geolycosa* spp.) are quite sedentary, with limited dispersal power and narrow habitat restrictions (Marikovski 1956; McCrone 1963; Miller 1989; etc.). They form small, localized colonies, in which about a half of the spiderlings establish their burrows in close proximity to the maternal burrows (although dispersal by ballooning was also reported; see McQueen (1978) and Miller (1989)). For some species, e.g. *Geolycosa turricola* (Treat, 1880) from the USA, even a sub-social organisation of aggregated broods was described (Miller 1989). Colonies of inbred burrowing wolf spiders similar to those described for other burrowing spiders with restricted juvenile dispersal, e.g., *Seothyra henscheli* Dippenaar-Schoeman, 1991 (Eresidae) from Namibia (see Henschel and Lubin 1997; Lubin et al. 2001; etc.), may also exist but there is no direct empirical evidence to support or reject such an assumption.

Future research directions

To summarize, it seems that SSD in *Zyuzicosa* can reasonably be explained by the differential mortality model, with dwarf males appearing as a side-effect of earlier maturation (i.e., selection for protandry)

(Vollrath and Parker 1992; Vollrath 1998; Huber 2005; Mas et al. 2009). However, as noticed by Blanckenhorn (2005), in order to thoroughly investigate the evolution of SSD in a given species, several hypotheses should be truly tested in an integrated manner. It also appears that the male dwarfism of certain burrowing wolf spiders is a trade-off to cope with environmental hazards, as with the sexually-dimorphic mygalomorphs (Main 1990), or is a mechanism for synchronizing mating seasons (Blanckenhorn et al. 2007). Both assumptions require detailed research on behavioural, life-history and demographic traits of a given species and the divergent mechanisms responsible for the origin/maintenance of sexual dimorphism in a given habitat. However, if selective pressures for small males are directly environmentally dependant, why do the majority of obligate burrowing wolf spiders exhibit low SSD? Or why has extreme SSD been found in only three species of a single genus within the family?

In the above discussion, little attention has been paid to selection for female fecundity (reviewed by Andersson 1994; Foellmer and Moya-Laraño 2007) as a possible reason for SSD in burrowing wolf spiders. If this is a selective factor, then why in the majority of burrowing lycosids are both sexes large (compared to vagrant species)? It appears that the phenomenon of extreme SSD in wolf spiders can be understood by addressing two main questions: (1) why obligatory burrowing groups of wolf spiders usually became larger than wandering species (i.e., what are the fitness costs of being large at the ecological, physiological, ontogenetic and genetic levels (Blanckenhorn 2000, 2005; Blanckenhorn et al. 2007; Fairbairn 2007), and (2) why the males of only certain burrowing Lycosidae became minute [or, alternatively, why they remained small; see Maklakov et al. (2004) and Huber (2005)]? The situation is further complicated by the fact that, potentially, extreme SSD in wolf spiders may have evolved in response to several causative factors (such as, fecundity selection, sexual selection, ecological divergence and/or unknown factors) acting simultaneously (see Shine 1989, for a general review). In my opinion, a solution to the problem of extreme SSD in wolf spiders should apparently be based on the life-history theory integrated with aspects of whole organism ontogeny, either as traditional life-history trade-offs or as modifications of life cycles and/or growth patterns in response to environmental conditions.

As virtually nothing is known about the biology of *Zyuzicosa* species which express the extreme SSD discussed herein, much empirical research is required in order to answer the above questions. It is hoped that this discussion will attract attention of other investigators to the phenomenon of extreme SSD in some burrowing Lycosidae and will stimulate field/laboratory studies of these unique animals.

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