



Factors affecting lifespan in bird-eating spiders (Arachnida: Mygalomorphae, Theraphosidae) – A multi-species approach

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ABSTRACT

Lifespan is a life-history trait being of utmost importance, as it is frequently closely related to individual fitness. However, interspecific comparisons are relatively rare, being hampered by the high effort to collect longevity data across taxa. We here compiled lifespan data for 85 species of bird-eating spiders (Theraphosidae) held in captivity, based on 2183 individual records from the animal record books of both zoological gardens of Berlin, Germany. Using a data-mining approach we sought for broad patterns of correlations between lifespan and an array of other variables as derived from the literature. We found that the subfamily Eumenophoriinae lived on average longest, followed by the Theraphosinae, Ornithoctinae, Grammostolinae, Selenocosmiinae, Ischnocolinae and finally the Avicularinae. Species inhabiting tropical, more humid and/or low-altitude environments lived longer, suggesting that more predictable environments facilitate the evolution of longer lifespans. Furthermore, large range size, low abundance, sub-terrestrial life-style, and aggressive behavior were all associated with longer lifespans. Evidence for resource allocation trade-offs was revealed as larger spiderling and prosoma size was negatively related to longevity. Our rather rough approach revealed several patterns worth of future investigations, and illustrate the value of zoo records for interspecific comparisons.

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1. Introduction

Lifespan is a life-history trait which is of utmost importance, as it is frequently closely related to individual fitness (Tatar, 2001; Zera and Harshman, 2001; Partridge and Gems, 2007; Vogt, 2012). This is because a minimum adult lifespan needs to be realized in order to secure any reproductive success, and as lifespan frequently correlates in a positive manner with reproductive output (Fischer, 2007; Bonduriansky et al., 2008). Despite its extraordinary importance, all sexually reproducing organisms are subject to senescence, eventually resulting in death (Williams et al., 2006; Hulbert et al., 2007). Several hypotheses have been put forward to explain the prevalence of senescence, including e.g. the disposable soma theory of aging stating that the available energy needs to be divided among competing functions, namely reproduction, maintenance, and repair (Stearns, 1992; Kirkwood and Austad, 2000). From a life-history perspective senescence can thus be understood as a consequence of resource allocation trade-offs, resulting in optimized rather than maximized phenotypes (Carey, 2001; Boggs, 2009).

Resource-allocation trade-offs result if a limited amount of energy needs to be divided among two or more competing functions. As somatic maintenance (and therefore longevity) requires substantial amounts of energy, lifespan is expected to be involved in trade-offs (Roff, 1992; Stearns, 1992). For instance, the energy expenditure allocated to reproduction, being measurable as e.g. fecundity or offspring size, has been repeatedly found to be traded off against longevity (Roff, 1992; Stearns and Partridge, 2001; Zera and Harshman, 2001). Other 'classical' trade-offs are those between present and future reproduction, which are also frequently found (Roff, 1992; Stearns, 1992). As a consequence of such trade-offs, lifespan is typically positively related to body size and/or storage reserves (Roff, 1992; Speakman, 2005a). As energy intake and metabolic rates depend strongly on environmental conditions, lifespan is generally strongly environment-dependent (Carey and Liedo, 1995; Carey, 2001; Hulbert et al., 2007). In addition to environmental factors lifespan may also be subject to genetically determined variation. For instance, Hughes and Reynolds (2005) list a number of transgenic and mutant alleles of *Drosophila melanogaster* which affect longevity. Longevity also shows striking variation across species and higher order taxa, suggesting a 'phylogenetic legacy' (Carey, 2001; Sgrò and Hoffmann, 2004; Hulbert et al., 2007). In general though, the heritability of lifespan appears to be low as expected for a trait closely related to fitness (Carey and Judge, 2001).

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Despite a strong interest in the evolution of lifespan and associated trade-offs, comparative data on this matter is exceedingly rare (Carey, 2001; Beck and Fiedler, 2009; Vogt, 2012). Such potentially very valuable studies are likely hampered by the high effort needed to collect longevity data across taxa. Against this background we here present data on 85 species of bird-eating spiders (Theraphosidae), on which hardly any systematic data on lifespans and their ecological correlates was available thus far. Theraphosidae are a family of mygalomorph spiders (Araneae), which mainly inhabit tropical and subtropical regions in both Americas, Africa and Asia, using a wide variety of habitats such as rainforests, woods, savannahs, grasslands, semi-deserts and deserts (Smith, 1988; Klaas, 2007). Data were compiled from the animal record books of both zoological gardens of Berlin, thus including exclusively animals which were kept under controlled environmental conditions in captivity. Using a data-mining approach we sought for factors affecting lifespan, using an array of predictor variables as derived from the literature (e.g. on climate, habitat, behavior, morphology and life history).

Obviously, the evolution of lifespan across species is shaped by a large array of selective forces, which may well vary throughout a species' range adding further complexity. Therefore, we are able here to examine some broad patterns of correlation only. Note though that this is a conservative approach. We will specifically test the hypothesis that more predictable environmental conditions should select for longer lifespans. This prediction rests on the assumption that random mortality (through e.g. predation, starvation, or catastrophic events) should be low in those environments, such that intrinsically longer lifespans may pay off (Sgrò and Hoffmann, 2004; Williams et al., 2006; Pruitt and Riechert, 2012). Apart from the above hypothesis we further investigate whether (1) the different subfamilies of Theraphosidae differ in lifespan, whether (2) lifespan is traded off against reproductive effort, and whether (3) lifespan is positively related to body size.

2. Materials and methods

2.1. Bird-eating spiders (Theraphosidae)

Within the Theraphosidae typically six or seven subfamilies are recognized, namely the Aviculariinae, Ischnocolinae, Eumenophoriinae, Grammostolinae, Theraphosinae, Ornithocticinae, and Selenocosmiinae, with Grammostolinae and Theraphosinae often being regarded as belonging to the same subfamily (Raven, 1985; Smith, 1988; Pérez-Miles et al., 1996; Schmidt, 2003). The Theraphosidae encompass 964 extant species, which have been described mainly based on morphological characters (e.g. Ausserer, 1871; Bücherl, 1962; Raven, 1985; Pérez-Miles et al., 1996; Platnick, 2013). Theraphosidae, often incorrectly named 'tarantulas', are distributed throughout the tropical and subtropical regions of South and Central America, central Africa, and Asia, including a few species that are adapted to desert habitats (Klaas, 2007).

2.2. Lifespan data acquisition

We compiled lifespan data for 85 species of Theraphosidae, based on 2183 individual records (range: 1–222 individuals per species). All lifespan data were obtained from the animal record books of both zoological gardens of Berlin (Zoo Berlin and Tierpark Berlin, the former West- and East-Berlin zoos). Thus, all data were derived from captive animals kept under standardized environmental conditions (see further below). In total, ca. 3500 invertebrate species have been maintained at both Berlin zoos, comprising one of the largest data source worldwide. Most species of Theraphosidae could be unambiguously identified (according to

Smith, 1988, Table 2), and all species for which an unambiguous identification was not possible were removed from the database. In our analyses we only included data of individuals for which the exact entrance date (either through birth or external acquisition, e.g. bought from breeders or other zoos) was known, and which died in the zoo for natural reasons. Thus, our lifespan data obviously underestimate the real lifespan of spiders at least in some cases (external acquisition), and therefore comprise minimum lifespans. Note though that (1) this is a recurrent problem also in the field (e.g. when data are based on mark-recapture studies in which the lifespan prior to the first and after the last capture event is unknown). Furthermore, (2) specimen derived from external sources were typically still young, and (3) more than 20 of the above species have been successfully bred in Berlin, for which consequently very accurate data are available. Finally (4), we included only individuals which had survived the adult stage for at least 10 days, in order to exclude juvenile mortality and confounding effects of stress during transport. Individuals were considered to be mature if having reached the size of a typical adult. We used size as a proxy because the identification of maturity in females is not a trivial matter. We acknowledge that only 10 days in the adult stage is a rather short period of time, and considering such individuals obviously lowers the mean values. However, as the same approach is used for all species, this should not affect our comparative analyses. Consequently, we are convinced that our database is robust enough for meaningful comparisons of broad patterns.

2.3. Rearing and maintenance conditions

In both zoos all spiders were maintained in tropical green houses or insectaria, i.e. at temperatures between ca. 25 °C (night) and ca. 30 °C (day), thus being similar to the temperatures typically encountered in their tropical and subtropical habitats. The light conditions were 12L:12D throughout. All individuals included in our analyses were cultured under these standardized conditions. We are aware of the fact that the species included may be adapted to different climatic conditions in the field, such that rearing them all under the same conditions might be problematic. Also, our settings are necessarily rather artificial. However, there is no alternative to such a 'common garden' approach, as keeping the species under an array of different conditions is not feasible for logistic reasons and due to a lack of knowledge on e.g. optimal temperatures for all the species involved. More importantly, controlling for environmental variation is absolutely crucial in comparative studies aiming at unraveling intrinsic differences among species. Otherwise, longevity data are entirely confounded by differences in environmental conditions. Except for mating, all adult spiders were kept individually in boxes, being provided house crickets (*Acheta domesticus*) for feeding twice a week and water ad libitum. Thus, the factors affecting longevity in ectotherms most strongly (food, temperature; e.g. Bauerfeind et al., 2009) were well standardized for all individuals included here.

2.4. Acquisition of additional data

In order to investigate broad patterns of correlations between lifespan and other factors (e.g. morphology, ecology), we compiled additional data on all 85 species included in our analyses. Data were obtained from the literature (Smith, 1988; Schmidt, 2003; Haack, 2007; Klaas, 2007), or, to a lesser extent, from unpublished zoo records (i.e. data on aggressive behavior). In total, data on 16 predictor variables could be obtained for all species (Table 1a). For many of these variables we obviously had to rely on rather broad categories, due to a lack of more specific information. Regarding seasonality, we only distinguished between species of tropical and other origin. Range size was classified as 'small' if a species had only

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