Life history of the bridge spider, *Larinioides sclopetarius* (Clerck, 1757)

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Bestätigung der sprachlichen Korrektheit

Die sprachliche Korrektheit der in englischer Sprache abgefassten Dissertation von Frau Anja Kleinteich (geb. Nioduschewski) mit dem Titel „Life history of the bridge spider, Larinioides sclopetarius (Clerck, 1757)“ wurde von dem Unterzeichnenden, Dr. Mason N. Dean, geprüft und bestätigt.

Sincerely,

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Zusammenfassung

Das Leben eines Organismus' wird durch das Erreichen der Geschlechtsreife in zwei Phasen geteilt: die Entwicklungs- und die Fortpflanzungsphase. Die Ausprägung der *life history* Parameter (Schlupf- oder Geburtsgröße, Wachstumsmuster, Alter und Größe zur Reife, Anzahl, Größe und Geschlechterverhältnis der Nachkommen, Fortpflanzungskosten, alters- und größenabhängige Mortalität und die Lebensdauer) wird durch intrinsische (physiologische und genetische) und extrinsische (ökologische) Faktoren bestimmt. Plastizität in *life history* Parametern ermöglicht Arten, sich schnell an neue Umwelten, wie zum Beispiel urbane Habitate, anzupassen. Die Brückenspinne *Larinioides sclopetarius* ist extrem erfolgreich beim Kolonisieren von Städten weltweit und bewohnt in großer Anzahl anthropogene Strukturen in Gewässernähe. Sie frisst Insekten, die aus dem Wasser schlüpfen und von künstlichem Licht angelockt werden, in dessen Nähe die Spinnen ihre Netze bauen. In Städten ist die Beuteverfügbarkeit sehr hoch, obwohl sie zeitlichen und räumlichen Schwankungen unterliegt. Veränderungen in der Beutedichte können – abhängig davon in welcher Lebensphase sie stattfinden – unterschiedliche Effekte auf die *life history* Parameter haben. Diese Arbeit beschreibt den Einfluss der Nahrungsverfügbarkeit während des gesamten Lebens (Entwicklungs- und Fortpflanzungsphase) auf die wesentlichen *life history* Parameter von *L. sclopetarius* untersucht. Ziel war es, die verantwortlichen Parameter für den Besiedelungserfolg der Brückenspinnen aufzudecken.

Sowohl die Weibchen als auch die Männchen zeigen abhängig von der Nahrungsverfügbarkeit ein hohes Maß an Plastizität in allen Entwicklungsparametern, d.h. in der Anzahl der Entwicklungsstadien, der Intervalle zwischen den Entwicklungsstadien und der Wachstumsrate. Nahungsbeschränkungen verursachen bei beiden Geschlechtern zusätzliche Häutungen und eine verlängerte Entwicklungszeit. Das Wachstum von Brückenspinnen folgt einem geometrischen Verlauf und kann daher unter konstanten Umweltbedingungen gut prognostiziert werden. Dennoch ist das Wachstumsverhältnis (Größenzuwachs pro Häutung) zwischen Häutungen nicht konstant, was zu einer Abweichung von der Dyarschen Regel führt, welche konstante Wachstumsverhältnisse zwischen Arthropoden-Häutungen postuliert.

L. sclopetarius zeigte in Bezug auf die Nahrungsverfügbarkeit während der Entwicklung auch Unterschiede in den *life history* Parametern Größe, Gewicht und Alter zur Geschlechtsreife. Hohe Futtermengen verursachten eine kürzere Entwicklungszeit, eine größere Adultgröße und ein höheres Adultgewicht. Männchen und Weibchen unterliegen verschiedenen Selektionsdrücken (Fekunditätsselektion vs. sexueller Selektion), was gewöhnlich zu einem Geschlechtsgrößendimorphismus führt (SSD = *sexual size dimorphism*). Die unterschiedlichen

Selektionsdrücke verursachen einen geringen männchengerichteten SSD (Männchen sind größer als Weibchen) bei Brückenspinnen, wobei die Weibchengröße unabhängig vom Futterlevel und daher kanalisiert (fixiert) war. Die größere Variabilität in der Männchengröße als in der Weibchengröße entspricht der Renschschen Regel, was im Gegensatz zu anderen Studien an Spinnen mit größerem SSD steht. Diese Studie ist die erste, die die Renschsche Regel in Kombination mit männchengerichtetem SSD für Spinnen bestätigt.

Die Schlüsselparameter Größe, Gewicht und Alter zur Geschlechtsreife sind aufgrund ihrer Bedeutung für Reproduktion und Überleben in hohem Maße fitnessrelevant. Um zu testen, wie Nahrungsverfügbarkeit während des Wachstums und die *life history* Parameter den Reproduktionserfolg beeinflussen, habe ich Brückenspinnenweibchen verpaart und sie während ihrer Fortpflanzungsphase bis zu ihrem Tod beobachtet. Zusätzlich kontrollierte und veränderte ich während dieser Phase die Futterbedingungen, um Auswirkungen der Nahrungsverfügbarkeit auf die Anzahl ihrer Nachkommen zu analysieren. Männliche Brückenspinnen geben nach der Adulthäutung den Bau von Radnetzen auf, so dass eine weitere Beeinflussung durch die Nahrung nicht mehr durchgeführt werden konnte. Weibchen, die unter hoher Futterdichte aufwuchsen, hatten eine erhöhte Fekundität und eine verlängerte Reproduktionsphase. Dennoch hat die Futterverfügbarkeit nach der Adulthäutung einen größeren Einfluss auf die Reproduktionsrate als die Futterverfügbarkeit während der Entwicklung. Hohe Futterverfügbarkeit während der Fortpflanzungszeit führt zu einer höheren Nachkommenszahl und kürzeren Intervallen zwischen den Gelegen. Weibchen, die in ihrem Leben wenig Futter zur Verfügung hatten, können die Nachteile durch ihre verzögerte Entwicklung teilweise kompensieren indem sie ihren Alterungsprozess (die Seneszenz) verlangsamen; sie können aber nicht so viele Nachkommen zeugen wie Weibchen, denen viel Nahrung zur Verfügung stand. Überraschenderweise konnte ich keinen Zusammenhang zwischen dem Eigewicht und der Nahrungsverfügbarkeit während des Lebens finden, was vermuten lässt, dass die Nahrungsmenge nur einen Einfluss auf die Quantität nicht aber auf die Qualität der Nachkommen hat.

Das Vorhandensein von großer Plastizität mit beschleunigtem Wachstum, die extreme Variabilität in den *life history* Parametern und die unmittelbare Reaktion auf die Nahrungsverfügbarkeit durch direkte Erhöhung des Reproduktionserfolges machen die Brückenspinnen *L. sclopetarius* zu einem extrem erfolgreichen Besiedler urbaner Habitate und demzufolge zu einem wichtigen Modell für Studien der Stadtökologie.

Summary

The life history of an organism is divided into two life stages termed developmental and reproductive period that are separated by maturation. The shape of life history traits (size at birth, growth pattern, age and size at maturity, number, size, and sex ratio of offspring, reproductive investments, age- and size-specific mortality schedules, and length of life) is determined by intrinsic (i.e. physiological and genetic) and extrinsic (i.e. environmental) factors. The plasticity in life history traits influences the ability of a species to quickly adapt to novel environments, such as urban habitats. The bridge spider *Larinioides sclopetarius* is an extremely successful colonizer of cities worldwide and inhabits buildings near water in huge numbers. The spiders feed on insects that emerge from the water and are attracted to artificial lights, where the spiders build their webs. Prey availability is high in this habitat although prone to spatial and temporal variation. Changes in prey abundance will have differential effects on life history traits, depending on the life stage they are acting on. In this thesis, I investigate the impact of food availability during the entire life (i.e. developmental plus reproductive period) on the major life history parameters of *L. sclopetarius*. Goal of this enterprise was to reveal the traits responsible for the invasiveness of bridge spiders.

All developmental parameters such as the number of instars, the interval between instars, and the growth rate showed a high degree of plasticity depending on diet in males and females. Dietary restriction caused additional molts and a prolonged developmental time in both sexes. The growth trajectory of bridge spiders followed a geometric progression and was thus highly predictable under constant environments. However, the growth ratios (size/weight gain per molt) were not constant, which is contrary to Dyar's rule that postulates constant growth ratios for successive instars in arthropods.

In relation to diet during development, *L. sclopetarius* further showed variability in the life history traits size, weight, and age at maturity. High feeding conditions caused a shorter development time and a larger adult weight and size. The sexes underlie different selection pressures (fecundity selection vs. sexual selection), which usually result in a sexual size dimorphism (SSD). In bridge spiders, these different selection pressures cause a weak male-biased SSD and female size at maturity was independent of feeding level and thus canalized. The higher variability in male body size than in female body size is in accordance with Rensch's rule, a finding that contrasts other growth studies in spiders with more pronounced SSD. This study is the first to validate Rensch's rule in combination with male-biased SSD for the taxon.

The key life history parameters size, weight, and age at maturity are highly fitness relevant due to their effects on reproduction and survival. To test how reproductive output is influenced by food availability during growth and life history traits, I mated female bridge spiders and followed them individually during their reproductive period until death. Feeding conditions also were altered during the reproductive period, to study proximate effects of diet on number of offspring. Male reproductive success was not considered because they stop building orb-webs after maturation and thus can no longer be influenced by variable diets. Females that grew under a rich diet had increased lifetime fecundity and a prolonged reproductive period. However, compared to the impact of diet during development, feeding condition after maturation had a more substantial impact on current reproduction. A rich diet during the reproductive period lead to higher offspring number and shorter intervals between successive clutches. Females that encountered limited food availability throughout their lives partly compensate disadvantages caused by delayed maturation and by slowing down senescence but they never produced offspring numbers comparable to females on a rich diet. Surprisingly, I found no link between lifetime diet and egg weight, suggesting an effect of food only on offspring quantity but not quality.

The high developmental plasticity with accelerated growth, the extreme variability in key life history parameters, and the immediate reaction to diet by current reproductive output makes the bridge spider *L. sclopetarius* an extremely successful invader in urban habitats and thus an important model in studies of urban ecology.

General introduction

The term 'life history' encompasses the lifecycles of organisms by characterizing their variability in the principal' traits such as (1) size at birth, (2) growth pattern, (3) age and size at maturity, (4) number, size, and sex ratio of offspring, (5) reproductive investments, (6) age- and size-specific mortality schedules, and (7) length of life (Stearns 1992). The lifespan of an organism and the related life history parameters are divided into the developmental and reproductive period that starts with sexual maturation. In invertebrates such as spiders, maturation is a distinct transition that not only affects the gonads but many other traits as well. Some life history traits are mostly influenced by events during the developmental period (so before maturation), others are exclusively influenced by events after maturation, while others yet, seem to be the result of events during both phases. For example, size at birth, growth pattern, and age and size at maturity are under the influence of events during development. Offspring number and reproductive investment are mostly dependent on events during the reproductive period while mortality and longevity are relevant during both, developmental and reproductive periods.

Life history research identifies the role of natural selection in different organisms in shaping traits that are beneficial for survival and reproductive success. Furthermore, by studying life history traits we can explain other biological patterns, such as phenotypic plasticity or sexual size dimorphism (Blanckenhorn 1998, Nylin and Gotthard 1998, Prenter et al. 1999, Blanckenhorn et al. 2007).

Life histories are shaped by intrinsic and extrinsic factors. Intrinsic factors include the genotype and trade-offs between life history traits, as a benefit for one trait often comes at the cost of another. Extrinsic factors are ecological impacts on survival and reproduction and comprise environmental factors such as food availability, population density, and temperature (Stearns 2000). For example, temperature is known to accelerate growth in ectothermal organisms (Atkinson 1994) and thus reduces the age at maturity. Similarly, an increased diet generally increases the size and weight at maturity (Roff 1992, Blanckenhorn 1998, Mayntz et al. 2003, Uhl et al. 2004, Marczak and Richardson 2008) and will also directly influence the quantity and/or quality of offspring (Wise 1979, Sota 1985, Parker and Begon 1986, Pékar 2000, Agarwala et al. 2008).

This thesis investigates the influences of intrinsic and extrinsic factors during development and reproduction on life history traits in an orb-web spider. The bridge spider, *Larinioides sclopetarius* (Araneae, Araneidae), is a synanthropic nocturnal orb-web spider with a holarctic distribution and can be overabundant along waterfronts in urban habitats (Burgess and Uetz 1982, Heiling 1999, Schmitt 2004, Schmitt and Nioduschewski 2007a, Schmitt and Nioduschewski 2007b). Their high population densities (up to 100 individuals per m^2, Nioduschewski and Kraayvanger 2005) on artificial structures (e.g. bridges, facades) and their waste (i.e. webs, droppings, exuviae) makes them a nuisance for inhabitants of buildings near water. Their presence can result in economic loss, especially in residential and office districts close to the waterfront.

Habitats that are occupied by bridge spiders often have no other orb-web spiders present (pers. observation). Other spiders are either completely outcompeted or are restricted to occasional patches with low population densities (e.g. *Zygiella x-notata*, *Araneus diadematus*). Although bridge spiders are ecologically and economically important in urban habitats, the biological base for their success is poorly known.

An explanation of the high densities of bridge spider population in urban habitat is the superabundance of prey associated with water. Illuminated structures and artificial light sources in urban habitats attract insects with positive phototaxis (Wigglesworth 1942). These insects are an enormous food resource for nocturnal predators such as bridge spiders. Along waterfronts of urban habitats, most of the insects attracted by light emerge from water dwelling larvae (e.g. Chironomidae, Oliver 1971). However, insect densities fluctuate throughout the season (Ziegler 2005) and periods of overabundance of prey items are followed by periods with less food. Thus it is likely that bridge spiders have evolved different life history strategies to respond to such fluctuations. To investigate the effects of different prey abundances on their life history, I reared *L. sclopetarius* under controlled laboratory conditions from birth until death and documented the impact of feeding conditions on the life stages development, maturation, and reproduction. The single Chapters of this thesis consider these three different life stages.

Chapter 1 focuses on the development of bridge spiders and considers their growth patterns and developmental plasticity. The development of arthropods can be described by three developmental parameters that determine the life history traits size, weight, and age at maturity: (1) number of instars (i.e. developmental stages), (2) intervals between instars, and (3) size/weight gain per molt. In response to variable environmental conditions, in arthropods at least two of the three developmental parameters are plastic (flexible) (Higgins and Rankin 1996). Many arthropods follow geometric growth rules that are described by a constant growth ratio (i.e. size/weight gain per molt) (Dyar 1890, Przibram and Megušar 1912, Hutchinson et al. 1997). The existence of constant growth ratios is contrasted by developmental plasticity and geometric growth progressions are likely to constrain the plastic responses to variable environmental conditions. Chapter 1 integrates developmental plasticity, growth patterns, and invasiveness in urban habitats.

Chapter 2 describes the plasticity and sex specific differences of the major life history traits size, weight, and age at maturity. These major traits are linked by trade-offs and are under the influence of three levels of selection (i.e. fecundity, sexual, and viability selection) that act differentially on males and females (Blanckenhorn 2000, Blanckenhorn et al. 2007). The sex specific selection pressures on life history traits often result in sexual size dimorphism (Blanckenhorn 2000, Blanckenhorn et al. 2007) with male size usually being more variable than female size (Rensch's rule, Rensch 1950, Fairbairn and Preziosi 1994, Fairbairn 2005, Blanckenhorn et al. 2007). Chapter 2 discusses the different selection pressures on life history traits and sexes, the trade-offs between those traits, and phenotypic effects such as sexual size dimorphism and Rensch's rule in *L. sclopetarius*.

Chapter 3 investigates the reproductive success (i.e. lifetime fecundity) of female bridge spiders and its relation to the diet at different life stages and lifespan. Lifetime fecundity in arthropods is often positively related to female body size (Wickman and Karlsson 1989, Honek 1993, Marshall and Gittleman 1994, Head 1995, Foellmer and Moya-Laraño 2007) and to feeding condition (Wise 1979, Sota 1985, Parker and Begon 1986, Pékar 2000, Agarwala et al. 2008). Under poor diet, animals extend their lifespan (Masoro 2005) and thus prolong the reproductive period. In Chapter 3, I investigate the trade-off between lifespan and offspring number in bridge spiders to reveal the reproductive strategies that are the basis for their success in urban habitats.

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Chapter 1

Developmental strategies in an invasive spider: constraints and plasticity

Abstract Growth defines the major life history traits such as size, weight, and age at maturity that determine an organism's fitness. Different models have been developed to describe growth by means of geometric progressions (e.g. Dyar's rule). However, growth along a geometric trajectory seems to be in contrast with developmental plasticity that is a common phenomenon in response to variable environmental conditions (e.g. food availability). We investigated growth patterns under varying food conditions in the bridge spider, *Larinioides sclopetarius,* an extremely successful species in colonizing urban habitats. Growth of *L. sclopetarius* does not follow Dyar's rule because growth ratios decreased over development. Nevertheless, growth can be described by geometric progressions that comprise a growth factor (weight gain per molt) and a growth coefficient (weight gain per development time). In *Larinioides sclopetarius*, all developmental parameters, including growth factor and growth coefficient as well as the intermolt duration and the number of instars, highly depend on food availability and show full plasticity. This study shows that plasticity does not necessarily preclude geometric growth patterns. However, the parameters of geometric growth are affected by developmental plasticity. Our study provides evidence that the ability of bridge spiders to successfully invade urban habitats is related to their high developmental plasticity.

Introduction

Adult fitness of any organism is to a large extent the result of life history strategies during development; juvenile growth is one of the principal life history traits. Growth determines size and age at maturity and often reproductive fitness (Stearns and Koella 1986, Vollrath 1987, Roff 1992, Stearns 1992). Growth itself is a function of environmental conditions in concert with the genetic disposition.

The ability to react adaptively to changing environmental conditions will define the trajectory between juvenile growth and adult fitness (Abrams et al. 1996). Growth patterns of animals are categorized into two separate dichotomies as determinate vs. indeterminate, continuous vs. discontinuous growth. Determinate growth stops at some point in life (e.g. certain size or age, usually after reaching sexual maturity) and indeterminate growth continuous as long as the animal survives (Karkach 2006). Discontinuous growth describes the stepwise growth of arthropods as well as the so-called "catch-up" growth of animals with a genetically determined final size (e.g. clams in the gulf of California) (Karkach 2006). In the latter example, individuals with slow growth early in life due to poor conditions will catch up if conditions improve. Continuous growth cannot be divided into discrete stages.

The main growth categories described above can be further divided into distinct developmental categories. Animals with metamorphosis go through a biphasic development (e.g. amphibians, holometabolous insects), while others develop directly (e.g. mammals, hemimetabolous insects). A biphasic development always includes a larval stage, a metamorphosis and an adult stage (Zissler 2003).

In contrast to indeterminate and continuous growth, determinate growth of hemimetabolous arthropods is characterized by consecutive stages each of which may have growth rates independent of other stages. Arthropods grow discontinuously due to their cuticle that prevents the exoskeleton from expanding outside molts. Theoretically, hemimetabolous growth may allow an animal to repeatedly adjust current growth decisions to prevailing conditions until maturation. Such a flexibility is known for insectivorous arthropods, while in many phytophagous (hemimetabolous or holometabolous) insects the flexibility to react to local conditions is restricted to the very beginning of their life (Nijhout and Williams 1974, Hatle et al. 2003).

In an attempt to explain the variability in arthropod growth patterns, Higgins and Rankin (1996) postulate that 1) three developmental parameters (change in size at ecdysis, intermolt duration, number of instars) determine age and size at maturity, but 2) never more than one is fixed (canalized), and 3) not all combinations of plastic (flexible) and canalized parameters occur in nature. Plasticity is the flexibility of an organism to react to internal or external environmental factors with a change in form, state, movement, or rate of activity (West-Eberhard 2003); canalization is the opposite. Canalization describes a genetic fixation of traits resulting in expression of the same phenotype regardless of environmental variation (Nylin and Gotthard 1998). However, most life history traits show phenotypic plasticity in response to changing environmental factors during development (Caswell 1983).

The potential to modulate growth adaptively is contrasted by the idea of growth rules, which postulate that animals can only grow at a distinct and constant ratio. Dyar (1890) proposed that arthropods grow with a regular geometrical progression a pattern known as Dyar’s rule. Later Przibram and Megušar (1912) determined the growth ratio (i.e. the size of one instar divided by the size of the preceding instar) to be 1.26. Cole (1980) listed additional growth ratios for 105 insect species. Comparable to Dyar’s rule for the increase of body size, Przibram and Megušar (1912) found a geometric progression for the weight increase of successive instars (by a factor of two).

The existence of a fixed growth factor implies that all individuals of a holometabolous or hemimetabolous arthropod species reach the same size at maturation unless the number of instars varies. The number of instars or molts determines in how many steps an individual reaches maturity and gains weight. However, growth of arthropods is also determined by intermolt intervals that determine the time an animal takes to gain weight between molts.

Empirical results are ambiguous although most studies support Dyar’s ideas (Moser et al. 1991, Alvan-Aguilar and Hamada 2003, Fusco et al. 2004, Hernandez-Livera et al. 2005, Massuretti de Jesus and Correa Bueno 2007, Panzavolta 2007, Rodriguez-Loeches and Barro 2008). Some insect species, however, are reported to follow Dyar’s rule in only some of their instars (Lauzon and Harper 1993), in only some morphological structures (Johnson and Williamson 2006), or in particular caste stages of social insects (Cnaani and Hefetz 2001). Other studies did not find constant growth rates between growth stages

(Klingenberg and Zimmermann 1992, Tomkins 1999, Calvo and Molina 2008) due to the effects of environmental changes such as crowding, temperature, and food availability (Daly 1985, Hutchinson et al. 1997, Mayntz et al. 2003, Guillen and Heraty 2004).

Spiders generally show a hemimetabolous, determinate growth, which is proposed to critically depend on food availability. In particular, spider species that are sit-and-wait predators depend on prey abundance due to their limited impact on numbers and kinds of prey (Mayntz et al. 2003). They can only influence their prey capture success by choosing web position, changing web size, or by varying mesh size (Olive 1982, Herberstein and Elgar 1994, Sherman 1994, Heiling and Herberstein 1998). As a consequence, sit-and-wait predators are well adapted to variable prey availabilities (Mayntz et al. 2003). Dyar's rule has been applied to very few spider species and the results allow no confident conclusion about its applicability. While an actively hunting wolfspider *Pardosa astrigera* (Lycosidae) showed deviations from a constant growth factor (Miyashita 1968), the orb-web spider *Nephila clavipes* (Nephilidae) exhibited fixed growth ratio between instars (Higgins 1992, Higgins 1993, Higgins and Rankin 1996). Enders (1976) found deviations from constant growth factors in several spider species of the families Salticidae and Lycosidae.

Dyar's rule would be most effectively tested through examination of a species with a particular advantage for developmental plasticity. In our study, we investigate growth trajectories and patterns under varying environmental conditions in an invasive orb-web spider, *Larinioides sclopetarius* (Araneidae). The bridge spider, *L. sclopetarius*, is extremely successful in colonizing urban habitats. It is a synanthropic species that is very abundant near water and considered a pest in large cities (Heiling 1999, Schmitt 2004, Schmitt and Nioduschewski 2007). The spiders aggregate near water, a consequence of the superabundance of insect prey that emerges from the water and is attracted of artificial lights in manmade habitats (Burgess and Uetz 1982, Heiling 1999). As an invasive species, *L. sclopetarius* is predicted to be particularly plastic because flexibility predisposes them to quickly adapt to novel environments. To test this assumption, we raised spiders from eggs and followed their growth until maturation while varying food supply across experimental groups. We hypothesized that these spiders do not show constant growth ratios between successive instars but display a high degree of plasticity in their growth factor (weight gain per molt), the number of instars, and the aging factor (instead of intermolt duration) that may allow them to be successful colonizers.

Methods

Study objects

The bridge spider *Larinioides sclopetarius* (Clerck, 1757) (Araneae: Araneidae) is very common in urban habitats. It is a nocturnal synanthropic species that is very abundant near water and lives in aggregations. Under laboratory conditions females produce up to 15 cocoons over a lifespan of 1.5 years. All developmental stages are present throughout the year, with adult males abundant mainly in September. Cocoons do not hibernate. Individuals of the spider *L. sclopetarius* were collected from their webs on bridges and facades in populations near the River Elbe in the HafenCity of Hamburg, Germany (53°33'N, 09°59'E), in 2006 from May to October and in April, 2007.

Parent generation

Spiderlings for experiments originated from 24 females; of these, 21 females were mated with virgin males in the laboratory and three females mated in the field. From the 21 female specimens that were mated in the laboratory, seven were collected in the field in the penultimate instar and 14 were derived from laboratory breeds. Altogether observed offspring were derived from 15 maternal lines (cp. Table 8 appendix). In addition to variation in locality and mating location, mothers differed in the duration between maturation and mating. From each mother we chose a single cocoon from which offspring were delivered for treatments (cp. Table 9 appendix).

Rearing conditions

Reproductive spiders were kept individually in 400 ml plastic cups at room temperature and under natural photoperiod. Spiders were fed 2-3 blowflies (*Calliphora sp.*) twice a week, and watered once per day, five days per week. After their final molts, females were weighed and transferred to Perspex frames (36 × 36 × 6 cm) where they built their orb webs. Females were mated 3-83 days (in average 42 days) following maturation. Males were maintained in individual 200 ml plastic cups, fed 5-10 *Drosophila melanogaster* twice a week, and watered five days per week. Mated females were transferred back to their plastic cups and checked for egg sacs five days per week. Deposited egg sacs were weighed, maintained in boxes (7 × 14.5 × 11.5 cm) and randomly assigned to three different temperatures – room temperature (20-25 °C), low temperature (20 °C) or high temperature (30 °C) in an incubator (cp. Table 8 appendix) – and watered daily five times a week.

Feeding treatments/Feeding experiments

Ten days after hatching, 15 full-sibling spiderlings were randomly assigned to three different diet regimes: (i) high feeding level, (ii) low feeding level, or (iii) very low feeding level. Due to the experimental design mothers that vary in locality, mating location, period elapsing between maturation and mating, successive number of egg sac were represented in all treatments. All juveniles were separated in the second instar because first molts occur inside the egg sac about three days after hatching. The first weighing of spiderlings was performed after the second molt. Animals in the high feeding treatment received *Drosophila melanogaster ad libitum*. *Drosophila melanogaster* were fed on a high nutrient diet with Carolina Biological Supply instant *Drosophila* medium Formula 4-24® and crushed dog food (Purina Matzinger Flocken-Vollkost Junior) according to Mayntz and Toft (2001).

Food was limited in the low and very low feeding treatment. The first feeding was performed fifteen days after hatching: spiders with low feeding level were fed three *D. melanogaster*, very low feeding level spiders received one *D. melanogaster* per week (cp. Table 7 appendix). With increasing age of spiders until maturation, we adjusted the number of fed fruit flies every 60 days by a factor of 1.5-2.

Spiderlings were fed twice a week, watered and checked five days per week for the presence of exuviae. Spiders were weighed after each molt (post-molt weight) using an electronic balance (METTLER TOLEDO XS105 DualRange) to an accuracy of 0.01 mg. For individuals on the high feeding treatment *Drosophila* were always available and therefore we cannot exclude that they fed before post-molt weight was determined. From September, 2006 to March, 2008 the development of 360 individuals (120 per treatment) was observed. Of this group, 93 individuals died (for mortality see results) or were lost during daily handling. The remaining 267 spiders reached adulthood, 138 females and 129 males. After death of adult spiders, the tibia-patella length of the first pair of legs was measured to the nearest 0.01 mm using a LEICA MZ 16 stereomicroscope and LEICA IM500 imaging software (Version 4.0).

In bridge spiders, sex cannot be assessed until the penultimate instar and so, coincidentally in some cases, the siblings allocated to a particular treatment were the same sex; as a result, some families are missing in some treatments. At the end of the study, the developmental time from birth to adulthood, the number of instars, post-molt weight, and inter-molt intervals of each individual were documented.

Developmental parameters

We examined the following developmental parameters: *growth ratio*, *number of instars*, *growth factor* (weight gain per molt), *aging factor* (age gain per molt, instead of intermolt interval), and *growth coefficient* (weight gain per development time).

The *growth ratio* of instar (n_i) is defined as weight of current instar (n_i) divided by weight of the previous instar (n_{i-1}). To exclude the possible effect of total number of instars on growth ratio, we used only individuals with the same number of instars for the comparison of growth ratios within the treatments. We started counting the *number of instars* (developmental stages) beginning with their hatching out of the eggs; the first instar is prior to the first molt.

To account for potentially different growth ratios between successive molts, we do not use mean growth ratios of successive instars for the description of growth in different treatments. To obtain values that are independent of the number of instars and describe each treatment, we use an exponential growth equation:

$$y_G = a \cdot F_G{}^x . \tag{1}$$

In this equation (1) y_G is the post-molt weight, x is the number of molt, F_G is the *growth factor*, and a is a constant with no biological relevance, representing the value of y for $x = 0$. The factor F_G describes the weight gain per instar.

To consider the potential plasticity in the intermolt duration of successive instars, we applied, an analogue to the *growth factor*, an aging factor F_A that can be derived from the exponential function:

$$y_A = a \cdot F_A{}^x \tag{2}$$

In this equation (2) y_A is the molting age, x is the number of molt, F_A the *aging factor*, and a is a constant. Rapid growth or aging is characterized by high values of F_G or F_A.

To determine the values for F_G and F_A, we use the linear representation of the equations (1) and (2):

$$ln(y_G) = ln(a) + ln(F_G)\,x \quad (3)$$

$$ln(y_A) = ln(a) + ln(F_A)\,x. \quad (4)$$

Linear regression of weight or age (ln(y)) over the number of molts (x) yields values for ln(F_G) and ln(F_A) (i.e. the slope of the regression equation).

Post-molt weight over development time (independent of the number of instars) can be generally described by the power function:

$$y_G = a \cdot x_t^{\,G}, \quad (5)$$

where y_G is the weight, x_t is the development time, a is a constant with no biological relevance, representing the value of y when $x_t = 1$, and G is the *growth coefficient* (based on Huxleys (1950) growth rate). Rapid growth is characterized by high values of G. The linear representation of equation (5) is:

$$ln(y_G) = ln(a) + G\,ln(x_t). \quad (6)$$

The value for G can be determined by linear regression of weight (ln(y_G)) over development time (ln(x_t)) and resembles the slope of the regression equation.

Statistical analysis

We used the *REML* (Restricted Maximum Likelihood) method for fitting mixed model *ANOVA*s (Analysis of Variance) to the data to estimate the effects of feeding treatment and sex on the number of instars, the growth factor, the aging factor, and the growth coefficient. Feeding treatment and sex were fixed factors and family was a random factor. An exclusion of the family effect in the model does not alter results. Response variables were transformed, if necessary. All residuals were normally distributed. Growth ratios and intermolt durations over instars are not normally distributed. To estimate the effects of the instar on the growth ratio and the intermolt duration we used the non-parametric *Friedman repeated measures analysis of variance on ranks*. For individual pairwise comparisons of least square means in the model we used *Student's t-test*. In case more than two parameters were present, we used the *Tukey's HSD* (Honestly Significant Difference) *test* to test all differences among the least square means. We used a chi-square contingency analysis where mortality was the fixed factor and the treatment was the response. The statistical analyses were performed using JMP® 7.0.2 (SAS Institute Inc.) for Microsoft® Windows. For models which are fitted with the *REML* method, JMP® does not calculate F-ratios or P-values for the random factor family.

Results

The family significantly influenced the number of instars, the growth factor, the aging factor and the growth coefficient (Table 1).

Table 1 Results of *ANOVA* for the effects of feeding level (treatment) and sex on number of instars, growth factor (base F_G in $y_G(weight)=a \cdot F_G^{x(molt)}$), aging factor (base F_A in $y_A(age)=a \cdot F_A^{x(molt)}$), and growth coefficient G (power of x in $y_G(weight)=a \cdot x(age)^G$) on spiderlings ($N = 267$).

		number of instars		growth factor F_G		ageing factor F_A X		growth coefficient G X	
variable	*DF*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
treatment	2	103.75	**<0.0001**	213.06	**<0.0001**	114.28	**<0.0001**	287.49	**<0.0001**
sex	1	132.85	**<0.0001**	0.15	0.7023	10.73	**0.0012**	6.04	**0.0146**
sex × treatment	2	8.28	**0.0003**	3.75	**0.0248**	2.82	0.0614	1.47	0.2328

Number of instars

Bridge spider development was plastic in the total number of instars. The number of instars depended on the feeding treatment and the sex. Females on average passed through one more instar than males (Fig. 1, 2, Table 1). Males needed at least six and a maximum of nine instars, females needed at least six but could take up to 10 instars (Table 2). The average number of instars of siblings within treatments was 6-9 for males and 7-10 for females (Fig. 2). With increasing food supply, both sexes required significantly fewer molts to reach adulthood (Fig. 1, 2, 3, Table 1, 2).

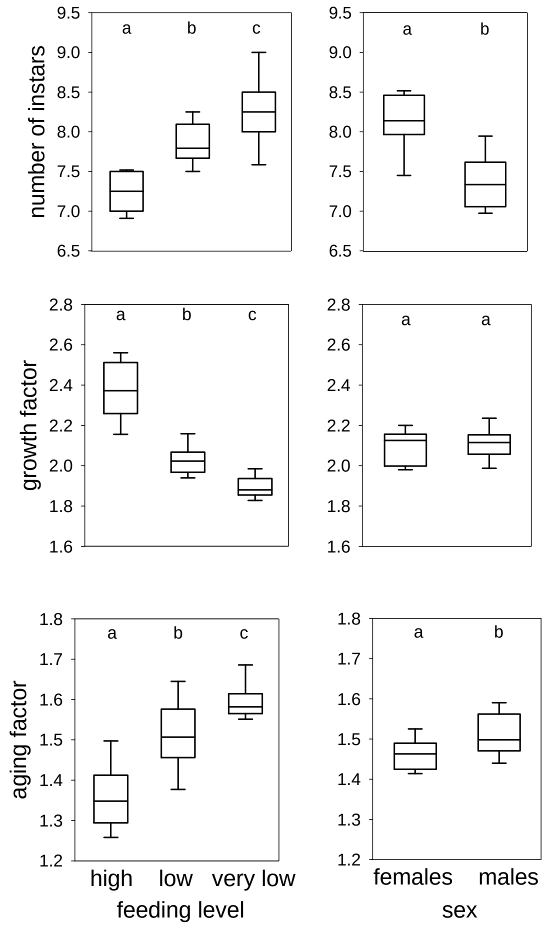

Fig. 1 Box plots for comparison of various developmental parameters (number of instars, growth factor, aging factor) of bridge spiders at different feeding levels (left) and sexes (right). Box plots that are not connected by the same letter are significantly different. Feeding level and sex influence all developmental parameters studied herein except for the growth factor, which is independent of sex. All values for siblings within the same treatment or sex were averaged.

Growth ratio

The growth ratio describes the weight gain between successive instars and decreases with increasing instar number in all food treatments except for those males under very low food conditions (Fig. 4, Table 3). In all treatments and sexes that had a decrease in growth ratio, at least the first and the last calculated growth ratios were significantly different (Fig. 4, Table 3). Better feeding conditions (i.e. more frequent feedings) resulted in a more rapid decrease of growth ratios of consecutive instars (Fig. 4). Mean values of growth ratios within instars ranged from 2.93 (female high, instar IV) to 1.59 (female very low, instar IX).

Table 2 *Larinioides sclopetarius* sample sizes and numbers of instars at different feeding levels. Relative values in percent given in parenthesis. Bold values show highest percentages inside treatments.

					number of individuals with		
	feeding level	*N* (%)	VI	VII	VIII	IX	X
					instars		
♀	high	44 (100)	3 (6.8)	**25 (56.8)**	16 (36.4)		
	low	47 (100)		1 (2.1)	**30 (63.8)**	15 (31.9)	1 (2.1)
	very low	47 (100)		1 (2.1)	16 (34.0)	**27 (57.4)**	3 (6.4)
♂	high	51 (100)	4 (7.8)	**45 (88.2)**	2 (3.9)		
	low	49 (100)		**32 (65.3)**	17 (34.7)		
	very low	29 (100)		9 (31.0)	**16 (55.2)**	4 (13.8)	

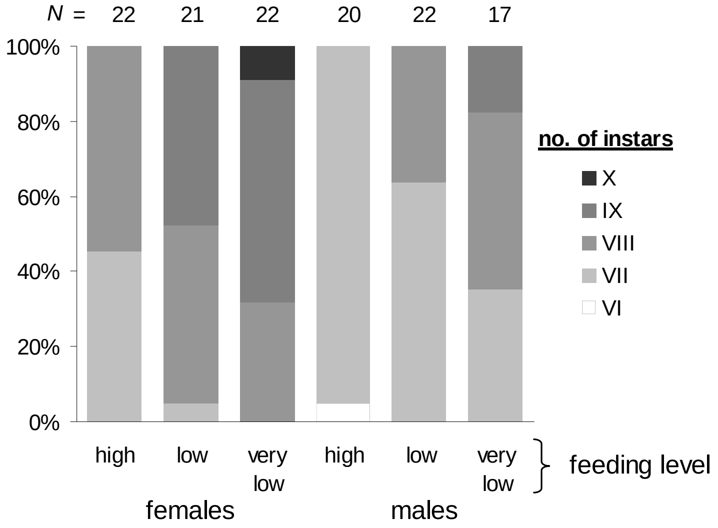

Fig. 2 Relative distribution of male and female spiders with n instars from hatching to adulthood at high, low, and very low feeding level. Lower food availability increases the number of instars for females and males. Average males have fewer instars than females in the same treatment. Females underwent seven to ten instars, males six to nine. All values for siblings within the same treatment and sex were averaged.

Growth factor

The growth factor F_G is a single value that describes the general growth trajectory from birth to maturation instead of using an averaged growth ratio for successive instars. A large value for F_G shows a rapid weight gain. Independent of sex, feeding treatments showed significant differences in the growth factor (Fig. 1, Table 1). Individuals experiencing high feeding conditions had the greatest weight increase over development

($F_G = 2.4$); in the very low treatment the weight gain over development was lowest ($F_G = 1.9$) (Table 5). The growth factor was not significantly different for males and females (Table 1) with a mean value of 2.0 (Fig. 1). Different feeding levels showed significant differences in growth factors for both males and females (Fig. 3). There was a significant interaction between sex and treatment (Table 1) but the response in growth factors to different treatments was the same for males and females (Fig. 3).

The relationship of post-molt weight over instar was well described by the exponential function (1); its regression equation (4) for determination of F_G yielded high correlation coefficients ($R^2 > 0.99$) (Table 5).

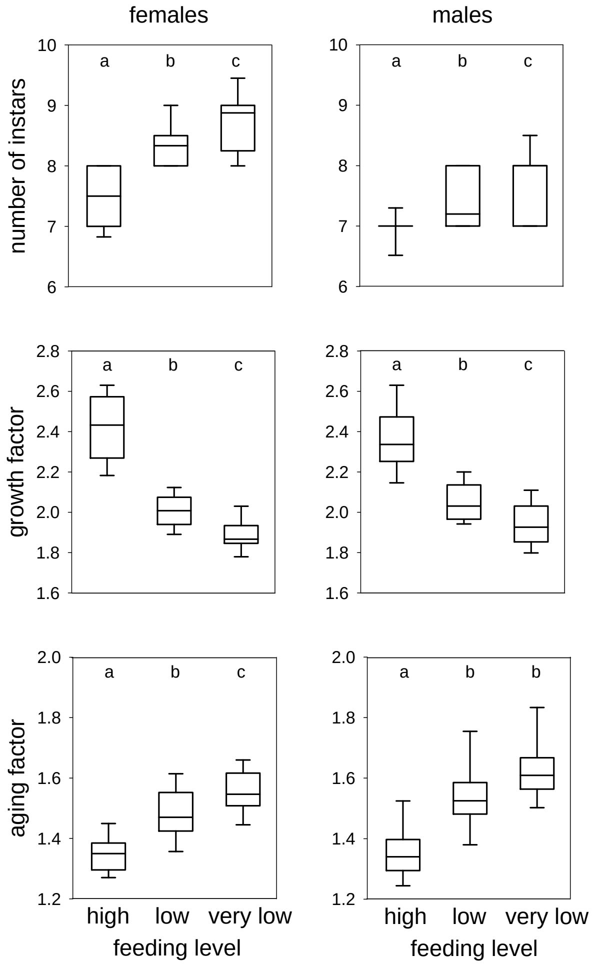

Fig. 3 Box plots for comparison of various developmental parameters (number of instars, growth factor, aging factor) at different feeding levels in female (left) and male (right) bridge spiders. Box plots that are not connected by the same letter are significantly different. Feeding levels influence all developmental parameters studied herein similarly for both sexes except for the aging factor of males at low and very low feeding level. All values for siblings within the same treatment and sex were averaged.

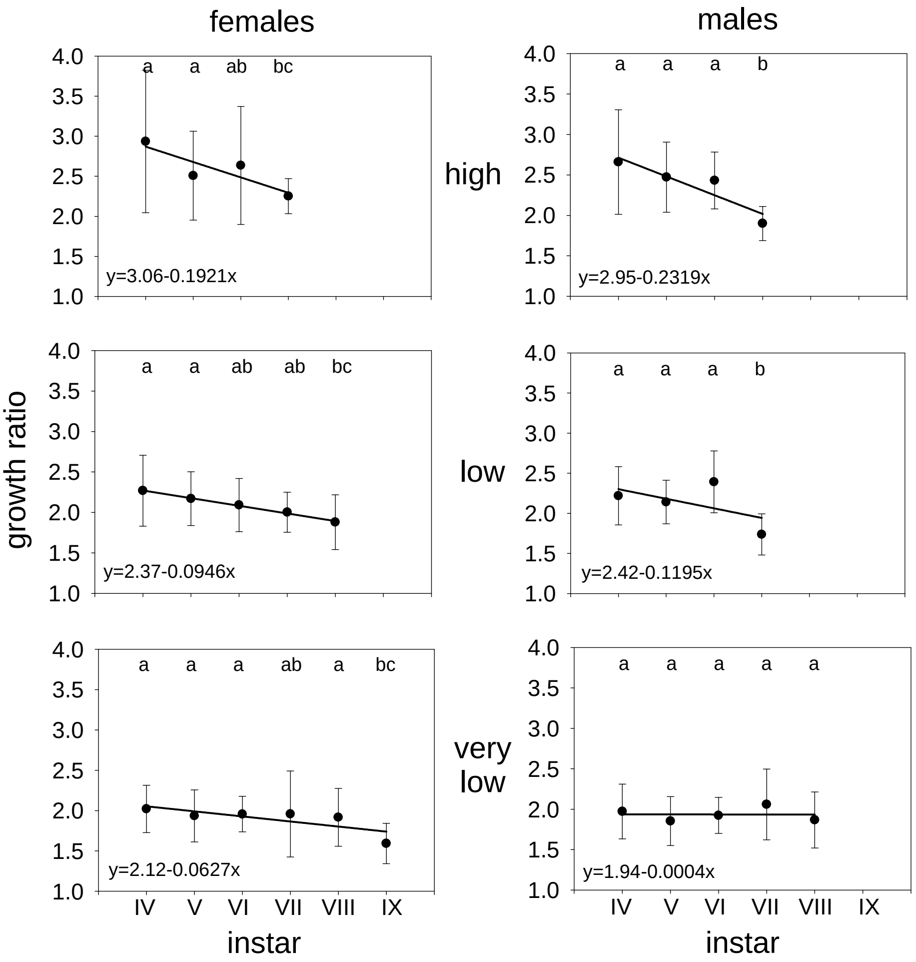

Fig. 4 Growth ratios (weight instar(n_i)/weight instar(n_{i-1})) of successive instars in female (left) and male (right) bridge spiders at high (top), low (middle), and very low (bottom) feeding levels. Instars that are not connected by the same letter are significantly different. Growth ratios between molts at the same feeding level are not constant and decrease except for the growth ratios of males at very low feeding level. The negative slope of the linear regression decreases with declining feeding level. (cp. Table 2 for sample sizes).

Table 3 Results of *Friedman repeated measures analysis of variance on ranks* for the effect of instars on growth ratios (weight instar(n_i)/weight instar(n_{i-1})).

	feeding level	total number of instars	*DF*	χ^2	*p*
♀	high	VII	3	13.636	**0.0003**
	low	VIII	4	10.993	**0.0270**
	very low	IX	5	22.691	**<0.0001**
♂	high	VII	3	54.971	**<0.0001**
	low	VII	3	40.779	**<0.0001**
	very low	VIII	4	0.629	0.960

Intermolt duration

The days between successive molts are considered as intermolt duration or intermolt interval. Overall mean values for intermolt durations ranged from 8.2 days (female high, instar IV) to 85.6 days (male very low, instar VII). Consecutive instars differed in their intermolt duration in all treatments and both sexes (Fig. 5, Table 4). Intermolt duration increased with successive instars (Fig. 5). Feeding levels affected intermolt duration; high feeding conditions resulted in shortest intermolt durations.

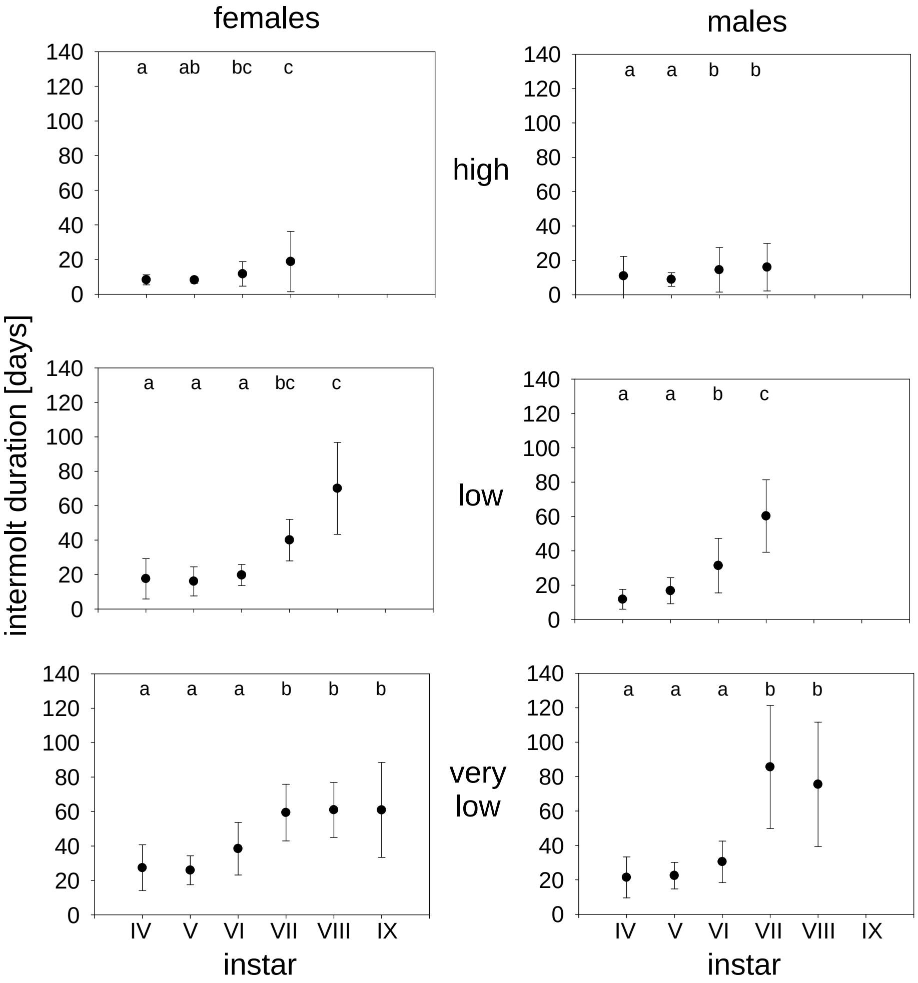

Fig. 5 Intermolt duration in days of successive instars in female (left) and male (right) bridge spiders at high (top), low (middle), and very low (bottom) feeding level. Instars that are not connected by the same letter are significantly different. Intermolt durations at the same feeding level are not constant and increase (cp. Table 2 for sample sizes).

Table 4 Results of *Friedman repeated measures analysis of variance on ranks* for the effect of instars on intermolt duration.

	feeding level	total number of instars	*DF*	χ^2	*p*
♀	high	VII	3	39.894	**<0.0001**
	low	VIII	4	82.734	**<0.0001**
	very low	IX	5	78.291	**<0.0001**
♂	high	VII	3	38.008	**<0.0001**
	low	VII	3	64.689	**<0.0001**
	very low	VIII	4	41.503	**<0.0001**

Table 5 Parameters of linear regression equation $ln(y_G) = ln(a) + ln(F_G)\,x$ for the growth factor F_G with weight (y) over molt (x) and *a* as constant and Pearson correlation coefficient R^2. F_G values that are not connected by the same letter are significantly different. All values for siblings within the same treatment and sex were averaged.

	feeding level	*a*	F_G	R^2
♀	high	0.29	2.42_{a}	0.9951
	low	0.36	2.01_{bc}	0.9928
	very low	0.41	1.89_{d}	0.9957
♂	high	0.32	2.35_{a}	0.9934
	low	0.36	2.06_{b}	0.9944
	very low	0.38	1.94_{cd}	0.9944

Table 6 Parameters of linear regression equation $ln(y_A) = ln(a) + ln(F_A)\,x$ for the aging factor F_A with weight (y) over molt (x) and *a* as constant and Pearson correlation coefficient R^2. F_A values that are not connected by the same letter are significantly different. All values for siblings within the same treatment and sex were averaged.

	feeding level	*a*	F_A	R^2
♀	high	10.91	1.35_{a}	0.9799
	low	10.86	1.47_{b}	0.9865
	very low	11.20	1.56_{c}	0.9773
♂	high	11.23	1.36_{a}	0.9784
	low	9.33	1.54_{c}	0.9805
	very low	10.05	1.63_{c}	0.9865

Aging factor

The aging factor F_A describes the aging over successive instars and is an alternative variable to the mean value for intermolt durations. High values for F_A represent long intermolt durations. F_A differed significantly in all treatments independent of sex (Table 1): under high food, intermolt intervals were the shortest and spiders aged with a mean F_A of 1.35. The mean F_A increased to 1.52 under low food and showed a further but slight increase under very low food (1.58). Males aged with a slightly higher mean aging factor than females (1.49 and 1.46, respectively). Feeding levels influenced the aging factors of males and females significantly (Fig. 3, Table 1); males at low and very low feeding level showed no significant differences in aging factors (Table 6). The relationship of age over instar was well described by the exponential function (2); the correlation coefficient for the linear regression that was used to determine F_A exhibited values of $R^2 > 0.97$ (Table 5).

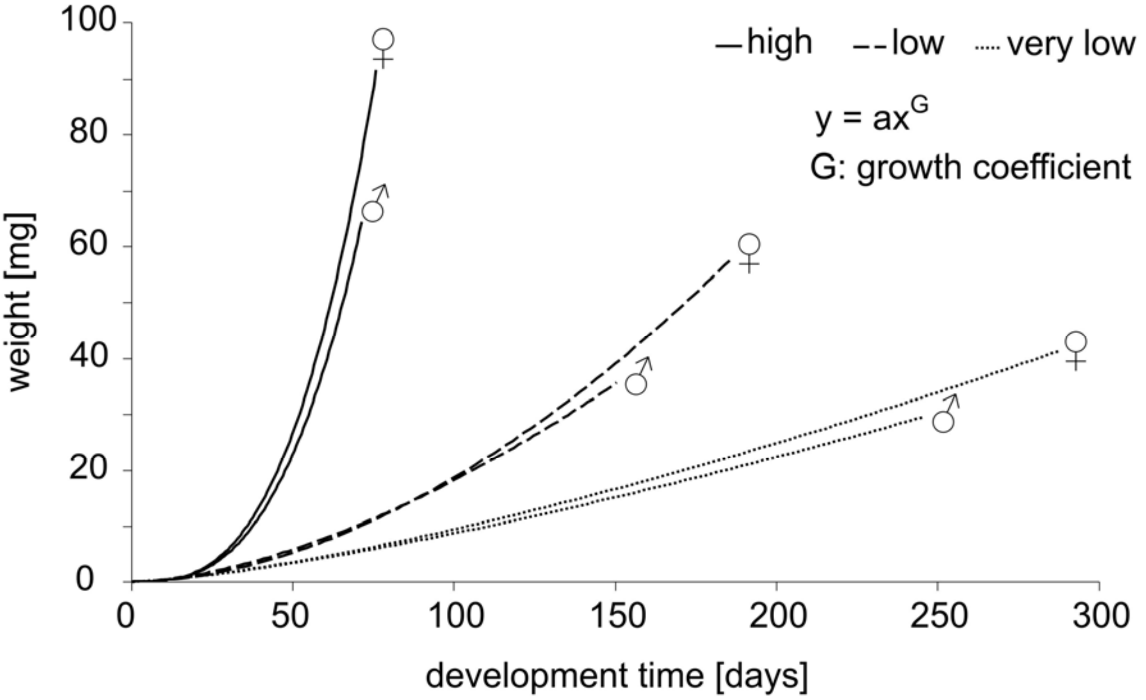

Fig. 6 Mean growth curves of female and male bridge spiders as a function of different feeding levels. Termination of each graph represents maturation. Individuals with high feeding level grow in a shorter time to a larger weight than individuals with less food. Growth coefficients (cp. Table 6) of different treatments are significantly different for both sexes (cp. Table 1). All values for siblings within the same treatment and sex were averaged.

Growth coefficient

The correlation between body weight and duration of development (Fig. 6) follows a power function (5) with growth coefficient G as power. G describes the weight gain over development time (days) independent of discrete instars. Large values for G depict a rapid growth. Overall feeding treatment and sex affected the growth coefficient significantly but there was no significant interaction between treatment and sex (Table 1). Individuals at high feeding level had the highest growth coefficients and those at the very low feeding level had the lowest. The growth coefficient differed significantly among feeding treatments for males and females (Table 7). Independent of feeding conditions, males and females shared the same mean growth coefficient of 2.07. The relationship of post-molt weight over development time was well described by the power function (5); the linear regression equation (6) that results in values for G had Pearson correlation coefficients of $R^2 > 0.97$ (Table 7).

Table 7 Parameters of linear regression equation: $ln(y) = ln(a) + G\ ln(x)$ with G as growth coefficient and Pearson correlation coefficient R^2. G values that are not connected by the same letter are significantly different. All values for siblings within same treatment and sex were averaged.

feeding level		*ln(a)*	*G*	R^2
♀	high	-8.30	2.96_a	0.9773
	low	-5.50	1.83_b	0.9837
	very low	-4.24	1.41_c	0.9780
♂	high	-8.26	2.91_a	0.9798
	low	-4.72	1.65_b	0.9765
	very low	-4.12	1.36_c	0.9853

Mortality

Out of 298 individuals, 10.4% died but there were no significant differences in the number of deaths per treatments (Pearson $\chi^2 = 5.389$, $p = 0.0676$). However, mortality was more likely in earlier instars (Pearson $\chi^2 = 40.652$, $p < 0.0001$): 64.5 % of the mortality occurred in instar II, contrasted with much lower values in instars III (16.1 %), IV (9.7 %), V (6.5 %) and VI (3.2 %).

Discussion

Growth models for bridge spider development

Our feeding experiments revealed extraordinary developmental plasticity in the bridge spider, *L. sclopetarius*, and a digress from various physiological rules. Our results are contrary to Dyar's (1890) and Przibram and Megušar's (1912) widely accepted assumption that growth ratios of successive instars are constant. Rather, we found that weight gain over molts is exponential and thus follows a regular geometric progression. The growth factor F_G describes body weight increases between molts; the postulated growth factor of 2.0 (Przibram and Megušar 1912), was only found under low feeding conditions. Depending on feeding conditions, F_G can be larger (high food) or lower (very low food) than 2.0. Hence the growth factor is influenced by feeding conditions and was 2.11 on average in *L. sclopetarius* given our experimental conditions.

The relationship of weight and development time followed a power function, meaning that weight gain in earlier instars is stronger than in later instars. The application of a power function to describe weight gain over development time was previously suggested by (Tammaru and Esperk 2007). We observed an overall decrease in growth ratios and an increase in instar durations with successive instars. Hutchinson et al. (1997) reviewed the literature on arthropod development to test their hypothesis that increase in size and instar duration are optimized (Investment Principle). The Investment Principle explains deviations from Dyar's rule. Hutchinson et al. (1997) introduced the variable α that describes the scaling of the rate of reserve accumulation with size. In arthropods, reserve accumulation rises less than body size ($\alpha < 1$). In case of high food availability (f in the model of Hutchinson et al. (1997)), the Investment Principle predicts decreasing growth ratios with consecutive instars. This prediction is confirmed experimentally by our results. Several studies on other arthropods also found that body size increase decelerated with increasing instars (Enders 1976, Klingenberg and Zimmermann 1992, Fantinou et al. 1996, Higgins and Rankin 2001, Mayntz et al. 2003, Calvo and Molina 2008, Marczak and Richardson 2008) while intermolt durations increased (Miyashita 1968, Mayntz et al. 2003, Uhl et al. 2004). Thus, the application of Dyar's rule for predictions of size and weight of different instars during arthropod development is limited. We confirm the statement of Klingenberg and Zimmermann (1992) on Dyar's rule „as a base of comparison against which specific adaptive hypothesis can be tested, rather than to search for an adaptive explanation for the rule itself".

High plasticity in developmental parameters

Under varying feeding conditions *L. sclopetarius* showed high plasticity in all developmental parameters: number of instars, growth factor (weight gain between molts), aging factor (intermolt duration), and growth coefficient. *Larinioides sclopetarius* shows the pattern of full plasticity in their postembryonic development (trajectory D in the terminology of Higgins and Rankin (1996)).

Trap building animals such as spiders have only limited control over their foraging success, which consequently may become unpredictable. Plasticity in life history traits allows the animal to tolerate stochastic fluctuations in the number and quality of prey items (Mayntz et al. 2003). Two other spider species, the orb-web spider *Zygiella x-notata* (Mayntz et al. 2003) and the cursorial wolf spider *Pardosa astrigera* (Miyashita 1968), show a similar degree of plasticity. Habitat and hunting strategies do not seem to drive these similarities as *Z. x-notata* (and *L. sclopetarius*) occur in urban habitats (Mayntz et al. 2003), while *P. astrigera* inhabits sunny open grasslands and hunts without a web (Miyashita 1968, Tanaka and Ito 1982, Tanaka 1993, Fujii 1998). Nevertheless, all three species share the absence of strictly seasonal life cycles. In *L. sclopetarius*, all developmental stages are present all over the year with a peak in summer (Schmitt and Nioduschewski 2007). *Zygiella x-notata* has an annual life cycle with overwintering egg sacs but some females survive through winter and built supplementary egg sacs in spring (Mayntz et al. 2003) . Furthermore, the population dynamic changes with increasing prey abundance; they reproduce earlier, and produce more and heavier eggs (Spiller 1992). In *P. astrigera*, there are two peaks in population density of nymphs; one in spring and the other in fall (Miyashita 1968). In contrast to the above examples, the golden orb-web spider *Nephila clavipes*, which is canalized to change size in ecdysis (Higgins 1992, 1995) is strictly seasonal (Higgins and Rankin 2001). These seasonal or non-seasonal life cycles may be related to different prey availabilities and life history patterns. Plasticity is proposed to be advantageous for non-seasonal species because it allows them to adapt to food fluctuations throughout the year.

Linking food availability to mortality

The high plasticity of *L. sclopetarius* appears to be associated with low mortality. Unlike other animals (see Blanckenhorn 2005), *L. sclopetarius* did not show higher rates of mortality when experiencing faster growth under laboratory conditions (i.e. without predation) suggesting that there are no intrinsic physiological costs of fast growth. However, mortality was very low in general across treatments (10.4% of all individuals) so we cannot draw meaningful conclusions about the potential influence of growth speed and mortality. In another spider species such as the golden orb-web spider *N. clavipes* (Nephilidae), individuals that grow faster due to high prey availability suffer an increased mortality risk (Higgins and Rankin 2001). *Nephila clavipes* tends to gorge food when prey is very abundant (Higgins and Rankin 2001) and encounter problems during molts that cause death. Under natural conditions, however, *N. clavipes* may not encounter sudden peaks in prey densities so that there is no selection to adapt to such conditions. Similar to *N. clavipes*, individuals of *Tetragnatha versicolor* died more frequently during molts under high food conditions whereas total mortality was higher under restricted food conditions due to unknown causes other than molting problems (Marczak and Richardson 2008). *Tetragnatha versicolor* is sometimes found on riverbanks where, similar to the bridge spider, it feeds on insects that emerge from the water. It may therefore encounter periods of overabundance of prey (Marczak and Richardson 2008) when insects emerge in bursts. However, since this is not their main niche (Aiken and Coyle 2000) it is possible that they have not evolved a mechanism to counter overfeeding. Comparable to our results, *T. versicolor* has variable growth rates and intermolt durations (Marczak and Richardson 2008). However, the total range of intermolt duration shows less variation (15-35 days) (see Figure 3b in Marczak and Richardson 2008) than in *L. sclopetarius* (8-86 days). Bridge spiders that live exclusively near water regularly experience an overabundance of prey due to the seasonal and diurnal hatching synchrony of chironomid species (Chironomidae) (spring, summer, and fall species) (Ziegler 2005). In particular, webs close to light sources are often loaded with large numbers of freshly emerged insects. Webs with untouched prey items are commonly observed (pers. observation).

Our results are based on continuous food regimes and it would be interesting to test whether mortality would be different under varying prey conditions. Even though the main prey of bridge spider underlies large seasonal fluctuations it is likely that these predators would easily cope since they can survive well in periods of starvation (as in our treatment with very low prey).

What makes bridge spiders an invasive species?

Plasticity is advantageous in a variable and heterogenic environment (Caswell 1983, Stearns 2000). Urban environments are probably not very variable but spatial heterogenic for bridge spiders. Urban habitits act as heat islands with a reduced species diversity but an increased species density (Shochat et al. 2006), favoring invasive colonization by plastic organisms such as *L. sclopetarius.* Invasive species (plants and animals) are native or nonindigenous species characterized by rapid proliferation allowing them to become locally dominant and increase in abundance in a short time period (Richardson et al. 2000, Kolar and Lodge 2001, Colautti and MacIsaac 2004). Shochat et al. (2006) recognized developmental plasticity as a beneficial trait for urban species, in addition to resistance to stress, disease and pollution. Plasticity will enable organisms to invade novel habitats rapidly and effectively. The vast majority of invasive species studies deal with invasive plants. And few studies propose general and consistent traits of invasive animals and of those, most have focused on birds (Kolar and Lodge 2001). *Larinioides sclopetarius* shares traits with invasive birds such as the production of several broods (or egg sacs, in the case of spiders) per year. Other traits are similar to those of invasive plants. Invasive plants grow in areas with high resource density and low predation (Blumenthal et al. 2009) and are characterized by early flowering, high initial growth rate, and high reproductive output (Garcia-Serrano et al. 2005). Similarly, *L. sclopetarius* experiences high prey densities when living in proximity to streets and buildings where illumination attracts insects. In contrast to many insects in cities that suffer high predation from birds (Shochat et al. 2006), *L. sclopetarius* are nocturnal and hide in crevices during the day where birds cannot easily access them. The short development in combination with the fact that egg development does not require a cold period enables these spiders to multiply and their populations to expand rapidly.

Phenotypic plasticity influences the invasiveness of plants if plasticity is related to fitness (Richards et al. 2006) because it allows colonization of new habitats without requiring environment-specific genetic adaptations (Sultan 2000). Although a comparison between plants and spiders has limited utility, we propose a mechanism similar to that seen in plants that explains the extreme success of *L. sclopetarius* as an invasive species in urban habitats.

Conclusion

Contrary to Dyar's rule, growth ratios in *Larinioides sclopetarius* decrease with successive instars. However, growth can be described by a geometric progression: either by an exponential function for weight increase over instar or by a power function for weight increase over development time. Bridge spider development shows full plasticity: all developmental parameters, including growth factor (respectively growth coefficient), the number of instars, and the aging factor, highly depend on food availability. High growth rates due to overabundance of prey had no effect on mortality, suggesting that bridge spiders experience no intrinsic physiological costs of fast growth. Accelerated growth, earlier maturation, and thus rapid reproduction under high prey densities allow bridge spiders to be an extremely successful invasive species in urban habitats. However, more studies on a larger variety of taxa are desirable to establish an overall connection between high developmental plasticity, invasiveness and urban habitats.

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Appendix

Table 8 Feeding concept: the number of *Drosophila melanogaster* fed per week to spiders in different treatments until maturation. Small values represent factors.

feeding level	age since hatching [days]												
	15 - 59		60 - 119		120 - 179		180 - 239		240 - 299		300 - 359		≥360
high	*ad libitum*												
low	3	1.7	5	1.6	8	1.9	15	1.4	21				
very low	1	2.0	2	1.5	3	1.7	5	1.4	7	1.4	10	1.5	15

Table 9 Ancestry of reared juveniles.

mother								juveniles (15 per egg sac)		
ID mother	**maternal line**	**locality**	**leg.**	**birth**	**maturation**	**days before mating**	**mated**	**cocoon no.**	**hatching**	**incubation temp.**
1	1	field	-	-	-	-	unknown	field	August 06	20-25
2	2	field	May 06		July 06	22	experimental	2	August 06	20-25
3	3	field	May 06		June 06	3	experimental	4	September 06	20-25
4	4	field	June 06		July 06	60	experimental	4	October 06	30
5	5	field	August 06		September 06	13	experimental	2	November 06	20
6	6	field	-	-	-	-	unknown	unknown	December 06	20-25
7	A	laboratory		August 06	October 06	23	experimental	1	January 07	30
8	B	laboratory		August 06	October 06	16	experimental	1	January 07	30
9	A	laboratory		July 06	November 06	77	experimental	2	February 07	20
10	2	laboratory		August 06	October 06	83	experimental	2	February 07	20
11	C	laboratory		July 06	November 06	80	experimental	2	February 07	20-25
12	D	laboratory		July 06	November 06	60	experimental	2	February 07	20
13	3	laboratory		July 06	October 06	36	experimental	6	March 07	20
14	14	field	October 06		November 06	7	experimental	6	March 07	20-25
15	4	laboratory		September 06	December 06	62	experimental	1	March 07	20
16	16	field	July 06		July 06	45	experimental	5	March 07	20-25
17	17	field	August 06		September 06	53	experimental	7	March 07	30
18	E	laboratory		October 06	January 07	43	experimental	1	March 07	30
19	5	laboratory		November 06	March 07	8	experimental	1	April 07	30
20	B	laboratory		September 06	December 06	60	experimental	1	April 07	30
21	A	laboratory		August 06	October 06	83	experimental	6	April 07	30
22	3	laboratory		July 06	October 06	4	experimental	9	April 07	30
23	6	laboratory		December 06	February 07	45	experimental	1	April 07	30
24	24	field	April 07	-	-	-	unknown	unknown	May 07	20-25

Chapter 2

Evidence for Rensch’s rule in an orb-web spider with moderate sexual size dimorphism

Abstract Body size, weight, and age at maturity are key life history parameters that characterize lifecycles. They are determined by development and are highly relevant for an individual’s fitness due to their effects on reproduction and survival. The sexes underlie different selection pressures (fecundity selection vs. sexual selection), which usually results in a sexual size dimorphism (SSD). Rensch’s rule, which states that male body size is more variable than female body size, applies to many but not all taxa. In spiders, SSD is extreme in cases of female gigantism and male dwarfism so that the assumptions of Rensch’s rule are not met. However, it is unclear, whether the rejection of Rensch’s rule in spiders is a general pattern or whether the better studied species with extreme reversed SSD are not representative. Therefore, I selected a spider species with moderate SSD and a high developmental plasticity to test sex specific variation in size and age at maturity. I experimentally varied food supply during the development of the bridge spider *Larinioides sclopetarius* and measured body size, body weight, and age at maturity for 267 male and female spiders from 15 matrilines. My results support Rensch’s rule because only male body size was affected by diet, while female body size was canalized. Females reacted to decreasing food levels by prolonging developmental time and adding extra molts, while males under poor diet were smaller than well-fed males despite adding extra molts and increasing age at maturity. Interestingly, reaction norms of matrilines to different food regimes differed suggesting a genotype × environment interaction. Unlike previously assumed, my results show that Rensch’s rule is relevant for spiders, but perhaps only for those species with no or reversed SSD.

Introduction

The body size of an organism is determined by the interaction of selective pressures that can act in opposing or congruent directions: fecundity, sexual, and viability selection (Blanckenhorn 2005). Selection on viability favors accelerated development and small body sizes (Blanckenhorn 2000, 2005) because a prolonged growth period results in a higher mortality risk due to predation, parasitism and starvation before the onset of reproduction. Selection on fecundity acts only on females as the fitness advantage of more and/or larger eggs and offspring favors enhanced growth since fecundity is often a direct function of body size. In general, males are more often a target of sexual selection than females (Roff 1992, Stearns 1992). Sexual selection and fecundity selection can oppose selection on viability if costly traits are favored that increase mating and fertilization success (equilibrium model of Arak 1988, Schluter et al. 1991, Fairbairn 1997, Blanckenhorn 2000, 2005).

Life history theory proposes a general and strong trade-off between size and age at maturity because everything else being equal, more time is needed to grow larger. The strengths of the various selection pressures and the balance between them naturally differ between the sexes resulting in differences in size and age at maturity. A species is said to exhibit sexual size dimorphism (SSD) if one sex is larger than the other (e.g. female spiders, insects, fishes, amphibians, reptiles; male birds, mammals) (Darwin 1874, Arak 1988, Le Boeuf and Reiter 1988, Shine 1988, Abouheif and Fairbairn 1997, Fairbairn 1997). Across taxa, the degree of SSD increases with body size in case males are larger and it decreases with body size in case of females are the larger sex, a pattern first described by Rensch (Rensch 1959, Abouheif and Fairbairn 1997).

Fairbairn and Preziosi (1994) developed a quantitative explanation of Rensch's rule by regression of the logarithm of female body size within a group of taxa or populations over the logarithm of male body size and showed that Rensch's rule is supported if male body size shows higher variability than female body size (Fairbairn and Preziosi 1994, Fairbairn 2005, Blanckenhorn et al. 2007).

Despite general support for Rensch's rule in most taxa, several studies (Abouheif and Fairbairn 1997, Fairbairn 1997, Foellmer and Moya-Laraño 2007) did not find allometry patterns consistent with Rensch's rule in spiders. Spiders are known for extreme SSD in species with giant females and dwarf males (for review see Foellmer and Moya-Laraño

2007) and have often been used as model organisms in which to examine the proximate causes for the evolution of SSD (Hormiga et al. 2000, Blanckenhorn et al. 2007, Foellmer and Moya-Laraño 2007, Wilder and Rypstra 2008, Moya-Laraño et al. 2009). The allometry patterns that are inconsistent with Rensch's rule may result from large variation in female size and an unusually weak correlation of male and female body size (Fairbairn 1997, Foellmer and Moya-Laraño 2007, Kuntner and Coddington 2009). However, it is not clear whether these are exceptions to the rule or not. Hence, Rensch's rule may only be relevant to spider taxa with weak or even male-biased SSD.

The bridge spider *Larinioides sclopetarius* shows only weak SSD; males and females apparently have about the same body size. There are no confounding effects such as sexual cannibalism, monogamous males, or maternal care that may alter selection pressures on extreme SSD. Thus, any life history strategy of both sexes is likely to be governed by the three major selection pressures (sexual, fecundity, and viability selection) and growth patterns as well as variation in size, age, and weight at maturity.

The absence of an extreme female-biased SSD suggests that Rensch's rule is applicable for bridge spiders. Based on Rensch's rule female body size is expected to be canalized due to stabilizing selection (Fairbairn 2005). However, bridge spiders show tremendous plasticity in all their developmental parameters (Chapter 1). This seems to be in contrast with the expectation of a canalized female size at maturity.

The integration of high developmental plasticity with an expected rigidity in life history traits and weak or no SSD makes bridge spiders an interesting model organism in which to investigate patterns of life history evolution. We performed feeding experiments to simulate three populations of bridge spiders with different food abundances to test for: (1) the impact of developmental plasticity on three life history traits: size, weight, and age at maturity; (2) sex related differences in these life history traits; and (3) sex specific responses to variable feeding conditions. We predict that Rensch's rule should apply to bridge spiders and we expect to find stabilizing selection on female size. Further, we hypothesize an increasing age at maturity in response to limited food. Stabilizing selection on body size on the costs of age at maturity would reflect the balance between opposing selection for fecundity and viability. We expect a different solution to the trade-off between size and age at maturation for males. These differences between the sexes predict an interaction between sex and feeding regime. Our results will contribute to the discussion on the selective pressures influencing major life history traits in arthropods.

Methods

Study objects

The bridge spider *Larinioides sclopetarius* (Clerck, 1757) (Araneae: Araneidae) is a nocturnal orb-web spider that is very abundant near water in urban habitats. Bridge spider colonies comprise individuals of all developmental stages. We collected spiders in the HafenCity Hamburg, Germany (53°33'N, 09°59'E) close to the River Elbe. Individuals were collected from their webs on bridges and facades in 2006 from May to October and in April, 2007.

The spiders examined herein are the same individuals used in Chapter 1; details on rearing conditions and feeding treatments are provided in that Chapter.

Rearing conditions

Field collected bridge spiders (parent generation) were kept individually in plastic cups (females 400 ml, males 200 ml) and watered five times per week. Females were fed twice a week with 3-5 *Calliphora sp.*; males were fed with 5-10 *Drosophila melanogaster*. After maturation, females were transferred to Perspex frames (36 × 36 × 6 cm) where they built their orb-webs and were mated. After mating, females were returned to plastic cups and treated similar to pre-mating conditions. Plastic cups inhabited by mated females were checked for the presence of egg sacs on five days per week. Egg sacs were weighed and then kept in Perspex boxes (7 × 14.5 × 11.5 cm) under temperatures between 20 to 30 °C. Egg sacs were watered five times per week until they hatched.

Feeding treatments

Ten days after hatching, fifteen full-siblings were randomly separated in three different feeding treatments (high, low, and very low feeding conditions). Hatchlings for feeding experiments were derived from 24 females with 15 maternal lines and are either the F1 generation or the F2 generation of the parent generation that was collected in the field (for details see Chapter 1 appendix Table 9). Spiderlings with high feeding conditions received *Drosophila melanogaster ad libitum*. In the low and very low feeding treatment, food was limited. The first feeding was performed fifteen days after hatching: spiders with low feeding level were fed three *D. melanogaster*, very low feeding level spiders received one *D. melanogaster* per week. With increasing age of spiders until maturation, we adjusted the number of fed *D. melanogaster* every 60 days by a factor of 1.5-2.

Spiderlings were fed twice a week, watered and checked five days per week for the presence of exuviae. Spiders were weighed after each molt (post-molt weight) using an electronic balance (METTLER TOLEDO XS105 DualRange) to an accuracy of 0.01mg.

Of 360 spiderlings in the experiment, 267 reached adulthood. We recorded the size, weight, and age at maturity (i.e. development time) for each spider. Size at maturity was measured after natural death of the spiders by measuring the tibia-patella length (TPL) of the first pair of legs to the nearest 0.01 mm using a LEICA MZ 16 stereomicroscope and LEICA IM500 imaging software (Version 4.0).

Statistical analysis

We used the *REML* (Restricted Maximum Likelihood) method for fitting mixed model *ANOVAs* (Analysis of Variance) to estimate the effects of feeding treatment and sex on the size, age, and weight at maturity. Feeding treatment and sex were fixed factors and family was the random factor. All residuals were normally distributed, except for the age at maturity (see Table 1). Further, the *REML* method was used to test the effects of development time on size and weight at maturity within treatments and sexes. Development time was the fixed factor; family was the random factor. An exclusion of the family effects in all calculated models did not alter results. To test all differences among the least square means in the model we used the *Tukey's HSD* (Honestly Significant Difference) test. The statistical analyses were performed using JMP® 7.0.2 (SAS Institute Inc.) for Microsoft® Windows. For models that are fitted with the *REML* method, JMP® does not calculate *F*-ratios or *p*-values for the random factor family.

Results

Size at maturity

Figure 1 and Table 1 show the relationship between size at maturity, feeding treatments, and sexes. Size at maturity in bridge spiders was significantly influenced by feeding treatment and sex. Bridge spiders under increased feeding conditions were larger than those in other treatments, regardless of their sex. Feeding treatment influenced size at maturity differently in the two sexes as reflected by the significant interaction between sex and treatment. Males attained a larger maximum size with increasing feeding level and reached a higher maximum tibia-patella length. Female size at maturity on average was not influenced by the feeding treatments (Fig. 2).

The distribution of size classes (i.e. separation of size ranges in 11 classes) differed between females and males (Fig. 3). Females that were reared in the high treatment occupied the narrowest range of size classes (size at maturity ranged from 4.5 to 6.0 mm). At low and very low feeding level the number of occupied classes increased; in the very low feeding treatment the range of size classes was widest (size at maturity ranged from 3.5 to 6.25 mm). In male bridge spiders, the occupation of size classes was shifted towards classes for larger sizes with increasing feeding level. The lowest classes were occupied by individuals that were reared under limited feeding conditions (size at maturity ranged from 4.25 to 6.5 mm); the highest classes were only occupied by spiders that had unlimited food (size at maturity ranged from 5.0 to 7.0 mm).

Table 1 Results of *ANOVA* for the effects of feeding level (treatment) and sex on size, weight, and age at maturity of spiderlings ($N = 267$).

		size at maturity		weight at maturity		age at maturity*	
variable	*DF*	*F*	*p*	*F*	*p*	*F*	*p*
treatment	2	10.22	**<0.0001**	61.71	**<0.0001**	1035.92	**<0.0001**
sex	1	50.00	**<0.0001**	293.08	**<0.0001**	59.38	**<0.0001**
sex × treatment	2	10.65	**<0.0001**	2.75	0.0656	11.41	**<0.0001**

* Residuals of age at maturity were not normally distributed. Re-analysis with a *GLMM* and Poisson distribution and a log link function revealed the same results as the *ANOVA*. For simplicity we kept the *ANOVA*.

Weight at maturity

The relationship of weight at maturity with feeding treatments and sexes is shown in Figure 1 with the statistical summary in Table 1. The weight at maturity depended significantly on feeding treatment and sex. There was no significant interaction of sex and treatment for the weight at maturity. Spiders that were reared under high feeding conditions were about 25% heavier than spiders that grew under low or very low feeding conditions. Regardless of feeding level, females were about 40% heavier than males. Average values for the weight at maturity were 60 mg (SE ± 1.42) for females and 38 mg (± 0.84) for males.

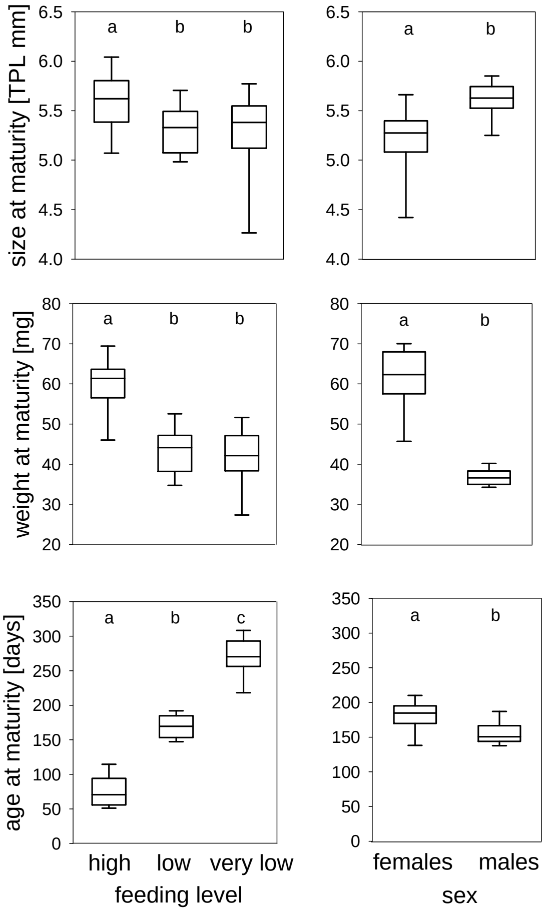

Fig. 1 Box plots for comparison of various life history traits of bridge spiders at different feeding levels (left) and sexes (right). Box plots that are not connected by the same letter are significantly different. Feeding level and sex influence all life history traits examined in this study. All values for siblings within same treatment or sex were averaged.

Age at maturity

The effect of feeding treatment and sex on the age at maturity is shown in Figure 1 and Table 1. Feeding treatment and sex significantly affected the age at maturity. Spiders that were reared under high feeding conditions reached maturity at a younger age than spiders under limited food. On average, spiders at high feeding level needed 71 days (± 2.33) until maturation; under very low feeding conditions, the period from hatching to maturation was extended by a factor of 3.7 (i.e. 269 ± 4.62 days). For females and males, the three feeding treatments significantly influenced the age at maturity (Fig. 2). Males matured on average 26 days earlier than females, however, under high feeding conditions, males and females matured at the same age.

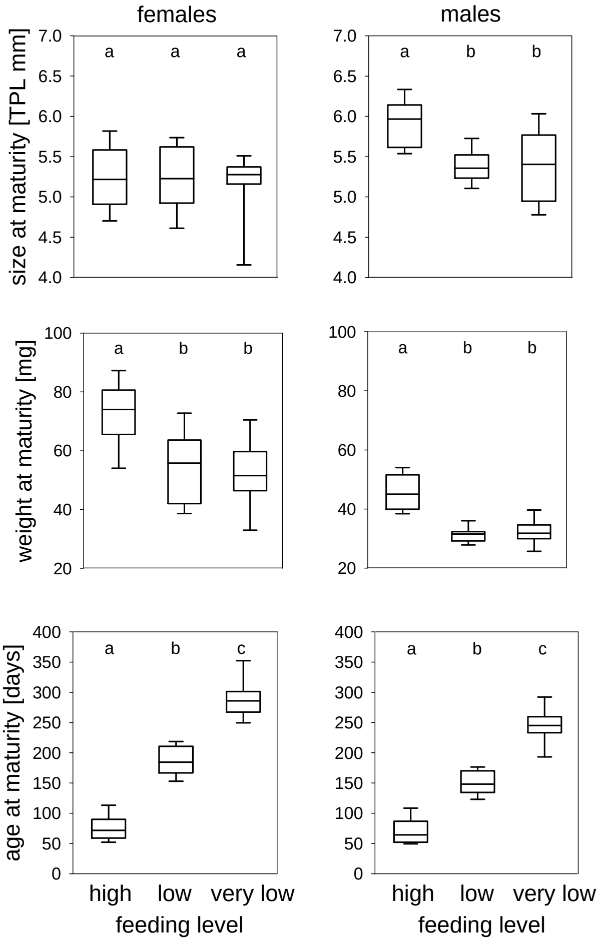

Fig. 2 Box plots for comparison of various life history traits at different feeding levels in female (left) and male (right) bridge spiders. Box plots that are not connected by the same letter are significantly different. Feeding level influence all life history traits examined in this study similarly for both sexes. Only the size at maturity of females is independent on food availability. All values for siblings within same treatment and sex were averaged.

The impact of development time on size and weight at maturity

The size at maturity significantly depended on the development time, except for females under high und males under low feeding conditions (Fig. 4, Table 2). For females on low and females and males on very low feeding level, size was positively correlated with development time. Males on high feeding level showed a negative correlation (Fig. 4).

Development time had a significant impact on the weight at maturity, except in the case of female spiders at high feeding level (Fig 4, Table 2). For females and males under low and very low feeding conditions, the weight at maturity increased with a prolonged development time; males on high feeding level showed a decrease in weight at maturity (Fig. 4).

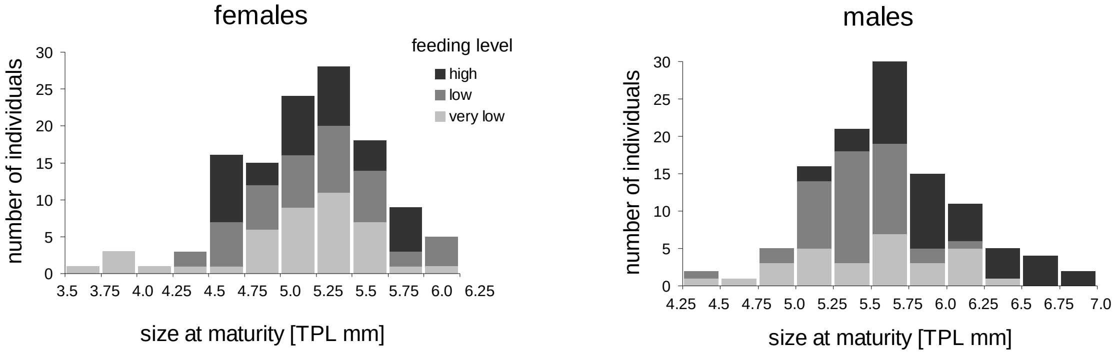

Fig. 3 Distribution of size at maturity (tibia-patella length = TPL) in female (left) and male (right) bridge spiders under varying feeding conditions (high, low, and very low). Females under very low feeding conditions occupy all size classes observed; under high feeding conditions females occupy a narrower range of size classes. Males under varying feeding conditions do not differ in the number of size classes occupied. Small size classes are only occupied by poorly fed males; only males under high feeding conditions attain the largest size classes.

Table 2 Results of *ANOVA* for the effect of age at maturity on size and weight at maturity, and the effect of weight at maturity on size at maturity separated by feeding level (treatment) and sex of spiderlings ($N = 267$).

				females		males	
x	y	feeding level	*DF*	*F*	*p*	*F*	*p*
age at maturity	size at maturity	high	1	0.81	0.3752	10.43	**0.0028**
		low	1	14.38	**0.0005**	0.21	0.6522
		very low	1	35.83	**<0.0001**	15.31	**0.0008**
age at maturity	weight at maturity	high	1	0.46	0.4995	11.68	**0.0020**
		low	1	61.20	**<0.0001**	39.64	**<0.0001**
		very low	1	43.04	**<0.0001**	20.49	**<0.0001**

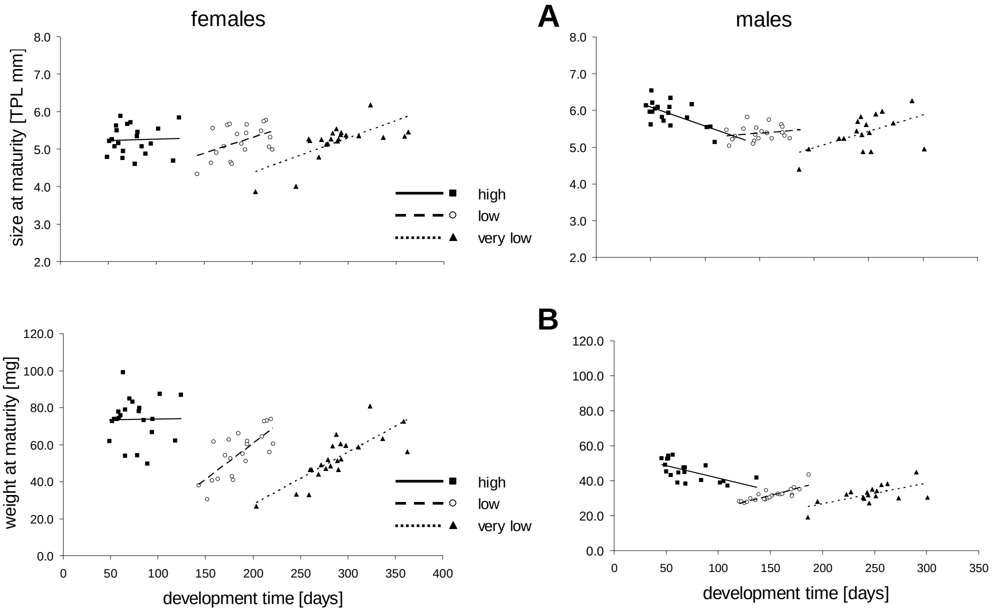

Fig. 4 Regression plots for the impact of development time on size (A) and weight (B) at maturity in female (left) and male (right) bridge spiders. Filled squares and solid line represent high feeding level, open circles and dashed line low feeding level, filled triangles and dotted line very low feeding level. Development time influences weight and size at maturity depending on feeding treatment and sex. All values for siblings within the same treatment and sex were averaged.

Family × treatment interactions

In each family there were three possible strategies in reaction to feeding treatment: first, the values for the life history traits size, weight, or age at maturity decreased with decreasing feeding level (solid line); second, the life history trait increased with decreasing feeding level (dashed line); and third, decrease and increase in the life history trait alternated between feeding levels (dotted line) (Fig. 5).

All three strategies were represented in the size at maturity in females. In four families, females increased their size with decreasing food, five families exhibited the inverse trend, and the other families did both. Males from five families decreased their size with decreasing food; one family showed an increase in size with decreasing food. None of the families showed an increase in weight with reduced feeding condition: either the weight decreased or there was no clear trend for increasing feeding level. This was true for females and males.

In all families, the effect of feeding condition on age at maturity was similar: they show an increase in age at maturity with decreasing feeding level, independent of sex. The number of molts generally increased under limited food in both sexes. Some families showed an alternating response to different feeding conditions.

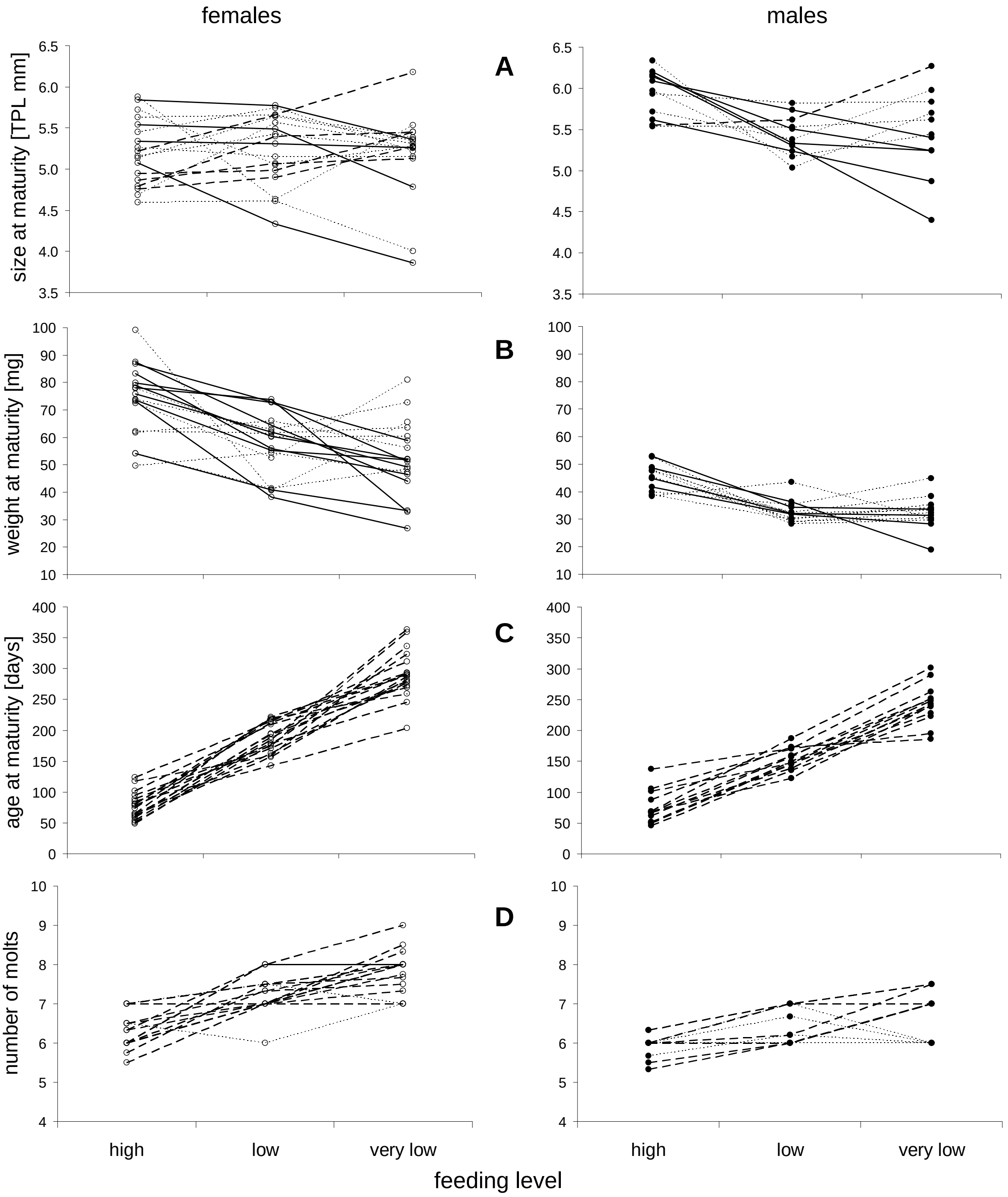

Fig. 5 Genotype by environment interactions for size at maturity (A), weight at maturity (B), age at maturity (C), and the number of molts (D). There are three possible reaction norms for individuals within families (i.e. genotypes) in response to different feeding treatments (i.e. environment): first, the life history trait (size, weight, or age at maturity) decreases with decreasing feeding level (solid line); second, the life history trait increases with decreasing feeding level (dashed line); and third, the life history trait decreases and increases between feeding levels (dotted line). Only genotypes that were represented by at least one individual within each treatment were considered.

Discussion

Our study verified a considerable impact of feeding treatments on major life history traits such as size, weight, and age at maturity of *Larinioides sclopetarius*. Size, weight, and age at maturity differed between male and female bridge spiders but differences in food availability had similar effects on life history traits for males and females, except for the size at maturity in female bridge spiders, which was unaffected by juvenile food availability. In accordance with our predictions we found evidence for stabilizing selection on female size at maturity. Trade-offs between development time (age at maturity) and size as well as weight at maturity were apparent in the food-restricted treatments and females showed a stronger relation (steeper slopes, Fig. 4) between size and weight at maturity over development time than males. We showed that the parentage of *L. sclopetarius* individuals influenced the reaction norm to alternating prey abundances.

Impact of food availability on life history traits

Bridge spiders that were raised under unlimited food availability grew larger and heavier and reached maturity at a younger age than individuals under limited food treatments. Similar results were reported for *Zygiella x-notata* (Araneidae) (Mayntz et al. 2003) and *Pholcus phalangioides* (Pholcidae) (Uhl et al. 2004). However, this pattern is not generally applicable to spiders: in *Lycosa tarantula* (Lycosidae), spiders that were reared with limited food were younger at maturity than individuals at high feeding level (Fernández-Montraveta and Moya-Laraño 2007). We suggest that there are two different strategies in response to limited prey abundances, either by optimizing the size at the expense of development time (*L. sclopetarius, Z. x-notata, P. phalangioides*) or by optimizing development time at the costs of size (*L. tarantula*). Thus, there might be differences in the relative selection strength for body size and timing of maturation that may be related to seasonality. If seasonality influences developmental strategies, we would expect for spiders with a short reproductive seasonal timeframe that selection constraints development time on the expense of size. In *L. sclopetarius*, seasonality and timing of reproduction might be less important for reproductive success than size at maturity.

Sex specific differences in bridge spiders

Weight: Females of *L. sclopetarius* are heavier than males although in Chapter 1 we showed that the growth rate (i.e. the weight gain over instars) shows no significant difference between males and females. The combination of a similar growth rate for the sexes with a longer development time for females inevitably results in females becoming the heavier sex at maturity.

Size: Male *L. sclopetarius* have a larger size (leg length) than females despite the shorter development time. Males are lighter at maturity, and as demonstrated in Chapter 1 pass through fewer instars. However, the male-biased sexual size dimorphism (SSD) in bridge spiders is moderate; the difference between sexes in leg length is about 10%.

Males invest more in body size and shorten developmental time through minimising the number of instars required at maturation. Females invest in weight gain and in size but grow more slowly. These differences follow the general pattern of females' maximising fecundity and males maximising body size. Spider species differ in the components and strength of sexual selection but large male body size is favoured under contest competition and under female choice. Male-male and female-male interactions were not the focus of this paper, however, male-male competition in bridge spiders is repeatedly observed in the field and during mating in the laboratory. It is often observed that several males court a single female (pers. observation). Thus, sexual selection, either by contest competition or female choice, might be a mechanism to increase male body size.

Besides sexual selection, male size is believed to be also a target of natural selection (Blanckenhorn 2000, 2005, Huber 2005). The effect of natural selection on the leg length of male spiders was previously demonstrated for *Argyoneta aquatica* (Cybaeidae). An increased leg length was proposed to increase the mobility of males under water (Schütz and Taborsky 2003). However, underwater locomotion is considerably different from terrestrial locomotion: on land, usually the smaller males are more mobile (Foelix 1996). That natural selection resulted in elongated leg length in male *L. sclopetarius* remains speculative at the moment.

Development time

In *L. sclopetarius*, males were protandrous with a shorter development time than females. Protandry is frequently observed in spiders (LeGrand and Morse 2000, Maklakov et al. 2004, Uhl et al. 2004). In seasonal species, protandry was hypothesized to be advantageous if: (1) females are more abundant early in the season (Andersson 1994), (2) mating occurs immediately after female molting (Robinson and Robinson 1980, Miyashita and Hayashi 1996, Foellmer and Fairbairn 2003), (3) mate-guarding takes place (Fromhage and Schneider 2005, Kuntner et al. 2009), and (4) first male priority occurs (Drengsgaard and Toft 1999). However, bridge spiders are non-seasonal (Chapter 1), and selective pressures for protandry are less obvious. In bridge spiders, receptive females are present throughout the year, due to overlapping generations. Thus, protandry likewise has no or little relevance for competition for females. We assume a connection between the shorter development time and the reduced weight at maturity of males (40% of female weight). Males are suggested to be lighter (and thus faster in development) because they have to allocate fewer resources for sperm production than females do in ova production (Darwin 1874, Andersson 1994).

Blanckenhorn et al. (2007) hypothesized, that differences in growth rate, rather than development time, are generally responsible for SSD. Our results on bridge spiders confirm the hypothesis by Blanckenhorn et al. (2007). Further, Blanckenhorn et al. (2007) showed that SSD in spiders was more related to differences in development time compared to other arthropods. However, in *L. sclopetarius*, the size differences between males and females are independent of differences in development time. On the contrary, although males develop faster, they are larger, in other words the shorter development time is overcompensated by a higher growth rate. The species of the Araneae in the study of Blanckenhorn et al. (2007) all had a female-biased SSD. However, in some arthropod species with male-biased SSD, males showed a tendency to grow faster than females (Blanckenhorn et al. 2007). This is analog to our results for bridge spiders and could be a more general trend for arthropods with male-biased SSD.

Sex specific differences in response to food availability

Female size at maturity is independent of food availability but the range of sizes varied with different prey abundances. In the high feeding treatment, more females reached the average (presumably "optimal") size than under low or very low feeding conditions; the range variation in size at maturity is lower for females with unlimited food. By increasing the development time, females under limited feeding conditions potentially reach the same size on average as females with unlimited food. These results show that high developmental plasticity does not necessarily force life history traits to be variable.

In contrast to females, male size at maturity did depend on the feeding treatment: a rich diet increases male leg length. Based on the assumption that body size in males and females is under different selective pressures (Blanckenhorn 2000, 2005), we suggest for *L. sclopetarius* that natural selection acts to stabilize female body size, while sexual selection acts directional to increase male body size. The comparatively higher variance of male size over female size in bridge spiders is consistent with Rensch's rule (Rensch 1950, Fairbairn 2005). This is surprising, because Rensch's rule was regularly found to not apply to spiders (Foellmer and Moya-Laraño 2007), except for *Lycosa tarantula*, which had female-biased SSD consistent with the rule (Fernández-Montraveta and Moya-Laraño 2007). Our results present the first evidence for Rensch's rule in a spider species with male-biased SSD.

Trade offs and genotype × environment interactions

The well-established life history trade-offs between age and size at maturity, and between age and weight at maturity do not apply for female and male *L. sclopetarius* under unlimited feeding conditions. A decrease in age at maturity is predicted to result in decreasing size and weight at maturity (Roff and Fairbairn 2007). Under unlimited food, however, for female bridge spiders there is no relationship between development time and either size or weight at maturity; in males, size and weight at maturity decrease with increasing age at maturity (Fig. 4).

The discrepancy between these expectations and our results may be due to two reasons: (1) a direct genetic impact on life history traits, and (2) genotype × environment interactions.

This study did not investigate genetic effects: if we separate the data into genetic lineages, the number of replicates is too low for robust statistical analyses on genetic effects. However, a preliminary statistical analysis that included only genetic lineages that were represented by at least three females and three males in each feeding treatment suggested a potential relationship between female, but not male, parentage and size or weight.

Genotype × environment interactions (GEI) describe variable responses to alternating environmental conditions by different genotypes (Falconer 1952, Via and Lande 1985).

There are two opposite patterns of reaction based on two proposed genotypes in *L. sclopetarius* (Fig. 5): (1) decrease of size and weight under limited feeding conditions (genotype I) and (2) increase of size and weight under limited feeding conditions (genotype II). Relative to individuals with genotype I, individuals with genotype II increase their number of molts substantially in favor of larger sizes and greater weights if exposed to decreased prey abundances.

The decrease in male size and weight with increasing age that was observed under unlimited feeding conditions might also be explained by GEI. Genotype I individuals may be optimized for fast development under high prey abundances and reach larger sizes. Males with genotype II will perform better under limited food conditions but worse with rich diet and thus be smaller even after longer development time. In spiders with genotype I, faster growth and thus earlier reproduction, can have a negative genetic correlation with longevity (Blanckenhorn 2000). Natural environments of bridge spiders are very heterogeneous; foraging sites can differ extremely in their quality (Heiling 1999, Schmitt 2004, Schmitt and Nioduschewski 2007a, Schmitt and Nioduschewski 2007b). This may select for some genotypes adapted to lower prey abundances thus avoiding intraspecific competition for high resource localities.

Conclusion

Our feeding experiment distinguished influences of prey abundance on major life history traits, including size, weight, and age at maturity in the bridge spider *L. sclopetarius*. High prey abundance resulted in larger and heavier spiders that reached maturity at a younger age, than spiders under limited food availability. Males and females show similar responses in their life history traits to variable prey availabilities, except in the case of size, where female spiders are canalized. We argue that the size at maturity of female spiders is under stabilizing selection and showed on average no response to different feeding conditions. In contrast, males showed more variability in their size, a pattern consistent with Rensch's rule. The comparison of males and females in our study exposed a male-biased sexual size dimorphism in bridge spiders, although males are the lighter sex with shorter development time. Thus, this makes bridge spiders the first documented case of male-biased SSD in combination with Rensch's rule in spiders. Future analysis of whether Rensch's rule is applicable to spiders should therefore not focus exclusively on species with extreme cases of female-biased SSD but should also include spiders with weak or male-biased SSD.

In addition to sex-related responses to variable environments, we also found genotype × environment interactions (GEI) in *L. sclopetarius*. Based on GEI, we propose the presence of two different life history strategies that are optimized for different environments. Genotypes may differ in their resource allocation: the genotype that will be outcompeted under rich diet could be beneficial under poor diet and *vice versa*. The combination of high phenotypic plasticity with possible variations in genotypes, may allow bridge spiders to be an extremely successful species in heterogeneous environments. However, the adaptive significance of GEI remains to be justified by future studies. Further, the mechanism that underlies GEI needs to be resolved. The integration of experimental life history research with molecular biology to explain different responses to variable environments will potentially reveal new insights in the evolution of life histories.

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Chapter 3

Dietary restriction increases lifetime fecundity and extends lifespan in a spider

Abstract The reproductive success (measured as lifetime fecundity) of an organism is determined by complex interactions of (i) the life history traits size, weight, and age at maturity, (ii) lifespan, and (iii) the respective trade-offs, as a benefit for one trait might entail a cost for another. Depending on environmental factors such as food availability, population density, and temperature, the reaction norm of life history traits will evolve to increase lifetime fecundity. This may result in the evolution of prolonged lifespans under poor feeding conditions. However, the effects of environmental factors likely differ in different life stages, such as developmental and reproductive periods. Thus, to draw a complete picture about the interactions between life history traits and environmental factors, it is essential to examine all periods of an individual's life. Here we investigate the impact of diet (before and after maturation) on lifetime fecundity in a highly developmentally plastic organism – the bridge spider, *Larinioides sclopetarius*. This species is known to respond to variable prey abundances during development by flexibly adapting growth patterns and life history traits at maturity. By changing food regimes after maturation, we demonstrate the absence of interactions between food availability during development and adult life stages. Females that experience low food and a long development are able to catch up to higher number of offspring during their reproductive stage if conditions improve. We show that a rich diet during development and reproduction increases lifetime fecundity and shortens lifespan while egg weight is not affected. This suggests that diet increases offspring quantity but has no effect on offspring quality. Offspring quantity and quality are traded-off as larger clutches contain lighter eggs. Furthermore, we found that egg weight is influenced by whether the egg is fertilized or not. In contrast to well-fed spiders, spiders that experienced a poor diet partly compensate for their delayed development by slowing down senescence and yet they still exhibit a lower lifetime fecundity.

Introduction

Age and size at maturity, number and size of offspring, and the reproductive lifespan and aging are the major life history traits (Stearns 1992). These traits are interrelated to each other and relations between different traits are complex. For example body size and fecundity (i.e. number of offspring) are often positively related (Wickman and Karlsson 1989, Honek 1993, Marshall and Gittleman 1994, Head 1995, Foellmer and Moya-Laraño 2007); whereas reproductive effort has been shown to decrease lifespan (Austad 1989).

Individuals regularly encounter trade-offs among life history traits, because resources that are invested to the benefit of one trait cannot be allocated to another. For example, a well documented trade-off exists between the number (quantity) and size (quality) of offspring. Another fundamental trade-off involves size and age at maturity; individuals that mature earlier are smaller (Roff 1980, Roff 1992).

In addition to these complex relationships between different life history traits, there are even more complex interactions with environmental factors such as temperature, density and food availability. The impact of food availability on the life history of organisms is well studied and can influence size, weight, and age at maturity, number and size of offspring as well as the lifespan itself. The size and weight at maturity of animals may increase with greater food availability and well-fed individuals often mature at a younger age (Roff 1992, Blanckenhorn 1998, Mayntz et al. 2003, Uhl et al. 2004, Marczak and Richardson 2008). Increased food may directly translate into increased numbers of offspring although this is not generally true (Wise 1979, Sota 1985, Parker and Begon 1986, Pékar 2000, Agarwala et al. 2008). Conversely, limited feeding conditions tend to increase the lifespan of animals (Austad 1989, Masoro 2005). The interrelations between life history traits can cause a consecutive reaction: if environmental factors impact one particular trait, other traits are subsequently, but indirectly affected.

Individuals may react differently to environmental factors, depending on their life stage (i.e. growth or reproduction period). Many predators change their range of prey throughout their lives. Larger individuals can handle larger prey items than smaller conspecifics (Enders 1976, Hutchinson et al. 1997). In some extreme cases, the dietary spectrum shifts completely (many holometabolous insects after maturation, Labandeira 1997), or feeding stops after maturation (e.g. mayflies Sternfeld 1907, adult male wasp spiders Foelix 1996). Thus, because of the exploitation of different food resources, the periods of growth and reproduction will be affected differently by prey fluctuations. However, the differential effects of diet on life history traits during different life stages are poorly known.

Orb-web spiders are suitable models to address diet effects on life history traits over life, as they are sit-and-wait predators and thus are directly affected by variation in prey densities (Anderson 1970, Mayntz et al. 2003). Furthermore, some species, such as the bridge spider *Larinioides sclopetarius,* show extraordinary levels of developmental plasticity in response to variable diets (Chapter 1, 2). In this species only the body size of females was canalized, all other life history traits (growth pattern, age and weight at maturity) were highly variable in response to diet (Chapter 2). But how this plasticity and different responses to variation in prey abundance affect lifetime reproductive success and lifespan is not known.

Here we examine the lifetime fecundity and lifespan of female bridge spiders that were reared under laboratory conditions and observed until death. Because adult males do not construct orb-webs and controlled feeding is difficult, we focus on females. We varied the food supply before (i.e. development) and after maturation (i.e. reproduction) to investigate the impact of food availability on reproductive performance and lifespan. For females under high feeding conditions after maturation we predict a higher number of offspring in a shorter reproductive period. Because we previously found no impact of feeding regime on female body size (Chapter 2), we expect female fecundity to be independent on juvenile feeding level. However, based on the observation that development is prolonged under poor diet (Chapter 1), we predict a shorter reproductive period that should result in a decreased fecundity. These contradictive predictions may reflect a trade-off between size and age at maturity, which effects lifetime fecundity under variable environmental conditions.

Methods

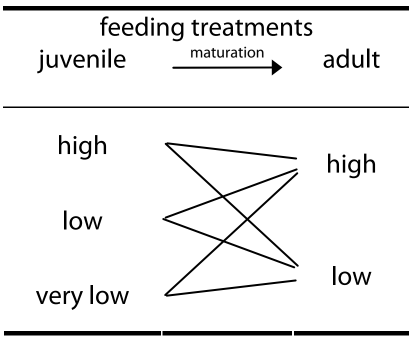
Study objects

The bridge spider *Larinioides sclopetarius* (Clerck, 1757) (Araneae: Araneidae) is a synthropic orb-web spider, which is very abundant near water. The parent generation of the laboratory stock of bridge spiders was collected from bridges and facades in the HafenCity Hamburg, Germany (53°33'N, 09°59'E). Details on origin and maternal lines are presented in Chapter 1. We observed the life of spiders from birth until death under controlled laboratory conditions from August 2006 to November 2008.

Feeding experiment

We followed 119 females throughout their lives. The spiders were reared under three different juvenile feeding conditions (high, low, and very low). For juvenile treatments, 15 spiderlings per egg sac of 24 females were randomly separated in the three feeding treatments 10 days after hatching. They were fed with different amounts of *Drosophila melanogaster* (high – *ad libitum*; low, very low – restricted) until sexual maturation. The juvenile feeding treatments are described in detail in Chapter 1 and 2. Immediately after maturation, each juvenile feeding treatment was randomly divided into two separate adult feeding treatments (high and low feeding level). Adult female spiders were fed with one blowfly (*Calliphora sp.*) daily (high feeding level) or weekly (low feeding level). The spiders were kept individually in plastic cups (400 ml) and watered five days a week.

Table 1 Experimental design for feeding treatments throughout life in bridge spiders.



Mating

Females were transferred to plastic frames (36 × 36 × 6 cm) where they built their orb webs and were mated seven days after maturation. Males were introduced into the web and removed after copulation was observed or after 3 days if copulation did not occur immediately. Fertilization was successful in most cases although 15 spiders laid unfertilized egg sacs. Twelve females died before they produced an egg sac. All female spiders were continuously fed according to their feeding treatments until they died. After mating females were transferred to upturned plastic cups (400 ml), which were visually inspected for the presence of egg sacs five days per week.

Incubation

Newly laid egg sacs were removed from the plastic cups, the dates were noted, and the egg sacs were weighed after the silk was removed. After weighing, the egg sacs were transferred to individual boxes and incubated under different temperatures (in climate chambers at 8, 20, 25, 30, 35°C or in the laboratory under room temperature of 20-25°C). Boxes with egg sacs were watered and inspected for the presence of hatched spiderlings five days per week.

The first day that spiderlings were present was noted as the hatching date. Most of the time, all spiderlings hatched on the same day, however on occasion, we found differences of up to three days in the hatching time of spiderlings from the same egg sac. To ensure that all spiderlings hatched from an egg sac and because handling of second instar spiderlings was easier, we waited approximately ten days and then counted all spiderlings and the remainder (unhatched/unfertilized) eggs.

Data recording

We recorded weight, and age at maturity for each individual (see Chapter 2 for details) and adult size by measuring the tibia-patella length (referred to as 'leg length') of the first pair of legs after the females died. This sclerotized body part does not change in size after the final molt.

After the females matured, we recorded: reproduction time (i.e. the time span from maturation to death), lifetime fecundity (total clutch size), number of egg sacs, fertilization success (i.e. the ratio of fertilized vs. unfertilized eggs within an egg sac), egg weight (i.e. the ratio between the weight of the egg sac and the total number (fertilized and unfertilized) of eggs), and the time interval between clutches including the time from copulation to first egg deposition. Unfertilized eggs were identified beyond doubt by comparison with egg sacs that were built by unmated females. Development time until maturation plus the reproduction time equals the total lifetime.

Statistical analysis

We used the *REML* (Restricted Maximum Likelihood) method for fitting mixed model *ANOVA*s (Analysis of Variance) to estimate the effects of (1) juvenile and adult feeding conditions and (2) size, weight, and age at maturity on female reproduction time, female lifespan, lifetime fecundity, number of egg sacs a female produces, mean weight of eggs from egg sacs with 100% fertilization success, and the mean interval between subsequent depositions of egg sacs. Feeding treatments and the life history traits size, weight, and age at maturity were fixed factors; family IDs were random factors.

We tested the residuals for normal distribution by applying the Shapiro-Wilk test. In cases where the distribution of residuals deviated from normal, we log transformed the data and repeated the test. In only a few cases residuals were non-normally distributed, but after visual inspection we picked the data type (original or log transformed) that was closest to a normal distribution, because it was previously shown that *ANOVA*s are robust to minor deviations from normal distributions at large sample sizes (Sokal and Rohlf 1995). Table 2 shows whether the data were normally distributed and which type of data was used.

For individual pairwise comparisons of least square means in the model we used *Student's t-test*. To test all differences among the least square means we used the *Tukey's HSD test* (Honestly Significant Difference). The statistical analyses were performed using JMP® 7.0.2 (SAS Institute Inc.) for Microsoft® Windows. For models which are fitted with the *REML* method, JMP® does not calculate *F*-ratios or *p*-values for the random factor family.

Results

We detected no significant interactions between juvenile and adult feeding treatment on any of the reproductive parameters or overall lifespan (Table 2) and thus considered both treatments separately.

Table 2 Results of *ANOVA* for the effects of juvenile and adult feeding level (treatment) and life history parameters size, weight, and age at maturity on lifetime fecundity, number of egg sacs, mean interval between egg sacs, egg weight, lifespan, and reproduction time of bridge spiders.

dependent variable	*N*		juvenile treatment (*DF* 2)	adult treatment (*DF* 1)	juvenile × adult treatment (*DF* 2)	*N*		size at maturity (*DF* 1)	weight at maturity (*DF* 1)	age at maturity (*DF* 1)
lifetime fecundity ^{b}	118*	*F*	3.63	26.67	1.50	104*	*F*	8.94	3.81	10.28
		p	**0.0298**	**<0.0001**	0.2286		*p*	**0.0035**	0.0538	**0.0018**
number of egg sacs	118*	*F*	2.24	0.38	0.49	116*	*F*	0.06	0.06	4.01
		p	0.1113	0.5392	0.6119		*p*	0.8020	0.8007	**0.0475**
mean interval between egg sacs $^{a, b}$	105	*F*	1.00	20.00	2.14	103*	*F*	1.92	0.14	1.21
		p	0.3728	**<0.0001**	0.1228		*p*	0.1690	0.7069	0.2735
egg weight $^{a, b}$ (100% fertilized egg sacs)	54	*F*	1.37	2.55	0.85	53	*F*	0.29	0.06	1.63
		p	0.2651	0.1174	0.4356		*p*	0.5914	0.8102	0.2079
lifespan	119	*F*	47.44	20.69	2.13	117	*F*	2.85	0.85	39.70
		p	**<0.0001**	**<0.0001**	0.1245		*p*	0.0941	0.3589	**<0.0001**
reproduction time	119	*F*	8.05	18.63	1.45	117	*F*	2.85	0.85	16.39
		p	**0.0006**	**<0.0001**	0.2390		*p*	0.0941	0.3588	**<0.0001**

* visually normally distributed
a: effects of juvenile and adult treatment on log transformed data
b: effects of life history parameters on log transformed data

Lifetime fecundity

Lifetime fecundity (i.e. the total number of eggs laid during life) depends on the number of clutches and on the numbers of eggs within each of the clutches and varied between 8 and 1,787 eggs. On average females produced 6 (± SE 0.34, range 1-15) egg sacs in their lifetime independent of feeding level. Hence the variation in lifetime fecundity is mainly due to variation in the number of eggs per clutch and not the number of clutches. The number of clutches was influenced only by the age at maturity such that females that developed more slowly produced fewer egg sacs (Fig. 1, Table 2).

Clutch size is directly and positively affected by the juvenile and the adult feeding treatment and is positively related to size and weight at maturity (although the correlation between weight and lifetime fecundity is not significant) (Fig. 2, Table 2). Interestingly, slow growing females had lifetime fecundity costs even though their size at maturity was not different from fast growing females (Chapter 2), suggesting a reproductive cost of decelerated development (Fig. 3, Table 2).

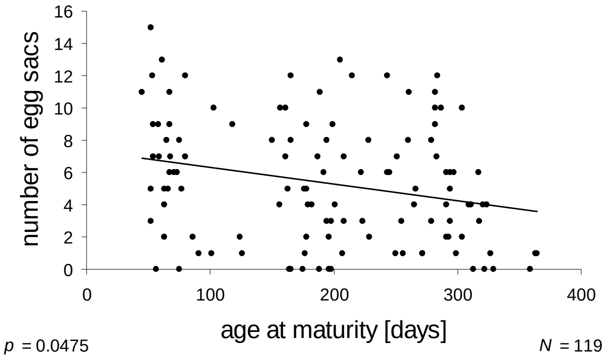


Fig. 1 Relationship of the total number of egg sacs and the age at maturity in bridge spiders. An increased age at maturity increases the number of egg sacs a female produces during life.

Intervals between clutches

The time between consecutive egg sacs varied between 2 and 132 days and was only affected by adult feeding treatment (Table 2). Females in the high feeding treatment had a significantly shorter mean interval between egg sac deposition than females under limited feeding conditions (Fig. 4, Table 2), suggesting that egg production is a direct function of the immediate nutrition.

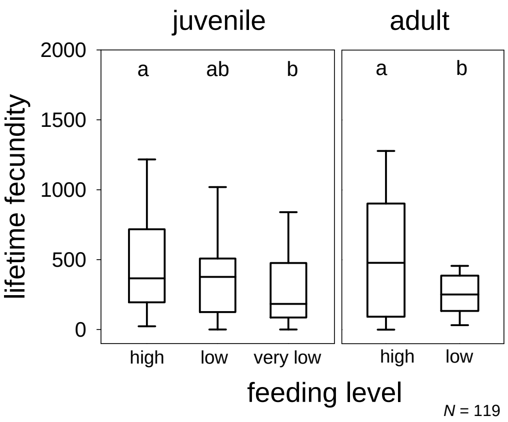


Fig. 2 Box plots for comparison of the effects of different juvenile (left) and adult (right) feeding conditions on lifetime fecundity. Box plots that are not connected by the same letter are significantly different. Food availability during development and reproduction influences lifetime fecundity of female bridge spiders. Limited food results in lower fecundity.

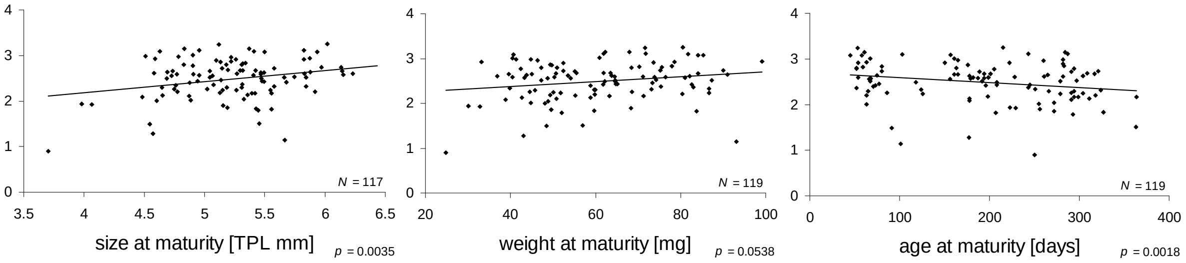


Fig. 3 Relationship of the logarithm of lifetime fecundity and life history parameters size (TPL = tibia-patella length), weight, and age at maturity. Increased size and decreased age at maturity of bridge spiders increase lifetime fecundity significantly. An increased weight at maturity has the tendency to increase lifetime fecundity.

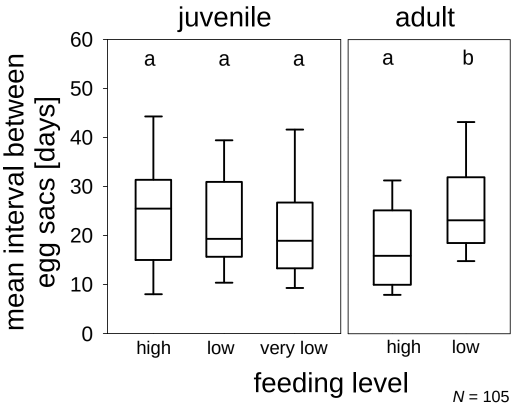


Fig. 4 Box plots for comparison of the mean interval between egg sacs of bridge spiders at different feeding levels during juvenile and adult life. Box plots that are not connected by the same letter are significantly different. Increased feeding condition after maturation decreases the mean interval between successive clutches. The feeding condition during growth has no influence on the interval between egg sacs.

Egg weight and embryonic development

The mean egg weight of a clutch (clutch weight/clutch size) significantly depended on the fertilization success (*ANOVA*, $F_{1,638}$=606.52, p<0.0001). Fertilized eggs had about twice the weight of unfertilized eggs (Fig. 5). Mean weight of fertilized eggs (only egg sacs with 100% fertilization success considered) was significantly and negatively correlated with clutch size (*ANOVA*, $F_{1,127}$=6.60, p<0.0114) (Fig. 6).

The egg weight produced by each female per egg sac was independent of the feeding treatment (juvenile and adult; Fig. 5, Table 2), independent of the size, weight, and age at maturity of the female (Table 2), and did not vary with the order number of egg sacs (Wilcoxon two sample test, $\chi^2_{8,127}$=4.15, p=0.8433).

Depending on the temperature, spiderlings hatched after an embryonic development time of 7.6 to 18.6 days. Embryonic development until hatching was significantly faster for egg sacs that were kept under higher temperatures (Mann-Whitney test, $\chi^2_{4,355}$=255.77, p<0.0001, Table 3). Temperatures of 8 and 35 °C were lethal for embryonic development. Under constant temperature (25 °C) the embryonic development time was not influenced by the egg weight (of egg sacs with 100% fertilized eggs) (*ANOVA*, $F_{1,53}$=1.22, p=0.2737).

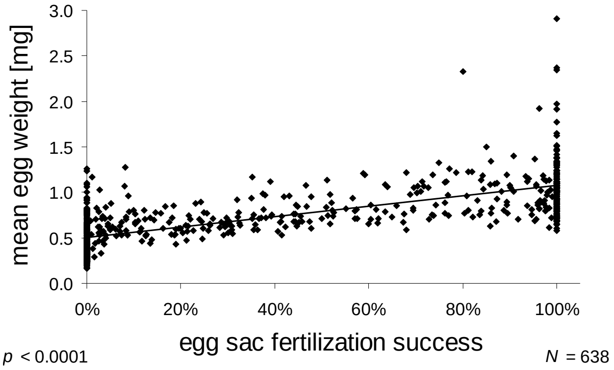


Fig. 5 The impact of egg sac fertilization success on mean egg weight. The mean egg weight within an egg sac increases depending on the number of fertilized eggs.

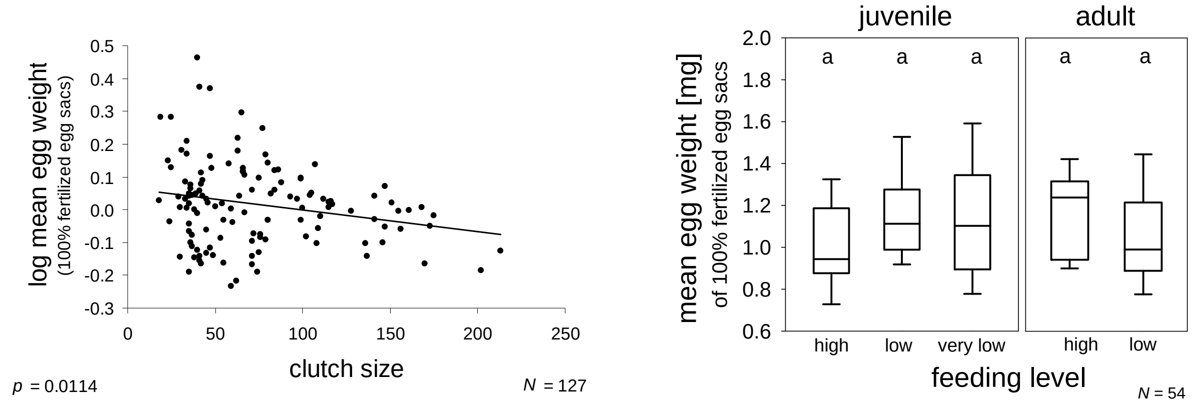


Fig. 6 The relationship of clutch size and log mean egg weight (left) and the effect of different feeding levels (juvenile and adult) on mean egg weight (right). In case a female produces more than one 100% fertilized egg sac, the mean egg weights were averaged for box plots. Box plots that are not connected by the same letter are significantly different. In egg sacs that have 100% fertilized eggs, (1) the mean egg weight within an egg sac decreases with increasing clutch size; (2) the mean egg weight is not under the influence of food availability during life.

Table 3 Influence of egg sac incubation temperature on embryonic development time in bridge spiders (*N* = 355).

incubation temperature [°C]	8	20	25	30	35
mean embryonic development time [days]	-	18.6 ±0.17	11.1 ±0.12	7.6 ±0.18	-

Reproduction time and lifetime

The duration of reproduction time (i.e. the time from maturation to death) depended significantly on the feeding conditions during juvenile growth and after maturation (Table 2). Juvenile and adult feeding treatments had a reciprocal effect on reproduction time: females that were reared under high feeding conditions had a longer reproduction time than females under limited food during development, however, after maturation, increased food availability resulted in shorter reproduction times (Table 2, Fig. 7). Reproduction time is significantly and negatively influenced by the age at maturity but independent of the size and weight at maturity. Females that were older at maturity had a significantly shorter reproduction time (Table 2, Fig. 7).

The total lifetime of female bridge spiders highly depended on the feeding conditions: spiders that had unlimited feeding conditions during development and reproduction (high lifetime feeding conditions) reached a mean age of 240 days; spiders under limited food during development and reproduction died on average 420 days after hatching (Table 2, Fig. 7).

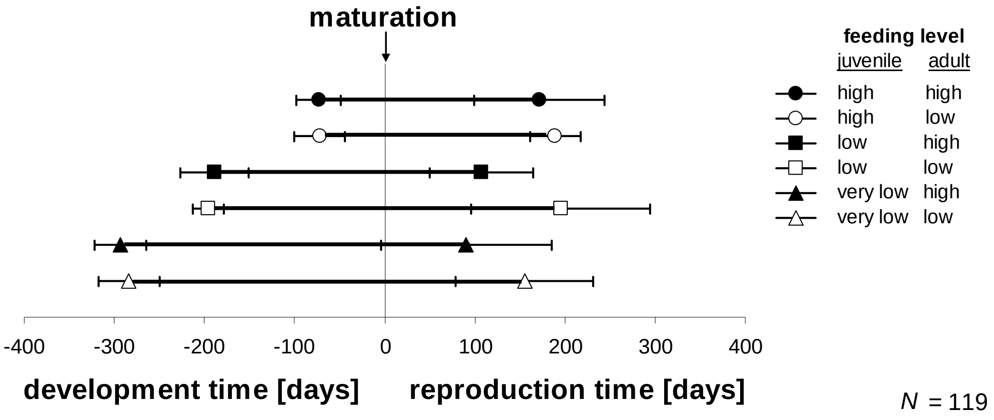


Fig. 7 The impact of feeding levels during development and reproduction on bridge spider lifespan. The time bar is rooted (time = 0 days) at maturation; development time has a negative sign. Lifespan of bridge spiders increases with decreasing food availability. Limited food during development shifts the ratio between development time and reproduction time towards development time, however, limited food after maturation leads to longer reproductions periods.

Discussion

Lifetime fecundity and lifespan of the bridge spider *Larinioides sclopetarius* is under the influence of feeding during growth and reproductive period. Spiders that were exposed to high prey availability throughout their entire life produced four times more offspring despite living half as long as spiders with poor prey availability. However, spiders with limited food throughout their juvenile and adult life partly compensated for the resulting disadvantages in growth and reproductive rates by increasing developmental and reproductive time.

Impact of food availability during developmental period on lifetime fecundity

The impact of food availability during development on lifetime fecundity in bridge spiders is mediated by the effects of different feeding conditions on the life history traits, size and age at maturation (see Chapter 2). However, the nature of the interactions between prey availability during development, fecundity, and life history traits remains cryptic. We assume that the influence of the juvenile feeding treatment on lifetime fecundity is caused by its effects on age, rather than size, at maturity. Among the three life history parameters examined in Chapter 2 feeding condition and lifetime fecundity are only related to age at maturity: females under limited food mature at an older age, which reduces lifetime fecundity. An increase in size at maturity increases the fecundity in female bridge spiders but we found no direct relation between size at maturity and juvenile feeding conditions in Chapter 2. In contrast, the weight at maturity, while significantly correlated to feeding level (Chapter 2) showed no significant link to lifetime fecundity, although we found a tendency for increasing offspring number with increasing female weight.

Our data suggest a life history trade-off in bridge spiders between size and age at maturity with fecundity (Roff 1992, Stearns 1992). Size at maturity is canalized suggesting that bridge spiders optimize their adult size at the cost of a prolonged developmental time (Chapter 2). The positive relation between size at maturity and female fecundity, and the negative relation between age at maturity and fecundity found in this study are in accordance with our previous hypothesis of an optimized female size (Chapter 2). The increase in fecundity of larger females is counterbalanced by a decrease in the number of egg sacs and eggs in spiders that mature at an older age. Thus we present experimental evidence in the bridge spider for the life history trade-off between size and age at maturity, which effects lifetime fecundity (Roff 1992, Stearns 1992).

The trade-off between size and age at maturity was often used to predict the body size of animals (i.e. the equilibrium model for body size, Arak 1988, Schluter et al. 1991, Fairbairn 1997, Blanckenhorn 2000, 2005). For females, the positive effect of size on fecundity is contrasted by the higher risk of mortality over a longer developmental period due to predation, parasitism, and starvation. In our laboratory experiment, extrinsic mortality costs on juvenile bridge spiders were absent implying that the negative effect of age at maturity on lifetime fecundity was caused by intrinsic factors. We suggest that those intrinsic factors were physiological costs that might be related to senescence.

Numerous studies have demonstrated positive effects of female body size on fecundity (Petersen 1950, Kessler 1971, Beck and Connor 1992, Head 1995, Spence et al. 1996, Brown et al. 2003, Hendrickx and Maelfait 2003, Walker et al. 2003, Foellmer and Moya-Laraño 2007). The increase in female fecundity can be due to an increase (1) in the number of eggs per clutch or (2) in the number of clutches. Bridge spiders increase their fecundity through an increase in the number of eggs per clutch because the number of egg sacs is not influenced by the size at maturity. Rather, the number of egg sac a female can produce is limited by the time available for reproduction.

Although a prolonged development time decreases the number of egg sacs, bridge spiders generally produce more clutches (on average 6.0 egg sacs, up to 15) than most other spider species (1-2 clutches, reviewed by Marshall and Gittleman 1994). There are only a few spider species that produce more than three clutches and usually an increased number of clutches is combined with a reduction in clutch size (Marshall and Gittleman 1994). Bridge spiders have a mean clutch size of 76.7 eggs, which fits well into the range of spider species with one or two egg sacs. The American house spider *Parasteatoda tepidariorum* produce an exceptionally high number of clutches (9.7) combined with a comparatively large clutch sizes (186.9 eggs) (Miyashita 1987). Like *L. sclopetarius*, *P. tepidariorum* is a successful cosmopolitan and synanthropic species (Levi 1967) and it can overwinter in juvenile and adult stages (Tanaka 1991). Non-seasonality in bridge and house spiders might be related to their anthropogenic habitats and was previously discussed as a general characteristic of urban species (Chapter 1).

Impact of food availability during reproductive period on lifetime fecundity and egg weight

High prey availability during the reproductive period is directly converted into lifetime fecundity by increasing clutch size and shortening the intervals between clutches. The positive correlation between food availability and reproductive success is a widespread phenomenon in arthropods (Wise 1979, Fritz and Morse 1985, Sota 1985, Pékar 2000, Allard and Yeargan 2005). The increase in clutch sizes and the shortening of intervals between consecutive clutches allows bridge spiders to immediately respond to high prey densities by increasing reproductive output. Trap building spiders frequently encounter variable prey densities and are generally thought of as being food limited (Wise 1979, Mayntz et al. 2003). There is general agreement that the possibility for spiders to respond to high food availability by immediately increasing their reproductive output evolved as an adaptation to temporal fluctuations in prey abundance (Anderson 1970, Wise 1979).

An unexpected result was that the mean egg weight was affected by whether the egg was fertilized or not. What makes fertilized eggs heavier than unfertilized eggs? There might be two reasons for this: (1) cryptic resource allocation of females and (2) processing of eggs after fertilization and deposition. Cryptic resource allocation between copulation and oviposition could be due to an egg provisioning mechanism that is directly coupled to fertilization. Bridge spiders produce egg sacs even when they are un-mated or their sperm reserves are depleted (pers. observation). It is conceivable that spiders with empty sperm stores invest fewer resources in egg sacs than spiders with sufficient sperm. This requires a mechanism for the female to measure sperm in storage and it raises the question why unfertilized clutches are produced to begin with. In addition, cryptic resource allocation can only explains differences between egg sacs that are 0 or 100 percent fertilized, but it cannot explain the gradual weight decrease of egg sacs that are fertilized to a lower degree than 100 percent.

The processing of eggs after fertilization may include chemical modifications that increase the hygroscopic character of fertilized eggs or that prevent fertilized eggs from drying out. Weight differences would then be due to differences in the amount of water. After oviposition, the egg mass hardens (pers. observation, Foelix 1996). In fish eggs, hardening increases the weight of fertilized eggs due to water influx (Lahnsteiner et al. 2001, Lahnsteiner and Patzner 2002). Although the mechanism remains unknown we propose a similar connection between egg hardening and egg weight increase in spiders.

The reproductive allocation patterns of *L. sclopetarius* are clearly shaped by the trade-off between clutch size and egg weight (i.e. between number and size of offspring). This trade-off was also found in the wolf spider *Pirata piraticus* (Lycosidae) (Hendrickx and Maelfait 2003) but not in the wolf spider *Hogna helluo* (Lycosidae), the pholcid spider *Holocnemus pluchei* (Pholcidae), and the crab spider *Misumena vatia* (Thomisidae) (Fritz and Morse 1985, Skow and Jakob 2003, Walker et al. 2003). The decrease in egg weight within larger clutches is independent of the feeding level because egg weights at different feeding levels were not significantly different. This suggests that feeding condition of the female does not affect the quality of eggs but the quantity. Thus, the trade-off between egg weight and egg number cannot be compensated for by larger amounts of food. Kessler (1971) and Wise (1979) also found no influence of the amount of food on egg weight in spiders.

Dietary restriction, lifespan, and fecundity

The effects of feeding conditions on life span and on the relative durations of development and reproduction are complex. High feeding conditions during the entire life of female bridge spiders resulted in a shorter development time and in shorter intervals between clutches after maturation. Reproduction time increased in spiders with high feeding conditions during growth but decreased with high feeding conditions after maturation. Lifespan is shortest in spiders that experienced high prey abundances over the entire life. Bridge spiders with limited food can compensate for temporal factors like intervals between clutches by prolonging lifespan. Thus, they produced the same number of clutches but they cannot increase the number of eggs per clutch.

The extension of life by dietary restriction in animals is a widespread phenomenon (for review see Masoro 2005). There are several hypotheses ranging from growth and metabolism to molecular processes to explain this pattern. However, the underlying biological mechanism for longevity under dietary or caloric restriction is still not known. Among the possible mechanisms that Masoro (2005) discussed, the *retardation of growth hypothesis* (lower growth under caloric restriction) and the *reduction of metabolic rate hypothesis* (lower metabolism under caloric restriction) are best applicable to bridge spiders.

Retardation of growth in *L. sclopetarius* was previously demonstrated in Chapter 1; growth rates under limited food were significantly lower than under unlimited food. The *retardation of growth hypothesis*, however, cannot explain the prolonged lifespan for spiders that grew under *ad libitum* conditions but had limited food after maturation.

Reduction of metabolic rate could slow down senescence in spiders because their metabolism is generally low compared to other ectothermal animals of similar size (Anderson 1970), and spiders can reduce their metabolism at hibernation (Foelix 1996). The low metabolic rates were proposed to be correlated with the periods of starvation frequently encountered by spiders (Anderson 1970). Although measurements of metabolic rates were beyond the scope of this paper, the responses in life history and reproductive parameters to limited food observed in this study and in Chapter 1 and 2, suggest that bridge spiders are able to down regulate their metabolic rates in periods of limited prey abundance.

In this study we investigated the link between longevity and fecundity and we found an inverse relationship between reproduction and survival. Similar results were found in a study on the bowl and doily spider *Frontinella pyramitela* (Austad 1989). In spiders, the costs of longevity are decreased lifetime fecundity and a higher extrinsic mortality risk due to longer development and reproduction time. Consequently, natural selection will favor spiders that increase their food intake at the cost of longevity if that raises fecundity. This might also explain why some spider species gorge food even though this behaviour results in greater mortality (Higgins and Rankin 2001, Marczak and Richardson 2008).

Conclusion

As expected, female *L. sclopetarius* that are exposed to high prey abundances exhibit higher numbers of offspring (many clutches with lots of eggs) during a short lifespan; dietary restrictions slow down senescence and cause an extended lifespan. The increase in reproductive output as response to high prey abundances makes bridge spiders very successful in colonizing new habitats. Surprisingly, the quality of eggs (egg weight) is independent of the feeding conditions females encounter during their lives. Although food availability was found to have no impact on female size (Chapter 2), size at maturity is positively correlated with lifetime fecundity. However, despite having similar size, females that grew under poor diet had lower fecundity and shortened reproductive periods due to longer development, which results in the predicted trade-off between size and age at maturity.

Food availability during developmental and reproductive period affected lifetime fecundity. However, the mechanisms determining how food alters fecundity differ between life stages. Juvenile feeding treatments influenced the reproductive output by changing the life history traits, especially the age at maturity; adult feeding treatment influenced the rate of egg deposition by decreasing intervals between clutches. The effects of feeding treatments on different life history stages can be: (1) equal (e.g. better feeding condition in juveniles and adults will increase fecundity), (2) counteracting (e.g. reproductive time is prolonged if a rich diet is received during development but shortened if it is received after maturation), or (3) one-sided (e.g. intervals between clutches are only affected by adult feeding treatment and not by juvenile feeding treatment). These complex interactions demonstrate the necessity to consider an organism's life stages when examining environmental impacts on life history.

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General discussion

The complexity of life history research

Life history strategies of organisms are very complex; different selection pressures and trade-offs between life history traits act during different life stages (Roff 1992, Stearns 1992). Thus, life stages should be considered separately but also concertedly to identify the extrinsic and intrinsic selection pressures and trade-offs that shaped life histories. The ability to respond to extrinsic factors, such variation in food availability should be expressed in an organism's life history traits and the most suitable models to target are invasive colonizers that rapidly expand into novel environments. The bridge spider *Larinioides sclopetarius* is a very successful colonizer of urban habitats that has the potential to expand exponentially. With bridge spiders as model organism, I investigated how life histories are shaped under varying selection pressures and trade-offs at different stages of life.

Life history strategies of laboratory reared bridge spiders

The first life stage – the developmental period – of bridge spiders is characterized by high developmental plasticity (Chapter 1). All developmental parameters such as the number of instars, the interval between instars, and the growth rate were affected by food availability in males and females. Growth of bridge spiders followed a geometric progression that unlike Dyar's rule (Dyar 1890, Przibram and Megušar 1912) has non-constant growth ratios between successive instars. Poor diet delayed growth by adding additional molts to reach larger sizes at maturity, which causes older ages at maturity (trade-off between age and size at maturity, Chapter 2). Nevertheless, females even aligned their body sizes irrespective of feeding conditions, suggesting that female body size is under stabilizing selection. Males became larger with increased food availability suggesting that their body size is affected by directional selection. The result that female size is canalized while male size showed higher variability is in accordance with Rensch's rule (Rensch 1950, Fairbairn and Preziosi 1994, Fairbairn 1997, Blanckenhorn et al. 2007).

The second life stage – the reproductive period – is characterized by female variability in reproductive output (Chapter 3). Females under rich diet during reproduction were able to produce high numbers of offspring in a short time (short egg sac deposition intervals). The offspring quality (egg weight) was not influenced by food availability but it decreases with increasing clutch size (trade-off between number and size of offspring). Poor diet caused delayed senescence and thus a longer reproductive period but also a decrease in lifetime fecundity.

So how can we combine these results to compare different trade-offs and selection pressures on distinct life stages? Feeding conditions during developmental and reproductive period have an impact on lifetime fecundity. However, there are four possible combinations on how diet influences lifetime fecundity in the experiment presented here. First, a rich diet at both life stages results in high numbers of offspring during a short life and thus the highest lifetime fecundity in the experiment. Second, poor diet throughout life extends lifespan but results in the lowest lifetime fecundity. Third, spiders that grew under poor diet but had unlimited food after maturation, compensated for their slower growth by having short intervals between clutches and by producing relatively high offspring numbers. Fourth, spiders that grew under unlimited feeding conditions but encountered a restricted diet during reproduction had a lifetime fecundity that was almost as low as in spiders with poor diet throughout life.

Although diet during development and reproduction altered lifetime fecundity, the effects of feeding conditions after maturation had a greater impact on reproductive success than diet during growth. Disadvantages caused by food limitations during development were almost compensated for by unlimited food after maturation while in contrast, poor diet during reproduction always resulted in lower fecundity, even in individuals that were well-fed during growth. Despite these unambiguous laboratory results, we have to interpret them according to the natural food environment bridge spiders experience in their natural environment. Thus, the results from this laboratory based thesis can then be applied to interpret the ecological success of *L. sclopetarius* in cities.

The ecological success of bridge spiders

The life history response to diet in bridge spiders is likely to be linked to local conditions in prey abundance. These spiders feed almost exclusively on chironomids that hatch from nearby water. I suggest that the timing of reproduction in bridge spiders in the field will coincide with periods of high prey abundance and thus should overlap with the seasonal emergence of chironomid larvae from water (spring, summer, and fall species, Ziegler 2005). Seasonal mass emergence is a common anti-predation strategy of many prey species (Ims 1990) and predators may have difficulties to adapt their life history traits to such conditions. The enormous flexibility in reproductive allocation and the high tolerance to low food availability, however, enables bridge spiders to survive and flourish under such conditions. While mass emergence events will limit reproduction to single or few peaks per season in a natural environment, illumination of cities provide food at all time by attracting additional insects from surrounding areas (Eisenbeis and Hassel 2000) and thus prolong the season and as a result the spiders become overabundant.

Food availability throughout life directly affected the lifetime fecundity of females and had a direct impact on current resource allocations. This rapid proliferation allows these spiders to become locally dominant in a short time period, which is characteristic for invasive species in general (Richardson et al. 2000, Kolar and Lodge 2001, Colautti and MacIsaac 2004). For example, in plants invasiveness is related to early flowering, high initial growth rate, and high reproductive output (Garcia-Serrano et al. 2005). Although a comparison of plants and spiders is of limited utility, there are some interesting parallels: (i) the young age at maturity in bridge spiders under high food (Chapter 2) is analogous to early flowering in plants, (ii) high initial growth rate in plants is similar to the rapid potential growth in bridge spiders (Chapter 1), and (iii) invasive plants and bridge spiders share a high reproductive output (Chapter 3).

Costs of rapid growth can be an increased mortality risk, which relates to molting problems that other spiders under unlimited food encounter (Higgins and Rankin 2001, Marczak and Richardson 2008). Unlike other spiders, in bridge spiders variation in growth and reproductive allocation did not influence mortality and bridge spider mortality is not increased at high feeding level. Conversely, even under extremely limited food availability, mortality was not affected by the laboratory experiment (Chapter 1) and because of the spatially and temporally limited presence of only a few predators feeding on bridge spiders (e.g. sparrows, tits, pers. observation), I do not expect a high extrinsic mortality in urban habitats. This suggests that life-history plasticity is not limited by intrinsic or extrinsic mortality. Further, bridge spiders can produce offspring also during periods of food limitation (Chapter 3).

With high food availability, female bridge spiders can produce up to 15 clutches per lifetime (Chapter 3). The production of several clutches (iteroparity) rather than investing in a single or few reproductive events (semelparity) is expected when adult mortality is low (Young 1990, Stearns 1992), a prediction that is supported by this study on *L. sclopetarius*. Indeed, the reproductive period of the bridge spider can exceed its developmental time (Chapter 3). Unlike most other spiders, including the coexisting species *Zygiella x-notata*, which produce maximally three clutches (Marshall and Gittleman 1994, Wherry and Elwood 2009) or species in which only one cocoon is laid (Fritz and Morse 1985, Beck and Connor 1992, Schneider and Lubin 1997, Salomon et al. 2005), *L. sclopetarius* immediately converts resources into eggs over an extended time period and will not only adapt clutch size to current conditions but can also modify intervals between clutches. The consecutive deposition of clutches in bridge spiders allows for rapid adjustment of reproductive effort to current prey availabilities throughout the year.

Bridge spiders do not show pronounced seasonality as all life stages are present throughout the year including mature males and females (except for egg sacs that do not overwinter) (Nioduschewski and Kraayvanger 2005, Schmitt and Nioduschewski 2007) The almost perpetual presence of spiderlings and egg sacs of bridge spiders is relevant for pest control in urban habitats, because cleaning of artificial facilities will only have a short term effect on their population densities.

The high population densities that bridge spiders can achieve and that resulted in their reputation as pest in cities with waterfronts are also favored by an unusual tolerance between conspecifics. Bridge spiders were previously considered parasocial (Schmitt 2004, Nioduschewski and Kraayvanger 2005), because they aggregate in loose communities with shared usage of retreats (Foelix 1996). The tolerance and reduced territoriality of bridge spiders likely result from the high resource availability (prey, space, retreats) in urban habitats.

Conclusion and outlook

Herein, I demonstrated a remarkably high flexibility in life history traits of bridge spiders at different life stages. Except for female size at maturity and offspring size (egg weight), all parameters that define a spider lifecycle are influenced by variable diet regimes. I suggested that bridge spiders are adapted to extreme fluctuations in prey abundance as is characteristic for mass emerging insects in their natural environment. In this study I did not simulate such extreme fluctuations but kept food availability constant within the two life stages (development and reproduction), but at different levels (high and low). Hence, conclusions about the adaptive significance of developmental and reproductive plasticity are only indirect. Further experiments on life histories under variable environmental factors should also alter diet within life stages, for example by varying developmental food supply after molts or by changing food amount at reproduction after the deposition of the first clutch.

To conclude on the conditions that spiders encounter in urban habitats it will be important for future studies to compare the life history traits of the laboratory reared spiders with spiders in the field. Differences in life history traits between field and laboratory populations could be due to differences in food quantity but also quality. Field experiments should thus also determine prey densities and prey composition. Further, the impact of food quality should also be assessed by an experiment that alters the nutritional intake at identical prey amounts (Toft and Wise 1999, Mayntz et al. 2003, Rickers et al. 2006, Wilder and Rypstra 2008, Kolss et al. 2009).

Bridge spiders are successful in invading urban habitats because they can exploit artificial structures (bridges, facades, artificial light sources) and high insect abundances that are attracted by light at night. However, there is a lack of data on rural (non-urban) bridge spider populations. A comparison between life histories of urban and rural bridge spider populations will enhance our knowledge on the characteristics of species that have the potential to become invasive in urban habitats and thus will contribute to our current understanding of urban ecology.

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