2005. The Journal of Arachnology 33:334–346

# GENDER SPECIFIC DIFFERENCES IN ACTIVITY AND HOME RANGE REFLECT MORPHOLOGICAL DIMORPHISM IN WOLF SPIDERS (ARANEAE, LYCOSIDAE)

**Volker W. Framenau**[1]: Department of Zoology, The University of Melbourne, Parkville, Victoria, 3010, Australia. E-mail: volker.framenau@museum.wa.gov.au

**ABSTRACT.** Sexual dimorphism of locomotory organs appears to be common in a variety of arthropods, however, the underlying evolutionary mechanisms remain poorly understood and may be the consequence of natural or sexual selection, or a combination of both. I analyzed the activity pattern of seven cohorts of a wolf spider, *Venatrix lapidosa,* over four consecutive years. Males appear to be the more active sex in search for a mate as they show temporarily higher activity prior to the periods of female brood care. Morphometric data on leg length showed comparatively longer legs for males than females. Allometric leg elongation in all four legs of males arises only after the final molt suggesting its significance in reproductive behavior such as mate search. A comparative analysis of two Australasian wolf spider genera with different activity profile of females, *Venatrix* (sedentary females) and *Artoria* (vagrant females) provides further evidence that limb elongation in males mainly arises due to indirect male mate competition.

**Keywords:** Sexual dimorphism, locomotion, leg length, mark and recapture, minimum convex polygon

Sexual dimorphism is thought to have evolved through sexual selection, ecological niche partitioning, differences in reproductive roles or a combination of these factors (e.g., Selander 1972; Hedrick & Temeles 1989; Shine 1989; Reynolds & Harvey 1994; Fairbairn 1997). Sexual selection arises through competition between members of one sex for reproduction with the other sex (Andersson 1994). Ecological niche partitioning may result in sexual dimorphism if each sex develops different structures as adaptations to different resources (Shine 1989; Walker & Rypstra 2001). Different reproductive success primarily arises through a fecundity advantage of large body size in females and is particularly evident in insects and spiders in which a common finding is that, throughout a wide range of sizes, female fecundity varies directly with mass (e.g., Head 1995; Prenter et al. 1999). Selection for early maturation of males (protandry) may also favor smaller male body size and thus result in sexual dimorphism (Bulmer 1983; Gunnarsson & Johnsson 1990). These explanations are not mutually exclusive and thus sexual dimorphism could evolve in a species through both sexual and natural selection. Therefore, it is often difficult to determine what mix of influences has resulted in sexual dimorphism in a particular species (Hedrick & Temeles 1989).

The difficulty of identifying selective pressures is especially evident in the sexual dimorphism of locomotory structures, like wings or legs, which is a common phenomenon in many arthropods (Montgomery 1910; Thornhill & Alcock 1983). The evolution of gender specific differences in locomotory organs may be favored by both selection on male mate searching behavior and natural selection on female movements in relation to foraging or oviposition. Therefore, sexual dimorphism of locomotory structures has generally not been considered in studies of sexual selection (Darwin 1871; Andersson 1994). Gender specific differences in locomotory structures have usually been attributed to a more active behavior of one sex, typically males, in search for mates (Thornhill & Alcock 1983; Gasnier et al. 2002). Higher mobility may increase encounter rates of males with females and therefore increase fertilization success. However, gender specific elongation of limbs, even if under the influence of

---

[1] **Current address:** Department of Terrestrial Invertebrates, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia

sexual selection, may not indicate an advantage in locomotion. Male elongated legs are important for direct male competition for mates in water striders (Tseng & Rowe 1999) and megalopodine beetles (Eberhard & Marin 1996), in grasping females during mating in mayflies or calanoid copepods (Peters & Campbell 1991; Ohtsuka & Huys 2001), in newt courtship displays (Malmgren & Thollesson 2001) and to reduce the risk of sexual cannibalism in some orb-web spiders (Elgar et al. 1990). In cursorial spiders, elongated segments of legs, in particular the first pair, have also been reported in combination with ornamentations in species with visual courtship display (Kronestedt 1990; Hebets & Uetz 2000). Therefore, it is vital to correlate activity and mobility patterns with sexual dimorphism of leg length to provide evidence of sexual selection acting on locomotion itself.

Sexual dimorphism in spiders has been studied extensively, however, the evolution of sexual size dimorphism remains controversial (e.g., Elgar 1991; Vollrath & Parker 1992; Head 1995; Hormiga et al. 1995). There are two main explanations for patterns of sexual size dimorphism in spiders (see Elgar 1998). Firstly, fecundity selection may favor larger females (Prenter et al. 1997, 1998, 1999). Alternatively, Vollrath & Parker (1992) suggest that sexual dimorphism may arise from differences in male and female lifestyles. In species with sedentary females, an increase in male mortality through mate searching behavior relaxes selection for large male body size and thus selection for protandry will favor smaller males. Ground living spiders are generally less size dimorphic than web-building species, which has been explained by their differing reproductive and foraging strategies (Enders 1976; Prenter et al. 1999). There is some evidence for sexual dimorphism in locomotory structures in ground living spiders (e.g., Gasnier et al. 2002). Montgomery (1910) reported that males have relatively longer legs than females, which he suggested is a result of the nomadic behavior of males after attaining sexual maturity. This idea is supported by a number of short term studies on the locomotory activity of wolf spiders, in which males were the more active sex (e.g., Hallander 1967; Richter et al. 1971; Cady 1984; Framenau et al. 1996a). However, wolf spiders differ in activity profiles due to varying life strategies that range from permanently burrowing (e.g., *Geolycosa* or *Lycosa* s. str.), to permanently vagrant animals (e.g., *Pardosa* and *Pirata*; e.g., Dondale & Redner 1990). These different lifestyles are reflected in mechanics of locomotion and activity response to variation in food supply (Ward & Humphries 1981; Walker & Rypstra 2001). Therefore, it is important to analyze sexual dimorphism in locomotory organs in conjunction with data on the general activity pattern over an adult spider's life span.

The goal of this study was to relate the activity profile of males and females of a cursorial wolf spider, *Venatrix lapidosa* (McKay 1974), to gender specific differences in the morphology of their locomotory organs. The activity profile of these spiders was generated by conducting a fortnightly mark and recapture survey over a period of more than three years, covering seven generations of adult spiders. This allowed an analysis of both the variation of spider activity over their entire adult life, and incorporated seasonal variation, thus contrasting with all previous studies of wolf spiders that typically observed individuals for only up to a day (Richter et al. 1971; Cady 1984). I was not only interested in each individual's activity (i.e. movement per unit time), but also the spatial aspect of movement (home range). Increases of both variables have the potential to augment fertilization success of males by increasing their encounter rates with females. However, these variables may not co-vary and higher activity may not necessarily increase home range size. Differential spatial use by males and females, as inferred from their home range, may also influence the operational sex ratio, thereby affecting the potential for male-male competition. Lastly, I analyzed locomotory structures of two Australasian genera of wolf spiders, *Venatrix* and *Artoria*, with different activity profiles of females to determine if differences in behavior are reflected in leg length dimorphism across a higher taxonomic level.

## METHODS

**Study species.**—*Venatrix lapidosa* is a nocturnal wolf spider inhabiting riparian gravel banks in southeastern Australia (McKay 1974; Framenau & Vink 2001). It is a vagrant species, but brood caring females, and all spiders during overwintering, dig excavations

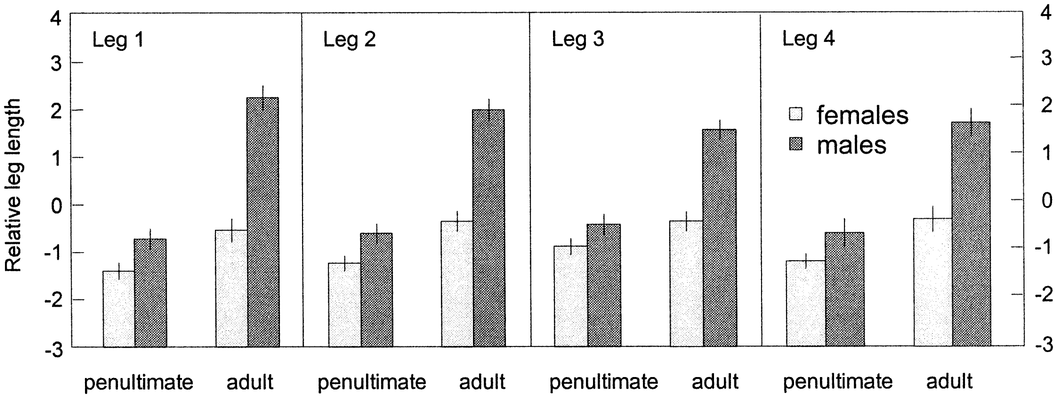

Figure 1.—Relative leg length (residuals of leg length on cephalothorax width) (mean ± s.e.) of female and male penultimate and adult *Venatrix lapidosa*. For statistical analysis (ANOVA) see Table 1.

under rocks that they line with a thin layer of silk (Framenau 1998, 2002a). *Venatrix lapidosa* is biennial, with juvenile development requiring up to 16 months. Adult life span of females may be up to eleven months and that of males up to ten months (this study; also Framenau & Elgar 2005). However, the average life span of adults of both sexes does not generally exceed 6 months. The life cycle of *V. lapidosa* in the Victorian Alps is characterized by the maturation of two distinct cohorts within each year (Framenau & Elgar 2005). In autumn maturing cohorts, most individuals mature between March and May, enter winter diapause, reproduce only after overwintering and die by December. In spring maturing cohorts, spiders molt to maturity between November and January, reproduce immediately and most spiders die by May. Overlap between adult individuals of both cohorts is minimal and generally limited to a low number of long-lived individuals that reach the maturation period of the following cohort. Laboratory-reared males and females of different cohorts readily mate (Cutler 2002) and this overlap permits gene flow between the different cohorts. Winter covers a large period of the adult life span of autumn maturing spiders, whereas adult individuals of the spring maturing cohorts live over summer, so cohorts were expected to differ considerably in their activity profile.

**Morphology of *V. lapidosa*.**—I collected adult (9 females, 15 males) and penultimate (15 females, 12 males) *V. lapidosa* from a variety of populations at ten rivers in seven major catchments during a survey of riparian gravel banks in the Victorian Alps between November 1999 and January 2000 (Framenau et al. 2002). Leg length (sum of all segments measured dorsally) of all four pairs of legs was determined under a stereomicroscope to the nearest 0.1 mm. Carapace width was measured above the coxae of the second pair of legs as an indicator of spider size (Hagstrum 1971; Jakob et al. 1996). I included penultimate spiders in the analysis to establish if an allometric increase in leg length occurs during the last molt, potentially indicating the importance of dimorphism for mature, sexually active spiders. Younger than penultimate spiders were not used as it was impossible to establish their sex. Gender specific differences in leg length were analyzed using the residuals of a least squares regression using leg length on cephalothorax width over both sexes and adult and penultimate spiders. This gives rise to measures of relative leg length, which were independent of body size. Residuals between the sexes and adult and penultimate spiders were compared by two-way ANOVA.

**Mark and Recapture.**—The mark and recapture study of *V. lapidosa* was conducted on a gravel bank at the Avon River near Valencia Creek in Victoria, southeastern Australia (37°48′S, 146°27′E). The climate of the region is moderate with mean daily maximum and minimum temperatures of 20.0 °C and 8.0 °C, respectively. Annual rainfall averages 594 mm (Data from Maffra Forestry Office; Bureau of Meteorology, Melbourne). The gravel bank studied was bordered by the Avon River

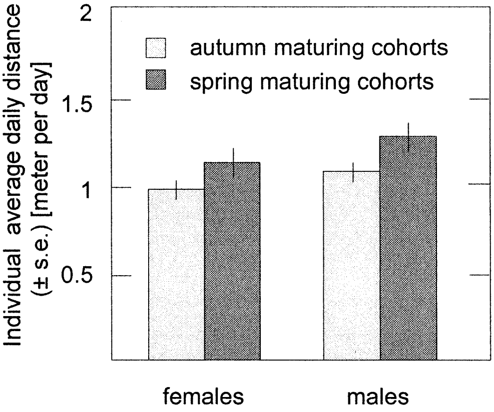

Figure 2.—Individual average daily distances (meters per day; mean ± s.e.) of female and male *Venatrix lapidosa* from the autumn and spring maturing cohorts at the Avon River. Average daily distance moved based on two-week interfix intervals. To determine individual average daily distances, all average daily distances measured during the life span of one individual were averaged.

on the southern side and a dense cover of vegetation (wattle, *Acacia trilobata*, willow, *Salix* sp. and blackberry, *Bromus* sp.) on a steep slope on the northern side, keeping spider immigration and emigration minimal. With the exception of a few *Acacia* and *Salix* shrubs, the gravel bank was bare of vegetation. When the survey commenced in 1996, the surface area of the bank was 1,830 $m^2$. In August 1998, it diminished in size to 1,540 $m^2$ due to a severe flood.

A 5 m × 5 m grid was established on the gravel bank using wooden pegs. One co-ordinate of this grid (‘Y’-value) was perpendicular to the river and therefore expressed the relative distance from the water. Surveys were conducted fortnightly, from 8 November 1996 to 2 May 2000. This observation period covered four spring maturing cohorts (1996–1999) and three autumn maturing cohorts (1997–1999) (Table 2). All rocks large enough to provide shelter for spiders were overturned and replaced. Each survey started randomly at either end of the gravel bank. Each grid was examined in a spiral from exterior to interior, in order to prevent spiders from leaving a grid while it was searched. Spider locations were determined to within an accuracy of 1 m. New adult spiders in the population were individually marked with a bee tag glued to their cephalothorax using a cyane-acrylate based adhesive (Supaglue Gel™). Cephalothorax width and body length were determined with vernier callipers to the nearest 0.1 mm. When returned, most spiders either remained without any movement under the same rock, or found shelter under the next available rock. Initial disturbance was therefore considered minimal. On subsequent encounters, only a spider’s position was recorded to avoid further disturbance.

Activity was determined using the average daily distance (‘velocity’ in Samietz & Berger 1997), which is defined as the distance between two consecutive fixes divided by the days between both observations. Not all spiders were recaptured every survey and average daily distances significantly decreased with the time lapsed between two consecutive fixes (two-, four-, six-, eight-weekly interfix intervals; $R^2 = 0.072$, $P < 0.001$, $n = 2{,}706$). Thus, only average daily distances based on recaptures within two weeks of a previous one were considered in the analysis. In addition, these shorter intervals provided the most accurate picture of a spider’s movement. I compared individual activity of males and females (‘individual average daily distance’) and autumn and spring maturing cohorts by their mean average daily distances over the whole observation period. To analyze seasonal variability of activity, average daily distances were also determined for each month of the year pooled over all individuals of each sex but analyzed separately for autumn and spring maturing cohorts. In this case, the average daily distance was obtained by analyzing captures within two consecutive months were assigned to the month that contained most days of the interfix interval. I pooled monthly data over all years after establishing that there was no between year variation.

**Home range.**—I estimated home ranges using 100% minimum convex polygons (MCP; Mohr 1947). For low capture numbers, MCPs increase with each additional fix until a stable home range is reached. Regression analysis identified nine as the minimum number of captures from which an increase in fixes did not result in a further, significant increase in home range size ($R^2 = 0.008$, $P = 0.397$, $n = 91$). Increment analysis of home ranges (Kenward & Hodder 1996) showed that nine fixes provided an average of 90% of the full home range. This conforms to results of Samietz & Berger (1997), who show that home ranges (100% MCP) for insects appear to be stable from 10 captures. Two-week observation periods guaranteed temporal independence of subsequent fixes, which is assumed if an animal can cross its home range within this period (White & Garrott 1990). As a measurement of home range shape, I calculated the range span as the distance of the furthest two points in a home range. Range centers were calculated as the mean of the X- and Y-values, corresponding to the established grid, of all fixes in a home range. Only one range in the spring maturing cohorts was based on more than eight fixes (Table 2). Therefore, between cohort analysis of home range size and range span was not possible.

Home range overlap was calculated for pairs of spiders that belonged to the same cohort and so could potentially meet. Two values of home range overlap could be determined for each pair of spiders, i.e. how much of the home range of spider A was overlapped by the range of spider B, and vice versa. I used the average of both values as the measurement of range overlap.

**Comparative morphology.**—The taxonomy of only two Australasian wolf spider genera, *Venatrix* Roewer (Framenau & Vink 2001; 23 species) and *Artoria* Thorell (Framenau 2002b; 11 species) is known sufficiently to allow interspecific comparative analyses. Both genera differ considerably in their mobility pattern, as most females of *Venatrix* dig permanent burrows or construct temporary excavations during brood care, whereas females of *Artoria* are vagrant throughout their life (Framenau 2002b; also pers. obs). Least squares regression of leg length on cephalothorax width for all pairs of legs over all species derived from the primary taxonomic literature of both genera (Framenau & Vink 2001; Framenau 2002b) provided measures of relative leg length (residuals) compared to a 'typical' lycosid. To test for sexual dimorphism within both genera, these residuals were compared between the sexes using two-sample t-tests.

**Statistical analysis.**—Home range and activity parameters were calculated using the software package 'RANGES V' (Kenward & Hodder 1996). Subsequent statistical analyses were performed with 'SYSTAT Version 9′ (SPSS Corp. 1998). Data that did not comply with ANOVA assumptions were log-transformed, in case of average daily distances (log +1)-transformed (Quinn & Keough 2002). If normality of data could not be achieved, nonparametric tests (Mann-Whitney U Test) were used to compare sexes. Measurements are given as mean ± standard error (s.e.) unless otherwise indicated. Voucher specimens of *V. lapidosa* were deposited at the Museum Victoria, Melbourne, and the Western Australian Museum, Perth.

## RESULTS

**Morphology of *V. lapidosa*.**—The carapace width (± s.e.) of adult female *V. lapidosa* (6.66 ± 0.18 mm, $n = 9$) was significantly larger than that of males (5.91 ± 0.06 mm, $n = 15$; separate t = 4.019, d.f. = 10.2, $P = 0.002$). The length of all legs was positively correlated with cephalothorax width and residuals of these regressions yielded measures of relative leg length (Table 1). All legs were comparatively longer in males than in females for adult and penultimate spiders (Table 1, Fig. 1). A significant interaction between age and sex for all legs indicates a proportionally higher elongation (allometric growth) for male legs during their last molt compared with females (Fig. 1).

**Mark and recapture survey.**—A total of 741 males and 712 females were individually marked over a period of 3.5 years, yielding an overall even sex ratio ($\chi^2 = 0.802$, $P = 0.37$) (Table 2). However, recapture rates, i.e. how often individual spiders were caught, differed significantly for males and females (Mann-Whitney U = 314226.5, $P = 0.008$) due to a higher number of males encountered only once. The total number of fixes analyzed was 4,963 yielding a detailed life cycle profile for each cohort in each year (see Framenau & Elgar 2005).

**Activity.**—Mean average daily distances of individual spiders, based on two-week interfix intervals, were significantly higher for males than females, and higher for individuals of the spring mating cohorts than of the autumn maturing cohorts (two-way ANOVA; sex: $F_{1,699} = 6.045$, $P = 0.014$; cohort: $F_{1,699} = 4.816$, $P = 0.029$; interaction: $F_{1,699} = 0{,}384$, $P = 0.536$) (Fig. 2).

Monthly average daily distances in the autumn cohort showed no significant difference between sexes (two-way ANOVA; $F_{1,1186} =$

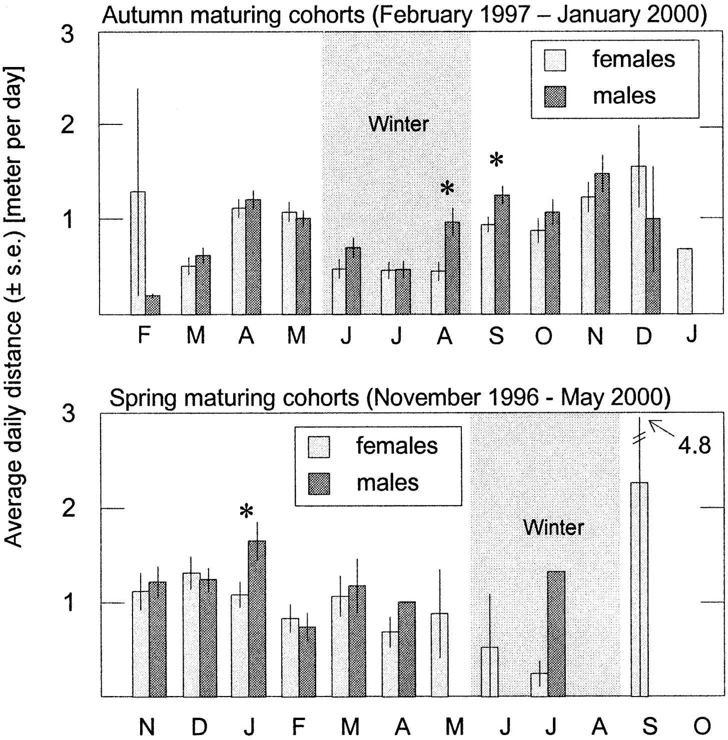

Figure 3.—Monthly average daily distances (meters per day; mean ± s.e.) of female and male *Venatrix lapidosa* from the autumn and spring maturing cohorts during the survey at the Avon River. The month on the far left in each graph represents the maturation of each cohort. Average daily distance moved is based on two-week interfix intervals. To determine monthly average daily distances, all average daily distances within a month were averaged over all individuals. Asterisk (*) indicates significant difference between sexes.

0.087, $P = 0.769$), however, there were significant differences between months ($F_{10,1186} = 7.908$, $P < 0.001$; interaction: $F_{10,1186} = 1.055$, $P = 0.394$; January excluded due to missing variation between sexes; Fig. 3). In the spring cohort, there was also no overall gender specific difference in monthly average daily distances (two-way ANOVA; $F_{1,389} = 1.514$, $P = 0.219$) and, in contrast to the autumn cohort, there was no differences between months ($F_{5,389} = 2.188$, $P = 0.055$; interaction: $F_{5,389} = 0.892$, $P = 0.486$; May–October excluded due to missing variance in sex or months; Fig. 3). However, a within months comparison of average daily distances between males and females revealed significantly higher male activity in August (pooled t = 3.048, d.f. = 28, $P = 0.005$) and September (pooled t = 2.199,

Table 1.—Comparison of relative leg length (residuals of leg length on carapace width) between male and female and adult and penultimate *Venatrix lapidosa*. Regression of leg length on carapace width: Leg 1: $R^2 = 0.543$, slope = 2.978, $P < 0.001$, $n = 51$; leg 2: $R^2 = 0.608$, slope = 2.972, $P < 0.001$, $n = 51$; leg 3: $R^2 = 0.689$, slope = 2.909, $P < 0.001$, $n = 51$; leg 4: $R^2 = 0.672$, slope = 3.457, $P < 0.001$, $n = 51$. Given are the $F_{1,47}$-values and significance level (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) of a two-way ANOVA.

| Factor | Leg 1 | Leg 2 | Leg 3 | Leg 4 |
|---|---|---|---|---|
| Sex | 60.918*** | 55.644*** | 35.171*** | 26.328*** |
| Age | 74.322*** | 76.209*** | 39.534*** | 39.378*** |
| Interaction: Sex * Age | 22.746*** | 18.380*** | 13.416** | 7.923** |

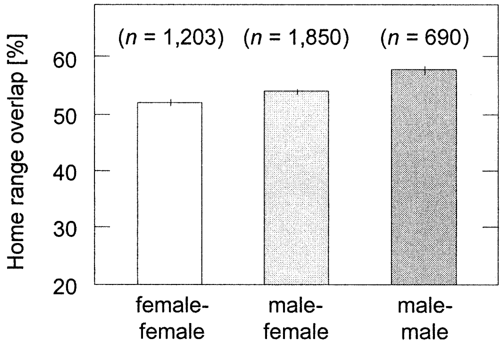

Figure 4.—Intra- and intersexual home range overlap (mean ± s.e.) in *Venatrix lapidosa* within the 1997 autumn maturing cohort. No other cohort provided a sufficient number of home range estimates to compare between and within sexes (see Table 1).

d.f. = 221, $P = 0.029$) for the autumn cohort and in January (pooled t = 2.673, d.f. = 120, $P = 0.026$) for the spring cohort (Fig. 3).

**Home range.**—Due to the major flood in 1998, home range overlap analysis was restricted to the autumn 1997 cohort when males and females were caught in sufficient numbers (minimum of nine fixes) to allow a comparison between the sexes (Table 2). Therefore, a comparison between cohorts was not possible. Home range estimates (100% MCP ± s.e.) did not differ significantly between males (302 ± 16 $m^2$, $n = 42$) and females (311 ± 17 $m^2$, $n = 49$; pooled t = 0.375, d.f. = 89; $P = 0.709$). Home range span also did not differ between males (55.4 ± 2.1 m, $n = 42$) and females (53.7 ± 2.2 m, $n = 50$; pooled t = 0.548, d.f. = 89; $P = 0.585$). Home range centers did not show a significant difference between sexes along the river (X-coordinate; pooled t = 1.732, d.f. = 89; $P = 0.087$), but the relative distance from the river (Y-value) was significantly higher for females (10.1 ± 0.2, $n = 49$) than males (9.3 ± 0.2, $n = 42$; pooled t = 3.156, d.f. = 89; $P = 0.002$). In addition, females carrying an eggsac were found significantly further away from the water (Y-coordinate ± s.e; 9.8 ± 3.3, n = 124) than females not caring for brood (9.0 ± 3.0, $n = 1{,}179$; pooled t = 2.372, d.f. = 1301; $P = 0.018$). Overall, range overlap was high (> 50%, Fig. 4), but it differed significantly between sexes, with male-male overlap highest and female-female overlap lowest (ANOVA; $F_{2,3743} = 19.315$, $P < 0.001$) (Fig. 4).

**Comparative morphology.**—There was a positive correlation between cephalothorax width and leg length in both *Venatrix* and *Artoria* and measures of relative leg length were obtained from the residuals of the respective regressions (Table 3, Fig. 5). Males had comparatively longer legs than females within the genus *Venatrix*, but there was no gender specific difference in the relative leg length in *Artoria* (Table 3, Fig. 5).

## DISCUSSION

There was a considerable difference in the activity and mobility pattern of male and female *V. lapidosa*, which corresponded to a pronounced sexual dimorphism in the length of their legs. The evolution of longer legs in

Table 2.—Capture statistics of the mark and recapture survey of *Venatrix lapidosa* at the Avon River, distinguished by cohorts. Average daily distance based on two-weekly interfix intervals only (see text). §Considered in analysis of average daily distances; ‡Considered in home range analysis.

| | Cohort | | | | | | |
|---|---|---|---|---|---|---|---|
| | Spring 1996 | Autumn 1997 | Spring 1997 | Autumn 1998 | Spring 1998 | Autumn 1999 | Spring 1999 |
| Males: | | | | | | | |
| Total number marked | 115 | 179 | 80 | 168 | 86 | 84 | 29 |
| Recaptured at least once§ | 58 | 157 | 35 | 121 | 43 | 67 | 9 |
| Minimum of nine captures‡ | 0 | 38 | 0 | 2 | 0 | 2 | 0 |
| Females: | | | | | | | |
| Total number marked | 127 | 176 | 105 | 140 | 77 | 66 | 21 |
| Recaptured at least once§ | 88 | 158 | 72 | 96 | 48 | 56 | 7 |
| Minimum of nine captures‡ | 1 | 48 | 0 | 0 | 0 | 0 | 0 |

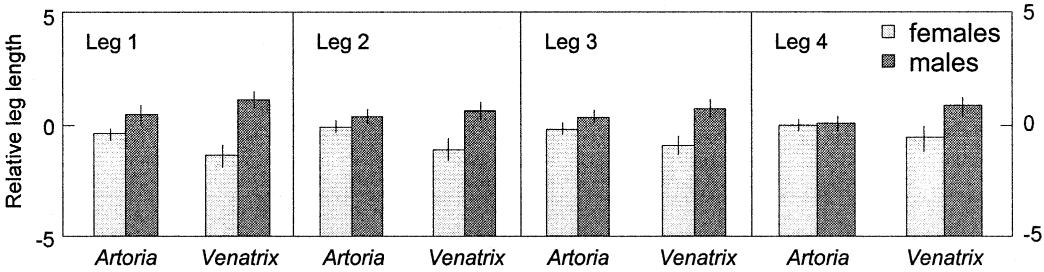

Figure 5.—Relative leg length (residuals of leg length on cephalothorax width) (mean ± s.e.) of female and male species of *Venatrix* and *Artoria*. For statistical analysis between sexes in each genus (t-test) see Table 3.

males may be the result of an increased likelihood to encounter more stationary females assuming a higher energy efficiency or speed as a result of leg elongation. The lack of sexual dimorphism in leg length in juvenile *V. lapidosa* and the genus *Artoria* (in which females are vagrant) supports this argument.

**Activity.**—*Venatrix lapidosa* is a comparatively immobile spider. Similar low activity occurs in other cursorial spiders inhabiting terrestrial-aquatic ecotones (Framenau et al. 1996a; Kreiter & Wise 2001). Limited mobility of riparian species may be a result of their fragmented habitat consisting of generally small isolated gravel banks. In addition, high prey availability near the water edge may render it unnecessary to move (Greenstone 1983). As expected for poikilothermic animals, activity between cohorts differed, most likely reflecting seasonal patterns. Activity was lower for individuals of the autumn mating cohort, due to a drop in movement over winter. Individuals of the spring mating cohorts, although more active than the autumn mating cohorts, showed no significant difference in activity between months. These individuals are adults mainly in summer. Temperature dependent movement patterns have also been reported in other wolf spiders, such as *Pardosa amentata* (Clerck 1757) (Ford 1978).

Activity patterns of males and females are similar within both cohorts, with males the more active sex. A variety of studies on wolf spiders have shown that an increase in male activity reflects mate searching (e.g., Hallander 1967; Framenau et al. 1996a). In *V. lapidosa*, significantly higher male activity appears to be temporary, emerging about three months after maturation (delayed in the autumn maturing cohort by winter diapause). In the autumn maturing cohort, males emerge earlier from diapause and are more active than females two months prior to female egg production, suggesting that males are searching for mates. Higher male activity in the spring mating cohort cannot be as easily explained in terms of mate searching, as male activity was particularly high in January, when females had already commenced egg production. Since higher male activity is observed for only a few months, females appear to move more than suggested by previous studies on wolf spiders (Richter et al. 1971; Hallander 1967). Initial female activity may be high due to increased foraging effort to meet energetic requirements for egg production (Kreiter & Wise 2001). Movement in female *V. lapidosa* may also be induced by the apparent preference of females to oviposit some distance from the water. Activity may subsequently drop, as females become sedentary to care for their brood (Hackman 1957; Hallander 1967; Framenau et al. 1996a, b; Nyffeler 2000). An unusually low proportion of ovipositing females in *V. lapidosa* (Framenau & Elgar 2005) compared to other lycosids (e.g., Framenau 1996a; Humphreys 1976) suggests a comparatively low number of stationary, broodcaring females and may partly explain why differences in activity between males and females is limited.

**Home range.**—Despite the temporary increase in male activity, home range size did not differ between males and females in *V. lapidosa*. The movements of *V. lapidosa* may have been restricted by the size of the study site itself, but average home range size and range span for both sexes were considerably smaller than the surface and length of the investigated gravel bank.

Table 3.—Comparison of relative leg length (residuals of leg length on carapace width) between males and females in species of the genera *Venatrix* and *Artoria*. Regression of leg length on carapace width: Leg 1: $R^2 = 0.899$, slope = 3.292, $P < 0.001$, $n = 51$; leg 2: $R^2 = 0.912$, slope = 3.037, $P < 0.001$, $n = 58$; leg 3: $R^2 = 0.903$, slope = 2.772, $P < 0.001$, $n = 58$; leg 4: $R^2 = 0.892$, slope = 3.512, $P < 0.001$, $n = 56$. Given are the *t*-values (pooled variance) with significance level (n.s. non significant; $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$) and degrees of freedom (d.f.).

| Factor | Leg 1 | Leg 2 | Leg 3 | Leg 4 |
|---|---|---|---|---|
| *Venatrix* | | | | |
| Sex | 4.140*** | 3.056** | 3.182** | 2.039* |
| d.f. | 33 | 34 | 34 | 34 |
| *Artoria* | | | | |
| Sex | 1.832 n.s. | 1.529 n.s. | 1.642 n.s. | 0.770 n.s. |
| d.f. | 19 | 20 | 20 | 18 |

Although home range size was similar between the sexes, there was a significant difference in the distribution of range centers between females and males. Female range centers were, on average, located further away from the water as ovipositing females retreat from the border of the gravel bank. Females may not tolerate a high degree of soil moisture, or they may look for more protected areas from varying water levels, before excavation of brood chambers. Site specificity in relation to abiotic factors occurs frequently in lycosids that build permanent burrows (e.g., Humphreys 1976; Milasowszky & Zulka 1998). Females of *A. cinerea* (Fabricius 1777) and *Trochosa ruricola* (DeGeer 1778), two lycosids inhabiting shore habitats, also move away from the water prior to brood care (Hackman 1957; Framenau et al. 1996b). Differential microhabitat preferences can have a strong influence on the activity and distribution patterns of individuals. In wolf spiders, intraspecific habitat preferences not only differ between females with and without eggsacs (Edgar 1971; Hallander 1967; Greenstone 1983), but also between sexes (Cady 1984) and adults and juveniles (Edgar 1969, 1971; Kronk & Riechert 1979).

The utilization of areas further away from the water, together with equal home range size, may explain the lower female-female range overlap compared to males. In wolf spiders, males and females do not encounter each other haphazardly. Males follow silk draglines laid by receptive females which contain sex-attracting pheromones (Hedgekar & Dondale 1969; Tietjen & Rovner 1982). In addition, strong agonistic behavior within sexes has been reported in wolf spiders (Aspey 1977a, b; Fernández-Montraveta & Ortega 1991). The effect of different habitat requirements, i.e. the search of a favorable location for brood care, appears to be stronger than male-female attraction or intrasexual aggression.

**Sexual dimorphism.**—*Venatrix lapidosa* is sexually dimorphic. Females are generally larger than males, but males have comparatively longer legs. The sex ratio of *V. lapidosa* was not biased in the autumn mating cohort, and limited to later months in the spring cohorts when many females were already caring for their brood (Framenau & Elgar 2005). Further, higher home range overlap between males suggests greater rather than less opportunity for male-male competition. Therefore, my data are not consistent with the underlying assumptions of the model developed by Vollrath & Parker (1992) that relates sexual size dimorphism in spiders to reduced male-male competition due to an increase in mortality caused by mate search. Sexual dimorphism in *V. lapidosa* most likely evolved through a fecundity advantage for larger females (Prenter et al. 1997, 1998, 1999); clutch size increases with body size in many wolf spider species (Marshall & Gittleman 1994; Simpson 1995).

While increased female fecundity may explain size differences between males and females, sexual selection through indirect male-male competition may explain the comparatively longer legs of males. Allometric growth leading to relatively longer legs only takes place in males and mainly during the final molt supporting an evolutionary hypothesis of leg elongation in males rather than leg shorting in females due to burrowing behavior. The production of longer legs may be ontogenetically costly and thus would be offset by energetically more efficient movement.

There are no experimental or comparative data of increased movement efficiency with longer legs in arthropods (J. Shultz pers. Comm.) and the relationship between leg dimensions (length and thickness) and metabolic rate are complex and also entail the mass of the spider. Simple lever mechanics predicts that if the length of the output lever arm increases, the velocity and excursion at the end of the lever will increase (and thus speed and distance moved per stride), but that the force the lever will exert will decrease (Manton 1977; Alexander 1982; Hildebrand & Goslow 2003). Males can compensate the loss of force by reducing their own mass which, in turn, augments selection for smaller males, providing a novel aspect in the explanation for sexual size dimorphism in vagrant spiders. Overall, longer-legged, smaller males are able to search faster and more extensively for females and potentially increase their encounter rates with females. This advantage would be favored by sexual selection if it provided males with a competitive edge in terms of fertilization success.

A limb elongation due to more efficient locomotion is also supported by the fact that all four legs show the same allometric pattern which was not required if the difference in leg length between sexes arose through sexual cannibalism (Elgar et al. 1990), male-male combats (Tseng & Rowe 1999), or in combination with leg ornamentation in used in courtship display (Kronestedt 1990; Hebets & Uetz 2000). In addition, sexual cannibalism and male-male combats are extremely rare in wolf spiders (Aspey 1977a). Alternatively, different foraging behavior between males and females could provide an explanation of sexual dimorphism based on different locomotory patterns (Givens 1978). However, due to lower metabolic requirements male wolf spiders attack considerably fewer prey than females (Walker & Rypstra 2001). Longer legs may also provide a sensory advantage due to an increased radius to mount olfactory chemoreceptors or trichobothria. In wolf spiders, olfaction plays some role in mate search, however, the main senses used by males to follow trail lines of females are situated on the dorsal side of the cymbium of the pedipalps (Tietjen an Rovner 1982).

The comparison in the pattern of leg-length dimorphism in *Venatrix* and *Artoria* provide further evidence that male mate-searching behavior favors relatively longer legs in males. Although males in *Artoria* also tend to have longer legs than females, this difference is not significant within the genus and is far less pronounced than in *Venatrix*. It appears unlikely that leg length dimorphism arises through shortening of female legs due to burrowing behavior, as allometric growth occurs between penultimate and adult spiders. In addition, there is no evidence that female *Venatrix* have comparatively shorter legs than vagrant *Artoria*.

This study provides evidence that longer legs in male wolf spiders are mainly caused by sexual selection through indirect competition with increased male activity in searching for a mate. To further elucidate the selective forces responsible for the elongation of male legs, future work should focus on three questions. Firstly, it is important to experimentally confirm the assumption that longer legs are more energy efficient in spider movement. Secondly, evidence that higher male activity will ultimately lead to higher fertilization success is required. This is strongly dependent on the species mating system in question, and requires an understanding of multiple mating and sperm priority patterns of wolf spiders (Austad 1984; Elgar 1998). Although *V. lapidosa* has been reported to mate multiply increasing the chance of male mate competition (Cutler 2002), there is no information on sperm priority patterns in this and other Lycosidae. Lastly, comparative studies in leg length dimorphism in comparison with the life time activity patterns of cursorial spiders on a broader taxonomic base may help us understand to what extent sexual dimorphism of limbs are under natural or sexual selection.

## ACKNOWLEDGMENTS

I am grateful to Melissa Thomas, Mark Elgar, Douglas Morse, and Mark Harvey for invaluable comments on earlier drafts of this manuscript. Jeff Shultz and Ken Prestwich provided important information on arthropod locomotion and energetics. Melissa Thomas, Fleur de Crespigny, Shar Ramamurthy, Elizabeth Dalgleish, Romke Kats, Karen Blaakmeer, and Jenny Maupin provided assistance in the field and laboratory. Casey and Elisabeth Klomp offered friendly accommodation at the Caravan Park in Stratford on the River Avon. Cath Handasyde provided access to her copy of 'RANGES V', and Graham Coulson provided further assistance in the analysis of home range data. This study was funded by the University of Melbourne (MRS), The Ecological Society of Australia, The River Basin Management Society, and the Donors Association for the Promotion of Science and Humanities in Germany (Stifterverband für die Deutsche Wissenschaft).

## LITERATURE CITED

Alexander, R.McN. 1982. Size, shape and structure for running and flying. Pp. 309–324. *In* A Companion to Animal Physiology. (C.R. Taylor, V. Johanson & L. Bolis, ed.). Cambridge University Press, Cambridge.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton.

Aspey, W.P. 1977a. Wolf spider sociobiology: I. Agonistic display and dominance-subordinance relations in adult male *Schizocosa crassipes*. Behaviour 62:103–141.

Aspey, W.P. 1977b. Wolf spider sociobiology: II. Density parameters influencing agonistic behaviour in *Schizocosa crassipes*. Behaviour 62:142–163.

Austad, S.N. 1984. Evolution of sperm priority patterns in spiders. Pp. 223–249. *In* Sperm Competition and the Evolution of Animal Mating Systems (R.L. Smith, ed.). Academic Press, New York.

Bulmer, M.G. 1983. The significance of protandry in social Hymenoptera. American Naturalist 121: 540–551.

Cady, A.B. 1984. Microhabitat selection and locomotory activity of *Schizocosa ocreata* (Walckenaer) (Araneae: Lycosidae). Journal of Arachnology 11:297–307.

Cutler, A.R. 2002. Courtship in the Wolf Spider *Venatrix lapidosa* (Lycosidae: Araneae). Honours Thesis, The University of Melbourne, Melbourne.

Darwin, C. 1871. The Descent of Man, and Selection in Relation to Sex. J. Murray, London

Dondale, C.D. & J.H. Redner. 1990. The Insects and Arachnids of Canada, Part 17. The Wolf Spiders, Nursery Web Spiders, and Lynx Spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Biosystematics Research Centre, Ottawa, Ontario.

Eberhard, W.G. & M.C. Marin. 1996. Sexual behavior and the enlarged hind legs of male *Megalopus armatus* (Coleoptera, Chrysomelidae). Journal of the Kansas Entomological Society 69: 1–8.

Edgar, W.D. 1969. Prey and predators of the wolf spider *Lycosa lugubris*. Journal of Zoology, London 159:405–411.

Edgar, W.D. 1971. The life-cycle, abundance and seasonal movement of the wolf spider, *Lycosa* (*Pardosa*) *lugubris*, in Central Scotland. Journal of Animal Ecology 40:303–322.

Elgar, M.A. 1991. Sexual cannibalism, size dimorphism, and courtship behaviour in orb-weaving spiders (Araneidae). Evolution 45:444–448.

Elgar, M.A. 1998. Sperm competition and sexual selection in spiders and other arachnids. Pp. 307—337. *In* Sperm Competition and Sexual Selection (T.R. Birkhead & A.P. Møller, ed.). Academic Press, New York

Elgar, M.A., N. Ghaffar & A.F. Read. 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. Journal of Zoology, London 222:455–470.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Annals of the Entomological Society of America 69:991–998.

Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Reviews in Ecology and Systematics 28:659–687.

Fernández-Montraveta, C. & J. Ortega. 1991. Owner-biased agonistic behavior in female *Lycosa tarantula fasciiventris* (Araneae, Lycosidae). Journal of Arachnology 19:80–84.

Ford, M.J. 1978. Locomotory activity and the predation strategy of the wolf spider *Pardosa amentata* (Clerck) (Lycosidae). Animal Behaviour 26: 31–35.

Framenau, V.W. 1998. Life cycles of *Lycosa lapidosa* McKay, 1974, and *Lycosa arenaris* Hogg, 1905, two riparian wolf spiders from south eastern Australia. Pp. 227—234. *In* Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997 (P.A. Selden, ed.). British Arachnological Society, Burnham Beeches, Bucks.

Framenau, V.W. (2002a). Taxonomy, Life History Characteristics, and Ecology of Riparian Wolf Spiders (Araneae, Lycosidae) in the Victorian Alps, South-East Australia. Ph.D. thesis, The University of Melbourne, Melbourne.

Framenau, V.W. (2002b). Review of the wolf spider genus *Artoria* Thorell (Araneae, Lycosidae). Invertebrate Systematics 16:209–235.

Framenau, V.W. & M.A. Elgar. 2005. Cohort dependent life history traits in a wolf spider (Araneae, Lycosidae) with bimodal life cycle. Journal of Zoology, London 265:179–188.

Framenau, V., M. Dieterich, M. Reich & H. Plachter. 1996a. Life cycle, habitat selection and home ranges of *Arctosa cinerea* (Fabricius, 1777) (Araneae: Lycosidae) in a braided section of the Up-per Isar (Germany, Bavaria). Revue Suisse Zoologie vol. hors série I:223–234.

Framenau, V.W., R Manderbach & M. Baehr. 2002. Riparian gravel banks of upland and lowland rivers in Victoria (South-east Australia): Arthropod community structure and life history patterns along a longitudinal gradient. Australian Journal of Zoology 50:103–123.

Framenau, V., M. Reich, & H. Plachter. 1996b. Zum Wanderverhalten und zur Nahrungsökologie von *Arctosa cinerea* (Fabricius, 1777) (Araneae: Lycosidae) in einer alpinen Wildflusslandschaft. Verhandlungen der Gesellschaft für Ökologie 26: 369–376.

Framenau, V.W. and Vink, C.J. 2001. Revision of the wolf spider genus *Venatrix* Roewer. Invertebrate Taxonomy 15:927–970.

Gasnier, T.R., C.S. de Azevedo, M.P. Torres-Sanchez & H. Höfer. 2002. Adult size of eight hunting spider species in central Amazonia: temporal variations and sexual dimorphism. Journal of Arachnology 30:146–154.

Givens, R.P. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). Ecology 59: 309–321.

Greenstone, M.H. 1983. Site-specifity and site tenacity in a wolf spider: a serological dietary analysis. Oecologia 56:79–83.

Gunnarsson, B. & J. Johnsson. 1990. Protandry and moulting to maturity in the spider *Pityohyphantes phrygianus*. Oikos 59:205–212.

Hackman, W. 1957. Studies on the ecology of the wolf spider *Trochosa ruricola* Deg. Commentationes Biologicae 16:1–34.

Hagstrum, D.W. 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and the field. Annals of the Entomological Society of America 64:757–760.

Hallander, H. 1967. Range and movements of the wolf spiders *Pardosa chelata* (O. F. Müller) and *P. pullata* (Clerck). Oikos 18:360–364.

Head, G. 1995. Selection on fecundity and variation in degree of sexual size dimorphism among species (class: Araneae). Evolution 49:776–781.

Hebets, E.A. & G.W. Uetz. 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 47:280–286.

Hedgekar, B.M. & C.D. Dondale. 1969. A contact sex pheromone and some response parameters in lycosid spiders. Canadian Journal of Zoology 47: 1–4.

Hedrick, A.V. & E.J. Temeles. 1989. The evolution of sexual dimorphism in animals: hyptheses and tests. Trends in Ecology and Evolution 4:136–138.

Hildebrand, M. & G.E. Goslow. 2003. Analysis of Vertebrate Structure. John Wiley & Sons, New York.

Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web-construction behaviour in *Phonognatha* and the phylogeny of Nephiline and Tetragnathid spiders (Araneae: Tetragnathidae). Australian Journal of Zoology 43:313–364.

Humphreys, W.F. 1976. The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch 1865) (Araneae: Lycosidae). Journal of Animal Ecology 45:59–80.

Jakob, E.M., S.D. Marshall & G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Kenward R.E. & K.H. Hodder. 1996. Ranges V. An Analysis System for Biological Location Data. Natural Environment Research Council, Dorset.

Kreiter, N. & D.H. Wise. 2001. Prey availability limits fecundity and influences the movement pattern of female fishing spiders. Oecologia 127: 417–424.

Kronestedt, T. 1990. Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the *pulverulenta* group. Zoologica Scripta 19:203–225.

Kronk, A.E. & S.E. Riechert. 1979. Parameters affecting the habitat choice of a desert wolf spider, *Lycosa santrita* Chamberlin and Ivie. Journal of Arachnology 7:155–166.

Malmgren, J.C. & M. Thollesson. 2001. Sexual size and shape dimorphism in two species of newts, *Triturus cristatus* and *T. vulgaris* (Caudata: Salamandridae). Journal of Zoology, London 249: 127–136.

Manton, S.M. 1977. The Arthropoda. Habits, Functional Morphology, and Evolution. Clarendon Press, Oxford.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8: 118–124.

McKay, R.J. 1974. The wolf spiders of Australia (Araneae: Lycosidae): 2. The *arenaris* group. Memoirs of the Queensland Museum 17:1–19.

Milasowszky, N. & K.P. Zulka. 1998. Habitat requirements and conservation of the ‘‘flagship species’’ *Lycosa singoriensis* (Laxmann 1770) (Araneae: Lycosidae) in the National Park Neusiedler See-Seewinkel (Austria). Zeitschrift für Ökologie und Naturschutz 7:111–119.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

Montgomery, T.H. 1910. The significance of the courtship and secondary sexual characters of araneads. The American Naturalist 44:151–177.

Nyffeler, M. 2000. Do adult female lycosids feed during the period of maternal care? Bulletin of the British Arachnological Society 11:388–390.

Ohtsuka, S. & R. Huys. 2001. Sexual dimorphism in calanoid copepods: morphology and function. Hydrobiologia 453:441–466.

Peters, W.L. & I.C. Campbell. 1991. Ephemeroptera (Mayflies). Pp. 279—293. *In* The Insects of Australia. A Textbook for Students and Research Workers (CSIRO, ed.). Melbourne University Press, Carlton.

Prenter, J., W.I. Montgomery & R.W. Elwood. 1997. Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. Journal of Zoology, London 243:341–349.

Prenter, J., R.W. Elwood & W.I. Montgomery. 1998. No association between sexual size dimorphism and life histories in spiders. Proceedings of the Royal Society of London, Series B 265: 57–62.

Prenter, J., R.W. Elwood & W.I. Montgomery. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. Evolution 53:1987–1994.

Quinn, G.P. & M.G. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Reynolds, J.D. & P.H. Harvey. 1994. Sexual selection and the evolution of sex differences. Pp. 53—70. *In* The Differences between the Sexes (R.V. Short & E. Balaban, ed.). Cambridge University Press, Cambridge.

Richter, C.J.J., J. den Hollander & L. Vlijm. 1971. Differences in breeding and motility between *Pardosa pullata* (Clerck) and *Pardosa prativaga* (L. Koch), (Lycosidae, Araneae) in relation to habitat. Oecologia 6:318–327.

Samietz, J. & U. Berger. 1997. Evaluation of movement parameters in insects—bias and robustness with regard to resight numbers. Oecologia 110: 40–49.

Selander, R.K. 1972. Sexual selection and dimorphism in birds. Pp. 180—230. *In* Sexual Selection and the Decent of Man, 1871–1971 (D.C. Campbell, ed.). Aldine, Chicago.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Reviews in Biology 64:419–461.

Simpson, M.R. 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology 76:795–800.

Thornhill, R. & J. Alcock. 1983. The Evolution of Insect Mating Systems. Cambridge University Press, Cambridge.

Tietjen, W.D. & J.S. Rovner. 1982. Chemical communication in lycosids and other spiders. Pp. 249—279. *In* Spider Communication: Mechanisms and Ecological Significance (P.N. Witt & J.S. Rovner, ed.). Princeton University Press, Princeton.

Tseng, M. & L. Rowe. 1999. Sexual dimorphism and allometry in the giant water strider *Gigantometra gigas*. Canadian Journal of Zoology 77: 923–929.

Vollrath, F. & G.A. Parker. 1992. Sexual dimorphism and distorted sex ratios in spiders. Nature 360:156–159.

Walker, S.E. & A.L. Rypstra. 2001. Sexual dimorphism in functional response and troph morphology in *Rabidosa rabida* (Araneae: Lycosidae). American Midland Naturalist 146:161–170.

Ward, T.M. & W.F. Humphreys. 1981. Locomotion in burrowing and vagrant wolf spiders (Lycosidae). Journal of Experimental Biology 92:305–321.

White, G.C. & R.A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego/London.

*Manuscript received 23 August 2004, revised 31 March 2005.*