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ARTÍCULO:

Bimodality in the body size distribution of Mediterranean tarantula juveniles: Humphreys' Russian roulette revisited

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Abstract

Bimodality in the distribution of body sizes within a cohort of organisms can be originated by different mechanisms. In the Mediterranean tarantula, *Lycosa tarantula* (Linnaeus, 1758), spiderlings disperse in two bouts, with approximately half of the spiderlings in the population dispersing before winter and the other half remaining in the burrow with their mothers until the onset of spring. Humphreys (1983) hypothesized that one advantage of early dispersal relative to late dispersal is that, after the winter, early dispersers will be several instars larger than late dispersers. If this is the case, we expect to find a bimodal distribution of spider sizes after the winter. We provide evidence for bimodality in a natural population of *L. tarantula*, hypothesize proximate mechanisms of biphasic dispersal and expand Humphreys' hypotheses on the costs and benefits of diphasic dispersal.

Key words: Araneae, Lycosidae, *Lycosa tarantula*, size bimodality, diphasic dispersal, cannibalism, territorial spider, burrowing wolf spider, Iberian Peninsula.

Bimodalidad en la distribución de tamaños de juveniles de tarántula mediterránea: una reconsideración de la ruleta rusa de Humphreys.

Resumen

Varios mecanismos pueden dar origen a bimodalidad en la distribución de los tamaños de una cohorte de organismos. En la tarántula mediterránea, *Lycosa tarantula* (Linneo, 1758) las arañitas recién emergidas del capullo se dispersan en dos momentos bien diferenciados: aproximadamente la mitad de las arañitas en la población se dispersan antes del invierno y la otra mitad permanence en el nido con las madres hasta la llegada de la primavera. Humphreys (1983) emitió la hipótesis de que una de las ventajas para las arañas que se dispersan tempranamente es que, después del invierno, se encontrarán en estadios más avanzados de su desarrollo y por lo tanto serán de tamaño superior que las arañas de dispersión tardía. Si la última hipótesis es verdadera, deberíamos observar una distribución bimodal de los tamaños de las arañas después del invierno. Se muestra evidencia de la existencia de dicha bimodalidad en una población natural de *L. tarantula*, se emiten hipótesis sobre los mecanismos próximos de la dispersión bifásica y se expanden las hipótesis de Humphreys sobre los costes y los beneficios de la dispersion bifásica.

Palabras clave: Araneae, Lycosidae, *Lycosa tarantula*, bimodalidad de los tamaños, dispersión bifásica, canibalismo, araña territorial, Araña lobo constructora de madrigueras, Península Ibérica.

Introduction

Size bimodality, the arising of two clusters in the distribution of sizes within a population or cohort, has been reported for both plant and animal populations. A bimodal size distribution can originate via different mechanisms, including competition, predation, cannibalism, differences in growth rate among individuals and a combination of the above and different abiotic factors (Huston & DeAngelis, 1987; Botsford et al., 1994). Huston and DeAngelis (1987) recognized four different critical factors for bimodality arising within a cohort: 1) the initial distribution of individual sizes; 2) the distribution of growth rates among the individuals; 3) the size and time dependence of the growth rate of each individual; and 4) mortality that may affect each size class differently.

A possible mechanism originating size bimodality is the existence of two peaks in the timing of dispersal within a cohort. This is because early dispersers would start growing before later dispersers, originating a bimodal distribution of growth rates, which in turn can originate a bimodality of size distributions. Diphasic dispersal dependent on wind patterns has been reported for tree seeds (Horn et al., 2001). Some of the seeds disperse very far away from the maternal tree during relatively strong winds and other seeds are just dropped beside the maternal tree in periods when there is no wind. The latter pattern is stochastic because it depends on turbulences, which is a stochastic process itself (Horn et al., 2001). Although

uncommon, deterministic (i.e., predictable) diphasic dispersal has been reported in animals. For example, in the meadow vole, *Microtus pennsylvanicus* (Ord, 1815), probably for minimizing inbreeding, individuals from sibling groups disperse earlier than individuals that live in groups of non-siblings (Bollinger et al., 1993). Sex differences in the timing of juvenile dispersal have been reported for the brushtail possum, *Trichosurus caninus* (Ogilby, 1836) (Barnett et al., 1982, as cited by Humphreys, 1983). Males of the brown thornbill, *Acanthiza pusilla* (Shaw, 1790) disperse diphasically, and late dispersers, which remain during autumn and winter in the parental nest, enjoy lower mortality and a higher chance of acquiring a breeding site in the local breeding population than earlier dispersers.

The Mediterranean tarantula, *Lycosa tarantula* (Linnaeus, 1758), is an exceptional wolf spider because maternal care can be extended for long periods of time with the spiderlings remaining on top of their mother for up to six months (Fabre, 1913). Humphreys (1983) reported a clear tendency for spiderlings of *L. tarantula* in captivity to disperse in two phases. In spite of the relatively warm laboratory conditions, Humphreys found that approximately half of the spiderlings from 12 females of a Croatian population dispersed before the winter and half after the winter. Later on, this diphasic dispersal was observed in nature by Parellada (1998) in a population from the North-East of the Iberian Peninsula. Humphreys hypothesized that such diphasic dispersal could be an adaptation in which female fitness would be maximized because their offspring would play a game of Russian roulette against environmental stochasticity. Humphreys, however, did not explicitly mention that the Russian roulette would evolve because it would maximize female fitness. In severe winters, early dispersers would have higher mortality and later dispersers would be favored by better survival in maternal burrows; whereas, during severe summer droughts early dispersers would be favored because by dispersing early they would have a higher growth rate because they would forage on warm days in the fall, and consequently be several instars ahead (i.e., larger size) in the summer, which would allow them to build deeper burrows or have a cannibalistic advantage. Spiderlings that remain in the burrow with their mothers do not obtain any source of food until they disperse after the winter (Humphreys, 1983; Parellada, 1998). Humphreys based the latter part of his hypothesis on the observation that larger individuals of the Australian ecological equivalent to *L. tarantula*, *L. godeffroyi* Koch, 1865 build deeper burrows that keep a relatively high moisture content (Humphreys, 1975), potentially allowing better survival during summer droughts. Although Humphreys' model is incomplete (i.e., it lacks a complete analysis of costs and benefits) field-collected data can still be used to show if any of his partial hypotheses is supported. An implicit prediction of Humphreys' conceptual model is that after the winter the size distribution of recently dispersed spiders should be bimodal,

with a cluster of large-early dispersers and a cluster of small-late dispersers. The latter would be evidence that diphasic dispersal can trigger size bimodality in a natural population. In a *L. tarantula* population for which diphasic dispersal has been reported (Parellada, 1998, J.M. personal observations) we document the size distribution of spiders at three different stages. We test whether there is a bimodal size distribution of recently dispersed juveniles after the winter and whether bimodality is maintained in later stages. We also test whether a bimodal distribution can be detected at birth, as it would be the case if size bimodality could be originated by a different mechanism than diphasic dispersal.

Materials and methods

The species

The Mediterranean tarantula is a cannibalistic, territorial burrowing wolf spider (Fernández-Montraveta & Ortega, 1990a, 1991; Moya-Laraño et al., 1996, 2002) that inhabits well-drained soils in open areas across the Mediterranean area. Spiderlings emerge from the egg sac in September and remain without feeding with their mothers for a period that can be exceptionally long (see above). During this period, the spiderlings survive from the nutrients that they have stored in their abdomens during development. These nutrients can be obtained either from their own egg, or by feeding on unfertilized eggs inside the egg sac (Moya-Laraño, 1999). Symptomatic behavior of aerial dispersal was observed by Fabre (1913) in captivity but has never been observed by the authors of the current paper, neither in captivity nor in the field, which suggests that dispersal takes place mostly by wandering. After dispersal, juveniles spend their first months of life wandering, building their first burrows when they reach one year of age (Orta et al., 1993; Moya-Laraño et al., 1996; Parellada, 1998). Fernández-Montraveta et al. (1991), however, report juveniles building burrows at earlier ages. During June and July of their second year of life, they become adults, with males maturing slightly earlier than females. Some females can live for an additional year (hereafter 2nd year females), building a second, smaller egg sac (Parellada, 1998; Moya-Laraño, 2002) using the sperm that they stored during the previous season (Fernández-Montraveta & Ortega, 1990b).

Data collection

We present size data on three different life stages which were collected within the same year (1996) in the Garraf Natural Park (North-East of the Iberian Peninsula), a *L. tarantula* population that has been studied in great detail (Orta et al., 1993; Moya-Laraño et al., 1996, 1998, 2000, 2003a, 2003b; Parellada, 1998; Moya-Laraño, 2002). The three stages (from three different cohorts) were: 1) recently emerged spiderlings (September), 2) 9-months-old non-burrowing spiders (early and

late dispersers after winter; i.e., June) and 3) antepenultimate and penultimate 18-months-old burrowing spiders (April). Although Humphreys' hypothesis predicts that the proportion of early and late dispersers should change from year to year according to variation in weather conditions, a bimodal size distribution of post-winter dispersers should be detectable every year whether or not there is year-to-year variation in the number of individuals present in every cluster. Although carapace width appears to be a more accurate measurement of spider size (e.g., Marshall & Gittleman, 1994) here we measure carapace length because in lycosids is longer than carapace width, and therefore it can be measured with relatively smaller error in the field. This is particularly important when taking measurements of small individuals (i.e., recently dispersed juveniles).

During September 1996 the carapace lengths of a sample of 170 recent emergers (10 spiderlings from each of 17 females – 14 first year breeders and 3 second year breeders) were measured to the nearest 0.005 mm under a dissection microscope. These spiderlings were collected during a field study documenting the effects of food limitation and age on female reproductive output (Moya-Laraño, 2002). During the latter study half of the female spiders were artificially fed. In order to avoid any potential bias in the size distribution of spiderlings due to the feeding treatment, only the offspring of females that were not artificially fed were included in the current analyses. To increase sample size, 10 emergers from an additional second year breeding female, which were collected in the same population and year, were included.

Data on size of early and late dispersers after winter were collected by one of us (M.C.) during two consecutive days (22 June and 23 June 1996). Non-burrowing individuals were located with the aid of a headlamp (Wallace, 1937). A total of 99 individuals were captured, measured and released during two consecutive days. To ensure that the same individuals were not re-measured during the second day, every captured individual was marked with green enamel on the legs. Only one previously marked individual was recaptured during the second day and it was not measured again. Marking and measurement was achieved by immobilizing each spider in a fine-mesh bag (Moya-Laraño et al., 1996). Carapace lengths were measured to the nearest 0.1 mm with a caliper.

Data on 18-month-old spiders came from a survey conducted by one of us (J.M.) prior to a food supplementation experiment (Moya-Laraño et al., 2003a). From 23 April to 1 May 1996 a total of 152 spiders were extracted from their burrows, marked, measured and released back into the burrows. Marking and measurement procedures were identical to the survey described above. This sample included both antepenultimate and penultimate instars. Because in most spiders sex differences are only apparent at the penultimate and ultimate instars, we were unable to distinguish the sexes

of all the animals included in this survey (Moya-Laraño et al., *in press*).
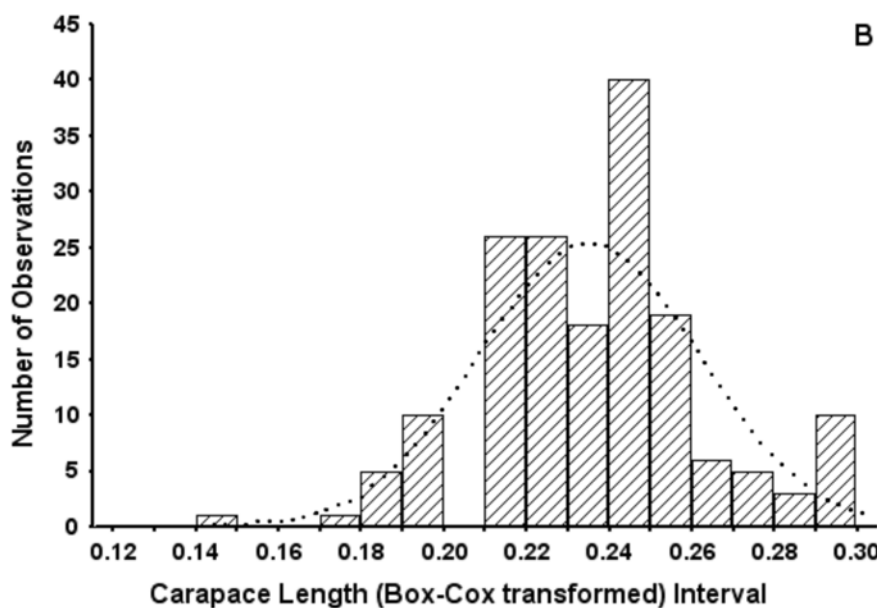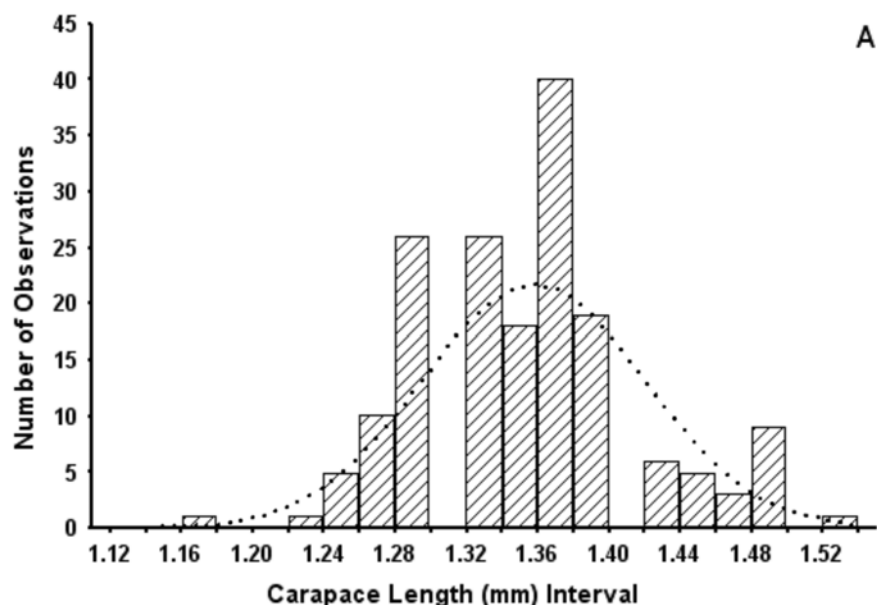
Statistical analyses

The presence of bimodality in distributions can be detected by testing for skewness (g_1) and kurtosis (g_2) (Hildebrand, 1971; Wyszomirski, 1992). Skeweness measures whether an observed distribution deviates from an expected normal distribution by virtue of its asymmetry: significant positive skewness indicates that the right tail of the distribution is longer than the left tail and negative skewness indicates the opposite. Kurtosis measures whether an observed distribution deviates from an expected normal by virtue of its shape: negative kurtosis indicates that the distribution is flatter than the expected normal (platykurtic) and positive kurtosis indicates that the distribution is pointier than the expected normal (leptokurtic) (Sokal & Rohlf, 1995). The kurtosis statistic ranges from –2 to infinite. A value of –1.2 indicates perfect flatness (i.e., the uniform distribution) and negative values smaller than that are conclusive proof of bimodality (Hildebrand, 1971). A distribution with significant skewness also will tend to have significant kurtosis (i.e., kurtosis depends on skewness), which means that in distributions that are not symmetric the kurtosis criterion may not be valid in detecting bimodality. Making the distribution symmetric prior to analyzing kurtosis will solve this problem (Wyszomirski, 1992). An asymmetric distribution can become symmetric by transformation of the data. The Box-Cox transformation finds, by Maximum Likelihood, the parameter λ by which transforming every data point (x_i) of a distribution using the expression $(x_i^\lambda -1)/\lambda$ will maximize the symmetry of the distribution (Sokal & Rohlf, 1995). Asymmetric distributions were Box-Cox transformed using the procedure TRANSREG in SAS (SAS Institute, 1990). Skewness and Kurtosis were tested for significance using z tests (Tabachnick & Fidell, 2001).

Results

There was a clear binomial size distribution of 9-month old non-burrowing instars in the field (Fig. 1). The distribution was symmetric ($g_1 = - 0.245$, $P(z) = 0.157$) and showed significant negative kurtosis beyond the uniform distribution ($g_2 = - 1.470$, $P(z) = 0.001$). Neither the size distribution of spiderlings nor the size distribution of older burrowing instars was bimodal (Figs. 2 and 3). Both the size distribution of spiderlings (Fig. 2A; $g_1 = 0.410$, $P(z) = 0.014$) and older burrowing instars (Fig. 3A; $g_1 = 0.878$, $P(z) < 0.0001$) were positively skewed. After Box-Cox transformations neither the size distribution of spiderlings (Fig. 2B; $\lambda = - 1.75$, $g_1 = - 0.016$, $P(z) = 0.466$; $g_2 = 0.457$, $P(z) = 0.109$) nor the size distribution of older burrowing instars (Fig. 3B; $\lambda = - 1$, $g_1 = 0.011$, $P(z) = 0.479$; $g_2 = 0.236$, $P(z) = 0.273$) showed significant skewness or kurtosis.
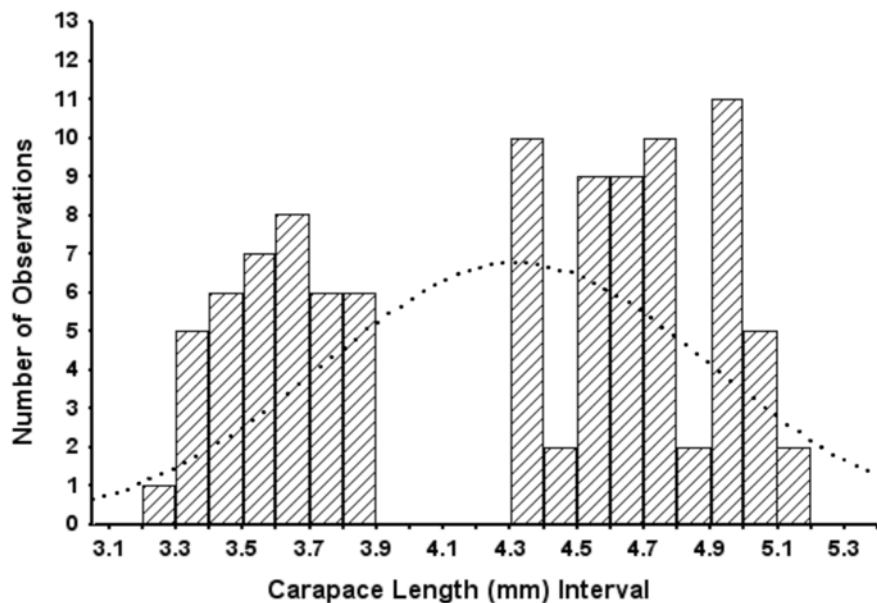
Fig.1. Bimodality in the size distribution of 9-month-old spiders. The dotted line shows the expected normal distribution (statistical analyses in the text).

Fig. 2. Size distribution of recently emerged spiderlings. **A:** Right skewness of untransformed data. **B:** Lack of bimodality in Box-Cox transformed data (statistical analyses in the text). Dotted lines show the expected normal distributions.
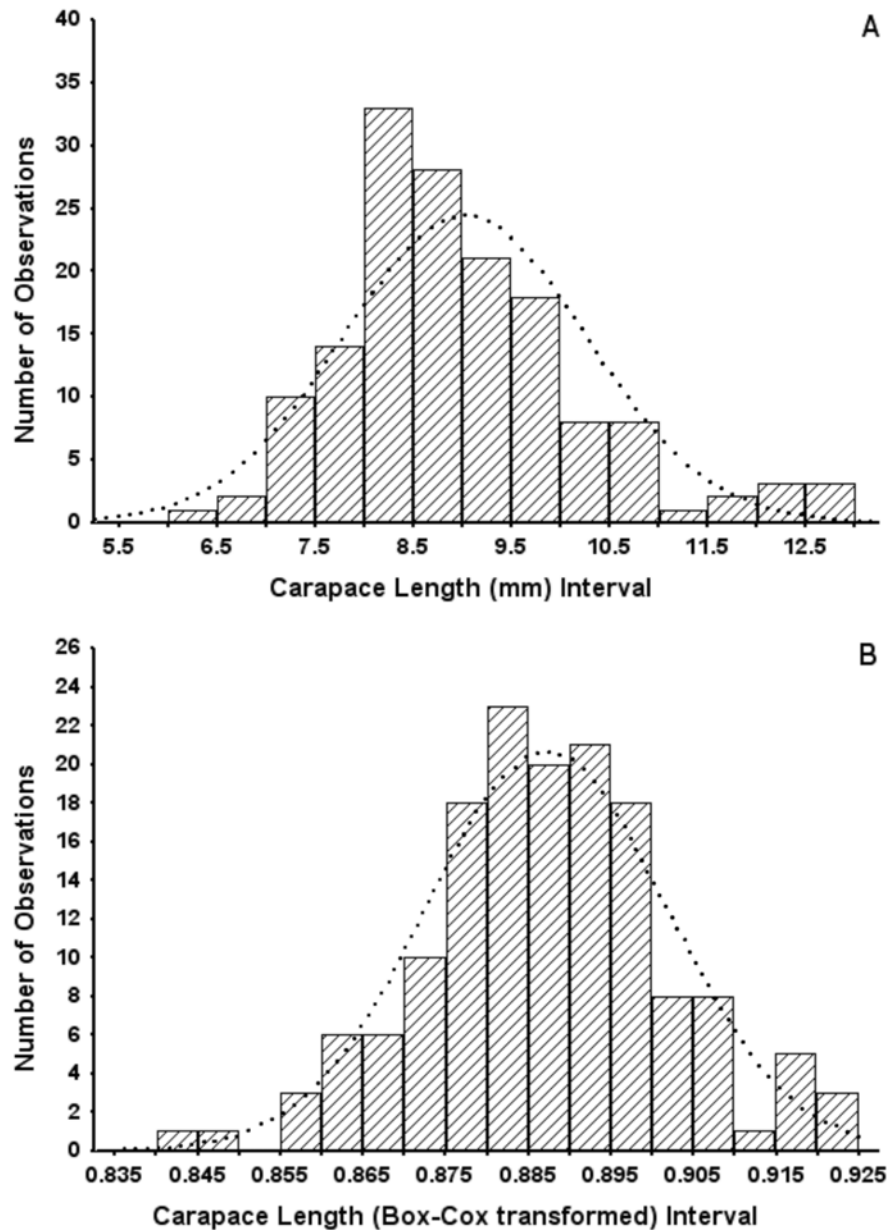
Fig. 3. Size distribution of pre-maturing burrowing instars. **A:** Right skewness of untransformed data. **B:** Lack of bimodality in Box-Cox transformed data (statistical analyses in the text). Dotted lines show the expected normal distributions.

Discussion

Size bimodality

Assuming that diphasic dispersal occurs every year in the studied population, we can conclude that the dispersal pattern of spiderlings from the same cohort was the cause of the bimodality observed in the size distribution of 9-month-old spiderlings. The assumption that diphasic dispersal occurs every year is not a strong one if we also assume that variation in weather patterns affects the proportion of spiders that disperse and survive before and after the winter. Therefore, we should detect a bimodal distribution every year, with the proportion of juveniles present in every cluster (small size or large size) depending on the weather of that year. Humphreys (1983) hypothesized that early dispersers would have a

higher growth rate (active outside the burrow) relative to the spiderlings that remained with their mom (inactive inside the burrow). The existence of a bimodal distribution supports this latter hypothesis. The alternative hypothesis that size bimodality could be important before dispersal was rejected because bimodality was not detected in the size distribution of spiderlings. Immigration of spiderlings of different size from a different population of, for example, different prey availability could also explain bimodality in the distribution of sizes. The studied population, however, is very isolated (J.M. personal observations), which makes immigration from neighborhood populations very

unlikely. Therefore a combination of different timing and rate of growth (Huston & DeAngelis, 1987) between early and late dispersers is the most likely explanation for the observed bimodality in the size distribution of juvenile spiders. To our knowledge this is the first time that diphasic dispersal is shown to be a source of bimodality in the size distribution within a cohort of any animal species.

Proximate causes of diphasic dispersal

Next we mention a series of potential proximate mechanisms that could explain the observed pattern of diphasic dispersal. How some of these mechanisms evolved and were maintained (i.e., the ultimate causes) is discussed in another section (see below).

Humphreys (1983) hypothesized that early dispersers would show metabolic differences relative to late dispersers based on his laboratory observations of early dispersers being unable to survive the winter without food. Late dispersers remained with the female without getting any source of food from their mothers and Humphreys suggested that they were in a better metabolic state than early dispersers. This last hypothesis, however, is not supported because the levels of activity of a dispersed spider, regardless of the initial metabolic conditions, will involve higher energy expenditure relative to spiders that do not disperse. In nature an early disperser will be actively searching, and probably finding, food. Early dispersers during Humphreys (1983) observations were probably actively searching for food (expending energy) but never found any (no energy intake) because they were not provided with prey in the laboratory, which probably explains why they died. Although metabolic differences can certainly be one of the proximate causes of diphasic dispersal, Humphreys´ reasoning is not supported. In the field, early dispersers will enjoy various months of foraging activity before it is too cold to do so, allowing them to grow at a faster rate than the spiderlings that remain in the burrow without foraging. However, a relatively higher level of activity of early dispersers in the laboratory, without the consequent higher food intake, will make them die at a higher rate than later, less active dispersers. This pattern would be observed even if, after emergence from the egg sac, the metabolic condition of early and late dispersers would be identical.

Parellada (1998) reported that only spiderlings from 2nd year reproductive females were early dispersers and that late dispersers were the offspring of 1st year females entirely. However, this observation was based on the fact that the totality of spiderlings from 2nd year females dispersed from their moms. Parellada did not count how many spiderlings were on top of 1st year females before and after the winter and could not reach an objective conclusion about whether or not some spiderlings dispersed before the winter from 1st year females as well. Indeed, Humphreys reported three females from which all spiderlings dispersed (probably 2nd year females) and 9 from which 25% to 60% of the

spiderlings remained with their moms until after winter (probably 1st year females). In fact, it has been observed that 2nd year females do not close their burrows with silk when they build their egg sac, whereas 1st year females close their burrow right after they build the egg sac (Moya-Laraño, 1999). When spiderlings emerge from the egg sac, 1st year females open their burrow, closing it again with the onset of the winter (J.M. personal observations). If 1st year females close the burrow before all spiderlings disperse, that alone could be a mechanistic explanation for the pattern of diphasic dispersal from 1st year females. In addition, the totality of spiderlings may disperse from 2nd year females because older females are missing abdominal hairs (Parellada, 1998; Moya-Laraño, 2002). It has been shown in another lycosid that the abdominal hairs play an important role in ensuring that the spiderlings remain on the back of the maternal abdomen (Rovner et al., 1973). Therefore, female age seems to be one mechanism explaining diphasic dispersal. One may argue that, if spiderlings from 2nd year females are larger because they disperse earlier, that alone could explain the observed bimodal distribution without the need of a differential growth of early dispersers. However, the size of spiderlings from 1st and 2nd year females is not significantly different, and the tendency is in the opposite direction (Moya-Laraño, 2002).

Three additional explanations as mechanisms triggering diphasic dispersal cannot be ruled out without further research. First, there is the possibility that the spiderlings fight with each other for remaining on the maternal back and that they establish a layer hierarchy, with some spiderlings closer to the female abdomen (the deeper layers) and some farther apart (sitting on top of other spiderlings). If that is the case, the larger spiderlings would probably be more likely to remain near the abdomen (i.e., the better fighters remain in deeper layers), forcing smaller spiderlings to remain on the external layers and, as a consequence, to disperse before the winter. This hierarchy could also be established according to a combination of different spiderling traits, not just size. Second, is the possibility for the existence of a behavioral polymorphism (Dingle, 1996; Toonen & Pawlik, 2001) by which two genetically different dispersal types (early and late) would coexist in the population. Lastly, sex-biased dispersal (Dingle, 1996) can be another possible mechanism, with one sex tending to disperse before the winter and the other after the winter. Future research will have to address all these possibilities.

Loss of bimodality

If bimodality arises every year in a similar way, then the fact that we did not detect bimodality in later burrowing instars suggests that it is lost before individuals mature. The loss of bimodality can be due to the same sort of mechanisms that cause it to arise (see introduction). Competition, however, seems the most likely mechanism by which bimodality is lost in this system. First,

burrowing instars are more likely to remain in their burrows until maturity if they are significantly larger than their neighbors (Moya-Laraño et al., 1996), suggesting that large, early-dispersing spiders will be better at maintaining territories. Second, and as already stated by Humphreys (1983), in cannibalistic systems, larger spiders will be at a cannibalistic advantage (Polis, 1981; see Samu et al., 1999 and Moya-Laraño et al., 2002 for wolf spider examples). Cannibalism of larger juvenile *L. tarantula* on smaller juveniles has been observed in the laboratory (J.M. personal observations). Cannibalism can be thought of as a kind of competition, in which competitors are eliminated from the population by killing and consuming them (Polis, 1981). Therefore, early-dispersing spiders will be most likely the cannibals of late dispersers. Third, the existence of a right skewed size distribution in pre-maturing burrowing instars can be thought as indirect evidence that competition favoring larger sizes has taken place (see Huston & DeAngelis, 1987 and references therein). This is because the left tail of the distribution (smaller individuals) is eliminated in favor of the right tail (larger individuals). Similarly, the right skewness of the size distribution of spiderlings could arise from competition of spiderlings for feeding on unfertilized eggs within the egg sac. Feeding on unfertilized eggs from egg sacs has been reported in a few spider families: Theridiidae (Valerio, 1974), Clubionidae (Peck & Withcomb, 1970) and Amaurobiidae (Kim & Roland, 2000). Egg sacs with unfertilized eggs have been found in the present *L. tarantula* population (Moya-Laraño, 1999) and if larger spiderlings are better at reaching unfertilized eggs within an egg sac, that alone could explain the observed right skewness of the distribution. All these ideas will need to be tested in future research.

The game of Russian Roulette revisited: the ultimate causes of dispersal

Humphreys (1983) built a conceptual model trying to explain the adaptive value of diphasic dispersal in *L. tarantula* (see the introduction). He based his model on his knowledge about the biology of the ecologically similar lycosid *L. godeffroyi,* and on the weather patterns of the Mediterranean region. However, his model was weak and lacked several alternative hypotheses that could explain the costs and benefits of biphasic dispersal. For instance, in his hypothesis abiotic factors played only a direct role as causes of death (cold in the winter and drought in the summer). It is well known that cannibalism is hunger-dependent (Polis, 1981; Dong & Polis, 1992) even in wolf spiders (Samu et al., 1999; Moya-Laraño et al., 2002). Therefore, in dry years of subsequent low prey availability cannibalism of early (larger) dispersers upon late (small) dispersers will be more frequent. Thus, the possibility of hunger-dependent cannibalism makes prey availability an additional biotic factor, that although it will be affected also by weather stochasticity, it may have direct consequences for the costs and benefits of early and late dispersal.

Table I.

The costs and benefits of the Game of Russian roulette. E = Early dispersers, L = Late dispersers. *Implicit assumption in Humphreys' (1983) model with a proposed, more realistic cost-and-benefit hypothesis between parentheses (see text).

	Survival	Growth Rate
Severe Winter	E < L	E = L (E = L)*
Severe Summer	E = L (E > L)*	E > L

Dispersing late in a year with high prey availability (i.e., a rainy year) may allow a larger proportion of late dispersers to survive cannibalism from early dispersers and the opposite will be true as well. In addition, staying with the mother over the winter can increase the probability of survival of the spiderlings for reasons other than cold (e.g. predation, starvation). Furthermore, Humphreys left out of his model what would be the differential growth rate of early vs. late dispersers in severe winters and what would be the differential survival in severe summers (Table I). We hypothesize that in a severe winter, the growth rate of early dispersers will be at least equal to that of late dispersers, which do not grow while in the burrow with their mother and that, in a severe summer, early dispersers will survive better because the competitive and cannibalistic advantages stated above (Table I).

One of the advantages proposed by Humphreys (1983) for early dispersal is that early dispersers could mature relatively earlier than late dispersers. He claimed that there could be a difference of 5 months in maturation times between early and late dispersers. However, such a large difference is very unlikely to be reached for two reasons: 1) the maximum difference between maturation times in the present population (i.e., maximum maturation time minus minimum maturation time) is 34 days (Moya-Laraño *unpublished data*) and 2) an effect of early maturation was not observed by artificially feeding some juvenile spiders in the present population (Moya-Laraño et al., 2003a), suggesting that prey availability, and its subsequent effect on growth rate, has no effect on maturation time. However, if diphasic dispersal depends on sex (see above), and males are most likely the early dispersers, then it would be possible that there is a link between early dispersal and early maturation time.

The fact that late dispersers are larger and most likely the cannibals, is consistent with the existence of a cannibalistic polyphenism (Crump, 1992; Hoffman & Pfenning, 1999; Michimae & Wacakara, 2002; Whiteman et al., 2003) by which cannibalistic individuals become phenotypically different than prey individuals. To our knowledge, cannibalistic polyphenisms have not been reported for arthropods. The *L. tarantula* system can be very helpful in understanding the ecology and evolution of cannibalism because the two different phenotypes can be readily distinguished in natural

populations by their different non-overlapping size distributions.

Finally, the evolution and maintenance of diphasic dispersal cannot be thoroughly understood without putting it in the context of sibling rivalry and parent offspring conflict (Trivers, 1974; Mock et al., 1998). In other words, whereas diphasic dispersal against environmental stochasticity may maximize the fitness of females (i.e., if dispersal is under their control), playing the wrong strategy (e.g. dispersing early before a severe winter) can reduce the fitness of an individual offspring to zero (the Russian Roulette). This situation is a typical example of a parent-offspring conflict. Thus, if diphasic dispersal is adaptive to the spiderlings as well, then it will have to be shown that there is a mixed Evolutionary Stable Strategy (ESS) played by the spiderlings and that is maintained by environmental stochasticity. This means that no pure strategy (disperse after winter only or disperse before winter only) will have an advantage over diphasic dispersal. This latter, more complex model, will also depend on whether or not there is a genetic mechanism underlying diphasic dispersal.

In conclusion, although we have established a link between diphasic dispersal and size bimodality, there is still a great deal of research to be done before we can understand the causes as well as the costs and benefits of early and late dispersal. The existence of this unusual diphasic dispersal in the Mediterranean tarantula makes this species a good model to study the evolution of animal dispersal in stochastic environments. Comparisons among populations across time, along with field manipulative experiments, will provide the best answers.

Acknowledgements

References

BARNETT, J.L., R.A. HOW & W. F. HUMPHREYS 1982. Habitat effects on organ weights, longevity and reproduction in the mountain Brushtail Possum, *Trichosurus caninus* (Ogilby). *Australian Journal of Zoology*, **30**: 23-32.

BOLLINGER, E.K., S. J. HARPER & G. W. BARRETT 1993. Inbreeding avoidance increases dispersal movements of the meadow vole. *Ecology*, **74**: 1153-1156.

BOTSFORD, L.W., B. D. SMITH & J. F. QUINN 1994. Bimodality in size distributions: the Red Sea urchin *Strongylocentrus franciscanus* as an example. *Ecological Applications*, **4**: 42-50.

CRUMP, M. L. 1992. Cannibalism in amphibians. In: *Cannibalism: ecology and evolution among diverse taxa*. Elgar, M. A. & Crespi, B. J. (eds.). Oxford Scientific Publications, Oxford. Pp. 256-276.

DINGLE, H. 1996. *Migration: the biology of life on the move*. Oxford Univ. Press. New York.

DONG, Q. & G. A. POLIS 1992. The dynamics of cannibalistic populations: a foraging perspective. In: *Cannibalism: ecology and evolution among diverse taxa*. Elgar, M. A. & Crespi, B. J. (eds.). Oxford Scientific Publications, Oxford. Pp. 13-37.

FABRE, J. H. 1913. *The life of the spider*. Dodd, Mead and Company. New York.

FERNÁNDEZ-MONTRAVETA, C., R. LAHOZ-BELTRA & R. ORTEGA 1991. Spatial distribution of *Lycosa tarentula fasciiventris* (Araneae, Lycosidae) in a population from Central Spain. *Journal of Arachnology*, **19**: 73-79.

FERNÁNDEZ-MONTRAVETA, C. & J. ORTEGA 1990a. El comportamiento agonístico de hembras adultas de *Lycosa tarentula fasciiventris* (Araneae, Lycosidae). *Journal of Arachnology*, **18**: 49-58.

FERNÁNDEZ-MONTRAVETA, C. & J. ORTEGA 1990b. Some aspects of the reproductive behavior of *Lycosa tarentula fasciiventris* (Araneae, Lycosidae). *Journal of Arachnology*, **18**: 257-262.

FERNÁNDEZ-MONTRAVETA, C. & J. ORTEGA 1991. Owner-biased agonistic behavior in female *Lycosa tarentula fasciiventris* (Araneae, Lycosidae). *Journal of Arachnology*, **19**: 80-84.

HILDEBRAND, D. K. 1971. Kurtosis measures bimodality? *The American Statistician*, **25**: 42-43.

HOFFMAN, E. A. & D. W. PFENNIG 1999. Proximate causes of cannibalistic polyphenism in larval tiger salamanders. *Ecology*, **80**: 1076-1080.

HORN, H. S., R. NATHAN & S. R. KAPLAN 2001. Long-distance dispersal of tree seeds by wind. *Ecological Research*, **16**: 877-885.

HUMPHREYS, W. F. 1975. The influence of burrowing and thermoregulatory behaviour on the water relations of *Geolycosa godeffroyi* (Araneae: Lycosidae), an australian wolf spider. *Oecologia*, **21**: 291-311.

HUMPHREYS, W. F. 1983. Temporally diphasic dispersal in siblings of a wolf spider: a game of Russian roulette? *Bulletin of the British Arachnological Society*, **6**: 124-126.

HUSTON, M.A. & D. L. DEANGELIS 1987. Size bimodality in monospecific populations: a critical review of potential mechanisms. *American Naturalist*, **129**: 687-707.

KIM, K.W. & C. ROLAND 2000. Trophic egg laying in the spider, Amaurobius ferox: mother-offspring interactions and functional value. *Behavioural Processes*, **50**: 31-42.

MARSHALL, S. D. & J. L. GITTLEMAN 1994. Clutch size in spiders: is more better? *Functional Ecology*, **8**: 118-124.

MICHIMAE, H. & M. WAKAHARA 2002. Variation in cannibalistic polyphenism between populations in the salamander Hynobius retardatus. *Zoological Science*, **19**: 703-707.

MOCK, D.W., G. A. PARKER & P. L. SCHWAGMEYER 1998. Game theory, sibling rivalry, and parent-offspring conflict. In: *Game Theory and Animal Behavior*. Dugatkin, L A. & Reeve, H. K. (eds.). Oxford Univ. Press. Oxford. Pp. 146-167.

MOYA-LARAÑO, J. 1999. Limitación por el alimento, territorialidad y canibalismo en la tarántula medirerránea, *Lycosa tarentula* (L.). (PhD dissertation) (microfish format). Autonomous University of Barcelona, Barcelona, Spain.

MOYA-LARAÑO, J. 2002. Senescence and food limitation in a slowly ageing spider. *Functional Ecology*, **16**: 734-741.

MOYA-LARAÑO, J., J. A. BARRIENTOS & J. M. ORTA-OCAÑA 1998. Possibles efectes de l'incendi de 1994 en una població de tarantula mediterrània. In: *II Trobades d'estudiosos del Garraf*. Monografies, 26. Diputació de Barcelona. Barcelona. Pp. 121-124.

MOYA-LARAÑO, J., J. A. BARRIENTOS & D. H. WISE 2000. Tria activa dels llocs de cacera a la taràntula mediterrània. In: *III Trobada d'estudiosos del Garraf*. Monografies, 30. Diputació de Barcelona. Barcelona. Pp. 101-103.

MOYA-LARAÑO, J., J. M. ORTA-OCAÑA, J. A. BARRIENTOS, C. BACH & D. H. WISE 2002. Territoriality in a cannibalistic burrowing wolf spider. *Ecology*, **83**: 356-361.

MOYA-LARAÑO, J., J. M. ORTA-OCAÑA, J. A. BARRIENTOS, C. BACH & D. H. WISE 2003a. Intriguing compensation by adult female spiders for food limitation experienced as juveniles. *Oikos,* **101**: 539-548.

MOYA-LARAÑO, J., J. M. ORTA-OCAÑA, J. A. BARRIENTOS & A. CASES 1996. Dynamics of a population of burrowing wolf spiders. Is there any competition? *Revue Suisse de Zoologie* (Special issue) Volume hors série: 491-499.

MOYA-LARAÑO, J., P. TAYLOR & C. FERNÁNDEZ-MONTRAVETA 2003b. Body patterns as potential amplifiers of size and condition in a territorial spider. *Biological Journal of the Linnean Society*, **78**: 355-364.

ORTA, J.M., J. MOYA & J. A. BARRIENTOS 1993. Datos fenológicos de una población de *Lycosa tarentula fasciiventris* L. Dufour, 1835, en el Noroeste de la Península Ibérica (Araneae, Lycosidae). *Bollettino della Accademia Gioenia di Scienci Naturali*, **26**(345): 15-26.

PARELLADA, X. 1998. Identificació i dades biològiques de tres espècies de taràntules (Araneae: Lycosidae) al Garraf. In: *II Trobades d'estudiosos del Garraf*. Monografies, 26. Diputació de Barcelona. Barcelona. Pp. 15-25.

PECK, W.B. & W. H. WHITCOMB 1970. Studies on the biology of a spider *Chiracanthium inclusum* (Hentz). *Bulletin of the Arkansas Experimental Station*, **753**: 3-76.

POLIS, G.A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, **12**: 225-251.

ROVNER, J. S., G. A. HIGASHI & R. F. FOELIX 1973. Maternal behavior in wolf spiders: the role of abdominal hairs. *Science*, **182**: 1153-1155.

SAMU, F., S. TOFT & B. KISS 1999. Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae). *Behavioural Ecology and Sociobiology*, **45**: 349-354.

SAS INSTITUTE. 1990. *User's Guide*. Cary. North Carolina.

SOKAL, R.R. & F. J. ROHLF 1995. *Biometry*. Freeman. New York.

TABACHNICK, B.G. & L. S. FIDELL 2001. *Using multivariate statistics*. 4th ed. HarperCollins. New York.

TOONEN, R. J. & J. R. PAWLIK 2001. Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertabrate. *Evolution*, **55**: 2439-2454.

TRIVERS, R. L. 1974. Parent-offspring conflict. *American Zoologist*, **14**: 249-264.

VALERIO, C. E. 1974. Feeding on eggs by spiderlings of *Achaearanea tepidatorium* (Araneae, Theridiidae), and the significance of the quiescent instar in spiders. *Journal of Arachnology*, **2**: 57-63.

WALLACE, H. K. 1937. The use of the headlight in collecting nocturnal spiders. *Entomological News*, **48**: 107-111.

WHITEMAN, H. H., J. P. SHEEN, E. B. JOHNSON, A. VANDEUSEN, R. CARGILLE & T. W. SACCO 2003. Heterospecific prey and trophic polyphenism in larval tiger Salamanders. *Copeia*, **2003**: 56-67.

WYSZOMIRSKI, T. 1992. Detecting and displaying size bimodality: Kurtosis, skewness and bimodalizable distributions. *Journal of Theoretical Biology*, **158**: 109-128.