Individual variation in ballooning dispersal by black widow spiderlings: The effects of family and social rearing

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Abstract Individual behavioral variation is ubiquitous across taxa and important to understand if we wish to fully use behavioral data to understand the ecology and evolution of organisms. Only recently have studies of individual variation in dispersal behavior become a focus of research. A better understanding of individual variation in dispersal behavior is likely to improve our understanding of population dynamics. In particular, the dynamics of critically small populations (endangered species) and large populations (pest species) may be driven by unique dispersal variants. Here we documented individual variation in the ballooning dispersal behavior of Western black widow spiderlings Latrodectus hesperus, an urban pest species found in superabundant infestations throughout cities of the desert Southwest USA. We found a great deal of family-level variation in ballooning dispersal, and this variation was highly consistent (repeatable) across time. Maternal egg investment was a poor predictor of this ballooning dispersal. Instead, we show that spiderlings reared in isolation are significantly slower to disperse than spiderlings raised in a more natural setting surrounded by full siblings. Thus, our study examines a widespread but poorly understood dispersal behavior (ballooning), and suggests urban pest population dynamics are likely driven by the interaction of variation in individuals, families and social environments [Current Zoology 61 (3): 520–528, 2015].

Keywords Individual variation, Dispersal, Spiders, Ballooning, Social rearing

Studies of individual variation are very common in the field of animal behavior (Sih et al., 2004, 2010, 2012). This recent surge of interest in individual behavioral variation has covered topics as far ranging as life-history trade-offs (Nicolaus et al., 2015; Schuett et al., 2015), sexual selection (Schuett et al., 2010), sexual cannibalism (Johnson and Sih, 2005), foraging voracity (Pintor et al., 2008), enemy avoidance (Dosmann et al., 2015) and social behavior (King et al., 2015). These works have demonstrated how ubiquitous individual variation is across species and phenotypic traits, and we now better appreciate the important role that individual variation plays in understanding critical issues in ecology and evolution such as extinction (Gonzalez-Suarez and Revilla, 2013), group dynamics (Holbrook et al., 2014), assortative mating (Potts et al., 1991; Steinmeyer et al., 2013), dispersal (Saino et al., 2014), invasion ecology (Pintor et al., 2008), and the maintenance of genetic variation (Dochtermann et al., 2015).

Most simply, natal dispersal is a behavioral ecological phenomenon that involves the permanent movement of individuals away from their birth site (Howard, 1960). Indeed, this simple definition is perhaps no longer sophisticated enough to support the growing field of dispersal ecology (reviewed in Bowler and Benton, 2005; Baguette et al., 2013). While we know dispersal behavior can vary between (Dahirel et al., 2015) and within (Greenwood and Harvey, 1982) species, a recent surge of studies have begun to ask how individual variation influences dispersal (Bonte and Lens, 2007; Bonte et al., 2009; Bowler and Benton, 2009; Hawkes 2009; Cote et al., 2010). Focusing on individual variation in dispersal behavior can yield powerful insights into changing population dynamics and genetic structure. For example, Debeffe et al. (2012) found that in the European roe deer Capreolus capreolus individuals significantly differed from one another in their dispersal distance. Here, dispersal distance increased linearly with body mass such that large individuals dispersed far from their natal range while small individuals were philopatric. This dispersal pattern has interesting implications for the natal herd as its phenotypic distribution shifts in favor of small, nondispersing individuals. Indeed, the failure to disperse by historically solitary taxa has been viewed as a necessary precondition for the evolution of sociality (Corcobado et al., 2012).
While many aspects of individual behavioral variation are attributable to genetic underpinnings (Bonte et al., 2007; Patrick et al., 2013), environmental effects also play an important role in shaping individual variation (Bengston et al., 2014; Scandolara et al., 2014). For example, an organism’s recent foraging success and/or body condition may influence its dispersal latency. Low energy reserves may motivate organisms to disperse sooner and/or further in search of food or resources (Mestre and Bonte, 2012; Rugiero et al., 2012), or alternatively high body condition may be required to make costly dispersal behaviors possible (Stamps, 2006).

As many organisms disperse soon after their egg/larval period, maternal investment in eggs may determine the dispersing organism’s body condition and dispersal latency (Massot and Clobert, 1995; Mestre and Bonte, 2012). For example, juvenile dwarf spiders Erigone dentipalpis are most reluctant to disperse after 2 generations of sustained food abundance (Mestre and Bonte, 2012). Starvation of either the parental or offspring generation has the effect of motivating spiderlings to disperse.

Additionally, an individual’s propensity to disperse could be strongly influenced by the social environment in which they were reared. The benefits of group living are commonly cited to explain why individuals fail to disperse (Jones and Parker, 2002). However, natal social environments can also result in competition among siblings, cannibalism/siblicide, and increased risk of inbreeding (Scandolara et al., 2014), thus making the potential costs of being philopatric high.

Spiders have been used as a model in studying dispersal and the environmental factors that influence it (Bonte, 2009; Johansson et al., 2012; Mestre and Bonte, 2012; Mestre et al., 2014). For example, many spiders employ a unique form of dispersal (ballooning). Ballooning involves passive, airborne dispersal in which small spiderlings release silk strands and are carried away on wind updrafts (Decae, 1987). Charles Darwin himself described this behavior in his journals while 60 miles off the coast of Argentina—noting that hundreds of tiny spiders were being caught in the sails of their ship, only to re-launch themselves on so-called ‘gossamer threads’ to continue their own oceanic voyage. As fascinating and impressive as ballooning behavior is, it remains relatively poorly understood, perhaps because researchers have been reluctant to try and quantify a behavior that usually involves such long distance travel (but see Bonte et al., 2007; Bonte, 2009; Mestre and Bonte, 2012; Mestre et al. 2014 for elegant studies of ballooning). Spiders have otherwise proven outstanding subjects for studies of individual variation across a variety of traits including foraging, web building/repair (Keiser et al., 2014), aggression (Kralj-Fiser and Scheider, 2012; Shearer and Pruitt, 2014), activity level (Shearer and Pruitt, 2014), and social behavior (Pruitt et al., 2011), making them particularly well suited for the study of how individual behavioral variation can influence dispersal.

1 Materials and Methods
1.1 Study system

Widow spiders (Latrodectus spp.) are often considered a troublesome pest taxa due to: 1) their propensity to form densely populated urban and agricultural infestations (Muller, 1993; Costello and Daane, 1998; Trubl et al., 2012), 2) their potential to invade non-native regions following long distance human-mediated dispersal events (Garb et al., 2004), 3) the negative side effects of the frequent use of widespread pesticide application to combat widow infestations (Johnson, personal observation) and 4) the toxicity of widow venom to humans (Lewitus, 1935; Orlova et al., 2000; Brown et al., 2008). The Western black widow Latrodectus hesperus has been the subject of past studies of consistent individual variation (Pruitt et al., 2011), but recent work in our laboratory has emphasized how incredibly plastic the black widow’s phenotype is (Halpin and Johnson, 2014).

Black widow spiderlings will balloon in a laboratory setting as young spiderlings (see Methods below), but we know nothing about the mechanisms that might shape individual variation in this behavior. Black widow sibships begin as a mass of eggs encased within a silken egg sac (D’Amour et al., 1936; Kaston, 1970). Field collections of egg sacs yield a range of egg numbers from 175 to 300 eggs per egg sac (Johnson et al., 2012). Individual eggs hatch within the egg sac after approximately 14 days (Kaston, 1970) and begin immobile pre-larval and larval periods (Foelix, 1996). Following the larval period, spiderlings begin a more mobile nymphal stage (approximately 7–14 days) in which they are active within the egg sac, usually molting one time before chewing their way out of the egg sac approximately 4 weeks after egg sac deposition (Kaston, 1970). Perhaps due to the drought-adapted nature of this organism, we have found black widow eggs to survive well outside of their egg sac, thus making them very conducive to developmental studies (Johnson et al., 2010; Johnson et al., 2012; Johnson et al., 2014; Still et
al., 2014). Specifically, egg sacs can be opened the day after they are laid, and individual eggs can be imaged, weighed, reared in isolation and tracked through development phases that usually occur within the egg sac. Upon emergence from the egg sac, spiderlings are initially densely congregated in their mother’s web for a period of approximately 7–14 days before dispersing to build solitary webs (Kaston, 1970).

Here we test for the presence and causes of individual variation in ballooning dispersal in *L. hesperus*. We hypothesize that juvenile black widow ballooning dispersal is typified by high levels of individual variation and that this variation is influenced, at least in part, by maternal egg investment and early social environment. Specifically, we predict that: 1) black widow lineages (full sibships) will affect average dispersal behavior, and that individuals within each lineage will be characterized by high degrees of consistent (repeatable) individual variation in ballooning behavior, 2) after accounting for egg investment, social rearing (i.e. increased sibling competition and cannibalism risk) will speed dispersal (de Meester and Bonte, 2010).

1.2 Methods

During the spring of 2014, penultimate-stage juvenile black widows were collected from urban habitats across metropolitan Phoenix, AZ (e.g. schoolyards, dumpsters, parking lots). Spiders were reared in the laboratory at room temperature (24.5°C) in plastic containers (10 × 10 × 12 cm). Females were each fed one 5-week old cricket *Acheta domesticus* weekly until they matured. Upon maturity, virgin females were paired with a virgin male and allowed to cohabit for 5 days before males were removed.

We checked females daily and found that eleven females (representing eight different sites) made an egg sac within 10 days of male removal. We call the day we found the egg sac “egg day 1”. On egg day 2, egg sacs were cut open and 100 eggs were weighed (µg) and digitally imaged using a Canon PowerShot 620 camera. ImageJ software was used to measure the area of each egg (mm²). Eggs were raised individually in small transparent plastic containers (4 × 4 × 5 cm). A square piece of cotton was placed on the bottom of the box to cushion eggs from damage. A pair of toothpicks was adhered to the side of each box in a tilted “X” formation to serve as a three-dimensional substrate for eventual webbuilding. Any remaining eggs in an egg sac after 100 were weighed and imaged were placed into a communal plastic container (4 × 4 × 5 cm) and allowed to develop with their full siblings. Neither these “social” spiderlings nor the “solitary” spiderlings described above were fed during the experiment. While social spiderlings had the opportunity to cannibalize their siblings, our previous work shows that even the most cannibalistic families refrain from sibling cannibalism until after day 31, when we began dispersal assays (see below).

1.3 Experimental arenas

Assays were conducted in a transparent 72-liter plastic tub (57 × 38 × 33 cm) filled with water to 1–2 cm depth to discourage spiderlings from dispersing on the ground (see Fig. 1). One piece of Styrofoam was cut into a hexagonal launching platform with half of the sides measuring 7 cm and the other half measuring 2.5 cm. At the start of each trial, filter paper was placed onto the launching platform. A 25 cm long bamboo stick was pushed into the platform 1 cm from the Styrofoam’s edge. This stick was oriented at a 45° angle so that it leaned over the edge of the Styrofoam launching platform. Two 13 cm long bamboo sticks were pushed into the middle of the platform and angled to contact the larger stick halfway up in a triangular formation. Both the filter paper and bamboo skewers were replaced between trials in order to minimize exposure to chemical cues from previous spiderlings.

![Fig. 1 The experimental container for our dispersal assays](https://example.com/figure1.png)

A second, larger Styrofoam piece was cut into a right trapezoid with the rectangular portion measuring 20 × 28 cm and the triangle measuring 28 × 15 × 31 cm. This piece served as a landing platform. An 18-cm high strip of mesh was glued to three skewers and attached along the two sides of this platform parallel to the sides of the tub. Both the right trapezoidal piece and the mesh “net” served as substrates on which dispersed spiderlings could land. A single-speed, miniature fan (Room Essentials 14.2 × 14.9 × 8.8 cm) was stationed on the exterior of the tub (12 cm outside and 5 cm above the tub facing the corner containing the launching platform). This fan
provided an unmeasured, but constant, wind source that proved suitable for ballooning.

1.4 Dispersal Trials

We conducted standardized dispersal trials to measure individual activity and latency to disperse of spiderlings. Dispersal trials took place at room temperature (24.5°C) with the lights on. While ballooning typically occurs in the dark cycle, we were concerned that trials in the dark would result in lost spiderlings. Regardless, we found spiderlings very eager to balloon during the light cycle (see below). The first set of trials for each family was conducted on Day 31 after egg sac production. Ten social and 10 solitary spiderlings from each family were selected at random for dispersal trials. For each trial a single individual spiderling was placed onto the launching platform. Spiderlings were allowed to climb on the end of a paintbrush and gently tapped into the experimental container. Every 60 seconds spiderlings were scored as either active or inactive. A score of “active” included any form of movement (e.g. walking, grooming, etc), and spiderling activity was estimated as the proportion (arc-sin transformed) of intervals where spiderlings were found active. The fan was turned on after 5 minutes of acclimation and left on until the end of the trial. We recorded the latency until each spiderling ballooned (i.e. launched horizontally and traversed to the landing platform). Trials were suspended after 15 minutes if a spiderling had not yet launched. After trials, solitary spiderlings were returned to their boxes and repeated measures were obtained on days 34 and 37. Social spiderlings were only assayed a single time on day 31.

1.5 Statistical analyses

All data met assumptions of normality and analyses were performed using SPSS version 18.0 (SPSS, 2009). We used simple univariate ANOVA with family entered as a random factor to establish the influence of family on our dependent measures. From that point forward, we relied on mixed models that included family as a random factor and either repeated measure or social rearing treatment as a fixed factor. To assess behavioral repeatability (i.e. individual consistency across repeated measures) we used the intraclass correlation coefficient. Dependent measures included spiderling activity and latency to ballooning dispersal.

2 Results

2.1 Family effects

As has been shown before (Johnson et al., 2014), we again found in the current study that egg mass ($F_{10,96} = 76.3, P < 0.0001$, see Fig. 2A) and egg size ($F_{10,96} = 66.8, P < 0.0001$) show very little variation among full-siblings ($n = 10$ per family) relative to the variation seen among families ($n = 11$). Furthermore, based on family averages, egg mass and egg size shared a strong
positive relationship \((R^2 = 0.66, F_{1,9} = 15.6, P = 0.004)\). Perhaps surprisingly, these two egg parameters had similarly weak effects on spiderling behavior, and below we only report analyses involving egg mass. Egg mass had no predictive relationship with either spiderling activity \((F_{1,9} = 0.02, P = 0.88)\) or latency to dispersal \((F_{1,9} = 0.38, P = 0.55)\). Family activity level did not predict latency to dispersal \((F_{1,9} = 3.11, P = 0.11)\).

Family effects also played a significant role in explaining variation in dispersal tendencies on day 31 (see Fig. 2C; \(R^2 = 0.492, F_{10,96} = 9.30, P < 0.0001\)), but not general activity levels (see Fig. 2B; \(R^2 = 0.156, F_{10,96} = 1.77, P = 0.08\)). Repeated measures following on days 34 and 37 showed similar results (Dispersal: all \(R^2 > 0.325, P < 0.0001\); Activity: all \(R^2 < 0.166, all P > 0.05\)). As such, we show great family-level variation in the majority of our dependent measures and below report mixed models that include family as a random factor.

### 2.2 Behavioral consistency

Overall, spiderlings showed no significant differences across repeated measures on days 31, 34 and 37 in their activity levels (see Fig. 3A: repeated measures: \(F_{2,122.1} = 2.62, P = 0.08\); family: Wald \(Z = 0.73, P = 0.47\)). In contrast, we found spiderlings significantly quicker to disperse on days 34 and 37 compared to day 31 (see Fig. 3B: repeated measures: \(F_{2,121.4} = 5.52, P = 0.005\); family: Wald \(Z = 3.13, P = 0.002\)). In addition, individual spiderlings were repeatable in their behavior: activity levels (intraclass correlation coefficient = 0.120, \(F_{106,212} = 1.41, P = 0.02\)), dispersal latency (intraclass correlation coefficient = 0.484, \(F_{106,212} = 3.81, P < 0.0001\)).

### 2.3 Effects of social rearing

Restricting our analysis to day 31 assays when we ran trials on both individuals raised in isolation from day 1 and individuals raised in “social” family groups, we found that spiderlings raised socially were both significantly more active (see Fig. 4A; social rearing: \(F_{1,201.2} = 17.98, P < 0.0001\); family: Wald \(Z = 1.37, P = 0.17\) and dispersed significantly sooner (see Fig. 4B; social rearing: \(F_{1,197.7} = 20.76, P < 0.0001\); family: Wald \(Z = 1.98, P = 0.05\)).

### 3 Discussion

We found a great deal of family-level variation in egg parameters and spiderling activity and dispersal,
though egg investment was a poor predictor of these spiderling behaviors. Ballooning dispersal proved to be both a highly repeatable trait and also significantly slower on day 31 relative to days 34 and 37. Lastly, social rearing produced spiderlings that were significantly more active and quick to disperse. Below we discuss the implications of these findings.

3.1 Consistent individual variation and family effects

We have shown previously that a great deal of the black widow’s early behavior and life history is influenced by a strong family effect (Johnson et al., 2010, 2014). For example, egg mass, larval development speed and sibling cannibalism tendency are all typified by low levels of variation among full siblings and high levels of variation among families. Here we add spiderling activity and ballooning dispersal to that list—showing that some families are almost three times faster to balloon than others (Fig. 2C). Furthermore, despite the fact that spiderlings tend to balloon faster as they age (see Fig. 3B), individual variation in ballooning latency is a relatively consistent trait at the individual level across the first week that spiderlings emerge from the egg sac when dispersal becomes possible.

Taken together, these data suggest that family effects are driving individual variation in an important ecological trait that has implications for the population dynamics of this urban pest species. For example, our data suggest that some families of black widows are very reluctant to disperse, and this reluctance is maintained 1) by every single individual tested in the family, and 2) across three developmental repeated measures. These extreme families may represent relatively philopatric lineages, which by staying close to home exacerbate localized urban infestations of black widows. Philopatry may offer a greater adaptive reward for exploiters of spatially homogenized habitats like cities if there is a very low probability that dispersal within a city leads to a better habitat. However, we have actually found high degrees of spatial heterogeneity in urban black widow population parameters (Trubl et al., 2012). As such, philopatric black widows may suffer fitness costs. In addition, as urban philopatry becomes more common, urban pests are likely subject to novel selection pressures such as inbreeding depression (Tabadkani et al., 2012). Interestingly, we have found no evidence that adult male black widows exhibit mating preferences that would be consistent with inbreeding avoidance (Bratsch and Johnson, in preparation).

Families, of course, share both genetic variation and environmental variation. Our data show a tight relationship between the area of an egg and its initial mass, but we found no relationship whatsoever between egg investment and spiderling activity and dispersal. Indeed, our past work indicates that egg and larval development speed is shaped by egg investment, but we have yet to find any spiderling behavior that is influenced by egg investment (foraging voracity, sibling cannibalism: Johnson et al., 2014; activity and dispersal: present data). Thus, we found no trends that would be consistent with a maternal effect of egg investment driving dispersal behavior. However, a manipulation of maternal body condition would be required to fully test this possibility (e.g. Mestre and Bonte, 2012). Given that our laboratory studies strive to control every other variable in parental environments (e.g. temperature, age, food availability, photoperiod), we suggest our data are consistent with genetic variation underlying family-level variation in dispersal. Paternal ½ sibling designs and/or selection experiments (perhaps designed to try and artificially select for highly philopatric lineages) would be required to more fully document genetic variation underlying these traits.

3.2 Social rearing effects on ballooning dispersal

We found that spiderlings raised socially with their full siblings were significantly more active and quicker to disperse than spiderlings that were separated from clutchmates as eggs and raised in isolation. Of course, this social rearing is far more representative of the natural setting in which black widows develop in the egg sac, and later in the maternal web, alongside hundreds of siblings. Nevertheless, it is interesting to note that this otherwise solitary, agonistic, territorial, cannibalistic spider relies upon early social experiences to shape its behavior and life history. In addition, many laboratory studies take advantage of the opportunity to rear individuals in isolation so as to better understand the biology of replicate individuals. Indeed, the current emphasis on consistent individual variation often requires laboratory studies to isolate individuals so as to allow the researcher to keep track of individuals across trials. Our data suggest that such protocols can alter the behavior of arthropods in unanticipated ways (see also Carducci and Jakob, 2000).

In general, differences in sociality in spiders are negatively correlated with dispersal tendencies (Corcobado et al., 2012), with nonsocial spiders having a greater ability to disperse over large distances (Johannesen et al., 2012). That said, for non-social species, early social cues may be critical in stimulating dispersal, as we show here for black widows. Several adaptive explana-
tions exist for social cues promoting dispersal. Living with one’s siblings may provide chemical cues in the maternal silk (Johnson et al., 2011) or in sibling cuticular hydrocarbons (Grinsted et al., 2011) that facilitate kin recognition and speed dispersal so as to avoid sibling cannibalism, sibling competition, and even later inbreeding opportunities. More simply, density dependence may prompt crowded spiderlings to disperse faster to reduce competition regardless of relatedness. Indeed, among subsocial spiderlings, food restriction hastens dispersal from natal habitat (Ruttan, 1990; Kim, 2000). If this is the case, it should be restated that all of our dispersal assays were performed on isolated spiderlings. As such, if “social” spiderlings are dispersing faster to avoid competition, this perceived competition was acquired during social rearing, but was absent at the time of the spiderling’s actual dispersal.

In conclusion, our survey of the ballooning dispersal behavior of black widow spiderlings suggests that individuals vary according to family and communal rearing but not egg investment. A better understanding of individual variation in dispersal behavior is likely to improve our understanding of population dynamics. In particular, pest populations such as urban black widow infestations may be triggered by unique dispersal variants. Mechanistically, we have shown that family variation alone may provide the necessary phenotypic variation for selection to act upon. If urban resource abundance has eliminated the benefits of ballooning dispersal, then selection may favor philopatry among urban black widows. For example, urban habitats may make ballooning dispersal costly if the probability of dispersing to a habitat as rich as the natal site is low, or if urban ballooning involves unusual mortality risks. Future works should quantify levels of genetic variation within and among urban habitat to determine levels of gene flow in urban black widows.

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References

Baguette M, Blanchet S, Legrand D, Stevens VM, Turlure C, 2013. Individual dispersal, landscape connectivity and ecological networks. Biol. Rev. 88(2): 310–326.

Bengston SE, Pruitt JN, Riechert SE, 2014. Differences in environmental enrichment generate contrasting behavioural syndromes in a basal spider lineage. Anim. Behav. 93: 105–110.

Bonte D, Lens L, 2007. Heritability of spider ballooning motivation under different wind velocities. Evol. Ecol. Res. 9: 1–11.

Bonte D, 2009. Inbreeding depresses short and long distance dispersal in three congeneric spiders. J. Evolution Biol. 22(7): 1429–1434.

Bonte D, De Clercq N, Zwertvaegher I, Lens L, 2009. Repeatability of dispersal behavior in a common dwarf spider: Evidence for different mechanisms behind short- and long-distance dispersal. Ecol. Entomol. 34(2): 271–276.

Bonte D, Van Belle S, Maelfait J, 2007. Maternal care and reproductive state-dependent mobility determine natal dispersal in a wolf spider. Anim. Behav. 74: 63–69.

Bowler DE, Benton TG, 2005. Causes and consequences of animal dispersal strategies: Relating individual behavior to spatial dynamics. Biol. Rev. 80: 205–225.

Bowler DE, Benton TG, 2009. Variation in dispersal mortality and dispersal propensity among individuals: The effects of age, sex and resource availability. J. Anim. Ecol. 78(6): 1234–1241.

Brown KS, Necaise JS, Goddard J, 2008. Additions to the known U.S. distribution of Latrodectus geometricus (Araneae: Theridiidae). J. Med. Entomol. 45: 959–962.

Carducci JP, Jakob EM, 2000. Rearing environment affects behavior of jumping spiders. Anim. Behav. 59: 39–46.

Corcobado G, Rodríguez-Gironés MA, Moya-Laraño J, Avilés L, 2012. Sociality level correlates with dispersal ability in spiders. Funct. Ecol. 26: 794–803.

Costello MJ, Daane KM, 1998. Influence of ground cover on spider populations in a table grape vineyard. Ecol. Entomol. 23: 33–40.

Cote J, Colbert J, Brodin T, Fogarty S, Sih A, 2010. Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. Philos. Trans. Roy. Soc. B. 365: 4065–4076.

D’Amour FE, Becker FE, van Riper W, 1936. The black widow spider. Q. Rev. Biol. 11: 123–160.

Dahirel M, Olivier E, Fuiller A, Martin MC, Madec L, Ansart A, 2013. Movement propensity and ability correlate with ecological specialization in European land snails: Comparative analysis of a dispersal syndrome. J. Anim. Ecol. 84: 228–238.

De Meester N, Bonte D, 2010. Information use and density-dependent emigration in an agrobiont spider. Behav. Ecol. 21: 992–998.

Debeffe L, Morellet N, Cargnelutti B, Lourtet B, Bon R et al., 2012. Condition-dependent natal dispersal in a large herbivore: Heavier animals show a greater propensity to disperse and travel further. J. Anim. Ecol. 81: 1327–1337.

Decaë AE, 1987. Dispersal: Ballooning and other mechanisms. In: Nentwig W ed. Ecophysiology of Spiders. Berlin & Heidelberg: Springer Verlag, 348–356.

Dochtermann NA, Schwab T, Sih A, 2012. Condition-dependent natal dispersal in a large herbivore: Heavier animals show a greater propensity to disperse and travel further. J. Anim. Ecol. 81: 1327–1337.

Edwards FM, 1996. The Biology of Spiders, 2nd edn. New York: Oxford University Press.

Garb JE, Gonzalez A, Gillespie RG, 2004. The black widow spider genus Latrodectus (Araneae: Theridiidae): Phylogeny, bio-
Sih A, Cote J, Evans M, Fogarty S, Pruitt J, 2012. Ecological implications of behavioural syndromes. Ecol. Lett. 15: 278–289.
Sih A, Stamps J, Yang LH, McElreath R, Ramenofsky M, 2010. Behavior as a key component of integrative biology in a human-altered world. Integ. Comp. Biol. 50: 934–944.
SPSS Inc. 2009. PASW Statistics for Windows, Version 18.0. Chicago: SPSS Inc.
Stamps JA, 2006. The silver spoon effect and habitat selection by natal dispersers. Ecol. Lett. 9: 1179–1185.
Steinmeyer C, Mueller JC, Kempenaers B, 2013. Individual variation in sleep behaviour in blue tits Cyanistes caeruleus: Assortative mating and associations with fitness-related traits. J. Avian Biol. 44: 159–168.
Still M, Gburek T, Miles L, Johnson JC, 2014. Adverse effects of fluorescent dust marking on the behavior of western black widow spiderlings. Entomol. Exp. Appl. 150: 28–31.
Tabadkani SM, Nozari J, Lihoreau M, 2012. Inbreeding and the evolution of sociality in arthropods. Naturwissenschaften 99: 779–788.
Trubl P, Highfill T, Miles L, Johnson JC, 2012. Black widows in an urban desert: Population variation in an arthropod pest across metropolitan Phoenix. Urban Ecosyst. 15: 599–609.