2010. The Journal of Arachnology 38:313–318

Is movement behavior of riparian wolf spiders guided by external or internal information?

Kevin Lambeets, Jelka Van Ranst and **Dries Bonte**: Terrestrial Ecology Unit (TEREC), Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium. E-mail: kevin.lambeets@gmail.com

Abstract. Orientation is an essential process preceding movement behavior. Information necessary for orientation toward suitable habitat can be gathered by acute and internal information. The former comprises directly detectable, external stimuli, whereas internal information includes earlier experienced environmental cues and inherited information related to an individual's origin. In habitats that can suddenly be disturbed (such as river banks), an accurate orientation is of prime importance for successful movement toward safe habitat. In a common-garden field experiment, we studied between-population variation in movement responses toward safe winter habitat (dike vegetation) of two sympatric riparian wolf spiders, the stenotopic riparian species *Pardosa agricola* (Thorell 1856) and the generalist *P. amentata* (Clerck 1757). Both responses to direct visual cues and orientation toward home habitat were investigated on an unfamiliar river bank upstream from the original populations. Movement toward safe habitat was mainly controlled by previously collected information on the riverbank location in the stenotopic species and additionally influenced by visual cues and the prevailing weather conditions. Movements in *P. amentata* were flexible and not systematically guided by either internal information or direct visual cues. Experience on the location of safe habitat consequently guided orientation in the stenotopic species. Internal information is therefore hypothesised to favor the stenotopic wolf spider by restricting unnecessary movements when sudden threatening situations emerge. Generalist species have less experience with the specific disturbance and do not show pronounced orientation capabilities toward safe habitat.

Keywords: Between-population variation, Lycosidae, orientation behavior, *Pardosa agricola*, *Pardosa amentata*

Efficient movement toward safe habitat is essential when sudden perturbations occur in the currently occupied habitat (Zollner & Lima 1999, 2005; Fahrig 2007). Optimal movements should therefore be preceded by precise orientation behavior. This orientation should be based on information either collected instantaneously from the local environment or based on internal information collected during an individual's life or on information shaped by natural selection (Dall et al. 2005).

Homeward orientation mechanisms, for instance, unidirectional zonal recovery in intertidal zones [e.g., sandhoppers (Borgioli et al. 1999a; Ugolini 2001), wolf spiders (Morse 2002)], are considered to be beneficial risk-avoiding strategies. Homeward orientation may lead to profitable outcomes in familiar environments, guiding such cursorial organisms as wolf spiders directly toward suitable conditions (Morse 1997, 2002). Visually detectable cues, either local landmarks such as vegetation structure (e.g., Bonte et al. 2004) or celestial cues (e.g., Papi 1955), also contribute to accurate orientation. By gathering information from the environment, organisms reduce the ecological uncertainty of that environment (Wehner 1997; Dall et al. 2005), eventually leading to movement or dispersal (Lima & Zollner 1996; Pulido 2007). Perception, however, mainly depends on an organism's sensory abilities (Wehner 1997). For cursorial spiders in particular, there is no doubt that detectable factors are integrated into orientation and movement decisions (Land 1971; Persons & Uetz 1996; Ortega-Escobar & Muñoz-Cuevaz 1999; Norgaard et al. 2007; Rypstra et al. 2007).

Organisms may also rely on information collected during their life or on inherited movement rules (Pullido 2007; Clobert et al. 2009). In this case, organisms do not need to spend time and energy to collect information on the most advantageous movement direction and rely on internally shaped movement rules (Papi & Tongiorgi 1963; Borgioli et al. 1999a; Morse 2002). However, since inherited information and experience might deceive an organism in unfamiliar or quickly changing conditions (Schlaepfer et al. 2002), their importance is relative to detectable sources of external information (Wehner 2003; Bowler & Benton 2005; Danchin et al. 2008). Moreover, orientation can be refined by learning (Papi & Tongiorgi 1963; Scapini et al. 1988; Collet et al. 2001). Learning results from the spatial relationships among objects in the organism's perceptible range and from previous experienced proximate cues (Persons & Uetz 1996; Giraldeau 1997). Since consistent movements shaped by internal movement rules can be disadvantageous (Bowler & Benton 2005), especially for organisms occurring in unpredictably disturbed environments (Lytle & Poff 2004), orientation behavior has to be flexible to some extent. Whenever different modalities that guide orientation decisions are opposed (e.g., accustomed cues on the location of natal or safe habitat vs. celestial information), inaccurate orientation and movement direction might emerge (Papi & Tongiorgi 1963; Borgioli et al. 1999b). Hence, plasticity in orientation or movement behavior will benefit organisms occurring in disturbed environments (Scapini et al. 1988, 2002; Bonte et al. 2007).

It is suggested that experience with long-term characteristics of the environment may be inherited (Danchin et al. 2008). Hence, species that differ in their ecological life history or originate from populations exposed to different environmental conditions possibly respond differently under stressful circumstances by integrating internal and external information in a different way (Dall et al. 2005; Danchin et al. 2008). Since flood events imply severe fitness costs for shore-inhabiting organisms (drowning or washing away), mobile species are expected to show a directed response away from the rising water level (moving ashore) and even withstand flooding during transient inundation events (Rothenbücher & Schaefer 2006; Lambeets et al. 2008). Since flooding is a constant component of the riparian environment, organisms that are familiar with this detectable yet unpredictable factor (riparian stenotopic species) are more likely to transmit knowledge about the directional component 'flooding' across generations than are their generalist congeners (Lytle & Poff 2004). Therefore, populations at opposite sides of the river might be expected to differ in their response to visual cues associated with the riparian environment. As proven by Morse (2002) for the intertidal *Pardosa lapidicina* Emerton 1885, external information, such as substrate structure, guides movements of the wolf spider away from the rising tide. Moreover, movements toward adjacent upland overwintering sites before the onset of long-lasting winter floods have been recorded for mobile, predatory arthropods from river bank habitats (Lang & Pütz 1999; K. Lambeets unpubl. data).

Here, we aimed to determine whether between-population variation in movement responses of riparian wolf spiders before the onset of the long-lasting winter flood remains consistent when they are subjected to different visual stimuli. These wolf spiders are short-lived (two-year life cycle with overwintering subadults), but able to build up experience with flooding during spring and autumn when riverbanks are subject to unpredictable flood events. This hypothesis was tested with two congeneric and sympatric wolf spiders (Lycosidae) with different ecological life histories. We considered the outcome of this orientation behavior as a good proxy for ashore movement toward suitable wintering habitats. *Pardosa agricola* (Thorell 1856) is a stenotopic riparian species (Harvey et al. 2002) that inhabits flood-disturbed riverbanks throughout the year (Lambeets et al. 2007). In contrast, *P. amentata* (Clerck 1757) occurs commonly in a wide range of rather humid habitats and rough growth (Alderweireldt & Maelfait 1988). Thus, the latter is considered to encounter the typical conditions met on riverbanks (e.g., flooding) more sporadically, since the surrounding grasslands are its main habitat. Both species are diurnal and actively hunt across the bare gravel or among the scarce, short riverbank vegetation (K. Lambeets, pers. obs.). Since *P. agricola* spends its life entirely in patchy distributed river banks, it is expected to be familiar with their dynamic character and the spatial arrangement of river bank structures. We therefore expected *P. agricola* to rely predominantly on inherited or experienced sources of information (population of origin) to restrict unnecessary movements. In contrast, cues from the vegetation are expected to act as an orientation landmark for the generalist wolf spider, *P. amentata*, leading to movements toward safe habitat.

METHODS

Experimental field set-up.—During August 2005 and 2006, before the onset of the long-lasting winter flood (Van Looy & De Blust 1995), individuals of *P. agricola* and *P. amentata* were collected from four highly isolated river banks in the downstream section of the Common Meuse. Voucher specimens are deposited at the Royal Museum of Natural History (KBIN) in Brussels. Two isolated populations of both species (mean interpopulation geographical distance = 2504 m ± 532 SE, mean F_{st} = 0.0248 ± 0.0046 SE; Lambeets et al. 2009) were sampled on both sides of the river. Only individuals occurring on the bare gravel were collected. The riverbanks were similar in flooding susceptibility (flooded at 179 m^3/s ± 13 SE), size (area: 10202 m^2 ± 1940 SE) and vegetation structure (Lambeets et al. 2007). Behavioral differences arising from dissimilar stand conditions may consequently be ruled out (Papi & Syrjämäki 1963). All individuals were collected in separate plastic vials with a humid plaster bottom and fed ad libitum with *Drosophila melanogaster* prior to testing (climatic chamber under ambient light conditions and constant temperature, 15° C). Earlier experiments had already shown that a short time under controlled conditions did not change behavior to tactile stimuli (Lambeets & Bonte 2009). Within a week, orientation behavior (ashore movement toward safe habitat, dike vegetation) was tested in a large arena constructed of transparent plexiglass sides (160 × 60 × 25 cm) with the bottom covered by a sand-gravel mixture. The arena was placed on an unfamiliar river bank upstream that was structurally the same as the natal river bank habitat (soft slope, bare gravel for > 20 m from the waterline onwards). Alternately, the arena was positioned directly along the waterline and the dike where vegetation was perceptible. These test locations were approximately 40m apart. For each test, weather conditions (sunny, overcast) were recorded. All spiders were tested in groups of ten individuals per population and per species. The sun was between the southeast and southwest quarter during the tests (Fig. 1). Since the river banks of origin were all oriented in an east-west direction (i.e., for river banks along the right side of the river the dike vegetation was present in the east and the waterline in the west, for banks at the left river side the other way around), diurnal variation in orientation was confined to a minimum. Each group of wolf spiders was successively released in the middle of the arena. We scored whether or not individuals within each group were inclined to move ashore. Ashore movement was considered a proxy for unidirectional orientation; i.e., away from the waterline or toward the dike vegetation. In this way, a simple proportional measure of orientation was recorded as the proportion of individuals moving ashore. For all groups, tests were repeated three times for the test locations (waterline, dike vegetation), but in random order to avoid newly gained experience (cf. Papi & Tongiorgi 1963; Persons & Uetz 1996). If ambient conditions exceeded 30° C the field experiment was stopped to prevent severe dehydration. In total, 28 groups of *P. agricola* and 21 groups of *P. amentata* were tested.

Statistical analysis.—We analysed whether orientation behavior differed according to population of origin (two populations from each river side), weather conditions (sunny, overcast), test locations (visual cues: waterline, dike vegetation) and their interactions. The binomially scored responses were analysed by Generalised Linear Mixed Models with logit-link (GLMM, SAS 9.1.3). Repeated tests and test groups were treated as random factors. Insignificant terms were sequentially removed. Corrected degrees of freedom were calculated by Satterthwait's procedure (Verbeke & Molenberghs 2000). Post-hoc Tukey tests were applied to reveal significant proportional differences in ashore movement.

RESULTS

Wolf spiders clearly differed in their orientation behavior according to their geographical origin, weather conditions and

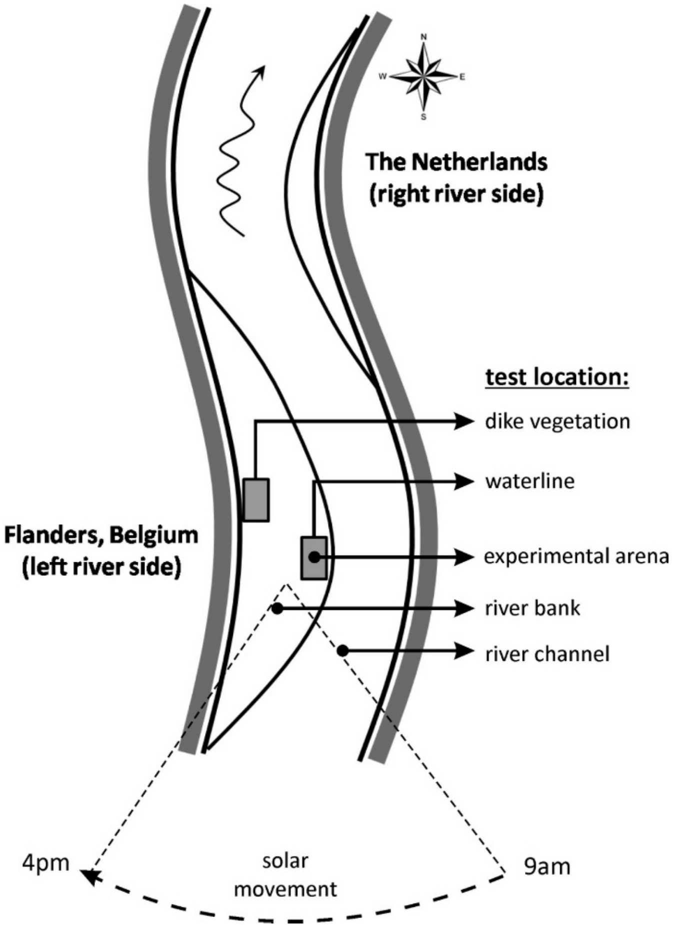

Figure 1.—Experimental field setup to test for orientation behavior preceding movement of riparian wolf spiders along the Common Meuse.

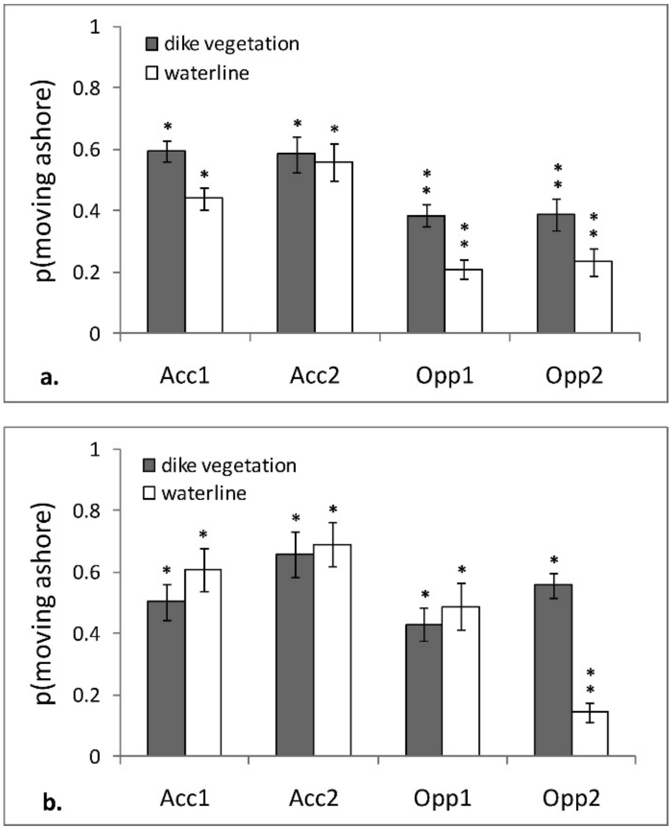

Figure 2.—Estimated mean proportions for orientation behavior per population of a) the stenotopic riparian wolf spider *Pardosa agricola* and b) the generalist *P. amentata*. Four populations, two from each side of the river, were tested during a field experiment, alternately at two locations (waterline, dike vegetation). Acc1, Acc2 indicate individuals collected on the same side of the river (accustomed) as where they were tested; Opp1, Opp2 point to individuals ascending from the opposite side. Columns represent the mean response per population during overcast conditions (see text for differences according to weather and test location). Error bars = standard error of the mean. A different number of asterisks indicate that populations proportionally differed in ashore movement (all $P < 0.001$).

location of testing (location*origin*weather*species: $F_{2,263} = 0.01$, $P > 0.9$; location*origin*species: $F_{3,263} = 4.94$, $P < 0.01$; location*weather*species: $F_{1,263} = 7.29$, $P < 0.01$). Therefore, further analyses were applied for each species separately (Fig. 2a–b).

The effect of origin in orientation behavior was clear for *P. agricola*. Individuals appeared to move ashore more when originating from the same river shore as where tested (accustomed populations) than when they originated from the opposite shore (Fig. 2a, origin: $F_{3,156} = 22.52$, $P < 0.0001$). Moreover, ashore movement increased proportionally when vegetation was perceptible (tests close to the dike vegetation) (+15.3% for location: $F_{1,156} = 28.44$, $P < 0.0001$) and increased marginally under sunny conditions (+6.1% for weather: $F_{1,155} = 3.29$, $P = 0.07$). Other factors were not explanatory (all $F < 1.52$, $P > 0.2$). Behavioral responses of *P. amentata* were more variable. There were no significant differences in orientation outcomes between the accustomed populations (Fig. 2b), nor between populations from different river shores (Fig. 2b: Opp1 vs. Acc1,2). Differences only appeared for those *P. amentata* groups originating from the opposite shore (Fig. 2b: Opp2, location*origin: $F_{3,116} = 7.22$, $P < 0.001$). Sunny weather conditions led to a significantly decreased tendency to move ashore only when tested at the waterline (−41.3% for location*weather: $F_{1,116} = 12.81$, $P < 0.001$), but not when tested adjacent to the dike. Marginally more individuals from accustomed populations of *P. amentata* moved ashore during overcast conditions (origin*weather: $F_{1,115} = 3.87$, $P > 0.05$). All other terms were insignificant (all $F < 2.1$, $P > 0.2$).

DISCUSSION

The stenotopic riparian wolf spider used both directly received information on the vegetation structure and internal information to perform optimal ashore movements toward safe habitat in response to future flooding. In contrast, a more generalist species not strictly bound to the river bank habitat used these sources of information in a less efficient and more variable manner. Our data suggest that inherited factors or experience (population of origin) and detectable external information (dike vegetation, waterline) guide orientation outcomes and movement behavior of wolf spiders on river banks.

Factors underlying variability in orientation of arthropods in unstable environments have been studied mainly in predictably disturbed intertidal zones (e.g., Scapini et al. 1988; Borgioli et al. 1999a,b; Morse 2002). Behavioral responses at infrequently disturbed habitats such as river banks were subject to earlier studies (Papi & Tongiorgi 1963; Papi & Syrjämäki 1963; Bates et al. 2006). These studies, however, merely considered typical riparian species, and did not compare behavioral traits between sympatric congeners (but see Lambeets & Bonte 2009). A comparative approach might elucidate the adaptive value of such behavior. Since a risk-avoiding strategy, thus evading the flood, has an obvious survival value along flood-disturbed shorelines, adjusting movement in response to predictable or sudden detectable environmental variation is essentially advantageous (Jander 1975; Scapini et al. 1999). From this, it is evident that a riparian species, which is assumed to be familiar with flood events (Lytle & Poff 2004), would benefit from weighing costs and benefits of movement by integrating various information sources. This is demonstrated here by the orientation behavior related both to population of origin (inherited information/experience) and externally collected (visual) cues. The two wolf spider species differ in their ecological history (riparian specialist vs. grassland generalist) and colonise the river banks quickly after the floodwater recedes in spring; however, they clearly show different orientation outcomes. Movement behavior can also be expected to change over the season or with the life stage (Papi & Tongiorgi 1963; Scapini et al. 1999), with orientation being mainly directed toward overwintering habitats before the onset of annually reoccurring floods (Lang & Pütz 1999). Correspondingly, Morse (1997) argued that the movement of intertidal wolf spiders increased when they occurred near the waterline (visual cue), and even more when being splashed by surf (tactile cue). On the other hand, Kraus & Morse (2005) clearly associated seasonal habitat shifts of an intertidal wolf spider with environmental variation.

Movements away from safe habitat when tested on the opposite side of the river were detected in the stenotopic riparian wolf spider. Papi & Syrjämäki (1963) proved that *P. agricola* relied on an internal solar compass as well, even adjusting its orientation according to the time of day (time-compensatory mechanisms; Jander 1975). Despite the apparent necessity of sunny conditions for orientation, *P. agricola* behaved more consistently than *P. amentata* under different weather conditions (Fig. 2a, b). Early-life experience with the river bank surroundings, whether visual or tactile, might explain this behavior, which has been suggested for other wolf spiders in disturbed environments as well (Papi & Tongiorgi 1963; Persons & Uetz 1996; Morse 2002). Differences in orientation, however, might be less pronounced after long-term captivity (Papi & Syrjämäki 1963; K. Lambeets, unpubl. data). Ortega-Escobar (2002) and Norgaard et al. (2007) also showed the necessity of external visual input during homing behavior of two wandering spiders. Since *P. amentata* prefers rough growth and grassy habitats, it is expected to lack sufficient information and/or experience for accurate orientation on the river banks and, consequently, to show increased variation in its responses to unfamiliar detectable visual cues in the direct vicinity (Fig. 2b). Therefore, it is expected to orientate primarily on external visual stimuli and much less on inherited information related to its population of origin. Morse (2002) noted similar behavior for *P. lapidicina*, since individuals that were familiar with tidal floods and typical cobble beach structures (scarce vegetation, bare ground) were more reluctant to orientate and move in the appropriate direction than individuals that lacked experience and lived in higher zones with denser vegetation. This might be the most beneficial (or least adverse) strategy for *P. amentata*, because gathering more information might be more costly than responding in a stereotyped way (DeWitt et al. 1998), since the latter will lead individuals directly to suitable habitats in a variety of situations. The presence of the waterline did not lead to an increased ashore movement for *P. amentata*, which indicates it is unfamiliar with the visual perception of flooding (Fig. 2b).

Our results indicate that internal factors related to the population of origin affect orientation outcomes less under benign circumstances than in stressful situations such as being washed offshore (Morse 1997; Lambeets & Bonte 2009). However, Papi & Tongiorgi (1963) and Riechert & Hall (2000) showed the ability of spiders to change their behavior quickly to their own benefit. Experience, for instance with geotactic landmarks such as bank inclination or a humidity gradient (Papi & Tongiorgi 1963), might be necessary to develop a precise orientation strategy (Scapini et al. 1999; Morse 2002). Moreover, other factors such as temperature, dietary conditions or population density can affect specific behavioral responses as well (Nylin & Gotthard 1998; for wolf spiders: Wagner & Wise 1997; Walker et al. 1999). Since factors related to both the population of origin and vegetation landmarks guide the movement behavior of a stenotopic riparian wolf spider, it leads to a more efficient movement strategy to carry it to its safe winter habitat in autumn. A generalist wolf spider, on the other hand, might be negatively affected by flooding, since its orientation behavior seems guided mainly by acute external information. Generally, decision-making that precedes movement is guided both by factors related to inherited information and external stimuli such as detectable visual cues (Clobert et al. 2009). Individuals from different populations, however, may convert inherited or experienced information into different behavior (Scapini et al. 2002; Bonte et al. 2006).

ACKNOWLEDGMENTS

We thank Martijn Vandegehuchte (UGent, TEREC), Viki Vandomme (UGent, TEREC) and Otto Cuppens for field assistance. Marcel Lambeets developed the plexiglass arena. Theo Blick (scientific staff member Senckenberg, Frankfurt) and Koen Van Keer (Belgian Arachnological Society, ARABEL) provided missing literature. Jean-Pierre Maelfait was a tremendous mentor, but left us too soon in February 2009. He stimulated the research of riparian wolf spiders. The first author was funded by a Ph.D. grant from the Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen; n° 41328).

LITERATURE CITED

Alderweireldt, M. & J.-P. Maelfait. 1988. Life cycle, habitat choice and distribution of *Pardosa amentata* (Clerck 1757) in Belgium (Araneae, Lycosidae). *In* Comptes Rendu de 10e Colloque Européen d'Arachnologie. (A. Canard, ed.). Bulletin de la Société Scientifique de Bretagne 59:7–15.

Bates, A.J., J. Sadler & A.P. Fowles. 2006. Condition-dependent dispersal of a patchily distributed riparian ground beetle in response to disturbance. Oecologia 150:50–60.

Bonte, D., L. Lens & J.-P. Maelfait. 2004. Lack of homeward orientation and increased mobility result in high emigration rates from low-quality fragments in a dune wolf spider. Journal of Animal Ecology 73:643–650.

Bonte, D., J. Vanden Borre, L. Lens & J.-P. Maelfait. 2006. Geographical variation in wolf spider dispersal behaviour is related to landscape structure. Animal Behaviour 72:655–662.

Bonte, D., B. Bossuyt & L. Lens. 2007. Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. Behavioral Ecology 18:438–443.

Borgioli, C., G.M. Marchetti & F. Scapini. 1999a. Variation in zonal recovery in four *Talitrus saltator* populations from different coastlines. A comparison of orientation in the field and in an experimental area. Behavioral Ecology and Sociobiology 45:79–85.

Borgioli, C., L. Martelli, F. Porri, A. D'Elia, G.M. Marchetti & F. Scapini. 1999b. Orientation in *Talitrus saltator* (Montagu): trends in intrapopulation variability related to environmental and intrinsic factors. Journal of Experimental Marine Biology and Ecology 238:29–47.

Bowler, D.E. & T.G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225.

Cézilly, F., E. Danchin & L.A. Giraldeau. 2008. Research methods in behavioural ecology. Pp. 55–95. *In* Behavioural Ecology: An Evolutionary Perspective on Behaviour. (E. Danchin, L.-A. Giraldeau & F. Cézilly, eds.). Oxford University Press, Oxford, UK.

Clobert, J., J.-F. Le Gilliard, J. Cote, S. Meylan & M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Collett, T.S., M. Collett & R. Wehner. 2001. The guidance of desert ants by extended landmarks. Journal of Experimental Biology 204:1635–1639.

Dall, S.R.X., L.-A. Giraldeau, O. Olsson, J.M. McNamara & D.W. Stephens. 2005. Information and its use by animals in evolutionary biology. Trends in Ecology & Evolution 20:187–193.

Danchin, E., L.-A. Giraldeau & R.H. Wagner. 2008. An information-driven approach to behaviour. Pp. 97–130. *In* Behavioural Ecology: An Evolutionary Perspective on Behaviour. (E. Danchin, L.-A. Giraldeau & F. Cézilly, eds.). Oxford University Press, Oxford, UK.

DeWitt, T.J., A. Sih & D.S. Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13:77–81.

Fahrig, L. 2007. Non-optimal movement in human-altered landscapes. Functional Ecology 21:1003–1015.

Giraldeau, L.-A. 1997. The ecology of information use. Pp. 42–68. *In* Behavioural Ecology: An Evolutionary Approach. (J.R. Krebs & N.B. Davies, eds.). Blackwell, Oxford, UK.

Harvey, P.R., D.R. Nellist & M.G. Telfer. 2002. Provisional Atlas of British Spiders (Arachnida, Araneae), Volume 2, pp. 205–406. Biological Records Centre, Huntingdon, UK.

Jander, R. 1975. Ecological aspects of spatial orientation. Annual Review of Ecology and Systematics 6:171–188.

Kraus, J.M. & D.H. Morse. 2005. Seasonal habitat shift in an intertidal wolf spider: proximal cues associated with migration and substrate preference. Journal of Arachnology 33:110–123.

Krebs, J.R. & N.B. Davies. 1997. The evolution of behavioural ecology. Pp. 2–12. *In* Behavioural Ecology: An Evolutionary Approach. (J.R. Krebs & N.B. Davies, eds.). Blackwell, Oxford, UK.

Lambeets, K., I. Lewylle, D. Bonte & J.-P. Maelfait. 2007. The spider fauna (Araneae) from gravel banks along the Common Meuse: riparian assemblages and species conservation. Nieuwsbrief van de Belgische Arachnologische Vereniging 22:16–30.

Lambeets, K., J.-P. Maelfait & D. Bonte. 2008. Plasticity in flood-avoiding behaviour in two congeneric riparian wolf spiders. Animal Biology 58:389–400.

Lambeets, K. & D. Bonte. 2009. Between-population variation in homeward orientation behaviour in two riparian wolf spiders. Behavioural Processes 82:62–66.

Lambeets, K., P. Breyne & D. Bonte. 2009. Spatial genetic variation of a riparian wolf spider *Pardosa agricola* (Thorell, 1856) on lowland river banks: the importance of functional connectivity in linear spatial systems. Biological Conservation 143:660–668.

Land, M.F. 1971. Orientation by jumping spiders in the absence of visual feedback. Journal of Experimental Biology 54:119–139.

Lang, O. & S. Pütz. 1999. Immigration into a wet polder in the Lower Oder Valley after winter inundation by carabid beetles and spiders. Pp. 171–195. *In* Das Untere Odertal. Limnologie aktuell 9. (W. Dohle, R. Bornkamm & G. Weigmann, eds.). Schweizerbart, Stuttgart.

Lima, S.L. & P.A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution 11:131–135.

Lytle, D.A. & N.L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19:94–100.

Morse, D.H. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae, Lycosidae). Journal of Arachnology 25:1–10.

Morse, D.H. 2002. Orientation and movement of wolf spiders *Pardosa lapidicina* (Araneae, Lycosidae) in the intertidal zone. Journal of Arachnology 30:601–609.

Norgaard, T., J.R. Henschel & R. Wehner. 2007. Use of local cues in the night-time navigation of the wandering desert spider *Leucorchestis arenicola* (Araneae, Sparassidae). Journal of Comparative Physiology A 193:217–222.

Nylin, S. & K. Gotthard. 1998. Plasticity in life-history traits. Annual Review of Entomology 43:63–83.

Ortega-Escobar, J. & A. Muńoz-Cuevas. 1999. Anterior median eyes of *Lycosa tarentula* (Araneae, Lycosidae) detect polarized light: behavioral experiments and electroretinographic analysis. Journal of Arachnology 27:663–671.

Ortega-Escobar, J. 2002. Evidence that the wolf spider *Lycosa tarentula* (Araneae, Lycosidae) needs visual input for path integration. Journal of Arachnology 30:481–486.

Papi, F. 1955. Astronomical orientation of the wolf spider *Arctosa perita* (Latr.). Zeitschrift für Vergleichende Physiologie 37:230–233.

Papi, F. & J. Syrjämäki. 1963. The sun-orientation rhythm of wolf spiders at different latitudes. Archives Italiennes de Biologie 101:59–77.

Papi, F. & P. Tongiorgi. 1963. Innate and learned components in the astronomical orientation of wolf spiders. Ergebenisse der Biologie 26:259–280.

Persons, M.H. & G.W. Uetz. 1996. The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). Animal Behaviour 51:1285–1293.

Pulido, F. 2007. The genetics and evolution of avian migration. BioScience 57:165–174.

Riechert, S.E. & R.F. Hall. 2000. Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider. Journal of Evolutionary Biology 13:541–550.

Rothenbücher, J. & M. Schaefer. 2006. Submersion tolerance in floodplain arthropod communities. Basic and Applied Ecology 7:398–408.

Rypstra, A.L., J.M. Schmidt, B.D. Reif, J. DeVito & M.H. Persons. 2007. Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. Oikos 116:853–863.

Scapini, F., M. Buiatti & O. Ottaviano. 1988. Phenotypic plasticity in sun orientation of sandhoppers. Journal of Comparative Physiology A 163:739–747.

Scapini, F., F. Porri, C. Borgioli & L. Martelli. 1999. Solar orientation of adult and laboratory-born juvenile sandhoppers: inter- and intra-population variation. Journal of Experimental Marine Biology and Ecology 238:107–126.

Scapini, F., A. Aloia, M.F. Bouslama, L. Chelazzi, I. Colombini, M. ElGtari, M. Fallaci & G.M. Marchetti. 2002. Multiple regression analysis of the sources in orientation of two sympatric sandhoppers, *Talitrus saltator* and *Talorchestia brito*, from an exposed Mediterranean beach. Behavioral Ecology and Sociobiology 51:403–414.

Schlaepfer, M.A., M.C. Runge & P.W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17: 474–480.

Ugolini, A. 2001. Relationships between compass systems of orientation in equatorial sandhoppers. Animal Behaviour 62: 193–199.

Van Looy, K. & G. De Blust. 1995. The Meuse naturally?! Impulse towards a large-scale project of nature development along the Common Meuse. Wetenschappelijke mededeling van het Instituut voor Natuurbehoud 1995(2):113.

Verbeke, G. & G. Molenberghs. 2000. Linear Mixed Models for Longitudinal Data. Springer, New York.

Wagner, J.D. & D.H. Wise. 1997. Influence of prey availability and conspecifics on patch quality for a cannibalistic forager: laboratory experiments with the wolf spider *Schizocosa*. Oecologia 109: 474–482.

Walker, S.E., S.D. Marshall, A.L. Rypstra & D.H. Taylor. 1999. The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae). Animal Behaviour 58:515–520.

Wehner, R. 1997. Sensory systems and behaviour. Pp. 15–41. *In* Behavioural Ecology: An Evolutionary Approach. (J.R. Krebs & N.B. Davies, eds.). Blackwell, Oxford, UK.

Wehner, R. 2003. Desert ant navigation: how miniature brains solve complex tasks. Journal of Comparative Physiology A 189:579–588.

Zollner, P.A. & S.L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology 80:1019–1030.

Zollner, P.A. & S.L. Lima. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108:219–230.

Manuscript received 22 May 2009, revised 5 October 2009.