

Low propensity for aerial dispersal in specialist spiders from fragmented landscapes

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Aerial dispersal by ballooning is a passive flight, by which wind drag generates an upward lift on a silk thread. It is likely to reflect an aerial lottery, in which the absence of flight direction control is a serious cost for long-distance dispersal in a fragmented landscape. For species occurring in one patchily distributed habitat type, dispersal should evolve in a different way from morphological traits, directly linked to active dispersal. Therefore, we expect that if the risk of landing in an unsuitable habitat is lower than the probability of reaching a suitable habitat, selection should benefit a well-developed ballooning behaviour. We investigated interspecific variation in the ballooning-initiating tiptoe behaviour as it is linked to spider dispersal performance. Our results indeed indicate that ballooning performance is negatively related to habitat specialization in spiders from patchy grey dunes, so habitat specialists are characterized by poorly developed dispersal behaviour. These findings are concordant with recent insights that dispersal is selected as risk spreading in generalists, while it is selected against in specialist species.

Keywords: evolution; dispersal; habitat specialization; phylogenetical background

1. INTRODUCTION

Dispersal in wingless arthropods occurs via passive transport in air currents, called ballooning if silk threads are used. Ballooning is known from many arthropod groups and initiated by behavioural adaptations that enable the individual to take off in the air. Spiders will initiate tiptoe behaviour, an observable behaviour by which the legs are stretched and the abdomen is raised before the silk thread is produced from the spinnerets.

Ballooning is particularly common in a large variety of spider families Araneae (e.g. Salmon & Horner 1977; Dean & Sterling 1985) and restricted to the juvenile instars from the larger species due to physical constraints (Humphrey 1987). It is triggered by innate responses to acute food shortage (Weyman & Jepson 1994) or to food shortage during juvenile development (Bonte *et al.* 2003a). Developmental temperature also explains a substantial part of the observed individual variation (Bonte *et al.* 2003a). Additionally, environmental factors influence ballooning propensity (Weyman 1995). In the field, effective take off occurs only during suitable meteorological conditions (Richter 1970; Van Wingerden & Vughts 1974; Greenstone 1990; Duffey 1998). High air temperatures and low wind velocities (less than 3 m s⁻¹) are particularly important for the initiation of ballooning dispersal (Vughts & Van Wingerden 1976).

Although climbing up in the vegetation and taking off are important factors that influence effective aerial dispersal (Weyman 1993), studies on the latency in initiating tiptoe behaviour are important for understanding the variation in the willingness of the spider to disperse by ballooning under suitable meteorological conditions, since it is only expressed in advance of aerial dispersal (Weyman

1993). In particular, the fact that ballooning proportions are constant during several tiptoe observation tests (Richter 1970) stresses the reliability of measuring variation in the performance of ballooning-initiating behaviour within a dispersal framework.

Ballooning is supposed to be an efficient mechanism for distant dispersal and hence for colonization of suitable but unoccupied habitats (Toft 1995; Duffey 1998). However, recent empirical investigation failed to prove the importance of ballooning in short-term colonization processes, although it was the best predictor to explain the patch occupancy resulting from long-term colonization and extinction dynamics (Bonte *et al.* 2003b). Indirect studies of ballooning dispersal also reduce the importance of ballooning for gene flow (Ramirez & Haakonsen 1999). Apparently, ballooning is not always an effective dispersal mode between populations, more a stochastic event, certainly in patchily structured populations.

Since passive aerial dispersal depends on air currents, wind directions and body mass, and dispersing individuals have no control over the flight direction (Compton 2002), ballooning dispersal is more of a lottery. In heavily fragmented landscapes, suitable habitats are patchily distributed within an unsuitable matrix. Aerial dispersal should involve a high risk in reaching potential suitable habitats (Samu *et al.* 1999; Compton 2002), particularly for species from these fragmented habitats. If patches are distantly located, low dispersal distances due to low wind velocities (Compton 2002) present additional complications for successful colonization.

Theoretical studies on the evolution of dispersal revealed that it is selected against by intrinsic costs and stable environmental heterogeneity (Holt 1985; Doebeli & Ruxton 1997, 1998; Parvinen 1999; Mathias *et al.* 2001), while it is favoured by kin selection (Hamilton & May 1977; Perrin & Lehman 2001; Lehman & Perrin 2002), inbreeding depression (Chesser & Ryman 1986; Perrin &

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Mazalov 1999, 2000) and temporal variability in habitat quality (Van Valen 1971; McPeck & Holt 1992). Recently, Kisdi (2002) found that risk spreading in stochastic environments and adaptation to the permanent properties of local habitats interplay in the simultaneous evolution of dispersal and habitat specialization. Roff (1981) analysed the relative costs and benefits of wind dispersal and Van Valen (1971) emphasized the trade-off between passive aerial dispersal and competitive abilities. Other authors (e.g. Roff 1975; Den Boer 1981; McLachlan 1985; McPeck & Holt 1992) suggested and confirmed that the advantages of well-developed dispersal abilities decline in stable and homogeneous habitats. Species inhabiting one fragmented habitat type should be characterized by similar ballooning behaviour propensities. However, interspecific differences have been observed (Van Wingerden 1980; Greenstone 1982; Miller 1984), so additional evolutionary processes must have generated this variation of the dispersal-linked behavioural trait.

Because of the apparently large cost of passive aerial dispersal in fragmented landscapes, we expect positive selection for the performance of the ballooning dispersal if the individual benefits from the dispersal. Natural selection should reduce a well-developed ballooning behaviour, if the risk of landing in an unsuitable habitat is high or if the species is strictly specialized to one (heavily fragmented) habitat type. Patterns of selection for reduced dispersal have been observed for wind-dispersed seeds in isolated plant populations (Carlquist 1966; Cody & Overton 1996). Thus, selection for dispersal in generalists favours risk spreading because of a suboptimal adaptation to the local habitat, while dispersal is selected against in specialists by adaptation to local environmental conditions (Kisdi 2002).

Vegetation of grey dunes includes Atlantic moss dominated dunes (mainly *Tortula ruralis*) as well as dune grassland (with a distinct organic soil layer) belonging to the *Cladonio-Koelerietalia* in the case of lime-rich grey dune and to the *Trifolio-Festucetalia ovinae* in the case of decalcified grey dunes (Provoost *et al.* 2002). Climatological conditions are extreme, with high temperature and low humidity in the summer. As a result, arthropod abundance peaks during winter and spring (Bonte *et al.* 2000, 2002b). Patch quality and isolation are the main determinants explaining the population dynamics of a typical spider species (Bonte *et al.* 2003b). To test the prediction of a reduced dispersal propensity in specialized species showing strong morphological, behavioural and phenological adaptation to this habitat type, we relate experimental data on the performance of ballooning behaviour by grey dune spiders to their degree of their habitat specialization.

2. MATERIAL AND METHODS

(a) *Study organisms: collection and testing instars*

Between April 1999 and May 2001, spiders were collected from grey dune vegetation from the coastal dunes in De Panne and Oostduinkerke (Belgium). Dwarfspiders (*Linyphiidae*), *Argemma subnigra* (*Dictynidae*), *Zelotes electus* (*Gnaphosidae*), *Ozyptila simplex* (*Thomisidae*) and *Hypsosinga albobittata* (*Araneidae*) were sampled by collecting moss and low-herb vegetation and manual extraction in the laboratory. Egg sacs (guarded by the female) of *Xysticus* species (*Thomisidae*) were

searched for during April–June in the moss vegetation and reared in the laboratory on Petri dishes with plaster of Paris under room temperature and an aerial humidity near to saturation. Wolfspiders (*Lycosidae*), with an attached cocoon or with juveniles on the back, were actively collected by hand (for species of the genus *Pardosa* and *Arctosa perita*) or passively by using dry pitfalls (for species of the genus *Alopecosa*). The pitfalls were emptied every 3 days during a two-week period in April–May 1999 (for species of the genus *Alopecosa*). Hand collections were performed in March (*A. perita*) and June–July for *Pardosa* species. Juveniles were reared in the laboratory under the same conditions as *Xysticus* spiderlings until the second or third instars (Collembolan *Isotoma viridis* as prey *ad libitum*).

Only adult dwarfspiders *Linyphiidae* and small juvenile spiders from the other genera were used for the experiment, as these have ideal masses for aerial dispersal (less than 1 mg; Greenstone *et al.* 1987). If possible, individuals were tested in the moulting instars in which they were already encountered as ballooning individuals in field situations (instar II, III for *Lycosidae* and *Thomisidae*, and instar III-subadult for *Argemma subnigra* and *Hypsosinga albobittata*; Bonte *et al.* 1998; Bonte & Mael-fait 2001).

(b) *Estimating ballooning propensity*

The propensity to express tiptoe behaviour was tested following Legel & Van Wingerden (1980) and Bonte *et al.* (2003a). Spiders were individually placed on a plastic frame or in groups of a maximum of five individuals (in the case of laboratory reared juveniles of *Pardosa* species) on a platform, so that intra-specific interactions were reduced. Recorded ballooning frequencies were similar in both testing designs (D. Bonte, unpublished data), thus data from all experiments could be used in the same analysis. The testing platform or frame was placed in an air tunnel with upward currents at a temperature of 30 ± 2 °C, aerial humidity of 40–50% and a light breeze: velocity $1\text{--}1.2$ m s⁻¹. To prevent the spiders from escaping by walking, the frame or platform was placed in a bath of water.

Observations were conducted for 20 min. Only if the tiptoe behaviour persisted for at least 3 s was the observation interpreted as valid (Bonte *et al.* 2003a).

Since nutritional conditions influence the ballooning behaviour (Bonte *et al.* 2003a) and, more specifically, starvation acts as the final trigger for the initiation of the tiptoe behaviour, spiders were fed in the laboratory with *Isotoma viridis* (*Collembola ad libitum*), and starved for one week before testing in the experimental chamber.

3. ESTIMATION OF HABITAT SPECIALIZATION

Species-specific levels of habitat specialization were estimated in two ways:

- (i) By using the level of maximal indicator value in the dichotomous and hierarchical clustering of the pitfall data from all kinds of coastal dune vegetation (as documented in Bonte *et al.* 2002a) as an approach of eurytopicity (Dufrene & Legendre 1997). This approach determines indicator species at different hierarchical or non-hierarchical levels of clustering by combining relative species abundance with its relative frequency of occurrence in the various groups of site within each level of clustering. Species with a maximal indicator value (IndVal) at the first

level are generalist eurytopic species in the dune area, occurring in many kinds of dune vegetation; those with maximal IndVal at the lower level (level 6) occur only in very specific habitats (grey dune) and are specialized stenotopic species. Species with a maximal IndVal at intermediate division levels are bound to more than one type of typical coastal dune habitat. Dispersing individuals accidentally trapped in a certain habitat will only marginally influence the IndVal calculation due to its specific algorithm (Dufrene & Legendre 1997).

- (ii) By counting the number of distinct habitat types, as given by Hänggi *et al.* (1995), in which species were regularly found in central Europe. The negative logarithms were taken to scale this measurement normally in the same way as the previous estimate.

(a) *Statistical analyses*

Data on individual tiptoe performance were used as binomial response variables in a generalized mixed linear model with logit link (glimmix procedure in SAS 8.1), with backwards elimination of non-significant variables. Habitat specialization was included as a continuous factor.

Phylogenetical background was included as a fixed factor. However, for our tested species only two parallel clades are currently distinguished (Coddington & Levi 1991): Orbicularia (including Araneidae, Linyphiidae and Tetragnatidae) and the RTA clades (including Gnaphosidae, Dictynidae, Thomisidae and Lycosidae).

Species was included as a random factor and tested against the χ^2 -distribution (d.f. = 1) of the log-likelihood difference between the models with and without the random factor.

4. RESULTS

(a) *Relation between habitat specialization and ballooning frequency*

The species used for the experiment and the numbers of tested individuals are given in table 1. The ballooning frequency differs between species and depends on the degree of habitat specialization and phylogenetic background. Variation explained by the random factor (species) is significant for the IndVal ($\sigma^2 = 0.827$; $\chi^2_1 = 287.1$; $p < 0.001$) and the Hänggi approach ($\sigma^2 = 1.094$; $\chi^2_1 = 95.5$; $p < 0.001$).

IndVal habitat specialization is negatively related with the ballooning frequency (model slope of -0.32 ± 0.27) and interacts significantly with the phylogenetic background in the case of the Hänggi habitat specialization (table 2). Here, model slopes are -1.027 ± 0.261 (s.e.) and -0.397 ± 0.313 (s.e.) for the Orbicularia and RTA clade, respectively. The phylogenetic background only explains significant variation in the case of the IndVal-model and does not interact with the degree of habitat specialization (table 2). In this case, model parameter estimates for the RTA and Orbicularia clades are 1.076 ± 0.442 (s.e.) and 0.495 ± 0.432 (s.e.), respectively.

The goodness-of-fit of the models (figure 1) is significant ($\chi^2_{\text{IndVal}} = 2011.94$ (d.f. = 2560); $\chi^2_{\text{Hänggi}} = 2011.14$ (d.f. = 2559); both $p < 0.0001$) and standardized res-

iduals are normally distributed (Shapiro–Wilk's $W_{\text{IndVal}} = 0.97$ and $W_{\text{Hänggi}} = 0.96$).

5. DISCUSSION

The present laboratory study demonstrates that spider species, characterized by a high degree of habitat specialization, show lower ballooning propensities than species occurring in a wide variety of habitats.

In general, ballooning dispersal is thought to be more common in species from unstable and ephemeral habitats (such as arable land), which quickly become unsuitable (Samu *et al.* 1999). Apparently, ballooning dispersal seems to have evolved in the same way as flight ability in winged insects (e.g. Roff 1975; Den Boer 1981; McLachlan 1985). Some authors confirm differences in ballooning frequency between species (Van Wingerden 1980; Greenstone 1982; Miller 1984), but intraspecific differences are not yet documented, although Bonte *et al.* (2003a) found genetic variation at the basis of the ballooning-initiating behaviour.

Our data suggest that variation in the pre-ballooning behaviour for species from one habitat type in a heterogeneous landscape is related to their degree of habitat specialization and phylogenetic background.

In addition to the earlier findings of Richter (1970, 1971), our results indicate that the evolution of this behavioural trait, linked to dispersal, also originates from factors other than the nature (stability) of the habitat (Southwood 1977). The ability of the species to survive in other habitats is apparently an important determinant of ballooning evolution in fragmented habitats within heterogeneous landscapes. Similar results on reduced dispersal in patchy habitats have also been found in specialized cactophilic *Drosophila* species from central American deserts (Markow & Castrezana 2000).

For eurytopic species that are able to survive in many habitat types, the cost of ballooning is certainly lower than for specialized species, and a well-developed ballooning behaviour is evolutionarily favoured. As already predicted by theoretical models (Kisdi 2002), the dispersal propensity in spiders from grey dunes is selected as being risk spreading in generalist species, while it is selected against in specialist species, the latter being adapted to local habitat conditions. Since only species from one habitat type were investigated, differences in habitat stochasticity cannot act as a selector for dispersal. Data on the population genetic structure are only available for one species with an intermediate degree of habitat specialization (*Pardosa monticola*; Bonte *et al.* 2003b) and indicate a very low genetic differentiation, even between very distant populations. Other studies on coastal dune arthropods confirm this low differentiation (Ramirez & Froehlig 1997; Boulton *et al.* 1998), suggesting similar environmental selection pressures (sand overblowing). Additionally, spider densities are very high (Bonte *et al.* 2000), therefore kin selection and inbreeding depression are less likely to select for dispersal. This new insight might explain the surprisingly high ballooning proportions in spiders from stable habitats (Miller 1984). Reduced dispersal by short-term selection has also been observed for wind-dispersed seeds in isolated plant populations (Carlquist 1966; Cody & Overton 1996).

Table 1. Species that were tested for tiptoe behaviour, with indications of their degree of habitat specialization. (IndVal level from Bonte *et al.* (2002a); number of habitat types in which the species occurs following Hänggi *et al.* (1995); observed ballooning frequency; and *n*, the number of tested individuals (with notes on the number of mothers in case of laboratory rearing).)

species and family	IndVal level	no. of habitat types	ballooning frequency (%)	<i>n</i>
<i>Alopecosa barbipes</i> (Sundevall 1833) (Lycosidae)	3	19	8.955	67 (6)
<i>Alopecosa fabrilis</i> (Clerck 1757) (Lycosidae)	6	8	0.000	21
<i>Alopecosa pulverulenta</i> (Clerck 1757) (Lycosidae)	2	72	16.364	55 (4)
<i>Arctosa perita</i> (Latreille 1799) (Lycosidae)	2	12	20.909	110 (7)
<i>Argenna subnigra</i> (O.-P. Cambridge 1861) (Dictynidae)	1	16	40.000	35
<i>Centromerita concinna</i> (Thorell 1875) (Linyphiidae)	2	38	56.364	55
<i>Erigone atra</i> (Blackwall 1833) (Linyphiidae)	1	79	96.000	300
<i>Erigone dentipalps</i> (Wider 1834) (Linyphiidae)	2	76	73.214	56
<i>Hypsosinga albobittata</i> (Westring 1851) (Araneidae)	3	16	33.333	15
<i>Meioneta rurestris</i> (C. L. Koch 1836) (Linyphiidae)	2	85	77.500	40
<i>Ozyptila simplex</i> (O. P. Cambridge 1862) (Thomisidae)	2	25	32.353	34
<i>Pachygnatha degeeri</i> (Sundevall 1830) (Tetragnathidae)	2	75	35.593	59
<i>Parapelecopsis nemoralis</i> (O. P. Cambridge 1884) (Linyphiidae)	2	12	10.569	123
<i>Pardosa monticola</i> (Clerck 1757) (Lycosidae)	4	16	8.084	569 (22)
<i>Pardosa nigriceps</i> (Thorell 1856) (Lycosidae)	1	31	42.268	97 (6)
<i>Pardosa pullata</i> (Clerck 1757) (Lycosidae)	2	67	15.730	89 (7)
<i>Pelecopsis parallella</i> (Wider 1834) (Linyphiidae)	5	47	20.588	34
<i>Styloctetor romanus</i> (O. P. Cambridge 1872) (Linyphiidae)	6	1	12.687	134
<i>Tenuiphantes tenuis</i> (Blackwall 1852) (Linyphiidae)	1	77	85.294	34
<i>Thyphochrestus digitatus</i> (O. P. Cambridge 1872) (Linyphiidae)	5	16	10.952	210
<i>Tiso vagans</i> (Blackwall 1834) (Linyphiidae)	3	56	46.875	32
<i>Trichopterna cito</i> (O. P. Cambridge 1872) (Linyphiidae)	3	16	22.989	87
<i>Walckenaeria monoceros</i> (Wider 1834) (Linyphiidae)	2	14	45.833	48
<i>Walckenaeria stylifrons</i> (O. P. Cambridge 1875) (Linyphiidae)	6	3	4.348	23
<i>Walckenaeria antica</i> (Wider 1834) (Linyphiidae)	1	59	88.235	34
<i>Xysticus kochi</i> (Thorell 1872) (Thomisidae)	3	43	32.308	65 (3)
<i>Xysticus nimii</i> (Thorell 1872) (Thomisidae)	5	6	0.000	21 (1)
<i>Xysticus sabulosus</i> (Hahn 1832) (Thomisidae)	4	6	13.636	110 (6)
<i>Zelotes electus</i> (C. L. Koch 1839) (Gnaphosidae)	2	16	36.000	25

Table 2. Results of logistic model for ballooning frequency with habitat specialization (HabSpec for both IndVal and Hänggi approach) and phylogenetic background (Phyl) as dependent variables.

specialization approach	variable	numerator d.f.	denominator d.f.	<i>F</i>	<i>p</i>
IndVal	HabSpec	1	32.1	33.00	< 0.0001
	Phyl	1	27.3	15.68	0.0005
	Phyl × HabSpec	1	34.5	1.06	0.311
Hänggi	HabSpec	1	27.4	14.35	0.0008
	Phyl	1	27.8	0.23	0.636
	Phyl × HabSpec	1	25.5	8.05	0.0080

Phylogenetic background, in which species from the Orbicularia perform a better ballooning behaviour in comparison with species from the RTA clade explains a substantial amount of the observed variation. Being dependent on the measurement of habitat specialization used, phylogeny is significant on its own or in interaction with the degree of habitat specialization. Different patterns in the approach of habitat specialization (IndVal levels have a much narrower range than the direct counts from Hänggi *et al.* (1995)) create this contrast, although the two

used measurements correlate well. In both cases, species from the Orbicularia show higher or equal ballooning propensities for a given degree of habitat specialization. This clade contains orb and cobweb spiders (Coddington & Levi 1991), species living in the higher strata of the vegetation and dependent on a well-developed silk production for web building. Their occupancy of patches of taller vegetation, and the more frequent silk production, probably increase the number of opportunities for ballooning. Many species of this clade are also small-sized

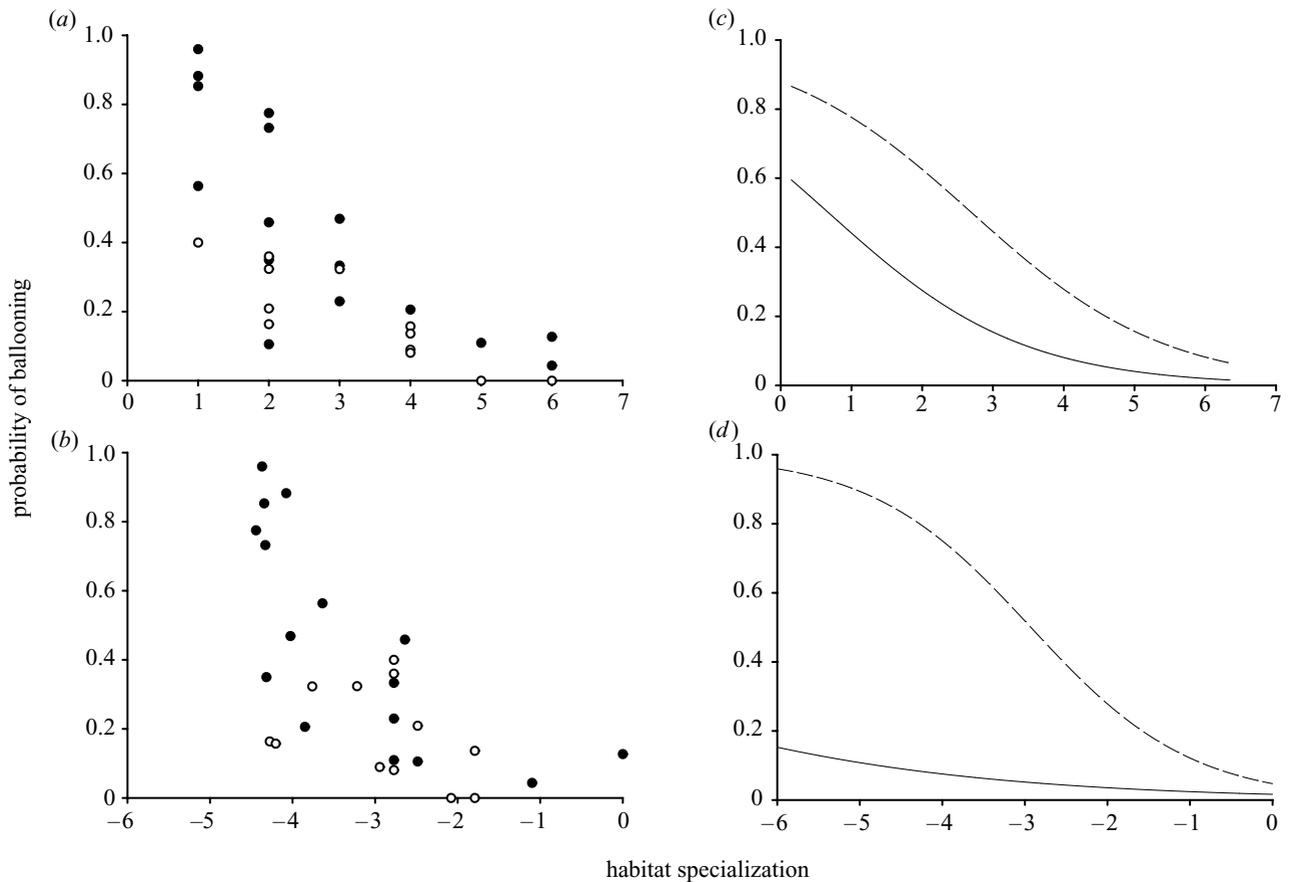


Figure 1. Relation between ballooning propensity and the degree of habitat specialization in grey dune spiders from the RTA clade (open circles and solid lines) and the Orbicularia (filled circles and dashed lines). (a) Mean species frequency and (c) logistic model for habitat specialization as derived from IndVal levels (Bonte *et al.* 2002a). (b) Mean species frequency and (d) logistic model for habitat specialization as derived from Hänggi *et al.* (1995).

(Linyphiidae) in the adult stages and can physically balloon during their entire life cycle, in contrast to the larger species (more represented in the RTA clade) in which ballooning is restricted to the (early) juvenile instars. This may also strengthen selection for dispersal. An interaction, or covariation between morphological and behavioural evolution related to dispersal is thus observed. Because only the phylogenetic clade separation is currently available, a considerable amount of variation, which is explained by the degree of habitat specialization, may actually result from weaker phylogenetic relationships rather than from habitat association *per se*. However, the effect of specialization is clear within related species from the same family (Lycosidae and Linyphiidae) and within species from the same genus (*Alopecosa*, *Pardosa*, *Xysticus*, *Wlackenaeria*), indicating a true effect of the degree of habitat specialization.

A well-developed dispersal capacity is the first condition for successful colonization (Den Boer 1970; Thomas *et al.* 2001; Bullock *et al.* 2002) and is related to local distribution (Malmqvist 2000) or patch occupancy in fragmented habitats (Hanski 1999). Effective wind dispersal has already been strongly linked to colonization ability in a number of plant species (Grime 1986; Dwzono & Loster 1992; Nakashizuka *et al.* 1993; Stöcklin & Bäumler 1996). Ballooning in spiders has also been shown to be effective in the colonization of recently cleared land (Meijer 1977; Weyman & Jepson 1994) and explains the occupancy pat-

terns of species (Bonte *et al.* 2003b). Our data suggest that in fragmented habitats, spider dispersal propensity declines in habitat specialists. As a result, habitat specialists will be exposed to higher extinction chances than their more eurytopic conspecifics. Thus, intrinsic rare species will become rarer due to reduced dispersal if fragmentation increases.

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