

1 Thermal conditions during juvenile development affect 2 adult dispersal in a spider

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9

Abstract:

Understanding the causes and consequences of dispersal is a prerequisite for the effective management of natural populations. Rather than treating dispersal as a fixed trait, it should be considered as a plastic process that responds to both genetic and environmental conditions. Here, we consider how the ambient temperature experienced by juvenile *Erigone atra*, a spider inhabiting crop habitat, influences adult dispersal. This species exhibits two distinct forms of dispersal, ballooning (long-distance) and rappelling (short-distance). Using a half-sib design we raised individuals under four different temperature regimes and quantified the spiders' propensity to balloon and to rappel. Additionally, as an indicator of investment in settlement, we determined the size of the webs build by the spiders following dispersal. The optimal temperature regimes for reproduction and overall dispersal investment were 20 and 25°C. Propensity to perform short-distance movements was lowest at 15°C while; for long-distance dispersal, it was lowest at 30°C. Plasticity in dispersal was in the direction predicted on the basis of the risks associated with seasonal changes in habitat availability; long-distance ballooning occurring more frequently under cooler, spring-like conditions and short-distance rappelling under warmer, summer-like conditions. Based on these findings we conclude that thermal conditions during development provide juvenile spiders with information about the environmental conditions they are likely to encounter as adults and that this information influences the spider's dispersal strategy. Climate change may result in sub-optimal adult dispersal behavior with potentially deleterious population level consequences.

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Key-words: *Erigone atra*, emigration, dispersal distance, immigration, behavior, plasticity, silk, body condition, seasonality

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1 \body

2 **Introduction**

3

4 The movement of dispersing individuals or propagules may have important consequences for
5 gene flow, the genetic cohesions of species, the global persistence of species in the face of
6 local extinction, speciation, inbreeding depression, the evolution of sociality and the evolution
7 of life-history traits (1-7). The dispersal phenotype is predominantly treated as a fixed
8 property in theoretical studies dealing with dispersal evolution and its consequences for
9 population persistence in changing environments (1). However, empirical work has
10 demonstrated high levels of dispersal plasticity (1). This is as expected according to the
11 hypothesis that, unless variation in habitat quality is highly unpredictable or information
12 acquisition is costly (1,3), the most successful strategy over evolutionary time has been for
13 individuals to make dispersal decisions based on information (8) obtained during their lifetime
14 (i.e., for individuals to adopt conditional strategies). There is mounting evidence that strong
15 selection pressures emerging from global change (i.e., land-use changes, climate change,
16 species invasions, pollution) is influencing the evolution of dispersal rate and dispersal
17 distance (1). Correlative and experimental studies have demonstrated rapid evolution of
18 morphological (e.g. wing and seed polymorphism; 9-12), physiological (13) and behavioral
19 (14) traits related to dispersal, but our understanding of the evolutionary ecology of plastic
20 dispersal strategies under environmental change remains rudimentary. Empirical
21 quantification of Genotype x Environment interactions by reaction norm analyses (15,16)
22 provides a highly promising approach for studying the adaptive potential of plastic dispersal
23 strategies. These analyses present formidable challenges if dispersal is to be quantified
24 under natural conditions or when dispersal morphology affects different types of movement
25 (17). This underlines the importance of selecting model species carefully. The species we
26 chose is a sheet-web spider from the family Linyphiidae and, because this species has a
27 short generation time and distinctive dispersal behavior, it appears to be an especially
28 appropriate subject for research on conditional dispersal strategies.

1

2 Like many other spiders, but also many mites and moth larvae (18), Linyphiidae
3 disperse predominantly by using silk threads as either a sail (*ballooning*) for long-distance
4 dispersal or as a bridging thread (*rappelling*) for short-distance dispersal. Both dispersal
5 modes are preceded by tiptoe-behavior (stretching out legs, raising the abdomen and making
6 long silk threads; 18). Ballooning spiders take-off attached to the silk thread and can travel
7 for distances of up to several hundred meters (19). When they rappel, spiders attach a
8 thread to the substrate before take-off, with the thread remaining attached while the spider
9 bridges short distances. These behavioral components can be quantified under highly
10 standardized laboratory conditions, making these spiders especially amenable to reaction-
11 norm analysis (15,16,20-22).

12

13 The temperature experienced by juvenile ectotherms during development can
14 influence their body condition and fitness (23-25) and may influence their adult life-history in
15 two distinct ways. Firstly, under conditions that are sub-optimal for development, inferior
16 body condition may place a severe constraint on particular traits, including how much the
17 animals invest in costly dispersal behaviors. Secondly, developing juveniles may use
18 temperature to determine those life-history characteristics that will be adopted by adults.
19 Under conditions where there is seasonal variation in the life-history characteristics that will
20 be optimal, ambient temperature experienced during development might be an especially
21 reliable indicator of the dispersal tactics that will be most advantageous for adults. In general,
22 direct behavioral responses to thermal conditions experienced at an earlier life stage are
23 poorly documented. However, in the Hymenoptera, adult oviposition and foraging behavior
24 depends on juvenile thermal conditions (26,27), but not on adult body condition.

25

1 Our objective is to determine how ambient temperature during ontogeny influences dispersal-
2 related life history traits in *Erigone atra*, a Linyphiid spider of agricultural landscapes. In
3 common with other agrobiont spiders, the species is adapted to life in a spatio-temporally
4 dynamic landscape where productive crop habitat is only seasonally available. *E. atra*
5 colonizes crop habitat when it becomes available (typically in the spring), breeding (often two
6 generations), and then abandoning the crop in late summer in favor of natural (non-crop)
7 habitat for subsequent breeding and over-winter hibernation (28). This cycle of mass
8 emigration from their hibernation sites in spring and subsequent immigration in autumn
9 (29,30) is most evident from the large amounts of gossamer (i.e. silk threads; 31) present in
10 late summer and autumn. In agricultural landscapes, natural (non-crop) habitat typically
11 constitutes only a small proportion of an area. This may have important consequences for
12 adaptive dispersal when spiders are moving to crop habitat as compared to when they are
13 moving to non-crop habitat. Spring dispersal from natural to crop habitat is less risky, as a
14 large proportion of the landscape is suitable for the spider. Under these conditions ballooning
15 is an effective means of distributing individuals over a wide area of productive crop habitat.
16 However, mortality risks are probably high for long-distance (uncontrolled) ballooning in
17 landscapes when dispersal is towards less widespread non-crop hibernation sites (e.g.
18 20,22). High mortality costs associated with ballooning are therefore expected to select for
19 the adoption of more controlled, lower-risk behavior, e.g. rappelling.

20 The hypothesis investigated was that *E. atra* uses the ambient temperature
21 experienced during development for determining which dispersal tactics will be adopted after
22 maturing (proximate mechanisms). The first prediction we consider is that maximal dispersal
23 rates are obtained under juvenile developmental temperatures that result in optimal body
24 condition. Secondly, we test the prediction that a higher proportion of spiders balloon when
25 they develop under cooler spring-like conditions when adult dispersal is towards crop habitat,
26 while a higher proportion rappel when they develop under warmer summer-like conditions
27 when adult dispersal will be towards the non-crop habitat. In following a half-sib breeding

1 design, we are additionally able to test the hypothesis that any condition-dependent dispersal
2 strategy has an innate basis (ultimate mechanisms).

3

4

1 **Results**

2

3 ***Fitness related traits***

4 Juvenile development time was significantly influenced by temperature during
5 development [$F(3,21.1) = 184.27$, $P < 0.001$]. Developmental time was shortest for
6 individuals raised at 30°C, was nearly twice as long at 20°C and was about three times as
7 long at 15°C (Fig 1a). Effects of the spider's sex [$F(1,352) = 0.67$, $P > 0.410$] and the
8 interaction of sex and temperature [$F(3,351) = 0.68$, $P > 0.566$] were not significant.
9 Longevity after maturation differed between sexes [$F(1,350) = 62.34$, $P < 0.001$], but was not
10 affected by temperature [$F(3,47.5) = 2.49$, $P > 0.071$] or by the interaction of temperature
11 with sex [$F(3,348) = 2.31$; $P > 0.075$]. Females (57 ± 2 days) lived on average 18 days longer
12 than males (39 ± 2 days).

13 The total number of eggsacs, number of eggs within the first eggsac and lifetime
14 numbers of eggs were strongly correlated (r_p ranged between 0.54 and 0.94; all $df = 230$, $P <$
15 0.001). Fecundity, in terms of the lifetime number of eggs, was highest for individuals reared
16 at 20°C and 25°C [$F(3,212) = 4.32$; $P < 0.006$; Fig 1b]. This is due both to the effect of
17 temperature on the number of eggsacs [$F(3,210) = 2.44$; $P < 0.065$] and the influence of
18 temperature on the number of eggs in the first egg sac [log-transformed data; $F(3,212) =$
19 3.90 , $P < 0.009$].

20

21

22 ***Dispersal motivation***

23 *Erigone atra* raised at 15°C on average attempted more climbing than those that developed
24 at higher temperatures [$F(3,34.28) = 25.21$, $P < 0.001$]. Effects of sex [$F(1,434.4) = 0.87$, $P >$
25 0.350] and interactions with temperature [$F(3,434.8) = 1.71$, $P > 0.162$], fecundity
26 [$F(1,227.4) = 1.24$, $P > 0.260$] or longevity [$F(1,366.5) = 1.09$, $P > 0.191$] were not significant.
27 The tiptoe duration per trial was highest for females [$F(1,363) = 15.28$, $P < 0.001$], highest at

1 developmental temperatures 20° C and 25°C [$F(3,49)=4.78$, $P < 0.006$] and positively
2 ($r=0.125 \pm 0.060SE$) related to longevity [$F(1,367) = 4.35$, $P < 0.037$].

3
4 Females rappelled more often than males [$F(1,437.7) = 4.46$, $P < 0.035$]. Rappelling
5 frequencies were lowest at 15° C compared to other developmental temperatures [overall
6 $F(3,61.51) = 2.87$, $P < 0.038$; Fig2a]. Females also ballooned more often than males
7 ($F(3,394.95) = 5.31$, $P < 0.004$). Ballooning occurred less frequently at 30°C compared to
8 other developmental temperatures [overall $F(1,358.7) = 9.22$, $P < 0.002$; Fig 2b]. For
9 ballooning, a positive relationship ($r=0.010 \pm 0.004SE$) with longevity was found [$F(1,367.7) =$
10 4.32 , $P < 0.039$]. Genotype*Environment (see table 1 in supporting information) interactions
11 were large for climbing activity ($\sigma=0.116 \pm 0.065 SE$) and ballooning frequency ($\sigma=0.389 \pm$
12 $0.187 SE$)

13

14

15 **Dispersal distance**

16 Duration of tiptoeing prior to ballooning was not significantly affected by any of the
17 considered parameters (i.e., temperature, fecundity, longevity), while duration of the tiptoeing
18 that preceded rappelling was significantly affected by temperature during development
19 [$F(3,143) = 4.30$, $P < 0.007$; Fig 3a) with the highest duration for individuals raised at 15°C.

20 The probability of ballooning was highest for females [$F(1,357.9) = 10.67$, $P < 0.002$], lowest
21 at developmental temperature of 30°C [$F(3,34.32) = 5.53$, $P < 0.004$; Fig 3b] and positively
22 related to longevity [$r=0.013 \pm 0.005SE$; $F(1,352.7) = 5.14$, $P < 0.024$]. Again no interactions
23 were significant and no additive effects of fecundity on female behavior were found. In
24 contrast, the probability of rappelling was not affected by sex [$F(1,443.9) = 1.40$, $P > 0.237$],
25 but significantly lower after development on 15° C [$F(3,50.37) = 5.65$, $P < 0.003$; Fig 3c]. In
26 females the effect of temperature disappeared [$F(3,15.8)=0.86$, $P > 0.481$] when controlling
27 for lifetime fecundity [$r=0.5341 \pm 0.2563SE$; $F(1,222.5) = 4.34$, $P < 0.045$]. Similarity among

1 kin due to paternal effects was restricted to the probability of ballooning ($\sigma=0.367 \pm 0.225$ SE;
2 see table 1 in supporting information).

3

4 **Settlement**

5 Females built larger webs than males [$F(1,261) = 93.28, P < 0.001$; Fig 4a]. Effects of
6 developmental temperature [$F(3,261) = 3.51, P < 0.017$] were only significant for females
7 [interaction $F(3,261)=3.76, P < 0.012$], with smallest webs produced after development at
8 15°C. Web size was positively related to longevity [$r=0.040 \pm 0.017$ SE; $F(1,261) = 5.32, P <$
9 0.022]. A significant temperature-fecundity interaction [$F(3,217) = 3.27; P < 0.022$] was found
10 for females (Fig 4b). Accordingly, only positive relationships between fecundity and web
11 building were prominent at 25°C ($r=2.34 \pm 0.97$ SE) and 30°C ($r =2.56\pm 1.01$ SE). At lower
12 temperatures during development, no positive relationship between fecundity and web size
13 was found. No parental effects were found (see table 1 in supporting information).

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1 Discussion

2 Our results demonstrate that thermal conditions during juvenile development can
3 strongly influence adult dispersal behavior, through effects on individual condition. Rappelling
4 motivation and duration of the rappelling (short-distance movements) was lowest for
5 individuals raised at 15°C. In contrast, long-distance dispersal (ballooning) showed opposite
6 patterns with lowest motivation and ability for individuals raised at 30°C. This suggests that
7 the spider, when it matures, used the temperature it experienced as a juvenile as a basis for
8 deciding which of the two dispersal tactics it adopts. Moreover, the chosen dispersal tactic is
9 optimal according to the spatial patterns of habitat availability the spider experiences as an
10 adult. Phenotypic plasticity was found to be responsible for most of the observed variation in
11 dispersal strategy. However, for general pre-dispersal activity and also for ballooning
12 behavior we found significant temperature interactions, indicating genetic variation within the
13 population for these characteristics. This suggests that natural selection may be able to act
14 more readily on long distance ballooning than on shorter-distance rappelling. The absence of
15 correlations among the explored dispersal behaviors suggest that dispersal motivation,
16 potential dispersal distance and settlement are independently influenced by thermal
17 conditions during juvenile development.

18
19 Our experiments revealed higher investments in rappelling when juveniles were
20 exposed to summer temperatures. Higher investments in behaviors that are most likely to
21 result in long-distance dispersal (i.e. longer rappelling threads and maximal ballooning
22 propensity) were prevalent when individuals were raised at spring temperatures. Thermal
23 conditions subsequently affect aeronautic dispersal both at the time of the dispersal event
24 (higher ballooning initiations when ambient temperature is high; 32,33) and in life phases that
25 precede the dispersal phase. Furthermore, plasticity in relation to thermal conditions during
26 juvenile development appeared to be adaptive (i.e. beneficial) with respect to optimal
27 seasonal dispersal movements. From earlier studies, we know that the costs of ballooning
28 become higher when suitable habitat becomes scarcer, both in terms of area and isolation

1 (15,22). Our results add to this evidence since ballooning motivation declines when spiders
2 are exposed to temperatures that represent the season with sparsely distributed winter
3 habitat.

4
5 Our study highlights the importance of adaptive plasticity for species inhabiting habitat
6 with severe cycles of disturbance, by using thermal conditions during development as a
7 reliable (but probably not the only; 34) source of information. Indeed, crop habitat shows a
8 spatially homogeneous distribution in spring and early summer, rendering ballooning
9 dispersal beneficial because unoccupied suitable habitat can be swiftly colonized without
10 risking mortality due to landing in unsuitable habitat. This is clearly reflected by increased
11 ballooning frequencies in individuals raised at temperatures of 15-20°C, but also in the higher
12 rappelling distances since longer threads are produced. In contrast, summer temperatures
13 during juvenile development favor rappelling. This dispersal comprises local movements at
14 low heights (above or even within the vegetation) and likely results in safer, short-distance
15 dispersal when available habitat is rare (35,36). However, short-distance displacements are
16 documented to be less directional and more broadly distributed through variable changes in
17 wind direction at short distances above the vegetation (37,38), and therefore be less efficient
18 for directional movements. It may consequently reflect higher tendencies to adopt a risk-
19 spreading strategy at limited spatial scales, i.e. as a response to a void local disturbance
20 (harvesting or ploughing in arable landscapes or flooding in natural habitats like regularly
21 inundating wetlands) or overcrowding by moving more randomly over short distances until
22 suitable habitat is reached. Moreover, our experiments indicate that high investments in
23 gossamer production in autumn do not result from increased ballooning dispersal (31), but
24 instead, from increased investments in low-risk short distance mobility. These results also
25 contradict theory that aeronautic dispersal in agrobiont spiders is solely determined by the
26 prevailing meteorological conditions during the life stage in which dispersal takes place (i.e.,
27 the dispersal window, 39).

1

2 The relationship between environmental thermal conditions and traits related to body
3 condition (growth rates, body size and fecundity) is generally parabolic (40), as observed for
4 fecundity in thermophilic butterflies (24,41) and spiders (23). Because silk production is an
5 energy demanding process (42), we expected a similar parabolic pattern for silk-related
6 dispersal in relation to juvenile thermal conditions. Our experiments demonstrated the
7 importance of body condition on the dispersal phenotype. In contrast to expectation, among-
8 treatment variation was only pronounced for rappelling probability in females. Within-
9 treatment variation explained more variation in the other behaviors. Dispersal in *E. atra* is
10 subsequently dependent on body condition (43). In contrast to studies on insects with
11 dimorphic wing development (10), we did not find a trade-off between dispersal and
12 fecundity, but instead a positive relationship between dispersal and fecundity under certain
13 environmental conditions. This suggests that dispersers are non-random samples from a
14 population, with the possibility that those individuals in the best condition are the best
15 dispersers (11, 44). Apart from the probability of rappelling, effects of developmental
16 temperature were additive. Thermal conditions consequently affected dispersal indirectly
17 through changes in individual body condition, and directly, probably through changes in
18 neurological development (see for example 26).

19

20 Female *E. atra* that experienced thermal spring conditions invested less in web-
21 building. Although this behavior covaries with body condition, as indirectly assessed by
22 fitness-related parameters, it potentially reflects different 'sampling' strategies of local prey
23 availability. Because prey is on average less abundant in the beginning of the season, a
24 more aggregated distribution can be expected (45). As agrobiont spiders select web
25 locations according to prey availability, lower investments in web-building (here shown to be
26 only a partially condition-dependent strategy) could be regarded as a sampling strategy of
27 micro-habitat before foraging is optimized.

1 Our main result, that ambient temperature during juvenile development can influence
2 the adult dispersal of organisms inhabiting spatio-temporally complex environments, has
3 potentially important implications in the context of global warming. Any substantial increase
4 in temperature may result in a mismatch between the dispersal strategy employed by adults
5 and the spatial patterns of habitat availability at different times of the year. For example,
6 juveniles developing during the spring may become less likely to balloon as adults and this
7 could lead to damaging population-level consequences as less crop habitat is colonized. The
8 genetic variation we observed for ballooning propensity suggests that adaptation to climate
9 change may be possible, and an interesting avenue for future work would be to investigate
10 the degree to which reaction norms are locally adapted to varying thermal conditions across
11 the species' range. For species where dispersal is condition-dependent, and especially
12 where temperature controls the propensity for long-distance dispersal, there may also be
13 interesting considerations in terms of predicting range-shifting dynamics. For *E. atra*, not
14 accounting for the temperature-dependence in dispersal might result in an overestimation of
15 the potential rate of range expansion as the extent of long-distance ballooning seems likely
16 to decline as temperatures increase. We argue that by using reaction norm analyses to gain
17 an improved understanding of plastic life history characteristics we will be better placed to
18 develop robust ecological management strategies for a period of rapid environmental
19 change.

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1 **Material and Methods**

2 Model species and aeronautic dispersal: *Erigone atra* (Blackwall 1833) is one of the
3 commonest aeronautic spiders in Western-Europe (18). It especially inhabits crops sown
4 during autumn (46). The species adopts both ballooning and rappelling dispersal tactics after
5 the initiation of tiptoe behavior. We deduced an individual's dispersal motivation from its
6 propensity to exhibit this tiptoeing and its frequency of ballooning and rappelling during the
7 trial. The potential covered dispersal distance is in first instance determined by the performed
8 dispersal mode (i.e., ballooning for long distance dispersal, rappelling for short distance
9 dispersal (18)). Secondly, the length of the thread is positively correlated to the duration of
10 the tiptoeing (16). The length of the produced silk thread also correlates with the potential
11 dispersal distance for rappelling, with longer rappelling threads resulting in larger covered
12 distances. The thread length may additionally determine the length of the ballooning event
13 because it is directly related to the drag velocity for individuals of similar weight (16). Finally,
14 we determined the size of the produced sheet web after dispersal as an indicator for the
15 energetic investment in settlement.

16 Experimental design: 520 individuals from 24 half sib families were individually reared
17 on moist plaster of Paris in Petri dishes with a diameter of 4 cm, which were randomly
18 assigned to four thermal conditions (15, 20, 25 and 30° C), simulating climatological
19 conditions during spring (15° C), summer (20-25° C) and an extremely hot summer (30° C).
20 Until one week after maturation, spiders were fed a diet with *Sinella curviseta*
21 (Collembola) and *Drosophila melanogaster* (Diptera). Spiders were checked every two days
22 for moulting (*E. atra* only shows full coloration the second day after moulting).

23 Seven days after final moulting, individuals were transferred to a wind tunnel with
24 upward wind velocity of 1.2 ± 0.2 m/s and ambient temperature of 25°C (see 16,20,21). They
25 were placed on a platform with vertical wooden sticks (diameter 6 mm, height of 20 cm) in a
26 water bath. After acclimatizing for one hour, the general activity (number of climbings on the
27 wooden sticks), duration of each tiptoe event and frequency of ballooning or rappelling were

1 scored during 15 min trials. During these trials, spiders were allowed to perform multiple
2 tiptoeing. Therefore, individuals were gently put back on the platform (hence minimizing
3 disturbance by the experimenter) after removing the previously produced silk threads from
4 the wooden sticks with a small brush. Individual variation in web-building investment was
5 assessed by placing individuals in terrariums with a grid of vertical sticks of 0.2 mm diameter
6 (1 cm² grid size) to allow web attachment. Size of the web was assessed after standardized
7 digitalization of the web surface (calculation of web surface after calibration of pixel
8 numbers). Earlier work showed significant individual repeatability of the behaviors at longer
9 time intervals, although aging and mating state have a strong influence (21, unpub. data).
10 Web building is not constrained by prior production of silk for dispersal; lower investments
11 are only recorded after sequential web destruction for > 10 days in spiders under food
12 deprivation (Bonte et al., unpub. data). In order to maximize the number of independent
13 trials, each individual was therefore only tested once in unmated condition, one week after
14 maturation. To test for condition-dependent dispersal, we recorded the following fitness-
15 related traits of each experimental individual: developmental time till final moult and longevity
16 after maturation (males and females), total lifetime numbers of egg sacs and eggs, and
17 number of eggs in first eggsac.

18 Data analysis: Reaction norms for ballooning or rappelling incidence were modeled
19 by multi-factorial mixed models for binomially distributed data (logit-link function). Poisson
20 models were applied to model frequencies of performed behaviors and numbers of eggsacs
21 (log-link function). Models for normally distributed data were used for duration of tiptoe
22 displays, age and numbers of produced eggs (log-transformed). Because parameters
23 showed different error distributions and were influenced by parental covariation, no
24 multivariate techniques were applied. Instead, we first performed Spearman correlations to
25 assess their correlated expression (see supporting information). Because of strong
26 correlations between the overall tiptoe frequency and the total duration of the tiptoeing within
27 one trial and the frequencies of the two dispersal modes (see supporting information), we

1 omitted analyses for tiptoe frequency. Breeding temperature and sex were treated as
2 categorical fixed factors. We allowed covariation with fitness-related traits to test for potential
3 condition-dependent dispersal. Sire, dam(sire) and interactions with fixed factors were
4 treated as random factors. Analyses of tiptoe duration for each dispersal event additionally
5 took account of individual variation (repeated measure), nested within dam(sire) variation.
6 We used the Satterthwaite procedure to approximate denominator degrees of freedom.
7 Analyses were conducted with Proc Mixed (normal models) and Proc Glimmix (Poisson and
8 Binomial models) (47).

9

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9 **References**

- 10 1. Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about
11 dispersal evolution. *Annu Rev Ecol Evol Syst* 38:231-253.
- 12 2. Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal
13 strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80:205-225.
- 14 3. Kokko H, López Sepulcre A (2006) From individual dispersal to species ranges:
15 perspectives for a changing world. *Science* 313:789-790.
- 16 4. Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. (2001) *Dispersal* (Oxford
17 University Press, Oxford)
- 18 5. Bullock JM, Kenward RE, Hails RS, eds. (2002) *Dispersal Ecology* (Blackwell,
19 Oxford)
- 20 6. Hanski IA, Gaggiotti OE (2004) *Ecology, genetics & evolution of metapopulations*
21 (Academic Press, San Diego)
- 22 7. Kremen et al. (2007) Pollination and other ecosystem services produced by mobile
23 organisms: a conceptual framework for effects of land-use change. *Ecol Lett* 10:299-
24 314.
- 25 8. Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW (2005) Information
26 and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187-193.

- 1 9. Imbert E (2001) Capitulum characteristics in a seed heteromorphic plant, *Crepis*
2 *sancta* (Asteraceae): variance partitioning and inference for the evolution of dispersal
3 rate. *Heredity* 86:78-86.
- 4 10. Roff DA, Fairbairn DJ (2001) The genetic basis of dispersal and migration and its
5 consequences for the evolution of correlated traits. In: *Dispersal*, eds. Clobert J.,
6 Danchin E., Dhondt, A.A. & Nichols JD (Oxford University Press), pp 191-202.
- 7 11. Saastamoinen M (2007) Mobility and lifetime fecundity in new versus old populations
8 of the Glanville fritillary butterfly. *Oecologia* 153:569-578.
- 9 12. Cheptou PO, Carrue O, Rouifed S, Cantarel A (2008) Rapid evolution of seed
10 dispersal in an urban environment in the weed *Crepis sancta*. *Proc Natl Acad Sci USA*
11 105: 3796–3799.
- 12 13. Haag CR, Saastamoinen M, Marden JH, Hanski I (2005) A candidate locus for
13 variation in dispersal rate in a butterfly metapopulation. *Proc R Soc London Ser B Biol*
14 *Sci* 272:2449-2456.
- 15 14. Philips BL, Brown GP, Travis JM, Shine R (2008) Reid's Paradox Revisited: The
16 Evolution of Dispersal Kernels during Range Expansion. *Am Nat*: S34-S48.
- 17 15. Bonte D, Bossuyt B, Lens L (2007) Aerial dispersal plasticity under different wind
18 velocities in a salt marsh wolf spider. *Beh Ecol* 18:438-443.
- 19 16. Bonte D, Lukac M, Lens L (2008) Starvation affects two aerial dispersal decisions in
20 *Erigone*-spiders in a different way. *Basic Appl Ecol* 9: 308-315.
- 21 17. Van Dyck H, Baguette M (2005) Dispersal behaviour in fragmented landscapes:
22 routine or special movements? *Basic Appl Ecol* 6: 535-545
- 23 18. Bell JR, Bohan DA, Shaw EM, Weyman GS (2005) Ballooning dispersal using silk:
24 world fauna, phylogenies, genetics and models. *Bull Entomol Res* 95:69-114.
- 25 19. Thomas CFG, Brañín P, Jepson PC (2003) Aerial activity of linyphiid spiders:
26 modelling dispersal distances from meteorology and behaviour. *J Appl Ecol* 40:912-
27 927.

- 1 20. Bonte D, Vandenbroeck N, Lens L, Maelfait J-P (2003) Low propensity for aerial
2 dispersal in specialist spiders from fragmented landscapes. *Proc R Soc London Ser B*
3 *Biol Sci* 270:1601-1607.
- 4 21. Bonte D, De Blauwe I, Maelfait J-P (2003) Environmental and genetic background of
5 tiptoe-initiating behaviour in the dwarfspider *Erigone atra*. *Anim Beh* 66:169-174.
- 6 22. Bonte D, Vanden Borre J, Lens L, Maelfait J-P (2006) Geographic variation in
7 wolfspider dispersal behaviour is related to landscape structure. *Anim Beh* 72:655-
8 662.
- 9 23. Li D, Jackson RR (1996) How temperature affects development and reproduction in
10 spiders: a review. *J Therm Biol* 21:245-274.
- 11 24. Karlsson B, Van Dyck H. (2005) Does habitat fragmentation affect temperature-
12 related life-history traits? A laboratory test with a woodland butterfly. *Proc R Soc Ser*
13 *B Biol Sci* 272:1257-1263.
- 14 25. Chamailé-Jammes S, Massot M, Aragon P, Clobert J. (2006) Global warming and
15 positive fitness response in mountain populations of common lizards *Lacerta vivipara*.
16 *Global Change Biol* 12:392-402.
- 17 26. Tautz, J, Maier, S, Groh, S, Rossler, W, Brockmann, A (2003) Behavioral
18 performance in adult honey bees is influenced by the temperature experienced during
19 their pupal development. *Proc Natl Acad Sci USA* 100:7343-7347.
- 20 27. Van Baaren J, Outreman Y, Boivin G (2005) Effect of low temperature exposure on
21 oviposition behaviour and patch exploitation strategy in parasitic wasps. *Anim Beh*
22 70:153-163.
- 23 28. Sunderland K (1999) Mechanisms underlying the effects of spiders on pest
24 populations. *J Arachnol* 27:308-316.
- 25 29. Schmidt MH, Tschardt T (2005) Landscape context of sheetweb spider (Araneae:
26 Linyphiidae) abundance in cereal fields. *J Biogeogr* 32:467-473.

- 1 30. Schmidt M, Thies C, Nentwig W & Tscharrnke T (2008) Contrasting responses of
2 arable spiders to the landscape matrix at different spatial scales. *J Biogeogr* 35:157–
3 166.
- 4 31. Toft S (1995) Two functions of gossamer dispersal in spiders? *Acta Jutlandica*
5 70:257-268.
- 6 32. Richter CJ (1970) Aerial dispersal in relation to habitat in eight wolf spider species
7 (*Pardosa*, Araneae, Lycosidae). *Oecologia* 5:200-214.
- 8 33. Thorbek P, Sunderland KD, Topping CJ (2003) Eggsac development rates and
9 phenology of agrobiont linyphiid spiders in relation to temperature. *Entomol Exp Appl*
10 109:89-101.
- 11 34. Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change.
12 *Science* 312:1477-1478.
- 13 35. Murrell DJ, Travis JMJ, Dytham C (2002) The evolution of dispersal distance in
14 spatially-structured populations. *Oikos* 97:229-236.
- 15 36. Rousset F, Gandon S (2002) Evolution of the distribution of dispersal distance under
16 distance-dependent cost of dispersal. *J Evol Biol* 15:515-523.
- 17 37. Suter RB (1999) An aerial lottery: the physics of ballooning in a chaotic atmosphere.
18 *J Arachnol* 27:281-293.
- 19 38. Finnigan J (2000) Turbulence in Plant Canopies. *Ann Rev Fluid Mech* 32:519-571.
- 20 39. Weyman, GS, Jepson, PC, Sunderland, KD (1995) Do seasonal changes in numbers
21 of aerially dispersing spiders reflect population density on the ground or variation in
22 ballooning motivation. *Oecologia* 101:487-493.
- 23 40. Roff DA (1992) *The evolution of life histories, theory and analysis* (New York)
- 24 41. Karlson B, Wiklund C (2005) Butterfly life-history and temperature adaptations: dry,
25 open habitats select for increased fecundity and longevity. *J Anim Ecol* 74:99-104.
- 26 42. Sherman PM (1994) The orb-web: an energetic and behavioural estimator of a
27 spider's dynamic foraging and reproductive strategies. *Anim Beh* 48:19-34.

-
- 1 43. Ims, RA, Hjermann, DO (2001) Condition-dependent dispersal. In: *Dispersal*, ed.
2 Clobert J., Danchin E., Dhondt, A.A. & Nichols JD (Oxford University Press), pp 203-
3 216.
- 4 44. Le Galliard J-F, Ferrière R, Clobert, J (2005) Effect of patch occupancy on
5 immigration in the Common Lizard. *J Anim Ecol* 74:241-249.
- 6 45. Harwood JD, Sunderland KD & Symondson WOC (2001) Living where the food is:
7 web-location by linyphiid spiders in relation to prey availability in winter wheat. *J Appl*
8 *Ecol* 38:88-99.
- 9 46. Downie I et al. (2000) Modelling populations of *Erigone atra* and *E. dentipalpis*
10 (Araneae: Linyphiidae) across an agricultural gradient in Scotland. *Agr Ecosys*
11 *Environm* 80:15-28.
- 12 47. SAS 9.1 (2003) SAS Institute Inc. (Cary, USA).
- 13

1 **Figure legends:**

2

3 Fig. 1. Effect of temperature during development on fitness related traits (mean values + se)
4 in *Erigone atra*. 1a: developmental time; 1b: egg production

5

6 Fig. 2. Effect of temperature during development on dispersal motivation (mean values + se)
7 in *Erigone atra*. 2a: rappelling frequency; 2b: ballooning frequency

8

9 Fig. 3. Effect of temperature during development on dispersal ability (mean values + se) in
10 *Erigone atra*. 3a: average rappelling tiptoe duration; 3b: probability of ballooning; 3c:
11 probability of rappelling

12

13 Fig. 4. Effect of temperature during development on settlement (web size; mean values + se)
14 in *Erigone atra*. 4a: effect of temperature on both sexes; 4b: effect of temperature on female
15 web size, controlled for lifetime fecundity







