Thermal conditions during juvenile development affect

2	adult dispersal in a spider
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- 7 **Supporting in formation:** one table (genetic variances) and s upporting information on
- 8 consistency of the dispersal behavior and among-trait correlations

Abstract:

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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 p lastic pro cess that re sponds to both genetic and en vironmental conditions. Here, we consider how the ambient temperature experienced by juvenile *Erigone* atra, a spid er inhabiting crop habitat, influences adult dispersal. This species exhibits two distinct forms of dispersal, ballooning (long-distance) and rappelling (short-distance). Using a hal f-sib design we rai sed individuals unde r four di fferent 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. Pro pensity 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 ball ooning occ urring more frequently under c ooler, 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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Introduction

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The movement of dispersing individuals or propagules may have important consequences for gene flow, the genetic cohesions of species, the global persistence of species in the face of local extinction, speciation, inbreeding depression, the evolution of sociality and the evolution of I ife-history trait s (1-7). The dispersal phen otype is predominantly treated as a fixed property in theoretical studies dealing with dispersal evolution and its consequences for population persistence in chang ing environ ments (1). However, empiric al work has demonstrated high levels of dispersal plasticity (1). This is as expected according to the hypothesis that, unles s v ariation in habi tat quality is highly unpredictable or information acquisition is costly (1,3), the most successful strategy over evolutionary time has been for individuals to make dispersal decisions based on information (8) obtained during their lifetime (i.e., for individuals to adopt a conditional strategies). There is mounting evidence that strong selection pressures emerging from global change (i.e., land-use changes, climate change, species invasions, pollution) is influencing the evolution of dispersal rate and dispersal distance (1). Corre lative and e xperimental studies have demonstrated rapid evolution of morphological (e.g. wing and seed polymorphism; 9-12), physiological (13) and behavioral (14) traits related to d ispersal, but our understanding of the evolutionary ecology of plastic dispersal strategi es u nder env ironmental change remains rudimentary . Empirical quantification of Genotype x Environment interactions by reaction norm analyses (15,16) provides a highly promising approach for studying the adaptive potential of plastic dispersal strategies. These analyse s pre sent formidable c hallenges if dispersal is to be quanti fied under natural conditions or when dispersal morphology affects different types of movement (17). This underlines the importance of selecting model species carefully. The species we chose is a sheet-web spider from the family Linyphiidae and, because this species has a short generation time and dis tinctive disper sal beha vior, it appears to be an especially appropriate subject for research on conditional dispersal strategies.

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

The temperature ex perienced b y juvenile ec totherms du ring de velopment c an influence their body condition and fitness (23-25) and may influence their adult life-history in two dist inct ways. Firs tly, under conditions that are sub-optimal for development, inferior body condition may place a se vere constraint on particular traits, including how much the animals i nvest in cost ly dispersal behaviors. Sec ondly, de veloping juveniles may use temperature to determine those life-history characteristics that will be adopted by adults. Under conditions where there is seasonal variation in the life-history characteristics that will be optimal, ambient temperature experienced during development might be an es pecially reliable indicator of the dispersal tactics that will be most advantageous for adults. In general, direct behavioral responses to thermal conditions experienced at an earlier life stage are poorly documented. However, in the Hymenoptera, adult oviposition and foraging behavior depends on juvenile thermal conditions (26,27), but not on adult body condition.

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Our objective is to determine how ambient temperature during ontogeny influences dispersalrelated life history traits in *Erigone atra*, a Li nyphiid sp ider of agric ultural landscapes. In common with other agrobiont spi ders, the species is adapted to life in a spatio-temporally dynamic landscape where p roductive crop habitat is only sea sonally available. E. a tra colonizes crop habitat when it becomes available (typically in the spring), breeding (often two generations), and then abandoning the crop in late summer in favor of natural (non-c rop) habitat for subsequent breeding and o ver-winter hibernation (28). This cyc le of ma ss emigration f rom their h ibernation sites in s pring and subsequent immi gration in autumn (29,30) is most evident from the large amounts of gossamer (i.e. silk threads; 31) present in late s ummer and autu mn. In agric ultural I andscapes, natural (non-c rop) habitat typically constitutes only a small proportion of an area. This may have important consequences for adaptive dispersal when spiders are moving to crop habitat as c ompared to when they are moving to non-crop habitat. Spring dispersal from natural to crop habitat is less risky, as a large proportion of the landscape is suitable for the spider. Under these conditions ballooning is an effective means of distributing individuals over a wide area of productive crop habitat. However, mortality risks are probably high for long-distance (uncointrolled) ba llooning in landscapes when di spersal is towards le ss widespread non-crop hibe rnation si tes (e.g. 20,22). High mortality costs associated with ballooning are therefore expected to select for the adoption of more controlled, lower-risk behavior, e.g. rappelling.

The hypoth esis investigated was that *E. a tra* us est he amb ient temperature experienced during development for determining which dispersal tactics will be adopted after maturing (proximate mechanisms). The first prediction we consider is that maximal dispersal rates are obtained under juv enile de velopmental temperatures that result in optimal body condition. Secondly, we test the prediction that a higher proportion of spiders balloon when they develop under cooler spring-like conditions when adult dispersal is towards crop habitat, while a higher proportion rappel when they develop under warmer summer-like conditions when adult dispersal will be towards the non-crop habitat. In following a half-sib b reeding

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

Results

Fitness related traits

Juvenile de velopment time was significantly i nfluenced by te mperature during development [F(3,21.1) = 184.27, P < 0.00 1]. Dev elopmental t ime was shortest for individuals raised at 30°C, was nearly twice as long at 20°C and was about three times as long at 15°C (Fig 1a). E ffects of the spider's sex [F(1,352) = 0.67, P > 0.410] and the interaction of sex and temperature [F(3,351) = 0.68, P > 0.566] were not significant. Longevity after maturation differed between sexes [F(1,350) = 62.34, P < 0.001], but was not affected by temperature [F(3,47.5) = 2.49, P > 0.071] or by the interaction of temperature with sex [F(3,348) = 2.31; P > 0.075]. Females (57 ± 2 days) lived on average 18 days longer than males (39 ± 2 days).

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

Dispersal motivation

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

developmental te mperatures 20° C and 25°C [F(3,49)=4. 78, P < 0. 006] and positively (r=0.125 ± 0.060sE) related to longevity [F(1,367) = 4.35, P < 0.037].

Females rappelled more often than ma les [F(1,437.7) = 4.46, P < 0.035]. Rappelling frequencies were lo west at 15° C compared to other developmental temperatures [o verall F(3,61.51) = 2.87, P<0.03 8; Fig2a]. Femal es als oballooned more often than nomales (F(3,394.95) = 5.31, P < 0.004). Ballooning occurred less frequently at 30°C compared to other developmental temperatures [overall F(1,358.7) = 9.22, P < 0.002; Fig. 2b]. For ballooning, a positive relationship ($r=0.010 \pm 0.004$ SE) with longevity was found [F(1,367.7) = 4.32, P < 0.039]. Genotype*Environment (see table 1 in supporting information) interactions were large for climbing activity ($\sigma=0.116 \pm 0.065$ SE) and ballooning frequency ($\sigma=0.389 \pm 0.187$ SE)

Dispersal distance

Duration of tiptoeing prior to ballooning was not significantly affected by any of the considered parameters (i.e., temperature, fecundity, longevity), while duration of the tiptoeing that prec eded rappel ling was significantly af fected by temperature during development [F(3,143)=4.30, P<0.007; Fig 3a) with the highest duration for individuals raised at 15°C. The probability of ballooning was highest for females [F(1,357.9)=10.67, P<0.002], lowest at developmental temperature of 30°C [F(3,34.32)=5.53, P<0.004; Fig 3b] and positively related to longevity $[r=0.013\pm0.005SE; F(1,352.7)=5.14, P<0.024]$. Again no interactions were significant and no additive effects of fecundity on female be havior were found. In contrast, the probability of rappelling was not affected by sex [F(1,443.9)=1.40, P>0.237], but significantly lower after development on 15° C [F(3,50.37)=5.65, P<0.003; Fig 3c]. In females the effect of temperature d isappeared [F(3,15.8)=0.86, P>0.481] when controlling for lifetime fecundity $[r=0.5341\pm0.2563SE; F(1,222.5)=4.34, P<0.045]$. Similarity among

kin due to paternal effects was restricted to the probability of ballooning (σ =0.367 ± 0.225 SE; see table 1 in supporting information).

Settlement

Females built larger webs than males [F(1,261) = 93.28, P < 0.001; Fig 4a]. Effects of developmental temperature [F(3,261) = 3.51, P < 0.017] were only significant for females [Interaction F(3,261) = 3.76, P < 0.012], with small est webs produced after development at 15°C. Web size was positively related to longevity $[r=0.040 \pm 0.017 \, SE; F(1,261) = 5.32, P < 0.022]$. A significant temperature-fecundity interaction [F(3,217) = 3.27; P < 0.022] was found for females (Fig 4b). Accordingly, only positive relationships between fecundity and web building were prominent at 25°C $(r=2.3 4 \pm 0.97 \, SE)$ and 30°C $(r=2.56\pm1.01 \, SE)$. At lower temperatures during de velopment, no positive relationship between fecundity and web si ze was found. No parental effects were found (see table 1 in supporting information).

Discussion

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Our results de monstrate that the rmal c onditions during juv enile development can strongly influence adult dispersal behavior, through effects on individual condition. Rappelling motivation and duration of the rappelling (short-distance mo vements) was lowest for individuals raised at 15°C. In contrast, long-distance dispersal (ballooning) showed opposite patterns with I owest motivation and ability for in dividuals raised at 30°C. This suggests that the spider, when it matures, used the temperature it experienced as a juvenile as a basis for deciding which of the two dispersal tactics it adopts. Moreover, the chosen dispersal tactic is optimal according to the sp atial patterns of habitat a vailability the spider experiences as an adult. Phenotypic plasticity was found to be responsible for most of the observed variation in dispersal s trategy. Ho wever, for general pre- dispersal a ctivity and also for ballooning behavior we found si re*temperature interact ions, i ndicating genetic variation within the population for these characteristics. This suggests that natural selection may be able to act more readily on long distance ballooning than on shorter-distance rappelling. The absence of correlations among the explored dis persal behav iors sugges t that dis persal motivation, potential d ispersal distance and settlement are independently influenced by thermal conditions during juvenile development.

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Our experiments re vealed higher in vestments in rappelling when ju veniles were exposed to summer temperatures. Higher investments in behaviors that are most I ikely to result in long-distance dispersal (i.e. I onger rappelling threads and maximal ballooning propensity) were prevalent when in dividuals were raised at spring temperatures. Thermal conditions subsequently affect aero nautic dispersal both at the time of the dispersal event (higher ballooning initiations when ambient temperature is high; 32,33) and in life phases that precede the dispersal phase. Furthermore, plasticity in relation to thermal conditions during juvenile development appeared to be adaptive (i.e. beneficial) with respect to optimal seasonal dispersal movements. From earlier studies, we know that the costs of ballooning become higher when suitable habitat becomes scarcer, both in terms of area and i solation

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

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Our study highlights the importance of adaptive plasticity for species inhabiting habitat with se vere cycles of disturban ce, by u sing thermal conditions during development as a reliable (but probably not the only; 34) source of information. Indeed, c rop habitat sho ws a spatially ho mogeneous distribution in spri ng and early s ummer, rendering ballooning dispersal beneficial because uno ccupied suitable habitat can be swiftly colonized without risking mortality due to landing in unsuitable habitat. This is clearly reflected by increased ballooning frequencies in individuals raised at temperatures of 15-20°C, but also in the higher rappelling distances since longer threads are produced. In contrast, summer temperatures during juvenile development favor rappelling. This dispersal comprises local movements at low heights (abo ve or even within the vegetation) and likely results in safer, short-distance dispersal when available habitat is rare (35,36). However, short-distance displacements are documented to be less directional and more broadly distributed through variable changes in wind direction at short distances above the vegetation (37,38), and therefore be less efficient for directional movements. It may consequently reflect higher tendencies to adopt a riskspreading strategy at limite d spatial scales, i.e. as a re sponse to a void local disturbance (harvesting or ploughing in arable landscapes or flooding in n atural habitats lik e regularly inundating wetlands) or overcrowding by mo ving more randomly over short distances until suitable habitat is rea ched. More over, our experiments indicate that hig h investments in gossamer production in autumn do not result from increased ballooning dispersal (31), but instead, from increased in vestments in I ow-risk short distance mobility. These results also contradict theory that aeronautic dispersal in agrobiont spiders is solely determined by the prevailing meteorological conditions during the life stage in which dispersal takes place (i.e., the dispersal window, 39).

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The relationship between environmental thermal conditions and traits related to body condition (growth rates, body size and fecundity) is generally parabolic (40), as observed for fecundity in thermophilic butterflies (24,41) and spiders (23). Because silk production is an energy demanding process (42), we expected a similar p arabolic pattern for silk-related dispersal in relati on to juvenile therma I conditions. O ur experiments demonstra ted the importance of body condition on the dispersal phenotype. In contrast to expectation, amongtreatment variation was only pronounced for rappelli ng probabilit y in fema les. Withintreatment variation explained more variation in the othe r behaviors. Dispersal in E. atra is subsequently dependent on body condition (4.3). In contrast to stud ies on in sects with dimorphic wing de velopment (10), we did not find a trade-off be tween disp ersal an d fecundity, but ins tead a positive relationship between dispersal and fecundity under certain environmental conditions. This suggests that dispersers are non-random samples from a population, with the possibility that those individuals in the best condition are the best dispersers (11, 44). Apart from t he probability of rappe lling, effe cts of de velopmental temperature were addit ive. Therma I conditions consequently affected dispersal indirectly through c hanges in individual body c ondition, and di rectly, probably through changes in neurological development (see for example 26).

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

Our main result, that ambi ent temperature during juvenile de velopment can influence the adult dis persal of organisms inhabiting spatio-temporally complex en vironments, has potentially important implications in the context of global warming. Any substantial increase in temperature may result in a mismatch between the dispersal strategy employed by adults and the spa tial patterns of habi tat availability at different times of the year. For example, juveniles developing during the spring may become less likely to balloon as adults and this could lead to damaging population-level consequences as less crop habitat is colonized. The genetic variation we observed for ballooning propensity suggests that adaptation to climate change may be possible, and an interesting avenue for future work would be to investigate the degree to which reaction norms are locally adapted to varying thermal conditions across the s pecies' range. For species where dispersal is condition-dependent, and especially where temperature controls the propensity for long-distance dispersal, there may also be interesting considerations in terms of predicting range-shifting dynamics. For E. atra, not accounting for the temperature-dependence in dispersal might result in an overestimation of the potential rate of range expansion as the extent of long-distance ballooning seems likely to decline as temperatures increase. We argue that by using reaction norm analyses to gain an improved understanding of plastic life history characteristics we will be better placed to develop robust ec ological management strat egies for a peri od of rapi d en vironmental change.

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Material and Methods

Model species and aeronautic dispersal: Erigone atra (Blackwall 1833) is one of the commonest aeronautic s piders in Western-Europe (18). It es pecially i nhabits crops sown during autumn (46). The species adopts both ballooning and rappelling dispersal tactics after the i nitiation of tiptoe behavior. We deduced an individual's dispersal motivation from it spropensity to exhibit this tiptoeing and its frequency of ballooning and rappelling during the trial. The potential covered dispersal distance is in first instance determined by the performed dispersal mode (i.e., ballooning for long distance dispersal, rappelling for short distance dispersal (18)). Secondly, the length of the thread is positively correlated to the duration of the tiptoeing (16). The length of the produced silk thread also correlates with the potential dispersal distance for rappelling, with longer rappelling threads resulting in larger covered distances. The thread I ength may additionally determine the length of the ballooning event because it is directly related to the drag velocity for individuals of similar weight (16). Finally, we determined the size of the produced sheet web after dispersal as an indicator for the energetic investment in settlement.

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

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

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scored during 15 min t rials. During these trials, spiders were allowed to perform mu Itiple tiptoeing. Theref ore, individuals were gently put back on the pl atform (hence minimizing disturbance by the experimenter) after removing the previously produced silk threads from the wooden sticks with a small brush. Indiv idual variation in web-bu ilding in vestment was assessed by placing individuals in terrariums with a grid of vertical sticks of 0.2 mm diameter (1 cm² grid size) to allow web attachment. Size of the web was assessed after standardized digitalization of the we bs urface (calc ulation of webs urface after calibration of pix el numbers). Earlier work showed significant individual repeatability of the behaviors at longer time intervals, although aging and mating state have a strong influence (21, unpub. data). Web building is not constrained by prior production of silk for dispersal; lower investments are only re corded after sequential web destruction for > 10 days in spiders under food deprivation (Bonte et al., unpub. data). In order to maximize the nu mber of independent trials, each individual was therefore only tested once in unmated cond ition, one week after maturation. To test for condition-de pendent dispersal, we recorded the following fitnessrelated traits of each experimental individual: developmental time till final moult and longevity after maturation (males and fe males), total lifetime numb ers of egg sacs and eg gs, and number of eggs in first eggsac.

Data analysis: Reaction norms for ball oning or rappelling incidence were modeled by multi-factorial mixed models for binomially distributed data (logit-link function). Poisson models were applied to model frequencies of performed behaviors and numbers of eggsacs (log-link function). Models for normally distributed data were used for duration of tiptoe displays, a geand numbers of produced eggs (log-transformed). Because parameters showed different error distribution sandwere influenced by pare ntal covariation, no multivariate techniques were applied. Instead, we first performed Spearman correlations to assess their correlated expression (see supporting information). Because of strong correlations between the overall tiptoe frequency and the total duration of the tiptoeing within one trial and the frequencies of the two dispersal modes (see supporting information), we

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

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Figure legends:

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- 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

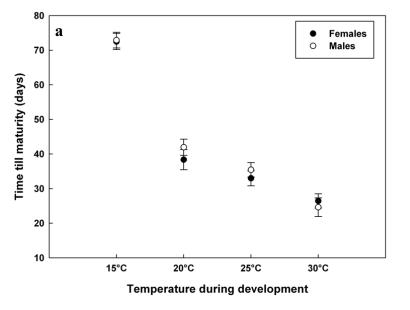
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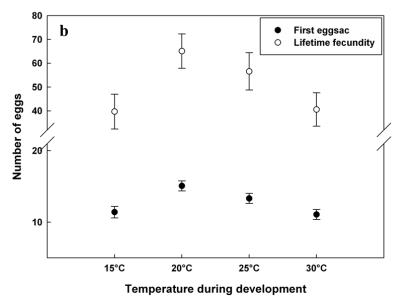
- 6 Fig. 2. Effect of temperature during development on dispersal motivation (mean values + se)
- 7 in *Erigone atra*. 2a: rappelling frequency; 2b: ballooning frequency

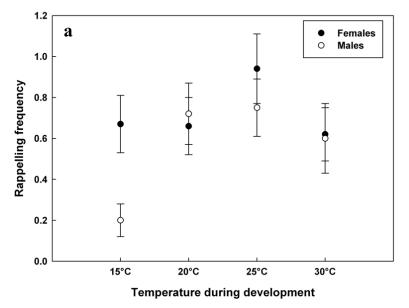
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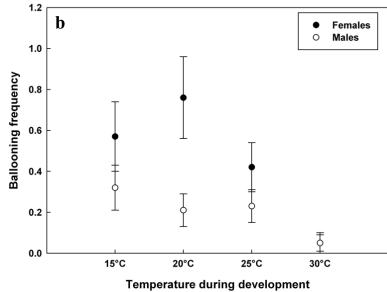
- 9 Fig. 3. Effect of tempera ture during development on dispers all ability (mean values + se) in
- 10 Erigone atra . 3a: a verage rappel ling tiptoe d uration; 3b: probability of ballooning; 3c:
- 11 probability of rappelling

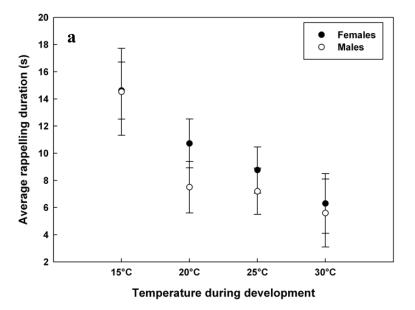
- Fig. 4. Effect of temperature during development on settlement (web size; mean values + se)
- in *Erigone atra*. 4a: effect of temperature on both sexes; 4b: effect of temperature on female
- web size, controlled for lifetime fecundity

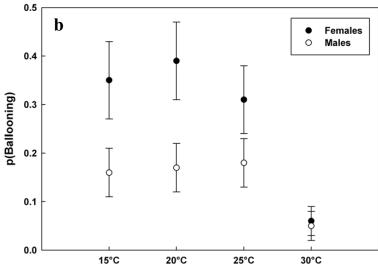












Temperature during development

