Density of conspecifics is considered as one of the main conditions affecting dispersal behavior and leading to a stabilization of population dynamics. Density-dependent dispersal can be induced by local competition at different phases during development and/or by density-related sources of social information. Here, we assessed the importance of population density on emigration rates and the degree to which the presence of silk threads at dispersal takeoff locations affects immediate dispersal decision making in the spider *Erigone atra*. By quantifying behaviors in wind tunnels under standardized laboratory conditions, silk-assisted long- and short-distance dispersal is quantified before the actual onset of the dispersal event.

Increased densities during juvenile development only affected short-distance dispersal behavior. In females, short-distance dispersal increased with the female density experienced during development, whereas responses in males increased under combined high male/low female-experienced densities. Elevated densities at the onset of dispersal led to a general increase of predispersal behaviors. The presence of silk threads at takeoff platforms similarly induced an increase of dispersal displays, with specifically an increase in long-distance dispersal in both sexes.

Our results demonstrate that the spider *E. atra* uses information related to density during development, most probably to avoid competition by performing short-distance dispersal. In contrast, density-related cues at the time of dispersal (i.e., increased densities and the presence of silk threads) increase general dispersal activities and long-distance ballooning events. Short- and long-distance dispersal strategies are consequently guided by differential density-related information use. Key words: araneae, density, dispersal, information, silk. [Behav Ecol 21:992–998 (2010)]

It therefore has a stabilizing effect on population dynamics (Ims and Hjermann 2001) and metapopulation survival (Hovestadt and Poethke 2006) due to feedbacks with decreasing local extinction and increasing colonization rates.

An essential prerequisite for density-dependent dispersal is the ability to perceive information related to local crowding (Clobert et al. 2009). In species with adult dispersal, this information can be gained at different phases during an individual’s life. Indirect cues on local density may be perceived by assessing lower body condition of conspecifics as a result of elevated levels of exploitative competition and decreasing resource availability (Bowler and Benton 2005). Similar information can be directly, in a nonexclusive way, perceived by assessing the number of competitors (Clobert et al. 2004) and/or investigating the different behavior of conspecifics as influenced by local densities (Cote et al. 2008). This information, acquired by monitoring individual interactions (social information), can potentially be based on inadvertent social cues from the performance of conspecifics (public information) and is hypothesized to be nearly cost free (Danchin et al. 2001).

Many correlative and empirical studies support the existence of positive density-dependent emigration in a wide range of taxa (insects: Harrison 1980; Denno and Peterson 1995 and birds and mammals: Matthysen 2005). Positive density-dependent emigration in insects with scramble competition is regarded as one of the most plausible causes of mass dispersal. For instance, overcrowding in grasshoppers induces both behavioral and morphological shifts from a sedentary to a gregarious life phase (Collet et al. 1998). Synchronized dispersal events (often more related to migration than to dispersal senso stricto) should, however, not directly be triggered by overcrowding and a shortage of resources as such but instead may be steered by environmental cues that provide...
Information on future adverse conditions. As an example, changes in light regimes or temperature are widely documented to onset migration in birds (Dingle 1996). Informed dispersal (defined as dispersal adjusted according to the prevailing and observable environmental conditions like local density and/or the availability of resources) minimizes costs during the entire dispersal process but is not cost free (Clobert et al. 2009). As a consequence, organisms are forced to gather reliable information about the potential dispersal costs. For instance, increased and turbulent wind velocities may blow aerially dispersing individuals into unsuitable habitat or induce direct mortality due to starvation and/or desiccation (Bonte et al. 2007). Therefore, individuals actively need to gather information on the prevailing (meteorological) conditions before eventually deciding to disperse (Clobert et al. 2009). In group-living species, including species living at high densities, a few individuals that have sampled the environment and subsequently emigrated may provide cheap (public) information for conspecifics on the suitability of the dispersal window (Danchin et al. 2004). This may be, for instance, the case when dispersing individuals leave behind specific chemical substances that can be perceived by others (Wilson 1970). Then, relatively few dispersing individuals can induce a cascade of emigration events, eventually leading to synchronized mass dispersal events.

Crop-inhabiting arthropods show distinct seasonal dispersal dynamics (Schmidt et al. 2004, 2005). These are especially prominent in spiders that engage in mass aerial dispersal events called ballooning (Bell et al. 2005). Aerial dispersal is possible through the production of silk threads that act as a sail to transport attached spiders by wind currents. It only occurs under suitable weather conditions (the meteorological window: low wind velocity, large differences between night and day temperatures inducing upward currents; Richter 1970) and is hypothesized to be induced by overcrowding (Weyman et al. 2002). Prior to dispersal, spiders collectively occupy elevated takeoff places in the landscapes, such as fences and large plants (Bell et al. 2005). We tested in a series of experiments whether individual dispersal propensity in the agrobiotic spider Erigone atra (Blackwall) is density regulated. The species is an excellent model species (see, e.g., Bonte et al. 2003, 2008a, 2008b, 2009; Goodacre et al. 2009) to investigate individual dispersal decision making because investments in both short- (i.e., rappelling) and long-distance (i.e., ballooning) dispersal can be explored before the onset of the actual dispersal event by scoring both general and specific predispersal behaviors under wind tunnel conditions.

Spiders like E. atra may disperse in a density-dependent way through various mechanisms. The species disperses in the adult life stage, both before and after reproduction (Bonte et al. 2009). Mass dispersal events occur especially in late summer, after the buildup of high local densities (Weyman et al. 2002; Bell et al. 2005). As with other arthropods (e.g., dragonflies: Anholt et al. 2001), males are time minimizers, trying to mate with as many females as possible, and females are energy maximizers, trying to attain as many sources as possible. Because males do not or hardly feed when adult, we therefore expect competition in females to be strictly female density dependent, whereas males are expected to adjust their dispersal according to the number of available mating partners relative to the density of male conspecifics. Because one of us (Bonte 2009) demonstrated that inbreeding depression may be severe after among-kin mating, sex-specific dispersal can be expected as an inbreeding avoidance mechanism that may be especially pronounced when population densities are high in populations established by few founding females. Erigone atra inhabits crops that are harvested in late summer, has 2 or 3 generations a year, and a massive reproductive output (De Keer and Maelfait 1988). This implies that high densities during the development of the parents will be directly correlated with competition between offspring in the next generation in the absence of any emigration. Increased female densities during development are therefore expected to induce higher emigration rates in females (Travis et al. 1999; Poethke and Hovestadt 2002). In contrast, increased male densities are expected to raise male emigration rates only under the condition that female densities remain low. So, only when the ratio males:females becomes highly unbalanced in favor of males, mate competition is expected. Because long-distance dispersal by ballooning involves substantial risks of arriving in unsuitable habitat, we specifically expect increased investments in short-distance rappelling dispersal in order to avoid local competition or to immigrate into scarcely distributed hibernation sites (Bonte et al. 2008b).

Spiders have to assess the suitability of the meteorological window by climbing up the vegetation at the cost of elevated predation risks (Bell et al. 2005). Therefore, we expect that densities at dispersal takeoff platforms provide a source of social information on the suitability of the meteorological conditions. As a consequence of this increased aerial dispersal activity, large amounts of silk threads are present in the landscape (Toft 1995). It is, however, unlikely that sudden changes in weather conditions induce mass dispersal because spiders inhabit the litter layer in which prevailing air currents above the vegetation cannot be perceived (Duffey 1956). Therefore, we tested the hypothesis that the presence of silk threads at takeoff places (public information on ongoing aerial dispersal) stimulates individual emigration propensity. Because costs of ballooning may significantly increase with adverse meteorological conditions (Bonte et al. 2007), we expect it to be more affected by information related to suitable dispersal conditions than short-distance rappelling.

MATERIAL AND METHODS

Study species

Erigone atra (Blackwall 1833) is an abundant small (3–5 mm) sheet web spider. The species especially inhabits crops (De Keer and Maelfait 1988; Downie et al. 2000) and is one of the commonest aeronauts in Western Europe (Bell et al. 2005). As in other Linyphiid spiders, adult individuals disperse predominantly by using silk either as a sail (so-called “ballooning”) for long-distance dispersal or as a bridging thread (so-called “rappelling”) for short-distance dispersal. Both dispersal modes are preceded by a stereotypic tiptoe behavior (stretching of the legs, rising of the abdomen, and production of long silk threads; Bell et al. 2005). Prior to ballooning, spiders produce a silk thread and take off attached to the thread for distances of up to several hundred meters (Thomas et al. 2003). In the case of rappelling, the threads are attached to the substrate prior to takeoff and are used to bridge short distances by climbing.

Dispersal trials

Individual dispersal motivation was quantified using previously established protocols (e.g., Bonte et al. 2008b, 2009; Bonte 2009). In the wind tunnel, adult spiders were placed on a platform in which escape was prevented by surrounding water. Aerial dispersal behavior is expressed after spiders climb on vertical wooden sticks (25 cm). A fan provided a wind current of 1 m/s, reflecting optimal conditions for aerial dispersal. During a time span considered to provide a representative image of the dispersal capacities of the spider, 10 min, different attributes of the predispersal behavior were recorded: the activity (frequency of climbing the sticks), latency to the first
tiptoe behavior, the duration of the tiptoe behaviors (tiptoe time, related to the length of the silk thread eventually determining dispersal distance in case of rappelling, see Bonte et al. 2008a), and the number of dispersal events within the trial of 10” performed by each focal individual (ballooning or rappelling frequency). All spiders were tested prior to egg production.

**Experiment 1: emigration in relation to population density during development**

Prior to all experiments, we collected >60 inseminated females at 3 different locations in Flanders in order to obtain sufficient genetic differentiation. Offspring from these females were crossed with nonrelated conspecifics under standardized conditions ($T = 25 \, ^\circ\text{C}$, high food availability) to obtain the experimental population for the 3 experiments. Hatched juveniles were subsequently randomly divided over 60 artificial populations (further referred to as “lines”) on 15 December 2008 (5 nonrelated males and females in boxes of $25 \times 15$ cm$^2$ with plaster of Paris pieces of moss to retain sufficient high humidity with which prey (Collembola: Sinella curviseta) ad libitum). When the main cohort of offspring reached adulthood (2–6 February 2009; further referred to as G2), a first set of behavioral trials were conducted. For these trials, we tested all males and females for dispersal in the wind tunnel. All lines were, if not extinct, tested a second time for responses during the following generation (referred to as G3) on 17–19 March. Because we aimed to explain variation in individual dispersal behavior in relation to population characteristics, we recorded the population structure (number of males, females, and juveniles) when a substantial proportion of the line reached adulthood (previously mentioned dates).

This estimate of local population (line) density therefore allows the separate estimation of male and female density (juveniles cannot be sexed) during the life phase when competition for space (web building) becomes severe and mortality becomes negligible. All lines received the same amount (and excess) of collembolan prey. However, due to demographic stochasticity, population structure within each of the 60 lines was highly variable, with substantial variation in density and sex ratio between populations (see Table 1). Average density within the lines ($F_{1,111} = 0.57; P > 0.05$) or sex ratio ($F_{1,55.4} = 0.57; P > 0.05$) did not change between the 2 test dates and reflect those met under natural conditions (Alderweireldt 1994). Our reason for generating random variation in population density rather than directly manipulating was 2-fold: on the one hand, it minimizes any artificial disturbance during development (by destroying webs and interference with the local individual distribution in the artificial population) and as such does not interfere with the natural use of density as a source of information during development. Second, this approach is expected to generate a more natural cohort and kin structure, the latter being one of the main drivers of sex-specific dispersal under high densities.

**Experiment 2: emigration in relation to density during dispersal preparation**

Offspring from 30 wild inseminated females, captured in September 2008, were individually reared in small boxes (diameter 4.5 cm) with prey (Collembola: Sinella curviseta) ad libitum. Once adult, test spiders were randomly selected from this breeding stock. Different characteristics of individual dispersal behavior (see higher) were recorded in relation to the species’ density on the test platform. We varied the number of spiders studied on the platform between 1 and 7 individuals. In case more than 2 individuals were tested, it was impossible to observe all individuals simultaneously. Therefore, we selected at random 2 focal individuals to assess their dispersal behavior. In total, we recorded detailed dispersal behavior of nearly 400 individuals, evenly distributed from the 30 parental lines.

**Experiment 3: emigration and public information (silk thread remains)**

In this experiment, we explored the difference between the dispersal behavior of spiders in the presence/absence of silk threads. The presence of these threads is hypothesized to be an indication of recently successful emigration by conspecifics. Indeed, before eventually departing, spiders leave lots of silk remains wired on the launching platform (see, e.g., Toft 1995; Weyman et al. 2002). Two platforms were simultaneously used in this experiment. In the first setting, no silk threads were present, and after each behavior protocol, the threads were removed. In the second setting, we induced the presence of silk threads by stimulating dispersal in 7 female spiders 15 min prior to the start of the experiments. To prevent individuals showing opportunistic behavior and using the “induced” silk to rappel, the silk was turned around the stakes. In this way, silk threads can solely be used as a source of information. Two spiders were tested at once on each platform. Nearly 200 individual spiders, randomly chosen from the stock populations described in experiment 2, were tested.

**Data analysis**

In the first experiment, we tested the proportion of dispersing male and female spiders per line relative to the total number of males and females in the respective line population. Therefore, we used the count of the number of dispersing males/females as a response variable with the total male/female population as an offset variable. Independent variables were total density of males and females, generation, and all interactions. For this analysis, we modeled a binomial error structure and logit link in the generalized mixed model. We analyzed changes in dispersal probability by full models, including sex (male or female), female density, and male density as independent factors. Generation was entered in the model as a repeated measurement component with “line” as subject to correct for genetic similarity among the 2 generations in the line populations. Due to the random effect error structure and the subsequent quasi-likelihood algorithm of the generalized mixed logistic models, no Akaike model selection criteria could be used for model selection.

For the second and third experiment, we tested the effect of treatments, sex, and the interaction of both on behavioral traits related to general dispersal activity (number of tiptoe displays and climbing activity) and specific rappelling and ballooning
behaviors (the latency, number, and absence/presence of the specific dispersal events). A Poisson error structure and log link was applied to model activity (number of stick-climbing events) and the number of rappelling and ballooning events during a trial. Individual ballooning or rappelling probability was analyzed assuming a binomial distribution and logit link. We added a random effect factor (code of the coupled experiment because we simultaneously tested dispersal on platforms with and without silk threads). Individuals were too small to mark, implying that we were not able to model potential dependency due to the common origin of each specific individual during the series of tests. All models were corrected for potential overdispersion by adding residuals variation as an R-side effect (see Verbeke and Molenberghs 2000). Degrees of freedom were approximated by Satterthwaite procedure. A backward procedure was used to eliminate all insignificant contributors in all analyses. All analyses were performed with SAS 9.2 (Proc mixed and Proc Glimmix; SAS Institute Inc., 2006).

RESULTS

Experiment 1: emigration in relation to population density during development

Rappelling probability was affected by the interaction between sex, male, and female density (Table 2). A separate analysis per sex revealed that female dispersal probability increased in relation to the recorded female density during development ($\beta = 0.099 \pm 0.045$ standard error; $F_{1,36.33} = 4.71; P = 0.0342$; Figure 1) but not in relation to the experienced male density ($F_{1,51.33} = 0.75; P = 0.38$) or the interaction between both ($F_{1,55} = 0.08; P = 0.785$). For males, a significant interaction between male and female density was observed ($F_{1,34.51} = 4.32; P = 0.045$), whereas additive separate effects of the male ($F_{1,36.15} = 0.52; P = 0.473$) and female density ($F_{1,35.20} = 0.01; P = 0.905$) were not significant. This interaction implies that rappelling probability increases with male density especially when female density is low (Figure 2). No population densities experienced during juvenile development nor sex influenced the ballooning probability of *E. atra* (Table 2).

**Table 2**

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<tr>
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<td>83.06</td>
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</table>

Results are from a generalized mixed binomial model with generation as repeated measure with line as subject.

Experiment 2: emigration in relation to density during dispersal preparation

The density at the platform had a significant positive effect on the climbing activity ($F_{1,36.3} = 11.27; P = 0.0009$) and tip toe frequency ($F_{1,36.3} = 4.77; P = 0.03$) of the spiders (Figure 3a,b). Increased densities led to an increased activity on the one hand and more tip toe on the other hand. There was no effect on the frequency of rappelling ($F_{1,34.3} = 1.03; P = 0.310$) or ballooning ($F_{1,35.0} = 0.01; P = 0.916$) behavior. Neither did we detect effects of sex for any of these measures (all $F < 6.07; P > 0.05$).

Experiment 3: emigration and public information (silk thread remains)

The presence of silk threads influenced the dispersal behavior of *E. atra*. When individuals experienced a setup without silk threads for an extended period of time, the rate of rappelling was 90% lower than in an experimental setup without silk threads (Figure 2).
threads, tiptoe latency increased significantly (mean of 284 ± 23.5 s) compared with a setup with silk (mean of 231 ± 21.7 s; \( F_{1,101} = 4.09; P = 0.046 \)). Individual predispersal activity increased when silk was present (\( F_{1,196} = 9.45; P = 0.002 \)). Similar results were found for tiptoe frequency (\( F_{1,187.9} = 7.31; P = 0.008 \)) and ballooning frequency (\( F_{1,190.2} = 6.81; P = 0.010 \)) (Figure 4). In addition, 14 % of the spiders will balloon at least once when silk threads are present, whereas only 3 % balloon when tested at a platform without any threads (\( F_{1,197} = 5.83; P = 0.020 \)). No effect of the presence of silk threads on the other variables (tiptoe and rappelling behavior) were found (all \( F \), 1.96; \( P \). 0.05). Females and males respond in the same way to the presence of silk threads (all main effects and interaction, \( F < 3.92; P > 0.05 \)).

**DISCUSSION**

A series of laboratory experiments demonstrated conditional emigration in the spider *E. atra* governed by the densities experienced at different phases during an individual’s life. *E. atra* shows a clear sex-specific density-dependent dispersal strategy, with increased female rappelling in relation to female density during development and increased male rappelling in relation to male density if female density is low. Increased densities during the onset of dispersal at takeoff platforms induced a general increase of behaviors in preparation of the dispersal (climbing activity and tiptoe behavior) but not an increase in effective short- or long-distance dispersal. Finally, the presence of silk threads from previously emigrating individuals led to an increase of dispersal displays, with specifically an increase in long-distance dispersal in both males and females. Our study consequently demonstrates that experiencing elevated densities and density-related cues complexly affect emigration decisions.

With the exception of the situation in which male densities are 2- to 3-fold higher than female densities, male dispersal probabilities are lower than those of females. Sex-specific dispersal patterns are known to be caused by sex-specific costs of dispersal (Gros et al. 2008), inbreeding avoidance, or sex-biased resource competition (Perrin and Mazalov, 2000). As demonstrated by Bonte (2009), inbreeding depression may be extremely severe after among-kin mating and related to a strong dispersal depression due to an overall decrease in body condition. Also in our study, the level of dispersal dropped on average by 75% from generation 2 to generation 3 (Figure 5). This implies that inbreeding avoidance is a likely mechanism underlying the species’ sex-specific dispersal strategy (Moore and Ali 1984). We can, however, not exclude direct sex-related dispersal costs as the cause of this sex-specific dispersal. It is, for instance, not unlikely that males, which also evolved to produce smaller sheetwebs (e.g., Vollrath and Selden 2007), may be more limited in silk production for aerial dispersal due to ultimately developed production constraints and/or because of possible lower levels of energy due to lowered foraging as an adult.

Neither inbreeding avoidance nor sex-specific dispersal costs explain the positive density-dependent rappelling strategy. Males and females increased their short-distance dispersal in response to elevated densities of the same sex during development. Males are assumed to compete more for females than vice versa (a polygynous breeding system with females performing multiple mating; Bonte D, unpublished data). This provides an explanation for the observed density dependency: males only show increased rappelling when their density is high relative to that of females (Figure 1b). We therefore attribute increased male–male competition for mating partners at the time of reaching adulthood as the key driver for male dispersal. In contrast, female rappelling dispersal only increased when their density increased. Because prey was...
plentiful, lack of sufficient resources prior to reproduction cannot be the reason for increased dispersal. Instead, we suggest the avoidance of increased densities for offspring to be the most plausible underlying mechanism. Given the high reproductive output—females may produce more than 100 offspring—it is likely that when females remain philopatric, competition for food and space among offspring will become extremely severe.

Spiders, like presumably many other arthropods, experience restricted dispersal time windows due to specific optimal meteorological conditions at the location of takeoff. Spiders are known to aggregate prior to dispersal at elevated locations in grassland vegetation (Bell et al. 2005) under low upward wind velocities (Vugts and Van Wingerden 1976). As such, increasing densities at these takeoff locations may act as a source of social information on the suitability of external dispersal conditions, that is, they provide individuals information on the reliability of their emigration decision with respect to optimal meteorological conditions. Our experimental results are consistent with this because spiders were more willing to prepare for aerial dispersal when densities at takeoff locations were high. However, no effects on effective long- and short-distance dispersal were observed, indicating that other cues influence effective emigration events.

The presence of silk threads, as an indicator of ongoing emigration events, induced a strong increase in long-distance dispersal. From a point of accurate information gathering, dispersal silk threads fragments provide reliable information on emigration efforts by conspecifics. Because chemicals, important in spider communication, are largely present on freshly produced silk (Roland 1983), this kind of information can potentially generate mass dispersal events (see, e.g., Weyman et al. 2002; Bell et al. 2005) in, at least, this agrobiont spider species.

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