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Inbreeding depresses short and long distance dispersal in three congeneric spiders

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Abstract

Dispersal is one of the most important precopulatory inbreeding avoidance mechanisms and subject to landscape related selection pressures. In small populations, inbreeding within and between populations may strongly affect population dynamics if it reduces fitness and gene-flow. While inbreeding avoidance is generally considered to be a key evolutionary driver of dispersal, potential effects of inbreeding on the dispersal process, are poorly known. Here, I document how inbreeding within a population, so by mating among relatives, affects the survivorship and the dispersal behaviour of three congeneric spider *Erigone* species (Araneae: Linyphiidae) that differ in habitat preference and regional rarity. The three species were chosen as a model because they allow the assessment of both long and short distance dispersal motivation (respectively ballooning and rappelling) under laboratory conditions. Inbreeding reduced both long and short distance dispersal modes in the three congeneric species. Because survival was depressed after inbreeding, with a tendency of reduced survival loss in the rare and highly stenotopic species, energetic constraints are likely to be the underlying mechanism. Inbreeding consequently depresses silk-related dispersal in three related spiders. This may induce an inbreeding depression vortex with important consequences for range expansion and metapopulation dynamics of aerially dispersing species from highly fragmented landscapes.

Introduction

Population dynamics are affected by the interaction between environmental fluctuations, emi-/immigration and population genetic structure. In small populations, inbreeding can greatly reduce the average individual fitness (i.e. inbreeding depression), and loss of genetic variability from random genetic drift can diminish future adaptability to a changing environment (Lande, 1988). Inbreeding relates to situations in which matings occur among relatives and to the expression of homozygous deleterious recessive alleles or the loss of heterozygote advantage (Charlesworth & Charlesworth, 1987; Keller & Waller, 2002; Roff, 2002). In general, two levels of inbreeding are recognized (Keller & Waller, 2002): (i) among-population inbreeding because of population subdivision and drift even when mating is random within the subpopulation and (ii) within-population inbreeding due to incestuous matings. Not all species are, however, similarly affected by inbreeding depression and many pre- and postcopulatory inbreeding avoidance strategies have emerged in the course of evolution (Blouin & Blouin, 1988; Pusey & Wolf, 1996). In addition, purging of genetic load because recessive deleterious alleles have increased probabilities to be subject to natural selection may be common in populations that have experienced a long-term history of inbreeding (Crnokrak & Barrett, 2002; Lavergne *et al.*, 2004; Bilde *et al.*, 2005).

While many theoretical and empirical studies have focused on the evolution of inbreeding avoidance strategies related to sexual selection (e.g. Fletcher & Michener, 1987; Wolff, 1992; Eberhard, 1996; Zeh & Zeh, 1996; Penn & Potts, 1999; Morbey & Ydenberg, 2001; Tregenza & Wedell, 2002; Bilde *et al.*, 2007a,b) or dispersal of one of the sexes (e.g. Pusey, 1987; Johnson & Gaines, 1990; Perrin & Mazalov, 1999, 2000; Bilde *et al.*,

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2007b), effects of inbreeding on these strategies have received little attention. These strategies are, however, subject to an omnibus of selection pressures. For instance, dispersal is known to be subject to landscape related selection pressures (Bowler & Benton, 2005). When habitats become extremely fragmented and isolated, rapid reduction of dispersal has been observed in both plants (Cheptou *et al.*, 2008) and animals (Bonte *et al.*, 2007). In isolated populations where inbreeding is substantial, opposing dispersal-enhancing selection pressures related to kin-competition (Hamilton & May, 1977) and/or inbreeding avoidance (e.g. Gandon, 1999; Perrin & Mazalov, 1999, 2000) may be important. Similarly, dispersal-reducing pressures related to increased dispersal costs (e.g. Perrin & Mazalov, 2000; Poethke *et al.*, 2003) are expected to become prevalent.

Inbreeding depression may lead to a substantial increase of the dispersal rate if costs of dispersal are not too high (Roze & Rousset, 2005). However, when an individual's condition is negatively affected, inbreeding load is predicted to directly suppress dispersal in case it is an energy-demanding process (Guillaume & Perrin, 2006), or negative body condition-dependent dispersal strategies may equally evolve under metapopulations conditions that select in general for philopatry (Bonte & de la Peña, 2009). Alternatively, inbreeding may indirectly affect dispersal by increasing demographic stochasticity through changes in reproduction (Guillaume & Perrin, 2006). Depressed dispersal after inbreeding is especially evident in plant species with anemochorous seed dispersal. Here inbreeding leads to reduced investment in pappus-structures through altered energetic allocations (Cody & Overton, 1996; Pico *et al.*,2003,2004; Mix *et al.*, 2006). Consequently, inbreeding depression may induce severe negative effects on one of the most important inbreeding avoidance strategies, i.e. dispersal.

Spiders typically perform aerial dispersal to move between and within habitats (Bell *et al.*, 2005). This aeronautic dispersal is behaviourally mediated through tiptoe behaviour, i.e. individuals climbing up vegetation or other fixed substrates, stretching their legs, raising the abdomen and producing silk threads from the spinnerets prior to take off. Dispersers may either detach from the fixed substrates and get passively carried by wind currents (ballooning) or they may move short distances by using silk threads as climbing structures (rappelling or ridging) (Weyman *et al.*, 2002). The suitability of ballooning for long distance dispersal and subsequent settlement is highly depending on the spatial abundance of suitable habitat ('aerial lottery' *sensu* Bonte *et al.*, 2003). Rappelling, on the other hand, results in short distance displacements (2–3 m) within habitats, thereby involving much lower risks of arriving in unsuitable habitat (Bonte *et al.*, 2008b).

The two distinguished dispersal strategies are subject to different ultimate and proximate influences in the spider *Erigone atra*, with 'rappelling' a plastic and 'ballooning' a partially inherited trait (Bonte *et al.*, 2008b, 2009). If inbreeding depression constrains body condition (like documented for a related species; Bilde *et al.*, 2007b), both dispersal modes are expected to be equally reduced because earlier studies indicated the existence of a positive overall dispersal-body condition relationship. Because low realized risk of inbreeding in the widespread and highly dispersive species may contribute to relaxed selection for inbreeding avoidance, more pronounced effects of inbreeding on life history traits compared with the geographically rare and dispersal-limited congeneric are subsequently expected *(*Crnokrak & Barrett, 2002).

Materials and methods

Dispersal behaviour was assessed in three related money spider species, belonging to the genus *Erigone* (Araneae, Linyphidae): *E. arctica* (White, 1852), *E. dentipalpis* (Wider, 1834) and *E. promiscua* (O.P.-Cambridge, 1872). Gravid females were collected in a dune slack of the nature reserve 'The Westhoek' (De Panne, Belgium) where the three species occur sympatrically and show different colonization patterns (Downie *et al.*, 2000; Bonte *et al.*, 2002). *Erigone arctica* is the first colonizer of coastal dunes and other early successional habitats. *Erigone dentipalpis* succeeds the former species in dune slacks and is the dominant species in nutrient-rich, short pastures (Downie *et al.*, 2000). *Erigone promiscua* is rare on the European mainland, with a restricted occurrence in coastal dune slacks (Bonte *et al.*, 2002). Because of their different life-histories and dispersal ability (assumed to be highest in *E. arctica*, intermediate in *E. dentipalpis*, lowest in *E. promiscua* because of the relation between habitat specialisation and dispersal ability in spiders; Bonte *et al.*, 2003), (meta-)population dynamics of the three species are assumed to differ too.

Offspring from seven gravid *E. arctica*, seven *E. dentipalpis* and 24 *E. promiscua* from a single dune slack were used as parents in a captive breeding experiment. Within-population inbreeding set-up was applied (Keller & Waller, 2002; Bilde *et al.*, 2007b) to measure the effects of inbreeding on survival and dispersal behaviour, i.e. by comparing the fitness and behaviour of progeny from out-crossed (random mating with nonsibs) individuals to those from inbred crosses (between sibs). In the inbred treatment, males were crossed with females from the same clutch (i.e. between siblings). In the outbred treatment, males and females were crossed with a randomly chosen partner from another clutch. In each F1 clutch, two males and two females were randomly selected to produce either 'inbred' or 'outbred' F2 offspring. This breeding design was balanced with respect to grandparental origin of the out- and inbred offspring. All F1 and F2 progeny were individually raised under optimal breeding conditions (20 °C, relative humidity

70%) in Petri dishes (diameter 4 cm) on moist plaster of Paris till adulthood. Spiderlings were fed with *Sinella curviseta* (Collembola) and *Drosophila melanogaster* (Diptera) *ad libitum* until 1 week after maturation. Seven days after maturation, ballooning and rappelling frequencies of 259 outbred (49 *E. arctica* from seven clutches, 46 *E. dentipalpis* from seven clutches, 164 *E. promiscua* from 24 clutches) and 206 inbred (36 *E. arctica* from seven clutches, 37 *E. dentipalpis* from six clutches, 133 *E. promiscua* from 22 clutches) F2 individuals were tested for dispersal behaviour during 15-min intervals under highly standardized conditions in a wind chamber (see Bonte *et al.*, 2008b for details).

In *Erigone* spiders, mainly adults disperse (Bell *et al.*, 2005). Individual dispersal probability only analysed, i.e. whether an individual engaged in one of either dispersal modes or not. The effect of treatment (inbreeding vs. outbreeding) on ballooning and rappelling probability and survival was analysed by generalized mixed logistic models (using logit-link and corrected for overdispersion) using proc Glimmix (SAS 9.1; SAS Institute Inc., Cary, NC, USA) with species, sex, treatment and their interactions as fixed factors. Similarities in offspring dispersal behaviour and survival may arise from either variation because of the parental origin of the dam and sire (i.e. females collected in the field) and clutch variation. Therefore, we included grandmother-ID, clutch and interactions with the modelled fixed factors as random factors in the model. To maximize statistical power while taking into account covariation because of common origin, we applied Satterthwaite correction when calculating the degrees of freedom of all fixed factors Verbeke & Molenberghs, 2000).

Results

Short distance dispersal

The three species showed a reduced rappelling probability under the inbred treatment (Fig. 1; $F_{1,461} = 18.78$; $P < 0.001$). The effect of inbreeding on rappelling probability did not differ between the three species ($F_{2,459} = 0.01$; $P = 0.998$) or between the sexes (rappelling: $F_{1,457} = 0.18$; $P = 0.140$). Neither did we detect significant species × sex interactions ($F_{2,457} = 0.66$; $P = 0.519$). As evidenced on Fig. 1, *E. promiscua* showed the highest (*post-hoc* Tukey test, $t > 4.7$, $P < 0.001$) tendency to perform rappelling compared with *E. arctica* and *E. dentipalpis* (no differences between the latter; *post-hoc* Tukey $t = 1.17$; $P = 0.457$). Both sexes showed similar rappelling probabilities for the three species ($F_{1,460} = 0.63$; $P = 0.429$), but differences due to inbreeding changed according to the species ($F_{2,461} = 18.50$; $P < 0.001$). Negligible variation because of grandmother-effects were found ($\sigma = 0.03 \pm 0.05$ SE). Similarity among siblings was low over the three species ($\sigma = 0.11 \pm 0.19$ SE).

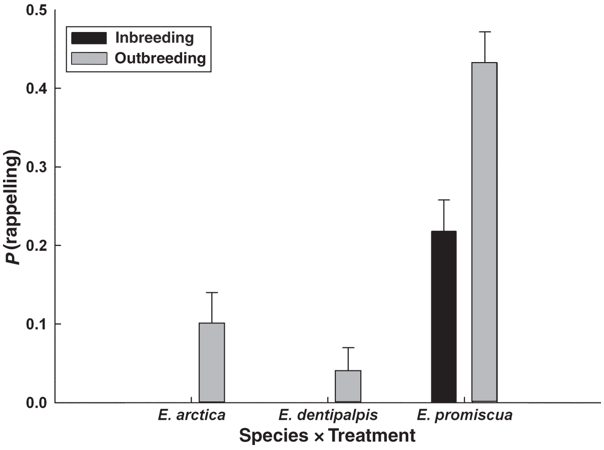

Fig. 1 Effects of inbreeding on rappelling probability in three species of *Erigone* spiders. Bars indicate mean probability; error bars represent SE.

Long distance dispersal

Inbreeding led to a decrease of ballooning dispersal probability among the three studied species (Fig. 2; $F_{1,460} = 4.51$; $P = 0.034$). As for rappelling, species differed in ballooning propensity ($F_{2,460} = 5.73$; $P = 0.003$), but now inverse interspecific patterns are obvious (Fig. 2) with *E. arctica* showing significantly higher ballooning rates than *E. promiscua* (*post-hoc* Tukey $t = 3.34$; $P = 0.026$). *Erigone dentipalpis* showed no significant differences compared with the other two species (*post-hoc* Tukey $t < 1.64$; $P > 0.19$). Ballooning probability neither showed an interaction between species and sex ($F_{2,442.2} = 2.02$; $P = 0.134$), treatment and sex ($F_{1,431.1} = 0.27$; $P = 0.606$) and species × treatment ($F_{2,120.7} = 2.67$;

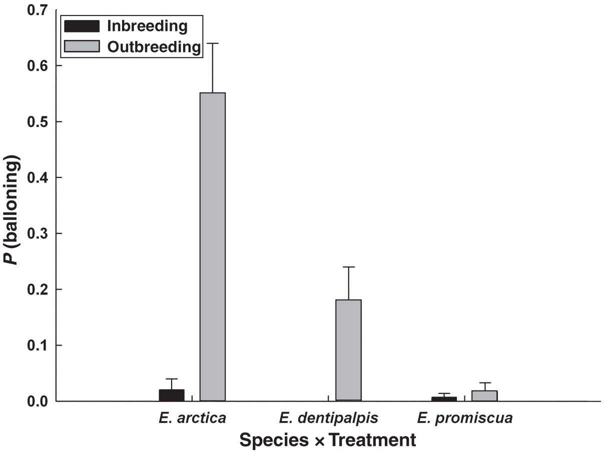

Fig. 2 Effects of inbreeding on ballooning probability in three species of *Erigone* spiders. Bars indicate mean probability; error bars represent SE.

$P = 0.073$). No differences between sexes were recorded ($F_{1,460} = 1.85$; $P = 0.174$). For the three species together, variation because of clutch ($\sigma = 2.85 \pm 1.18$ SE) and grandmother ($\sigma = 1.11 \pm 0.91$ SE) were substantial.

Survival

Inbreeding resulted in a reduction of survival till maturity of approximately 30% in *E. arctica*, 15% in *E. dentipalpis* and 5% in *E. promiscua* ($F_{1,64} = 6.48$; $P = 0.03$; Fig. 3). Effects of inbreeding on survival tended to differ between species (interaction: $F_{2,64} = 2.94$; $P = 0.056$; species-effect: $F_{2,64} = 1.57$; $P = 0.216$).

Discussion

By comparing survival, short distance (rappelling) and long distance dispersal (ballooning) behaviour between inbred and randomly mated congeneric spider species, I provide evidence of severe inbreeding depression on survival and the two dispersal modes. Differences in dispersal behaviour were in accordance with predictions based on the species' habitat preference (Bonte *et al.*, 2003). In this study, the species from widespread habitat disperses predominantly by high-risk ballooning because mortality risks by ending-up in unsuitable habitat are low. In contrast, the rare habitat specialist showed lowest ballooning rates as expected from the high risks of landing outside suitable habitat (here dune slacks with very small area). Presumable to avoid local competition, the latter species invests in safe, short distance rappelling dispersal. More interestingly, both long and short distance dispersal behaviour are equally reduced after inbreeding. Because the magnitude of inbreeding effects on dispersal did not differ between the three species, purging mechanisms and subsequent inbreeding tolerance appeared to be absent. For survival, however, a tendency of purging in the rare species was found.

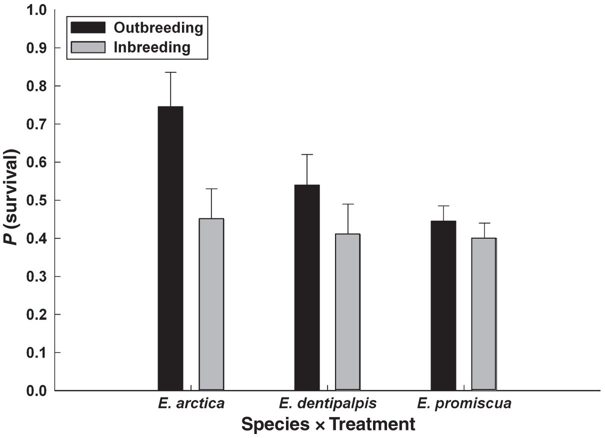

Fig. 3 Effects of inbreeding on survival till maturity in the three species of *Erigone* spiders. Bars indicate mean probability; error bars represent SE.

There is currently increasing awareness that dispersal in organisms is not solely determined by the environment or the species' evolutionary background, but that dispersal phenotypes are the result of Genotype × Environment interactions (Clobert *et al.*, 2009). Here, we provide evidence of genetic effects on dispersal which are not caused by an individual's evolutionary background, but by the individual's genetic environment, i.e. the individual's mating history and subsequent level of inbreeding. This non-heritable source of genetic information has been largely neglected in previous empirical and theoretical dispersal research but may be an important factor that generates variation in body condition and related dispersal strategies. Obviously, because inbreeding avoidance is hypothesized to be driven by the balance between inbreeding depression and the costs of outbreeding (Bengtsson, 1978; Waser *et al.*, 1986), other avoidance strategies than dispersal may have evolved in wild, already inbred populations that experience high dispersal costs. In this study, borderline significant interspecific differences in survival according to the expectations of the species' habitat preference and mobility possibly point at an inbreeding tolerance with respect to survival costs in the geographically restricted, rare species.

Reduced dispersal rates are selected in stable environments or in metapopulations with high dispersal mortality (see Bowler & Benton, 2005; Ronce, 2007 for reviews). I here show that inbreeding can be considered as an additional, yet highly significant, inhibitor of dispersal capacity. The degree of inbreeding induced in this study may be considered irrelevant under natural conditions, given the high local population densities of our study species (Weyman & Jepson, 1994). However, as *Erigone* spiders belong to the initial pioneers of isolated terrestrial ecosystems or ephemeral habitats (Bell *et al.*, 2005), populations in fragmented landscapes can be expected to founded by a small number of fertile females. Because both ballooning dispersal and rappelling dispersal (with respectively high and low dispersal mortality costs) are affected by inbreeding, a general body conditional dependency of the aerial dispersal strategy is expected. The likelihood of this constraint mechanism is obviously confirmed by previous investigations that demonstrated either a direct effect between dispersal and starvation (Bonte *et al.*, 2008a) or between dispersal and body condition-related life history parameters (Bonte *et al.*, 2008b). No direct relationships were studied between individual body condition and dispersal in this study. Therefore, inbreeding may equally induce dispersal depression through internal (i.e. physiological) mechanisms that are not linked to the energetic state of the surviving individuals. Alternatively, it also remains plausible that decreased dispersal rates after inbreeding have evolved as a negative body condition-dependent strategy. Especially in metapopulations where kin-competition is strong, alike strategies can evolve (Bonte & de la Peña, 2009).

In nature, the onset of dispersal will evidently not solely depend on individual condition, but also on other prevalent environmental factors related to habitat quality, the social environment and population density (Clobert *et al.*, 2009). Here, I showed that inbreeding leads to the suppression of individual dispersal behaviour. Because of the simultaneous action of inbreeding on survival, feedback mechanisms with population density and the social environment are very likely. For instance, both theory and empirical work predicts a positive density-dependent relationship of dispersal propensity (Kaufman *et al.*, 2000; Andreassen & Ims, 2001; Poethke & Hovestadt, 2002; Metz & Gyllenberg, 2001) and increased dispersal rates under kin competition (Hamilton & May, 1977; Lena *et al.*, 1998; Perrin & Mazalov, 1999; Poethke *et al.*, 2007). As a consequence, dispersal rates in nature will be governed by the prevailing balance between individual condition, demography and population genetic structure (i.e. relatedness at local spatial scales). Therefore, dispersal strategies may be overruled by physiological effects of dominance after inbreeding.

Genetic inbreeding effects, alongside natural selection, may consequently induce rapid changes in dispersal rates in strongly isolated populations, and may operate at shorter time intervals than natural selection (Keller & Waller, 2002). This may have severe consequences for range expansion or metapopulation dynamics. Isolated habitat patches are not only difficultly colonized, range expansion at species' boundaries or stepping-stone dispersal dynamics in metapopulations may become additionally restricted due to inbreeding effects. These results therefore highlight the interesting avenue for future work to take into account effects of inbreeding (or broader the relationship between population demography and genetics) when predicting range-shifting dynamics. For *Erigone*-species, classical adaptive metapopulation or range-expansion models may seriously overestimate colonization dynamics by not considering dispersal depression after inbreeding. Moreover, a hump-shaped relationship between inbreeding levels and dispersal rate can be expected, with increased dispersal as a strategy of kin competition avoidance at the start of the inbreeding event and decreased dispersal under severe inbreeding due to constraints in the later phase of inbreeding.

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