

Offspring-driven local dispersal in female sand lizards (*Lacerta agilis*)

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Abstract

We report on a field study in which determinants of female breeding dispersal (i.e. the shift in the mean home range coordinates between successive breeding events) was investigated. Offspring were released in full sib groups (or half sib ones if there was within-clutch multiple paternity) at a separation distance from the females that varied between 'families'. This allowed for analysis of 'offspring nearness' effects on maternal dispersal. When a female's offspring were released more closely to her, she responded with greater dispersal. Furthermore, when the data set was truncated at 100 m maternal–offspring separation distance at offspring release (because perception at longer distances is likely to be unrealistic), maternal dispersal resulted in greater separation distance between female and offspring in the following year. A corresponding analysis for juveniles revealed no effect of maternal nearness on offspring dispersal but identified a significant effect of clutch size, to our surprise with dispersal declining with increasing clutch size. We discuss this result in a context of the 'public information hypothesis' (reinterpreted for juveniles in a nonsocial foraging species), suggesting that conspecific abundance perhaps acts as an indicator of local habitat quality. Thus, our analysis suggests a microgeographic structuring of the adult female population driven by genetic factors, either through inbreeding avoidance, or from simply avoiding individuals with a similar genotype regardless of their pedigree relatedness, while a nongenetic factor seems more important in their offspring.

Introduction

Dispersal is the tendency of organisms to move from one area to another and can from a perspective of life history theory be divided into two processes, (i) natal dispersal, when a neonate leaves its birth place to eventually start reproducing elsewhere and (ii) breeding dispersal, when an adult shifts its breeding home range (or territory when there is site defense) from one breeding episode to another (Clobert *et al.*, 2001). The present study deals with the latter of these processes.

The importance of dispersal for understanding many fundamental principles in evolutionary biology is per-

haps best illustrated by the attention of some of the most influential researchers in this field, e.g. Sewall Wright and Ronald Fisher, who represented strongly opposing views on how natural populations are structured and why. Fisher believed that most natural populations were large and close to panmictic, i.e. with matings being largely random (Fisher, 1930; Provine, 1985). Wright, on the contrary, saw natural populations as being 'broken up' with 'rapid differentiation of local strains' (Wright, 1930; Provine, 1985). Their conflict over this matter (and others) lasted more than 30 years (Provine, 1985). Their lead in this field was followed by some of the most influential biologists of our time. In Bill Hamilton's autobiography, he reflects: '...like a volcano at the back of my mind...more than sex itself...the new problem was that of dispersal' (Hamilton, 1996). What he referred to was a joint contribution (Hamilton & May, 1977), in

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which optimal parent-induced offspring dispersal was modelled.

Since then, a large number of factors have been suggested to influence dispersal from the proximate to the ultimate level, such as hormones and body condition (Dufty & Belthoff, 2001; Ims & Hjernann, 2001), genetics and inbreeding avoidance (Barton, 2001; Perrin & Goudet, 2001; Roff & Fairbairn, 2001), habitat selection (Stamps, 2001), predation and parasitism (Boulinier *et al.*, 2001; Weisser, 2001), population dynamics and density-driven processes (Hanski, 2001; Holt & Barfield, 2001), mate choice (Parker, 1983), and antagonistic interactions (for instance those between predator and prey, or host and parasite) (van Baalen & Hochberg, 2001). In the present paper, with a genetics focus, we will return to the effects of relatedness on dispersal and, in particular, that of inbreeding.

This wide variation in dispersal mechanisms identified throughout the literature (reviewed in Clobert *et al.*, 2001) can be further extended with theory framed around cognition and dispersal in social foragers. One such hypothesis, the 'public information hypothesis', posits that animals – especially those with large cognitive ability – have the capacity to monitor the reproductive success of their conspecifics and choose a breeding site near successful pairs (Valone & Giraldeau, 1993; Doligez *et al.*, 2002). A similar capacity to 'spy' on conspecifics has been demonstrated in nonsocial species such as fish, where females may choose their partner based on his ability to win male–male contests (Herb *et al.*, 2003), and males alter their fighting behaviour accordingly (Johnsson & Åkerman, 1998; Clotfelter & Pagling, 2003). Thus, nonsocial species too may adjust their behaviour in immediate response to cognitive cues, or following memory processing.

Research on what factors drive the evolution of dispersal thus has a long-standing tradition among both theoreticians and empiricists. In the present paper, we attempt to follow this example with an experimental analysis of the effects of relatedness (offspring presence) on female dispersal. Unlike our previous work in this field, in which we addressed spatial distribution (females having a home range size about a tenth that of males, ca. 100 vs. 1000 m²), risk of inbreeding as a determinant of natal dispersal (i.e. targeting sibling interactions; Olsson *et al.*, 1996), and breeding dispersal in an adult parent–offspring situation (Olsson *et al.*, 1997), we here test the effect of genetic relatedness as a driving force of dispersal between a mother and her neonatal offspring. Factors that we previously identified as correlates of dispersal (e.g. reproductive output and partner relatedness) are here incorporated into our new analyses in order to identify independent dispersal triggers.

The model species we have used for this project is particularly suited for this purpose for the following reasons: (i) offspring viability and survival are strongly influenced by parental consanguinity (Olsson *et al.*, 1996;

Olsson & Madsen, 2001a, b), thus, there ought to be selection for inbreeding avoidance, although the mechanisms involved are sometimes insufficient to prevent copulations between close relatives (Olsson & Madsen, 2001a, b); (ii) our recent work confirms odour-related preferences of partners with respect to MHC relatedness (females prefer to associate with odour samples from less related males in staged laboratory experiments; Olsson *et al.*, 2003); (iii) in the natural population, relatedness of observed pairs is lower than expected by chance (Olsson *et al.*, 2003). Thus, this scenario suggests that females could perceive relatedness based on odour, and adjust their spatial structuring accordingly. Testing for such effects using offspring as relatives is the aim of this project.

Materials and methods

Sand lizards (*Lacerta agilis*) are small (up to 20 g, 90 mm snout to vent), ground-dwelling lizards with one of the widest distribution ranges of all reptiles (Bischoff, 1984), from England to Russia, and mid-Sweden to France. This work was conducted 1998–2002 at Asketunnan, 50 km south of Gothenburg on the Swedish west coast. Detailed descriptions of field protocols have already been made elsewhere (e.g. Olsson, 1994), and therefore we only give a brief account of essential techniques.

Sand lizards emerge from hibernation in late April. Upon emergence, males and females were captured using a noose, had a blood sample taken from *v. angularis* (in the corner of the mouth), were photographed and claw-clipped (for long-term identification), weighed (to the nearest 0.1 g), and measured snout to vent (to the nearest 1 mm). We then counted their ectoparasites (ticks, *Ixodes ricinus*), marked them with a numbered cloth tape on their backs for temporary identification, and released them at the site of capture within hours. Throughout the mating season (ca. 3–5 weeks, late April to late May, depending on weather conditions), pairs were monitored, and the number of observations with males was used to index a female's success in acquiring partners. When females started to show egg contours on their body sides, oviposition was imminent and they were brought to facilities at the Department of Zoology, University of Gothenburg.

Subsequent to capture, females were kept in separate cages (or with a maximum of two females per cage), with crickets and mealworms dusted with multivitamin provided *ad libitum*. The cage was provided with a deep layer of sand and a flat rock under which the sand was kept moist. This directed female oviposition behaviour and guaranteed that females laid their eggs in a place where the eggs did not desiccate (mean clutch size = 8.5 ± 2.2 , SD). The eggs were incubated at 25 °C in moist vermiculite, which has proven the ideal incubation conditions for offspring development (Olsson & Madsen, 2001a). Subsequent to oviposition, females were released at their

place of capture. After ca. 40 days the eggs hatched, after which the hatchlings were measured and weighed using the same procedures as for adults and released as a sib unit at a place picked at random at the Asketunna locality.

During the following summer, the juveniles were recaptured at the study site and their – as well as their mother's – mean home range Cartesian coordinates were calculated. The shift in mean Cartesian coordinates between years was used to index dispersal of females (i.e. as a shift in home range distribution), and dispersal in relation to the coordinates of offspring release. The average number of observation per female on which this estimate was based, was 4.2 ± 2.5 (SD) per female and each female was only used in one year-to-year dispersal event to avoid pseudoreplication. We also looked for effects of partner relatedness on female dispersal using band sharing data from screenings of the MHC Class I loci using a species-specific sand lizard probe, under the assumption that females in more closely related pairs would tend to separate further from their partner (see Madsen *et al.*, 2000).

Results

The Asketunna study site is a rocky peninsula with the sightings of lizards very much localized to its periphery (Fig. 1; mean home range coordinates of all individuals during the study period). This is likely to reflect the lizards' basking behaviour along the shoreline where basking opportunities are more predictable.

The shift in mean female home range coordinates between years was 10.0 m (± 15.6 m, SD, $n = 80$), with no significant difference among years (Kruskal–Wallis

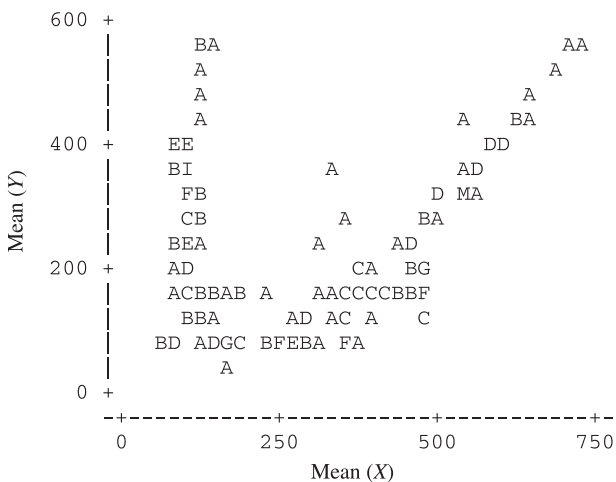


Fig. 1 Plot of mean home range coordinates for all individuals at the Asketunna study site during 1998–2002 (the true peninsula outline closely follows the periphery of the SAS plot of mean home range coordinates). A = 1 observation, B = 2 observations, etc.

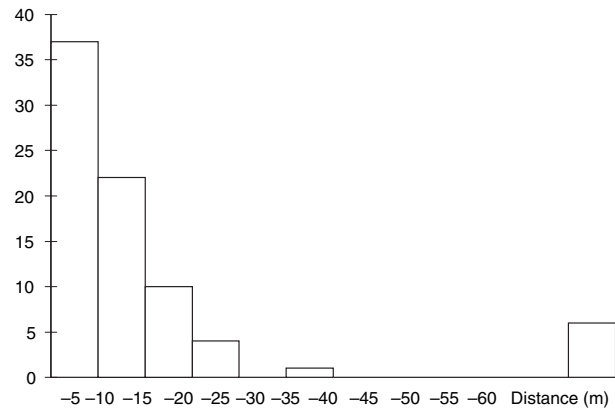


Fig. 2 Distribution of dispersal distances in female sand lizards. Frequencies of observations in 5-m dispersal classes are plotted to illustrate dispersal tendencies. Only six females of 80 (7.5%) showed dispersal further than 50 m.

nonparametric analysis of variance, χ^2 approximation = 0.19, d.f. = 3, n.s.). The distribution of dispersal distances was clearly left-biased, i.e. most females shifted their home ranges relatively little (<5 m), but six females of 80 (7.5%) moved more than 10 times this distance (mean = 57 m \pm 9.0, SD; Fig. 2). For these females, unfortunately, we had no offspring available for release (the females could never be recaptured before laying) and therefore these 'families' could not be included in the analysis of offspring nearness as a predictor of female dispersal. We also investigated among-year differences in mean separation distance between mean female home range coordinates and the release coordinates of the offspring, but also this analysis was nonsignificant at the 0.05 level (Kruskal–Wallis nonparametric analysis of variance, $\chi^2_3 = 6.7$, $P = 0.08$). As there were no significant differences among years in female dispersal, or female-offspring separation at offspring release, we pooled the data sets for the separate years in order to increase the power of our statistical analyses (see Table 1 for all descriptive data).

In order to assess the effect of our predictor variables on maternal and juvenile dispersal, we performed two

Table 1 Descriptive data on variables analysed as potential predictors of maternal dispersal distance.

Trait	<i>n</i>	Mean	SD	Median	Min	Max
Number of observations with partners	34	1.62	2.13	0.50	0.00	7.0
Clutch size	34	8.50	2.22	8.00	2.00	15.0
Female dispersal (m)	34	6.8	10.6	4.00	0.00	56.3
Maternal-offspring separation distance (m)	34	187.7	121.6	192.9	4.95	409.3
Number of ticks	203	10.7	16.8	6.0	0	175
Band sharing (MHC)	27	0.81	0.11	0.84	0.63	1.0

Table 2 Multiple regression analysis of predictors of between-year maternal dispersal in female sand lizards. Within brackets is given the results of a corresponding model using the residual scores from a clutch size-body size regression as an estimate of reproductive effort. In that model, maternal-offspring separation distance is also significant ($T = -2.37$, $P = 0.025$).

Parameter estimate (β)	β	SE	T	P
Maternal-offspring				
Separation distance	-0.87	0.29	-3.03	0.0052**
Offspring dispersal distance	-0.19	0.26	-0.75	0.461
Clutch size	-0.16	0.12	-1.10	0.278
Residual clutch size - body mass	0.09	0.29	0.33	0.744
Number of partners	-0.34	0.26	-1.31	0.200
Number of ticks	0.09	0.06	1.41	0.168

Model statistics: $F_{5,28} = 2.76$, $P = 0.038$, $R^2 = 0.33$.

sets of analyses. In the first, we looked for significant relationships between maternal dispersal distance and two non-normal variables, male-female MHC band sharing and time between release and mean recapture date, which both turned out to be nonsignificant in a Spearman's rank order correlation ($r_s = -0.23$, $P = 0.10$, $n = 53$, and $r_s = 0.004$, $P = 0.98$, respectively). We then analysed the effects on dispersal of five predictors in a multiple regression analysis (Table 2). The only variable in this analysis that came out significant was maternal-offspring separation distance at offspring release ($P < 0.0$; Table 2). None of the variables mean offspring dispersal distance, clutch size, number of partners, or ectoparasite load significantly influenced maternal dispersal distance (Table 2).

In order to establish whether dispersal indeed resulted in further separation of females and their offspring, we also looked for a correlation between maternal dispersal and the distance separating the mean female home range coordinates and those of her recaptured offspring in the year following dispersal. This relationship could not be confirmed for the entire data set ($P > 0.05$). However, because it may be unrealistic that females and their young can detect each other's presence at long distances (up to 400 m separation at release in this data set), we truncated the data at an arbitrarily chosen separation distance of 100 m (as there is no information available on at what distance perception would be possible). In this sub-sampled data set ($n = 11$), there was a strong correlation between maternal dispersal and final maternal-offspring separation (Spearman's rank order correlation coefficient, $r_s = 0.66$, $P < 0.05$, $n = 11$), supporting that female dispersal resulted in enhanced offspring avoidance. Visual inspection of release sites in relation to density (Fig. 3) suggested that elevated female and juvenile dispersal as a result of female-offspring nearness is not coincidental with high density of juveniles (Fig. 3) or adults (Fig. 1), as relatively longer dispersal in relation to closely related offspring could take place anywhere at the study site regardless of lizard density.

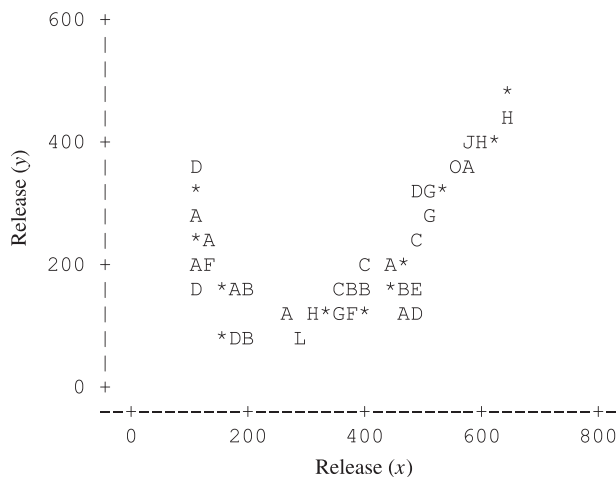


Fig. 3 Descriptive plot of the distribution of offspring release sites around the Asketunnan peninsula 1998-2002 (the true peninsula outline closely follows the periphery of the SAS plot of release coordinates). The * symbols represent the 11 release sites with offspring separated <100 m from the female (and for which we had dispersal data of both females and young). As can be visually confirmed, these sites are uniformly distributed around the peninsula and sampled randomly in relation to offspring density. A = 1 observation, B = 2 observations, etc.

Table 3 Multiple regression analysis of predictors of between-year juvenile dispersal in female sand lizards. Sex ratio is based on a within-clutch average score where 1 = son, and 0 = daughter (thus 1.0 = all sons). The data set were truncated for maternal-offspring separation distances longer than 101 m.

Parameter estimate (β)	β	SE	T	P
Maternal - offspring				
separation distance	-0.12	0.21	-0.57	0.575
Body mass	-1.53	2.26	-0.68	0.501
Clutch size	-0.14	0.06	-2.26	0.029*
Sex ratio	-0.57	0.82	-0.71	0.485

Model statistics: $F_{4,41} = 1.67$, $P = 0.17$, $R^2 = 0.14$.

We then performed a corresponding multiple regression analysis of potential predictors of juvenile dispersal (Table 3). Juveniles dispersed on average 52 m (± 46 m, SD). There was, however, no significant effect of maternal-offspring separation distance at offspring release on offspring dispersal distance ($P = 0.575$, Table 3), or of offspring body mass ($P = 0.501$), or offspring sex ratio ($P = 0.485$). Thus, juvenile dispersal *per se* does not seem to contribute to female-offspring separation. The only factor showing significant effects on offspring dispersal was clutch size, i.e. the number of young released at a given coordinate, and this effect was to our surprise negative, with shorter dispersal when clutches were larger ($P < 0.05$, Table 3).

Discussion

The results of this study paint a coherent picture with females in a natural population dispersing further when their offspring are released relatively closer. What might explain this effect? One factor that may contribute is that females simply avoid closely related individuals regardless of age, perhaps via odour detection. We doubt this scenario. If so, females with relatively closely related partners would also shift their home ranges relatively more, which they did not. An alternative explanation is that perception of related individuals is either not odour related, or if it is, is mediated via some other part of the genome than MHC, which we used to assess partner relatedness. Two observations cast doubt on this proposition. First, Olsson *et al.* (2003) demonstrate that females in staged trials in the laboratory prefer to associate with odour samples from males less closely related at the MHC. Thus, this confirms that females do respond to odours that are either directly or indirectly linked to MHC genotype, and are capable of adjusting their spatial patterns accordingly.

Given that some discrimination at an individual level must take place in order to explain offspring-induced female home range shifts in the wild, it appears near impossible that this is visually based, since there is no parental care in this species and females characteristically leave their home ranges for oviposition (Olsson, 1988). Thus, a female has never seen her offspring prior to (or subsequent to) their release. One possibility is that selection for relatedness-based, odour-mediated mate recognition could result in a sensory bias that selects for female offspring avoidance (this mechanism could still operate even if females do not alter their spatial distribution in the wild in relation to partner relatedness).

Our results may also cast new light on the proposition that availability of oviposition sites is driving females to leave their home ranges for egg laying (Olsson, 1988; Olsson *et al.*, 1997; Olsson & Shine, 1997). The present study suggests that females may be selected to lay their eggs outside of their normal home ranges to avoid competition with their own offspring with which they have food niche overlaps (Olsson & Madsen, 2001b), and, later in life, to reduce the risk of mating with their own sons (Olsson *et al.*, 1997; Olsson & Madsen, 2001a).

This study was not primarily initiated to analyse determinants of juvenile, but maternal, dispersal. However, our data admits such analysis and revealed some interesting results. First, dispersal does not seem to be at all influenced by maternal nearness and, hence, is driven by different processes than in adults. More importantly, and contrary to findings in the congeneric common lizard (*Lacerta vivipara*, Massot *et al.*, 1992; Lecomte *et al.*, 1994), our multiple regression analysis suggests that factors relating to high juvenile density promotes philopatry in neonatal sand lizards. In common lizards, density-related processes, such as competition, seem to

promote dispersal rather than philopatry. Thus, this prompts the question 'how robust are these results'? The two additional factors included in our multiple regression model remove the ambiguity that body size which has been identified as a promoter of dispersal in another lizard species (Olsson & Shine, 2003), confounds these results. Furthermore, the potentially confounding effect of same-sex sib competition is also removed (no effect of sex ratio), as this parameter is also included in the model. A neglected factor, however, is the potential for preparturient maternal effects, e.g. maternal corticosterone level, which has been demonstrated to drive dispersal in experimental enclosures of *L. vivipara* (De Fraipont *et al.*, 2000). Although common lizards are viviparous in most of their distribution range, and, hence, maternal effects could be expected to be higher than in the oviparous sand lizard, work on oviparous populations of common lizards also confirm such results (De Fraipont *et al.*, 2000). Thus, we cannot exclude the possibility that unknown maternal effects also influence our results.

Our study thus demonstrates that females are positively influenced by offspring nearness. In fact, we could not identify any other significant predictors of maternal dispersal, despite incorporating several factors that have been demonstrated to have such effects in previous work, e.g. reproductive output (significant here also when analysed separately). In offspring, however, the only significant factor influencing dispersal was the number of siblings in their surroundings. This may thus lend some support to the 'public information hypothesis', which states – in the case of sand lizard neonates – that near siblings are used to assess surrounding food abundance, or, that neonates are under selection to judge maternal reproductive output as an indicator of high productivity in recent history. Thus, these results are a stimulating challenge for future experimental work.

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