

Genetic, prenatal, and postnatal correlates of dispersal in hatchling fence lizards (*Sceloporus occidentalis*)

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Similarity of dispersal behavior among siblings is common in vertebrates. However, little is known about the factors (genetic, prenatal, postnatal) generating this similarity. Here we analyzed potential influences on the dispersal patterns of multiple families of hatchling fence lizards, *Sceloporus occidentalis*. We captured near-term females from the field, incubated their eggs in the laboratory, measured various traits of the hatchlings and dams, and then released the hatchlings at a number of sites in nature. We recaptured hatchlings 5–6 weeks later and measured the direct distance to the release site. Because we treated hatchlings (from eggs to release) randomly with respect to sibship, we eliminated the possibility that any observed sibling similarity in dispersal is merely an artifact of common postnatal influences. To analyze dispersal, we developed a new method that does not make an arbitrary choice of a threshold distance separating dispersers from nondispersers. We found a significant family effect on dispersal. We suspect that this family effect originates from genetic influences rather than from prenatal ones. Indeed, hatchling dispersal was remarkably unrelated to numerous traits (of clutches, mothers, or hatchlings) that might reflect prenatal effects. However, we did find that males were more likely to disperse than females, as predicted for polygynous species. Finally, characteristics of the release site did not appear to influence dispersal. *Key words*: dispersal, family resemblances, lizards, *Sceloporus occidentalis*, sex-biased dispersal. [*Behav Ecol* 14:650–655 (2003)]

Dispersal is of interest to evolutionary biologists primarily because of its impact on gene flow and on individual fitness (Johnson and Gaines, 1990; Stenseth and Lidicker, 1992). Most evolutionary theories of dispersal have assumed that differences in dispersal are genetically based (Johnson and Gaines, 1990; Stenseth, 1983), but no convincing evidence of such a genetic basis has been reported for vertebrates (Johnson and Gaines, 1990). Similar dispersal behavior among vertebrate siblings has been reported (reviewed in Massot and Clobert, 2000). However, this pattern could reflect either genetic variation in dispersal or the fact that siblings share common pre- and postnatal environments (for prenatal influences, see Massot and Clobert, 1995, 2000; for postnatal influences at birth site, see Arcese, 1989; Massot and Clobert, 2000; van Noordwijk, 1984). Distinguishing genetic from environmental determinants of dispersal is thus an open challenge, as a response to selection on dispersal behavior requires that it have a genetic basis (Johnson and Gaines, 1990).

As part of a study of the evolutionary ecology of hatchling lizards (see below), we conducted an experimental study of dispersal of families of hatchling fence lizards (*Sceloporus occidentalis*). Our primary goals were to determine whether dispersal was influenced by (1) family membership (genetic or prenatal influences), (2) characteristics of the dams or of the hatchlings themselves, and (3) the characteristics of the

release sites (postnatal habitat influences). A previous experimental study examined developmental processes of dispersal in the live-bearing lizard *Lacerta vivipara* and found that siblings had similar dispersal propensities dependent on prenatal effects (Massot and Clobert, 2000). Viviparity is expected to promote prenatal influences (Massot and Clobert, 2000). Correlative studies in birds showed family resemblances due only to postnatal effects (Arcese, 1989; Ferrer, 1993; van Noordwijk, 1984), a result expected given that extensive parental care provides more opportunities to develop postnatal influences (Massot and Clobert, 2000). In contrast, our experimental study of an oviparous species that does not have parental care is of considerable interest, as any observed family resemblance is likely to be less dependent on pre- and postnatal influences.

Sex-biased dispersal is widespread and has been extensively studied in birds and mammals (Greenwood, 1983). However, the ultimate causes of sex-biased dispersal (resource competition, competition for mates, inbreeding, kin competition) remain debatable. Nevertheless, studies of taxa other than birds and mammals can help evaluate the universality of sex-biased dispersal and clarify its causes (Doughty et al., 1994; Massot and Clobert, 2000; Pusey, 1987). In any case, all competing hypotheses predict male-biased dispersal for polygynous species such as *Sceloporus occidentalis* (Clarke et al., 1997; Dobson, 1982; Favre et al., 1997; Greenwood, 1983). Accordingly, we tested whether male hatchlings are more likely to disperse than females.

Many studies of dispersal use an arbitrary threshold distance to separate dispersers from nondispersers. We developed a new method that instead searches for the optimal distance to separate them. In addition, previous studies of dispersal have usually been complicated because siblings shared common pre- and postnatal environments as well as common genes (Massot et al., 1994). Consequently, the

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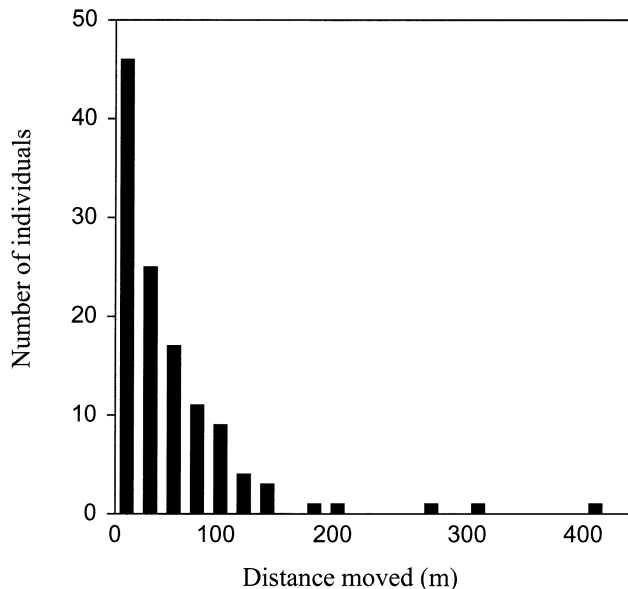


Figure 1
Distance moved by hatchlings from their release to recapture sites. Median distance = 27.5 m, mean distance = 45.6 m, maximum distance = 420 m, $N = 120$.

dispersal behavior of siblings may not be statistically independent. We circumvented this problem in two ways. First, we controlled postovipositional influences by separating clutches and incubating eggs individually in a common garden and also by releasing siblings systematically at different sites in the study area such that sibs were never released together. Thus, any similarity among siblings cannot be due either to a family-specific incubation or a family release-site environment. Second, when we detected a residual family effect on hatchling dispersal, we used a statistical approach that corrects for overdispersion of data induced by their non-independence.

METHODS

The species

The western fence lizard, *Sceloporus occidentalis*, is a semi-arboreal iguanid lizard found in western North America from Mexico north to Washington State. At our study area in south-central Washington, these lizards are abundant on logs, trees, and under small shrubs in open oak-pine forests. These lizards are oviparous and breed in late spring. Eggs hatch in July and August. Lizards do not reach sexual maturity until at least 2 years of age. At our study site, lizards hibernate from about September (adults) or October (hatchlings) until April.

This study was part of a series that investigating the evolutionary ecology of hatchling western fence lizards. Tsuji et al. (1989) showed that various hatchling traits (e.g., body size, speed, stamina) are similar among siblings. Van Berkum et al. (1989) found that an individual's relative speed and stamina (but not its relative body size) were repeatable over long periods of time. Sinervo et al. (personal communication) found that strong directional selection favored small egg size in this cohort and also that short-term survival is family-dependent. Bennett and Huey (1990) reported preliminary analyses on phenotypic selection on physiological performance (locomotion) and on morphology.

Data collection

This study was conducted at the Tuthill Ranch, Klickitat County, Washington, USA (permits from the Department of Wildlife). Methods of obtaining laboratory-raised hatchlings are detailed in Tsuji et al. (1989) and in van Berkum et al. (1989). In brief, we captured 33 gravid females in early June 1985, transferred them to a laboratory (University of Washington), and then collected and incubated (30°C) their eggs ($N = 483$) in individual egg cups. The position of eggs in the incubator was randomized with respect to sibship and also shifted frequently, thus eliminating the possibility that interfamily differences in dispersal were confounded by a family-specific incubation environment.

Within a few hours after hatching, lizards were individually measured and toe clipped. After several days (Tsuji et al., 1989), we began measuring their speed and stamina (see below). Finally, we remeasured the size of hatchlings on 18 August and then released them ($N = 296$; average age at release = 23 days and range 19–28 days) the following day onto marked sites near the area where dams were originally captured. We intentionally released only one hatchling per family at a given site, thereby eliminating the possibility that interfamily differences in dispersal could be confounded with a release-site effect. Between 5 and 6 weeks later (28 September–7 October), we recaptured 120 hatchlings (from 30 families) and measured the straight-line distance between release and recapture sites. Any mark-recapture study of dispersal must confront the possibility of failing to detect long-distance movements of animal away from the study area (Koenig et al., 1996). Such long-distance movements were probably rare by these lizards, as the study area was bounded by forest. Nevertheless, we made an effort to search in patches of open habitat as far as 420 m outside the main area. Most movements were less than 100 m (Figure 1), even though we attempted give the same capture effort to all sites within the study area.

Maternal traits

Because dispersal behavior of offspring might be influenced by maternal attributes, we tested for several traits of each dam: snout-vent length (SVL), speed and stamina after laying (Tsuji et al., 1989), and a postlaying condition index (residuals from the relationship between body mass vs. SVL). We also tested several traits of each clutch: laying date, residual clutch size (corrected for its relationship with SVL), sex ratio (proportion of males within clutches), and hatching success (proportion of eggs that hatched). We used a multivariate model to test for relationships between these maternal traits and hatchling dispersal.

Hatchling traits

Because dispersal might be influenced by hatchling's phenotype, we measured several hatchling traits. We used a multivariate model that included SVL at hatching, condition index at hatching (as above), speed (residuals from the relationship between speed vs. SVL), stamina, age at release, and prerelease condition index. Methods of measuring maximal speed and stamina are detailed in van Berkum et al. (1989) and in Tsuji et al. (1989). In brief, we determined burst speed by chasing hatchlings along a 1.2 m racetrack with photocell detectors at 0.1-m intervals. A computer estimated the fastest 0.2-m speed for each run. Stamina was indexed as the total time a lizard could maintain station while running slowly on the moving belt (at 0.225 km/h) of a motorized treadmill. We determined speed eight times over 2 days (when lizards averaged 13 [range 12–15] and 19 [18–21] days old), whereas stamina was measured only twice (when lizards

averaged 16 [15–18] and 21 [20–23] days old). We selected the fastest speed and the longest run as estimates of maximal speed and stamina, respectively (see van Berkum et al., 1989).

Habitat characteristics

We released lizards in groups of 8 (all non-sibs) onto 37 marked sites in an oak woodland. These sites, which were generally small clearings with logs or shrubs (or both), were all judged suitable for lizards, as evidenced by the presence of native lizards or their spoor. We recorded physical characteristics of all release sites: size and shape (length/width) of the clearing as well as presence of the different microhabitats (pine logs, oak logs, debris [branches, small logs, or barks], cracks, or shrubs).

Statistical methods of classifying dispersers

The main operational difficulty for studies of dispersal is correctly distinguishing dispersers from individuals that are merely making routine movements within their home range (Gaines and McClenaghan, 1980). We chose not to use the straight-line distance moved for two reasons. First, the suitable habitats for the fence lizard are patchily distributed in our study area. Thus, the distance a given lizard moved would depend in part on the patchiness of the immediate environment as well as on that individual's dispersal propensity. Second, previous studies show that differences in distance moved may be due to movements unrelated to dispersal (e.g., differences in the size of home range may bias estimates of distances moved; Massot, 1992).

Many studies define "dispersers" as individuals that move farther than one home range diameter and define "philopatric individuals" as those moving less than one home range. The average home range diameter is often used as the threshold distance (e.g., Harris and White, 1992; Sandell et al., 1990). However, other studies set higher thresholds, such as the upper 95% confidence limit of the home range diameter (Caley, 1987; Clobert et al., 1994) or the largest diameter observed (Holekamp et al., 1984). These higher threshold approaches may help avoid misclassifying many philopatric individuals as dispersers (many truly philopatric individuals move farther than the average of the home range diameter). In any case, any a priori choice of a threshold distance is inevitably somewhat subjective. For example, it may be inappropriate to use the home range estimate of individuals (with regard to age, sex, etc.) studied for dispersal if their dispersal depends on other individuals. For example, if inbreeding avoidance is the cause of dispersal (e.g., Wolff et al., 1988), then dispersal of one sex should be relative to the home range of the other sex. Similarly, if offspring dispersal depends on parent-offspring conflict (e.g., Ronce et al., 1998), then dispersal of offspring should be relative to the home range of adults.

Another problem is that philopatric and dispersing animals may often overlap in their distance moved because there is generally no clear shift in frequency distributions of distances moved (Figure 1). If so, then when trying to classify individuals as philopatric versus dispersing, it is better to discard individuals that move intermediate distances, as such individuals cannot reliably be classified (Clobert et al., 1994; Massot and Clobert, 2000).

For all these reasons, we used a new approach that does not make an arbitrary choice of a single threshold distance, but rather searches for an expected pattern (e.g., the classical sex-bias in dispersal) from several analyses with differing distance

Table 1

Test of the family effect on hatchling dispersal with generalized linear models on families that included at least two hatchlings with a known dispersal status

Distance moved >	Sample sizes			Model \hat{p}_m	Family effect p	Family \times sex p
	Nf	Np	Nd			
20 m	29	46	73	.018	.913 ^a	.256 ^a
30 m	27	44	59	.017	.887 ^a	.265 ^a
40 m	24	41	42	.044	.648 ^a	.358 ^a
50 m	24	41	36	.054	.162	.107
60 m	23	40	30	.072	.063	.326
70 m	20	37	23	.274	.020	.405
80 m	18	35	19	.353	.012	.657
90 m	17	34	15	.496	.009	.788
100 m	14	32	10	.621	.046	.769

Hatchlings were always defined as philopatric when they moved <20 m. Dispersers were successively defined for longer and longer distances. Nf = number of families; Np = number of philopatric hatchlings; Nd = number of "dispersing" hatchlings; \hat{p}_m = test of the fit of models (a significant probability means that the model does not fit the data reasonably well).

^a Tests corrected for unfitted models (correction of overdispersion of data by the DSCALE option of the GENMOD procedure; see Methods).

thresholds. If, for example, sexes differ in their dispersal tendencies, then analyses comparing relatively "pure" samples (i.e., with ambiguous individuals discarded) should be more likely to yield significant results compared to analyses that include inadvertently misclassified individuals. In our study, we defined philopatric hatchlings as those that moved less than 20 m (a conservative value for the fence lizard: estimates of mean home range diameters in another population are 55 m for adult males and 22 m for adult females; Tanner and Hopkin, 1972), and the different thresholds to define dispersers were 20 m, 30 m, . . . , 90 m, and 100 m. For example, in the second case (i.e., 30 m), we defined as dispersers the individuals that moved farther than 30 m and thus excluded any individuals that moved between 20 and 30 m. To search for the optimal threshold, and based on previous findings in literature, we used tests on the family resemblance and sex-bias in dispersal. Family resemblance among siblings has been found in 10 out of 14 species (review in Massot and Clobert, 2000). Sex-biased dispersal, which is widespread in birds and mammals (Greenwood, 1983), has also been found in lizards (Clobert et al., 1994; Doughty et al., 1994; Olsson et al., 1996).

We used generalized linear models (GENMOD procedure; SAS Institute, 1996) to test for differences between philopatric and dispersing individuals. This maximum likelihood method performs likelihood ratio tests to estimate the significance of relationships (McCullagh and Nelder, 1989). However, analyses of data involving siblings are complicated because siblings cannot a priori be assumed as statistically independent (Massot et al., 1994). In our study population, for instance, many traits run in families (Tsuji et al., 1989), including survivorship (Sinervo et al., personal communication). To solve this problem, we used generalized linear models in which we corrected for overdispersion of data (DSCALE option of the GENMOD procedure; SAS Institute, 1996). This is known to efficiently correct the non-independence between individuals (Anderson et al., 1994; Lebreton et al., 1992). Because the determinism of dispersal could differ between sexes (Boonstra and Craine, 1988), we controlled for the sex effect in all analyses.

Table 2
Relationship between hatchling dispersal and maternal traits in interaction with the sex of hatchlings

Maternal traits	Relationship with dispersal		Interaction with sex	
	χ^2 (1 df)	<i>p</i>	χ^2 (1 df)	<i>p</i>
Snout-vent length	0.46	.4957	0.04	.8445
Laying date	0.02	.8958	0.58	.4466
Condition index after laying	1.49	.2215	0.12	.7280
Speed after laying	0.29	.5873	0.01	.9108
Stamina after laying	1.21	.2720	0.32	.5721
Residual clutch size ^a	1.05	.3050	0.01	.9259
Sex-ratio within clutch	1.69	.1942	0.12	.7345
Hatching success	0.12	.7336	<0.01	.9451

Tests performed with a generalized linear model: stepwise analysis with all the main effects and their first-order interaction with sex.

^a Residuals from the relationship between clutch size versus snout-vent length ($r = .78$, $n = 29$, $p < .001$).

RESULTS

Family and sex effects

We defined philopatric individuals as those moving less than 20 m (a conservative value for the species; average home range diameter of 22 m for adult females and 55 m for adult males estimated by Tanner and Hopkin, 1972). For the reasons discussed above, we did not fix an arbitrary threshold distance to define dispersers, but searched the best threshold to find two common effects (family and sex).

When dispersers were defined as having moved at least 20, 30, 40, 50, or 60 m, we found no significant family effect, no significant interaction between family effect and hatchling sex; and models fitted the data poorly (Table 1). However, when dispersers were defined as having moved at least 70 m, a significant family effect was consistently detected (Table 1; no significant interaction family \times sex); and the models fitted the data well. Note that *p* values for the family effect decreased regularly when the disperser's category was restricted to increasing long distances (Table 1), even though the sample

Table 3
Relationship between hatchling traits and dispersal in interaction with the sex of hatchlings

Hatchling traits	Relationship with dispersal		Interaction with sex	
	χ^2 (1 df)	<i>p</i>	χ^2 (1 df)	<i>p</i>
Snout-vent length at hatching	0.02	.8870	0.38	.5364
Condition index at hatching	0.21	.6501	0.39	.5319
Speed before release ^a	0.01	.9343	0.39	.5307
Stamina before release	0.38	.5392	0.17	.6832
Tail broken before release	0.04	.8399	3.43	.0640
Age at release	0.16	.6863	0.10	.7543
Condition index at release	0.03	.8529	0.08	.7746

Tests performed with a generalized linear model: stepwise analysis with all the main effects and their first-order interaction with sex.

^a Residuals from the relationship between speed versus snout-vent length ($r = .36$, $n = 69$, $p = .003$).

Table 4
Relationship between habitat characteristics and dispersal in interaction with the sex of hatchlings

Habitat characteristics	Relationship with dispersal		Interaction with sex	
	χ^2 (1 df)	<i>p</i>	χ^2 (1 df)	<i>p</i>
Site area	0.01	.9282	1.60	.2054
Shape area	0.21	.6474	0.95	.3287
Presence of pine logs	0.01	.9169	2.24	.1341
Presence of oak logs	0.11	.7453	0.18	.6722
Presence of debris	0.17	.6767	0.15	.6983
Presence of cracks	0.15	.6962	0.22	.6420
Presence of shrubs	<0.01	.9944	1.44	.2302

Tests performed with a generalized linear model: stepwise analysis with all the main effects and their first-order interaction with sex.

sizes declined progressively (from 29 to 14 families and from 119 to 42 hatchlings; see Table 1). Such a regular decrease in *p* values is unlikely to occur by chance, simply because statistical power declines with decreased sample sizes. Thus, the decreased *p* values likely reflect improved classification of individuals.

Tests on the sex effect gave the following pattern: *p* = .105 with dispersers defined for distances >20 m, *p* = .192 with 30 m, *p* = .075 with 40 m, *p* = .044 with 50 m, *p* = .061 with 60 m, *p* = .033 with 70 m, *p* = .053 with 80 m, *p* = .091 with 90 m, and *p* = .069 with 100 m (one-tailed tests because the proportion of dispersers in males was always higher than in females, as expected in a polygynous species). Again, probabilities of the test shifted from nonsignificant for shorter distances to significant or marginally significant values for longer distances. The lowest *p* value of the sex effect (.033) was found with dispersers defined for distances higher than 70 m: hatchling males were more likely to disperse (45.5 %, $n = 33$) than females (22.2 %, $n = 36$).

The above sex effect is unlikely to be an artifact of our excluding individuals with intermediate distances. If hatchlings with intermediate distances (between 20 and 70 m) were truly a mixture of philopatric and dispersing hatchlings, then philopatric hatchlings (distance <20 m) should show the lowest proportion of males, hatchlings with intermediate distances (between 20 and 70 m) an intermediate proportion of males, and dispersers (>70 m) the highest proportion of males. This was the case, with males accounting for 39.1% of all individuals with distances <20 m ($n = 46$), 47.1% for distances between 20 and 70 m ($n = 51$), and 65.2% for distances >70 m ($n = 23$). This expected pattern was significant (one-tailed Jonckheere-Terpstra test: $p = .03$).

For the remaining analyses (see below), we used a threshold of 70 m, which seemed to represent a good compromise between sample quality and size with respect to results on the family effect (Table 1). This was also the distance where the expected sex effect had the lowest *p* value and is compatible with the 55 m estimated for the average home range diameter in adult males (Tanner and Hopkin, 1972).

Tests on maternal, hatchling, and release-site characteristics

To test influences of maternal, hatchling, and release-site characteristics on hatchling dispersal, we used generalized linear models corrected for overdispersion of data (see Methods) to take into account the above family effect on dispersal. None of the maternal traits (maternal measurements and reproductive characteristics) was associated with

hatchling dispersal (Table 2), and similarly none of the hatchling traits was significantly related to hatchling dispersal (Table 3). Moreover, no overall effect of release sites was found ($\chi^2_{17} = 16.95$ $p = .458$). This was verified by the lack of relationships between release-site characteristics and hatchling dispersal (Table 4).

DISCUSSION

We reared eggs in a common garden, measured traits of the hatchlings and their dams, and then released siblings at different sites; thus our results for siblings are not confounded by family-specific incubation or release environments. We then recaptured individuals and measured transit distance from release to recapture. Consequently, we were able to search for associations between dispersal and characteristics of dams, hatchlings, and release sites. Remarkably, dispersal was related only to family membership and sex, but not to specific traits of the dams, the hatchlings themselves (other than sex), or release site characteristics.

Genetic, prenatal, and postnatal determinants of dispersal

Hatchling dispersal was significantly influenced by family (Table 1). Most previous studies that have searched for resemblance in the dispersal of siblings have also found a significant family effect (in 10 out of 14 species, reviewed in Massot and Clobert, 2000). This pattern has been reported in mammals (e.g., Beacham, 1979; Hilborn, 1975; Ims, 1989), birds (e.g., Arcese, 1989; Ferrer, 1993; Keppie, 1980), and also in one reptile (Massot and Clobert, 2000 in *Lacerta vivipara*). This similarity of sibling dispersal could be due either to their sharing common genetic, prenatal, and/or postnatal influences. Distinguishing among these determinants is difficult in descriptive studies because many factors (e.g., shared habitat effects) may confound such analyses. Although some postnatal effects have been identified in previous descriptive studies (Arcese, 1989; van Noordwijk, 1984), experiments that control for common environmental effects should be a powerful tool to explore the causes of resemblances among siblings. In particular, experiments are necessary to discriminate between the effects of the prenatal versus postnatal environments, which may often be autocorrelated in nature.

Here we used an experimental approach and tested postnatal influences and family effects after systematically assigning sibs to different postnatal environments. To our knowledge, only one other study has performed such an experiment on dispersal (Léna et al., 1998; Massot and Clobert, 2000). That study showed that juvenile dispersal in the common lizard (*Lacerta vivipara*) was influenced by both postnatal and family effects. In our study, we found that dispersal also ran in families but was independent of any postnatal habitat effects (Table 4). In addition, we found that dispersal was independent of diverse characteristics of dams or of hatchlings (other than sex and family membership; Tables 2 and 3). In a comparable study on the common lizard (tests with five maternal traits and three hatchling characteristics), dispersal was related to litter sex-ratio and to hatchling condition index (Massot and Clobert, 2000). However, the common lizard is a viviparous species, in which prenatal influences should be more frequent (different prenatal effects on dispersal are shown in de Fraipont et al., 2000; Massot and Clobert, 1995, 2000; Sorci et al., 1994).

Postnatal effects (i.e., characteristics of the release site) were detected in the common lizard (Léna et al., 1998; Massot and Clobert, 2000) but not in the present study. The lack of postnatal influences in our study is not a consequence of homogeneity of the release sites, as they differed strikingly

(ranges were from 5 to 50 m² for site area, and from 1 to 20 for shape area; pine logs occurred in 60% of sites, oak logs in 51%, debris in 68%, cracks in 22%, and shrubs in 65%). However, we did not quantify the density of native hatchlings or adults at the release sites, and the number of such resident individuals might in fact influence dispersal. In the common lizard, for example, juvenile dispersal is influenced by adult density (Léna et al., 1998). Similarly, in *Uta stansburiana*, juvenile dispersal is influenced by interactions with other juveniles and adults (Sinervo B, personal communication). It is also possible that hatchlings released immediately after hatching would show a postnatal effect, but this would require an additional study.

The observed resemblance of siblings in dispersal could originate from genetic or from common environmental (prelaying only) influences. No maternal trait (Table 2) was associated with offspring dispersal. Moreover, no hatchling trait was associated with dispersal either, even though many of the examined traits are similar among siblings in this population (Tsuji et al., 1989). Thus, the observed family effect suggests that dispersal might be heritable in this population, although we cannot exclude a prelaying maternal effect unrelated to measured traits. Maternal feeding level affected juvenile dispersal in the common lizard (a viviparous species), but not via influencing hatchling body size, body mass, and condition index at birth (Massot and Clobert, 1995). Again, such prenatal effects are less likely in oviparous lizards such as *Sceloporus occidentalis* because embryos experience a common maternal environment for a relatively short time. Further work will be required to evaluate a genetic basis of dispersal (e.g., breeding experiment) and also to study fitness consequences of dispersal to assess its adaptive basis.

Sex-biased dispersal

Males dispersed more frequently than females, as predicted for polygynous species (Clarke et al., 1997; Dobson, 1982; Favre et al. 1997; Greenwood, 1983). Three previous studies on polygynous lizards also show male-biased dispersal (Clobert et al., 1994 for *Lacerta vivipara*; Doughty et al., 1994 for *Uta stansburiana*; Olsson et al., 1996 for *Lacerta agilis*). It should be interesting to study other reptile species with different mating systems, in which male-biased dispersal would not be expected.

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REFERENCES

- Anderson DR, Burnham KP, White GC, 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780–1793.
- Arcese P, 1989. Intrasexual competition, mating system and natal dispersal in song sparrows. *Anim Behav* 38:958–979.
- Beacham TD, 1979. Dispersal tendency and duration of life of littermates during population fluctuations of the vole *Microtus townsendii*. *Oecologia* 42:11–21.

- Bennett AF, Huey RB, 1990. Studying the evolution of physiological performance. *Oxf Surv Evol Biol* 6:251–284.
- Boonstra R, Craine ITM, 1988. Similarity of residence times among *microtus* littermates: importance of sex and maturation. *Ecology* 69:1290–1293.
- Caley MJ, 1987. Dispersal and inbreeding avoidance in muskrats. *Anim Behav* 35:1225–1233.
- Clarke AL, Saether B-E, Roskaff E, 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438.
- Clobert J, Massot M, Lecomte J, Sorci G, de Fraipont M, Barbault R, 1994. Determinants of dispersal behavior: the common lizard as a case study. In: *Lizard ecology: historical and experimental perspectives* (Vitt L, Pianka R, eds). Princeton, New Jersey: Princeton University Press; 183–206.
- de Fraipont M., Clobert J, John-Alder H, Meylan S, 2000. Increase pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. *J Anim Ecol* 69:404–413.
- Dobson SF, 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav* 30:1183–1192.
- Doughty P, Sinervo B, Burghardt GM, 1994. Sex-biased dispersal in a polygynous lizard, *Uta stansburiana*. *Anim Behav* 47:227–229.
- Favre L, Balloux F, Goudet J, Perrin N, 1997. Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. *Proc R Soc Lond B* 264:127–132.
- Ferrer M, 1993. Ontogeny of dispersal distances in young Spanish imperial eagles. *Behav Ecol Sociobiol* 32:259–263.
- Gaines MS, McClenaghan LR Jr, 1980. Dispersal in small mammals. *Annu Rev Ecol Syst* 11:163–196.
- Greenwood PJ, 1983. Mating systems and the evolutionary consequences of dispersal. In: *The ecology of animal movement* (Swingland IR, Greenwood PJ, eds). Oxford: Clarendon Press; 116–131.
- Harris S, White PCL, 1992. Is reduced affiliative rather than increased agonistic behaviour associated with dispersal in red foxes? *Anim Behav* 44:1085–1089.
- Hilborn R, 1975. Similarities in dispersal tendency among siblings in four species of voles (*Microtus*). *Ecology* 56:1221–1225.
- Holekamp KE, Smales L, Simpson HB, Holekamp NA, 1984. Hormonal influences on natal dispersal in free-living Belding's ground squirrels (*Spermophilus beldingi*). *Hormones Behav* 18:465–483.
- Ims RA, 1989. Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. *Ecology* 70:607–616.
- Johnson ML, Gaines MS, 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu Rev Ecol Syst* 21:449–480.
- Keppie DM, 1980. Similarity of dispersal among sibling male spruce grouse. *Can J Zool* 58:2102–2104.
- Koenig WD, van Vuren D, Hooge PN, 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol Evol* 11:514–517.
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR, 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118.
- Léna J-P, Clobert J, de Fraipont M, Lecomte J, Guyot G, 1998. The relative influence of density and kinship on dispersal in the common lizard. *Behav Ecol* 9:500–507.
- Massot M, 1992. Déterminisme de la dispersion chez le lézard vivipare (PhD dissertation). Paris: University of Paris XI.
- Massot M, Clobert J, 1995. Influence of maternal food availability on offspring dispersal. *Behav Ecol Sociobiol* 37:413–418.
- Massot M, Clobert J, 2000. Processes at the origin of similarities in dispersal behaviour among siblings. *J Evol Biol* 13:707–719.
- Massot M, Clobert J, Chambon A, Michalakis Y, 1994. Vertebrate natal dispersal: the problem of non independence of siblings. *Oikos* 70:172–176.
- McCullagh P, Nelder JA, 1989. *Generalized linear models*. New York: Chapman and Hall.
- Olsson M, Gullberg A, Tegelström H, 1996. Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*). *J Evol Biol* 9:229–242.
- Pusey AE, 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol Evol* 2:295–299.
- Ronce O, Clobert J, Massot M, 1998. Natal dispersal and senescence. *Proc Natl Acad Sci USA* 95:600–605.
- Sandell M, Agrell J, Erlinge S, Nelson J, 1990. Natal dispersal in relation to population density and sex ratio in the field vole, *Microtus agrestis*. *Oecologia* 83:145–149.
- SAS Institute, 1996. *SAS/STAT software changes and enhancements through release 6.11*. Cary, North Carolina: SAS Institute.
- Sorci G, Massot M, Clobert J, 1994. Maternal parasite load increases sprint speed and philopatry in female offspring of the common lizard. *Am Nat* 144:153–164.
- Stenseth NC, 1983. Causes and consequences of dispersal in small mammals. In: *The ecology of animal movement* (Swingland IR, Greenwood PJ, eds). Oxford: Clarendon Press; 63–101.
- Stenseth NC, Lidicker WZ Jr, 1992. The study of dispersal: a conceptual guide. In: *Animal dispersal—small mammals as a model* (Stenseth NC, Lidicker WZ Jr, eds). London: Chapman & Hall; 5–20.
- Tanner WW, Hopkin JM, 1972. Ecology of *Sceloporus occidentalis longiceps* Baird and *Uta stansburiana* Baird and Girard on Rainier Mesa, Nevada Test Site, Nye County, Nevada. *Brigham Young Univ Sci Bull Biol Ser* 15:1–39.
- Tsuji JS, Huey RB, van Berkum FH, Garland T Jr, Shaw RG, 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Evol Ecol* 3:240–252.
- van Berkum FH, Huey RB, Tsuji JS, Garland T Jr, 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird & Girard). *Funct Ecol* 3:97–105.
- van Noordwijk AJ, 1984. Problems in the analysis of dispersal and a critique on its “heritability” in the great tit. *J Anim Ecol* 53:533–544.
- Wolff JO, Lundy KI, Baccus R, 1988. Dispersal, inbreeding avoidance and reproductive success in white-footed mice. *Anim Behav* 36:456–465.