

Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*)

M. Olsson¹, A. Gullberg² and H. Tegelström²

¹*The University of Sydney, School of Biological Sciences, Zoology Building A08, N.S.W. 2006, Australia*

²*Uppsala University, Department of Genetics, Box 7003, S-750 07 Uppsala, Sweden*

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Abstract

We demonstrated that sand lizards (*Lacerta agilis*) are more likely to have malformed offspring when they mate with siblings. Offspring with malformations, such as deformed limbs and heads, have zero survival in a natural population. Normal-looking siblings of malformed hatchlings also had a reduced survival in the wild, compared to offspring from clutches in which all siblings appeared normal. The proportion of malformed hatchlings in the natural population was ca. 10%, in spite of differences in juvenile dispersal between males and females. Male juveniles disperse significantly further from their natal sites than do female juveniles.

Introduction

Matings at both ends of the 'inbreeding-outbreeding' continuum sometimes yield deformed offspring in species across both the animal and plant kingdoms (see e.g. Shields, 1982; reviews in Wilmsen–Thornhill, 1993). Although the detrimental effects of such matings are widely appreciated, there is still no consensus about its genetic underpinnings. Three main hypotheses have been claimed, by themselves or in combination, to account for genetic phenomena related to inbreeding, inbreeding depression, and the results in the present paper. The 'dominance' hypothesis argues that inbreeding depression arises mainly from an increase in the exposure of detrimental recessives in homozygotes (Waser, 1993a). The 'overdominance' hypothesis claims that inbreeding depression is caused by the resulting *decrease* in heterozygosity (in this hypothesis heterozygotes are supposedly superior to homozygotes) (Waser, 1993a). The epistasis hypothesis (e.g. Hamilton, 1993) questions the importance of heterozygote advantage, and also suggests that a significant

part of heterosis effects, arising from outcrossings between inbred strains, could be due to epistatic multiple homozygosity.

Most empirical knowledge of inbreeding effects in natural populations has been accumulated on a limited set of taxa, predominantly plants, some box-nesting passerine birds, and mammals (e.g. *Plants*: Cornelius and Dudley, 1974; Griffin and Lindgren, 1985; Schemske and Lande, 1985; Holtsford and Ellstrand, 1990; Waser, 1993b; Willis 1993; *Birds*: Greenwood et al., 1978; Van Noordwijk and Scharloo, 1981; Johnsson and Gaines, 1990; Rowley, Russell, and Brooker, 1993; *Mammals*: Greenwood, 1980; Moore and Ali, 1984; Dobson and Jones, 1985; Harvey and Ralls, 1986; Ralls, Harvey and Lyles, 1986; Ralls, Ballou and Templeton, 1988; Charlesworth and Charlesworth, 1987; Johnsson and Gaines, 1990; Moore, 1993; Smith, 1993).

Far fewer studies deal with inbreeding in invertebrates and lower vertebrates (but see reviews in Wilmsen–Thornhill, 1993). In reptiles, there are only three published observations of inbreeding effects (in Waldman and McKinnon, 1993). Apart from Madsen et al.'s (1992) preliminary observation that still births and malformations in newborn adders (*Vipera berus*) are likely to be caused by inbreeding, there is to our knowledge no published field study yet of the extent, or the effects, of inbreeding in reptiles.

The circumstances and levels of inbreeding under which mechanisms for inbreeding avoidance may evolve have been modelled by several researchers (Bengtsson, 1978; Packer, 1979; Parker, 1979, 1983; Lande and Schemske, 1985; Waser et al., 1986; Johnsson and Gaines, 1990). However, these models differ in the predictions that they make depending on the costs of inbreeding avoidance, mating systems, and different levels of inbreeding tolerance in males and females (Waser et al., 1986). Until recently, not only was there little data for testing the predictions of these models, but there was only weak evidence of selection opposing inbreeding in the wild (Wilmsen–Thornhill, 1993; Caughley, 1994; Partridge and Bruford, 1994). However, two recent studies clearly demonstrate that selection can strongly oppose inbreeding in song sparrows (Keller et al., 1994) and white-footed mice (Jiménez et al., 1994). In contrast to the scant previous evidence, selection arising from matings with close kin has been widely assumed to drive the evolution of traits with significant somatic costs such as sex-specific dispersal.

Mechanisms yielding reduced risk of inbreeding effects have enjoyed little attention in studies of reptilian populations. To our knowledge there are only two studies that analyze sex-specific differences in juvenile dispersal in reptiles. Doughty et al. (1994) demonstrated experimentally that male juveniles of the lizard (*Uta stansburiana*) disperse more than females in some years. Clobert et al. (1994) recently demonstrated that dispersal is male biased in the common lizard (*Lacerta vivipara*), and strongly family dependent.

We focus on the detrimental effects arising from matings with close kin in the Swedish sand lizard (*Lacerta agilis*) – i.e. inbreeding and inbreeding depression (reduced viability and survival). The background for this study were observations of malformed offspring from sand lizard females in a natural sub-population with low genetic diversity (Olsson et al., 1994a), which is part of a larger, fragmented

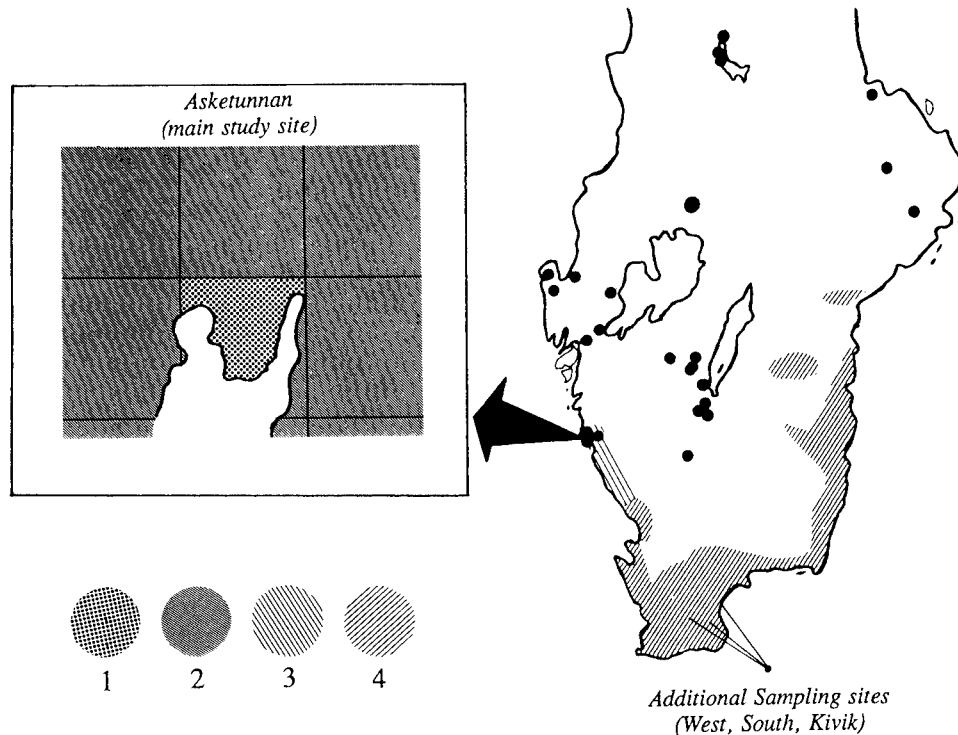


Fig. 1. Distribution of the sand lizard in Sweden. The map was redrawn from Andrén and Nilson (1979), and updated with the most recent fauna survey available for sand lizards (Ahlén and Tjernberg, 1992). The distance from the main site (Asketunnan) to the 'Additional sampling sites' is approximately 300 km. The inflated map of the study site shows the peninsula, approximately 400 m long, on which the field work was performed. The areas marked in the figure represent: (1) the core area of the study site, (2) the area searched for migrating lizards annually but in which less time was invested than in area (1), (3) update (Ahlén and Tjernberg, 1992) of Andrén and Nilson's (1979) original distribution map (4). Filled black circles represent relic populations (Andrén and Nilson, 1979).

population (Fig. 1; Ahlén and Tjernberg, 1992; Olsson, 1992a). This made us hypothesize that hatchling malformations could be due to inbreeding. To look for mechanisms of pre-copulatory inbreeding avoidance in sand lizards, we estimated sex-specific juvenile dispersal.

Is there potential for inbreeding in sand lizards?

Sand lizards may live for over ten years; mean longevity is 5–6 years (Olsson, 1992a), and the lizards become mature at an age of ca. three years in males and four years in females (Olsson, 1992a). Thus, generations overlap, and there is, demographically, opportunity for matings between close kin. Male sand lizards are

polygynous and female receptivity is asynchronous so that larger males can monopolize more females than smaller males, which may skew the operational sex ratio and, hence, reduce the effective population size (Olsson, 1992a, 1994a; Olsson et al., in prep.). Thus, the life history and the geographic distribution of sand lizards suggest that close relatives may interbreed. We designed a study comprising both laboratory and field work. In the laboratory, we staged matings between siblings, to investigate if these matings (i) would result in the same or similar malformations in the offspring as those observed under natural conditions, and (ii) whether these malformations would occur in higher frequency in females mated to brothers, than when some of these brothers and sisters were drawn at random and re-mated with a sample of non-related individuals. In a complementary field study we monitored the malformations of offspring in clutches laid by wild females, and recorded recapture rates of these offspring after one year. The first year in a sand lizard's life cycle is characterized by a high mortality rate (Corbett, 1979; Olsson et al., 1994a), and hence should coincide with stages of ontogeny during which selection on offspring viability is most intense. The sand lizard has a continuous distribution in the coastal areas of the provinces Halland, Skåne (Scania), Blekinge, and eastern Småland (Fig. 1; Ahlén and Tjernberg, 1992). In other parts of Sweden there are isolated, relic populations, which probably have very little gene flow with the zone of continuous distribution.

Sand lizard females are approximately uniformly distributed within a study site, the home range center is usually a rock or log which is used for shelter and thermoregulation. Males visit several females during the mating season, have much larger home ranges than females, and defend an area around the female that is currently courted or mate guarded (Olsson, 1992a). Thus, males do not defend a site-related territory throughout the mating season. The home range size for males is approximately 1100 m² on average and the corresponding figure for females is ca. 140 m² (Olsson, 1984, 1986). These figures were arrived at by only including individuals in the analysis that had a relationship between number of observations and home range area with a derivative that asymptotically approached zero; thus, additional observations did not yield a larger home range size (Rose, 1982). These figures also corresponded well with home range size estimated by the A4-index (Jennrich and Turner, 1969), and following Jennrich and Turner's correction (1969) there was no correlation between number of observations and home range size ($r_s = 0.08$, $P > 0.05$; Olsson, 1992a).

Materials and methods

Laboratory study

All our sampling sites were situated within the zone of continuous distribution in southern Sweden (Fig. 1); no sampling was made from the isolated relic populations for the present study. Our main study site was situated at Asketunnan (Halland) (Fig. 1). In 1987, we collected lizards at four sites (Fig. 1; marked

Table 1. Geographic origin of lizards that sired the groups 'sibling' and 'unrelated partners', which were compared with respect to the proportion of malformed young in a clutch.

Mother	Father	Fcmale ID No.	Male ID No.	Clutch size	Proportion (%) deformed young
Sibling partners					
A-tunnan	Kivik	4040	5010	11	9
A-tunnan	Kivik	5030	5050	6	0
A-tunnan	Kivik	43	44	7	43
A-tunnan	West	54	52	5	20
A-tunnan	A-tunnan	203	204	9	0
A-tunnan	A-tunnan	303	204	6	33
A-tunnan	A-tunnan	504	1002	14	43
A-tunnan	A-tunnan	503	1001	8	0
				Mean \pm SD:	18.5% \pm 19.0
Unrelated partners					
A-tunnan	South (♀)	203	1000	10	0
South	South (♂)				
A-tunnan	A-tunnan (♀)	303	10000	8	0
A-tunnan	South (♂)				
A-tunnan	A-tunnan (♀)	303	1224	9	0
A-tunnan	South (♂)				
A-tunnan	A-tunnan (♀)	504	4050	10	0
A-tunnan	Kivik (♂)				
A-tunnan	A-tunnan (♀)	11	5050	9	0
A-tunnan	A-tunnan (♂)				
South	Kivik (♀)	2002	1002	6	0
A-tunnan	A-tunnan (♂)				
A-tunnan	A-tunnan (♀)	1121	1001	9	0
Kivik	Kivik (♂)			Mean:	0

Asketunnan, West, South and Kivik), and transported the lizards to facilities at the University of Göteborg where they were kept in glass terraria ca. 40 cm \times 50 cm \times 60 cm. In each cage a 40 W spotlight allowed thermoregulation and maintenance of preferred body temperature. Fresh water and crickets (*Gryllus*) were provided ad libitum.

Matings were staged between siblings. Female sand lizards lay multiple clutches when feeding ad libitum (Olsson et al., 1994b). Therefore, both females and males from the sib-mating group could be drawn at random and remated with unrelated individuals. There is no post-ovulatory sperm storage in sand lizards (Olsson et al., 1994b). After the matings the females were kept separately, and without exception laid eggs in the moist sand provided under a flat rock in the cage. The cages were checked twice or three times daily for freshly laid eggs, which were transferred to a 1.3 l plastic container filled to one quarter with vermiculite mixed with water in the

volume ratio 10:1 (vermiculite:water). The eggs were incubated at 25 ± 1 °C in a climate chamber until hatching. Evaporating water condensed on the walls of the containers suggesting saturated humidity. Hatchlings were monitored for morphological deformities, such as kinked vertebral columns, missing or twisted extremities, cranial abnormalities such as deformed jaws, when necessary under a stereoscope. The grandparents of the hatchlings sired in sibling-matings came either from the same population, or from different populations in the wild (Tab. 1).

Field study

From a marked population of sand lizards at Asketunnan in Halland, S W Sweden (see Olsson, 1992a, b, 1994a for more details), females mated in the wild were brought back to the laboratory for egg laying as described above. The hatchlings from wild females were scored for malformations in the same way as those from females mated in captivity. In 1989–1990, the hatchlings were marked by toe-clipping and released within one week of hatching at random geographic sites within the study area. The survivors were recaptured after one year, and were sexed by sex-specific differences in head and tail base morphology, and coloration (Olsson, 1992a).

Adult and subadult lizards in the natural population for which hatching dates were not known, were aged with skeletochronology (Hemelaar, 1985; Olsson, 1992a; Olsson, 1994a).

Each observation of a marked lizard was identified in the field relying on fix points and was assigned a polar coordinate. The polar coordinates were then transformed to cartesian (X, Y) coordinates for statistical analyses. For every year a mean coordinate of an individual's home range was calculated. Males are sighted more often than females during the mating season, while females are sighted more often than males during the time elapsing between matings and oviposition (Olsson, 1984). However, over the whole season there was no statistically significant difference between the sexes in the mean (or variance) of the number of observations that were made per individual (Wilcoxon two-sample test, $Z = -1.71$, $P > 0.05$; Kruskal Wallis analysis of variance, $\chi^2 = 2.9$, $P > 0.05$, $N_{\text{females}} = 114$, $N_{\text{males}} = 149$). The shift (in meters, along a straight line) of the mean home range coordinate between two subsequent years was used as an estimate of the shift in home range site between years. Each year a 0–600 m circumference around the study area was searched, depending on the distance to the open water surrounding the peninsula on which the study site was situated. This was done to confirm that lost lizards had not simply left the study area, but had died (Olsson, 1992a; Olsson and Madsen, 1995).

Results

Description of malformations

The malformations observed in all offspring (Appendix 1), both those hatched from eggs laid by females in the natural population and those from females mated

by siblings in captivity, could be assigned to the following categories: cranial abnormalities (such as short skulls and jaws), missing and/or fused toes, deformed and twisted extremities (apparently semi-paralysed or paralysed), and deformed tails. Thus, there was no difference in the way that malformations were scored in offspring from clutches laid by females mated in the wild or from females mated by siblings in the laboratory.

The risk of having malformed offspring when mating with siblings

Matings with siblings resulted in clutches with significantly higher proportions of malformed offspring (mean = 18.5% ± 19.0, SD), compared to when males and females from the sib-matings were mated with unrelated lizards (mean = 0%, ± 0, SD; $T = 2.4$, $DF = 13$, $P = 0.03$, arcsine transformed proportions, Tab. 1). Since sample sizes were small, we also performed a non-parametric Wilcoxon two-sample test between the two groups which was in agreement with the parametric test ($Z = -2.0$, $P = 0.04$, $N_1 = 8$, $N_2 = 7$).

Malformations in offspring from females mated in the wild, and selection on malformed offspring

The clutches from females mated in the wild and hatched in captivity were assigned to either of the two groups with or without at least one malformed offspring. Henceforth, 'normal' young will be used to denote young from clutches with no malformed young, whereas 'normal-looking' young will be used to denote young without malformations but with at least one malformed sibling. There was no difference in clutch size between these groups (mean = 8.5 eggs ± 1.96, S.E., $N = 25$, versus mean = 8.6 ± 2.00, S.E., $N = 49$; $T = -0.211$, $P = 0.83$, $DF = 68$).

Offspring from seven clutches in Appendix 1 were not included in the following analyses since they all died before being released in the wild. Offspring from two of these clutches were 'normal-looking'. Thus the following tests of relationships between malformations and recapture rates are conservative. No morphologically malformed offspring were recaptured, and, hence, the recapture rate of the malformed young was significantly lower than for normal young (mean = 0%, S.E. = 0, $N = 18$, versus mean = 10.1%, ± 13.0, $N = 49$; $T = -3.75$, $P = 0.0004$, arcsine transformed data).

The average recapture rate of normal-looking young from clutches including at least one malformed young was 3.0% (± 6.0, SD, $N = 18$). The difference in recapture rate between normal-looking hatchlings from clutches with malformed young, and normal young was statistically significant ($T = -2.27$, $DF = 65.0$, $P = 0.03$, $Z = -2.26$, $P = 0.024$, $N_{\text{malformed}} = 18$, $N_{\text{normal}} = 49$). Thus, offspring with malformed within-clutch siblings, or half-siblings when there is multiple paternity (Olsson et al., 1994a–c), had higher mortality than offspring from clutches in which no such malformations were recorded.

There was no effect of female age on the probability of having malformed offspring; older females were no more likely to have malformed offspring than younger females ($r = 0.04$, $P = 0.73$, $N = 59$).

Sex-specific juvenile dispersal

Juvenile or subadult females (<4 calendar years old) dispersed on average 25.5 m between years (± 35.9 , SD, min = 0, max = 182.1), while males (<3 years old) dispersed more than twice as far, 57.2 m per year (± 74.8 , SD, min = 0, max = 399.8). The difference in dispersal distance between the sexes was statistically significant ($T = -2.3$, DF = 88.0, $P = 0.02$; Wilcoxon two-sample test, $Z = -2.39$, $N = 42_{\text{females}}$, $N = 48_{\text{males}}$, $P = 0.02$). Furthermore, the variation in dispersal distance also differed between juvenile males and females ($F' = 4.33$, DF = 47, 42, $P < 0.00001$, Kruskal-Wallis Test, Chi-square approximation, $\chi^2 = 5.74$, DF = 1, $P = 0.02$).

When considering gender-specific dispersal tendencies throughout the entire life cycle, the yearly shift in mean home range coordinates was negatively correlated with age and snout-vent lengths in males ($r_s = -0.27$, $P = 0.01$, $N = 84$, and $r_s = -0.28$, $P = 0.005$, $N = 95$, respectively). However, the corresponding correlations in females were not statistically significant ($r_s = -0.13$, $P = 0.26$, $N = 81$, and $r_s = -0.05$, $P = 0.67$, $N = 87$, respectively).

Adult females (≥ 4 calendar years old) shifted their mean home range coordinate by 27.6 m (± 35.3 , SD, min = 0, max = 196), while the corresponding figure for adult males (≥ 3 years old) was 41.3 m (± 60.7 , SD, min = 0, max = 399.8). The difference in dispersal distance between adult males and females was not statistically significant ($T = 0.24$, $P = 0.81$, DF = 91; Wilcoxon two-sample test, χ^2 approximation = 0.66, $P = 0.42$, DF = 1, $N_{\text{females}} = 45$, $N_{\text{males}} = 48$).

Discussion

How robust are our observations?

Since female sand lizards mate multiply in the wild, we cannot safely reconstruct pedigrees for juveniles from mothers for which both mating history and hatchling data were recorded. We therefore cannot provide direct evidence that malformations among the wild hatchlings were caused by inbreeding. However, our support for this assumption stems from three observations: (i) the malformations in offspring from sibling-matings in the laboratory agree in detail with those observed in the natural population, (ii) Murphy et al. (1987) observed similar malformations, e.g. cranial abnormalities, after a single generation of inbreeding in captive rattlesnakes, and (iii) our study population has little genetic variation, with an average band sharing between individuals of 66% using DNA-fingerprinting (Olsson et al., 1994a, b).

Can the malformations we observed be of a non-genetic origin? Our study site consists of a rocky peninsula surrounded by the sea to the east, south, and west and a summer house area with a non-cultivated forest to the north. Thus, it is unlikely that e.g. pesticides used in forestry or agriculture caused the malformations. In any case, pesticides cannot explain the increased risk of having malformed offspring in sibling matings in the laboratory.

Other factors that may influence reptilian morphology are temperature and humidity during incubation (Fox, 1948; Fox et al., 1961; Murphy et al., 1978; Shine and Harlow, 1994). However, all our lizards were incubated at the same temperature and humidity; hence, differences in malformations between laboratory groups cannot be referred to differences in incubation conditions. Thus, our conclusion is that the mechanism explaining malformations in hatchlings is genetic and due to inbreeding.

Could our results be explained by genetic effects due to the crossing of lizards from different geographic areas?

We doubt this interpretation. First, all the lizards in our crossing experiments were collected within the zone of continuous distribution in southern Sweden where there is likely to be gene flow between different sites. Second, if outcrossing effects explained the higher frequency of malformations in the sib-matings, then between-sites crossings should have resulted in malformations also in the 'sibling' generation (i.e. the parental generation to the malformed young in the experiment); there were no malformations in either 'siblings', or the lizards which sired the 'siblings'. Furthermore, two of four matings between Asketunnan siblings resulted in malformed offspring, the corresponding figure for the siblings with parents from different sites was three out of four matings; thus, malformed young occurred in high frequencies in both these 'groups', which strongly suggests that geographic origin of parents had no influence on siblings that sired malformed young. Third, *if* there were differences in allelic frequencies between sites, this difference should be largest between Asketunnan and the three sites in Scania. Then, it would be important that alleles from these areas were equally represented in the parental generations to the compared groups of 'sibling partners' and 'unrelated partners' (Tab. 1). The site Asketunnan was represented by 12 of 16 (75%) partners siring the sibling group. In the unrelated group, Asketunnan was represented by 18 of 28 (64%) partners yielding these lizards (calculated over the two generations for which we have data). Thus, although there is a slight difference in the genetic influence that these two 'areas' could have on allelic frequencies in the 'sibling' versus the 'unrelated' group, this difference is not statistically significant (Fisher's exact test, two-tailed, $P = 0.52$).

Dispersal – a selected mechanism for inbreeding avoidance?

Olsson et al. (1994a, c) demonstrated that females in a natural population (the same as in this study) of sand lizards that mated multiply were at a selective

advantage because they produced more viable young than monandrous females. Irrespective of what mechanism that initially selected for female 'promiscuity', this behaviour seems to reduce the effects of inbreeding. In the following discussion we will focus on pre-copulatory mechanisms that may reduce the effects of inbreeding.

In female sand lizards mate rejection seems to occur only when females are not physiologically and behaviorally ready to mate (Olsson and Madsen, 1995). Olsson and Madsen (1995) could not demonstrate female choice on male size, age or colour. Furthermore, no females in the laboratory refused, or hesitated, to mate with their brothers. Although one should be cautious about inferring mating behavior in natural populations from experiments in captivity, Olsson and Madsen's (1995) observations in the laboratory and in the field agreed in full, and with the observations reported here. Female sand lizards mated with all males that courted them, regardless of whether these males were kin or not; hence, inbreeding was not avoided by mate choice.

Restriction of kin matings in sand lizards is more likely to be explained by differences in dispersal between the sexes than by selective matings. Can the difference in dispersal of juvenile males and females be due to differences in the foraging ecology of juveniles? Hatchlings do not vary in head size and body proportions in the way typical for adults (Olsson, 1992a). It is therefore highly unlikely that ecological factors determining microhabitat use, such as prey choice, will result in the observed difference in dispersal in this insectivorous generalist (Olsson, 1992a). In sand lizards sex-specific juvenile dispersal could be the result of selection (i) acting on the juvenile, and/or (ii) acting on the adult. In the latter case characteristics of juvenile dispersal would be correlated effects, due to pleiotropy, arising from selection on adults (e.g. Gould, 1977; Cheverud, Rutledge and Atchley, 1981).

Are males and females likely to differ in how pre-adapted for dispersal they are?

If dispersal is the result of selection on adults, adult males would need to be better pre-adapted for dispersal than females, or females would need to be better pre-adapted for site tenacity. Can such gender-related pre-adaptation for dispersal, or site tenacity, be identified in sand lizards? Male sand lizards have much larger home ranges than females (Olsson, 1986, 1988), and are thus more mobile than females, possibly due to selection for mate acquisition (Olsson, 1986). Females are also larger than males in any given age-class (Olsson, 1992a), which is likely to incur greater energy expenditure, and hence costs, per unit distance moved.

The sex-specific dispersal occurs primarily in juvenile sand lizards and males move more than twice as far as females. However, there is considerable variation in dispersal tendencies and some males and females hardly disperse at all. The lack of dispersal in some individuals of both sexes, the lack of kin-mate rejection in females, and the risk of overlapping sisters' or mothers' much smaller home ranges in the adult male, make some inbreeding expected. If dispersal tendency is heritable, such consanguineous matings are even more likely to occur.

The 10% malformation rate recorded in hatchlings may be an underestimate as the average hatching success is 77% in this natural population (Olsson et al., 1994a, b), and malformed young may die undetected in early pre-hatching developmental stages. The malformations are likely to be the outcome of matings between close kin in this population with low level of genetic variation. Selection against inbreeding is strong; no offspring with malformations were ever recaptured. The siblings of these malformed offspring were also likely to harbor non-detected detrimental alleles. Less than 3% of the normal-looking siblings of malformed hatchlings survived their first year in the wild.

In conclusion, male juveniles disperse more than females, a behaviour which may be a pleiotropic effect of sexual selection for adult male mobility. Inbreeding avoidance is imperfect, malformed offspring are produced, most likely due to consanguineous matings, and are strongly selected against.

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Corresponding Editor: R. Bijlsma

Appendix 1

Malformations in sand lizards hatchlings. The number of young affected in each clutch are given in parentheses.

Females in the natural population

<i>Year</i>	<i>Female No.</i>	<i>Malformations</i>
1991	0	Deformed extremities, semi-paralysed (1)
	1	Deformed extremities, semi-paralysed (1)
	152	Curled, deformed tail (1)
	594	Missing toes (1)
		Short skull (1)
		Fused toes (1)
		Missing toes (1)
		Deformed, stumped tail (1)
		Curled and deformed tail (1)
		Deformed, stumped tail (1)
1990	80	Fused toes (1)
		Curled tail (1)
	250	Deformed extremities, semi-paralysed (1)
	338	Deformed extremities, semi-paralysed (1)
		Curled tail (1)
	357	Missing toes (1)
		Curled tail (1)
	392	Missing toes (1)
	552	Deformed extremities, semi-paralysed (1)
	553	Deformed extremities, semi-paralysed (2)
		Curled, deformed tails (2)
	584	Deformed extremities, semi-paralysed (4)
		Curled, deformed tail (2)
585	Deformed, stumped tail (1)	
882	Deformed extremities, semi-paralysed (1)	
	Curled, deformed tail (1)	
896	Deformed extremities, semi-paralysed (2)	
	Curled, deformed tail (1)	
1989	223	Deformed, stumped tail (1)
	284	Deformed extremities, semi-paralysed (4)
		Missing toes (1)
	323	Curled tail
	384	Short deformed lower jaw (1)
		Deformed extremities, semi-paralysed (1)
	396	Missing finger (1)
	397	Deformed extremities, paralysed (1)
	398	Curled tail (1)
	433	Short skulls (2)
	568	Curled tail (1)

Females in the laboratory experiment

43	Short skulls (2)
	Missing extremities (1)
54	Deformed extremities, semi-paralysed (1)
303	Deformed and curled tails (2)
504	Deformed and curled tails (6)