# Genetic and Maternal Determinants of Effective Dispersal: The Effect of Sire Genotype and Size at Birth in Side-Blotched Lizards

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ABSTRACT: We assessed genetic factors on progeny dispersal due to sire color morph genotypes in a field pedigree and lab crosses, and we measured maternal effects by studying both natural and experimentally induced egg size variation. Progeny were released into nature upon hatching, but we recorded dispersal distance at maturity, which reflects effective dispersal after viability selection has run its course. Progeny dispersal was significantly affected by sire genotype. Progeny from orange sires dispersed the farthest. Progeny from blue sires dispersed intermediate distances. Progeny from yellow sires were the most philopatric. Sire genotype effects interacted with egg size. In particular, enlarged progeny from orange sires dispersed farther, while enlarged progeny from yellow sires were more philopatric. Progeny from blue sires were unaffected by egg size manipulations. Egg manipulations and natural variation generally had concordant effects indicative of causation. However, asymmetry of gigantization and miniaturization on progeny dispersal from some sire genotypes suggest the involvement of maternal factors besides egg size. Results of laboratory crosses with progeny released into nature confirmed key sire genotype effects and identified additional maternal effects that modulated dispersal as a function of progeny gender. We discuss the adaptive implications of progeny dispersal in the context of male (rock-paper-scissors) and female strategies (*r*- and *K*-density cycle) that are associated with color morphs.

*Keywords:* effective dispersal, color morph, maternal effect, genetic determinant of dispersal, disperser phenotype.

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Dispersal, the movement from natal site to the first breeding site or between successive breeding sites, is one of the most important life-history traits. However, the genetic components of dispersal remain poorly understood (Clobert et al. 2004). There are several reasons why the evolution of dispersal remains enigmatic. First, there is confusion between definitions of dispersal and migration. Migration is a seasonal or recurrent movement that typically is not associated with a change in reproductive location. Second, the confusion is exacerbated by use of the term migration rather than dispersal in the population genetic literature. The distinction between migration and dispersal is not clear-cut in all cases (e.g., nomadic species; Dingle 1996), and that has made the study of the genetic basis of dispersal difficult.

The best examples of a genetic basis for movement are derived from studies of avian migration (Berthold 1988; Berthold and Pulido 1994) and insect activity, wing morphs, and flight duration (Roff and Fairbairn 2001). In insects, activity, wing morphology, and flight duration are not necessarily linked to dispersal ability because dispersal requires appropriate morphology and physiology as well as behavioral adaptations (e.g., decision to leave and

settle). Moreover, factors operating in insects are not necessarily the same as those at work in avian migration (Belliure et al. 2000). This might explain why genetical studies of movement in *Drosophila* spp. have yielded contradictory results depending on experimental conditions and which traits were scored (Connolly 1966; Van Dijken and Scharloo 1980; Roff and Fairbairn 2001).

While migration seems to be under more direct genetic control than dispersal, dispersal seems to be more phenotypically plastic (Ims and Hjermann 2001). This does not imply that dispersal is not under genetic control (e.g., Trefilov et al. 2000), rather that its control is not simple. There are theoretical reasons to think that dispersal is a complex phenomenon (Clobert et al. 2001). First, it is increasingly recognized that dispersal has a multicause origin (Gandon and Michalakis 2001; Perrin and Goudet 2001; for examples, MacKay and Wellington 1977; Massot and Clobert 2000; Massot et al. 2002). Second, dispersal is often condition dependent (Ims and Hjermann 2001; Ronce et al. 2001) and potentially affected by maternal as well as environmental effects. Under such conditions, dispersal may evolve in connection with suites of traits to constitute behavioral and physiological syndromes (Dufty et al. 2002). The identification of these syndromes is of prime importance to the study of dispersal.

In addition to establishing genetic and environmental causation, a key step in analyzing the adaptive value of dispersal is identifying the selective causes underlying movement. In this regard, kin interactions (Hamilton and May 1977; Ronce et al. 1998; Perrin and Goudet 2001) appear to be a dominant force in the evolution of dispersal. In birds, kin helping is linked to philopatry versus dispersal (Komdeur et al. 1997). In lizards, mother-offspring competition appears to govern dispersal (Léna et al. 1998; Ronce et al. 1998; Le Galliard et al. 2003). In fact, kin interaction is possibly the easiest piece of information for parents to predict. Parents can manipulate offspring dispersal in many ways and also confer an advantage to philopatric or dispersing offspring (Léna et al. 1998; Murren et al. 2001). However, studying parental effects is particularly difficult because parental strategy and progeny fate should both be measured. This may be most readily achieved in species with alternative strategies that include genetic strategies of space use and defense (Zamudio and Sinervo 2000; Calsbeek et al. 2002; Sinervo and Clobert 2003).

In species with a clear association between genetically based morphological traits and dispersal, adaptive value of dispersal can be studied in connection with other life-history traits. For example, cat coat color markers, in particular the orange allele in male cats, are linked to body condition, aggressiveness, and spatial movement (Pontier et al. 1995), suggesting both a genetic basis and genetic

covariance between dispersal and life-history traits. However, pure maternal effects could cause these associations, such that a measure of sire influence on offspring strategy would be necessary to ascertain the genetic influence on dispersal and the associated traits. Given the possibility of maternal effects on dispersal, maternal genotype is always confounded with maternal effects plasticity. Thus, to ascertain the genetic basis of dispersal, it is necessary to study effects of sire genotype per se.

*Uta stansburiana* is an ideal system to study such influences. Alternative strategies in side-blotched lizards have a genetic basis (Sinervo et al. 2000*a*, 2001; Sinervo 2001; Sinervo and Zamudio 2001), and egg size and offspring condition are amenable to experimental manipulation (Sinervo 1990, 1998; Sinervo and Huey 1990; Sinervo and Licht 1991*a*, 1991*b*; Sinervo et al. 2000*a*). Finally, extensive mark-recapture studies of metapopulations allow us to recapture even the farthest-dispersing individuals (Doughty and Sinervo 1994). Male side-blotched lizards display one of three genetically based alternative strategies of territoriality. Males with orange throats are usurpers with the ability to take over territory during the reproductive season (Calsbeek et al. 2002). Blue-throated males are mate-guarders with a more restricted territory, but they also participate in cooperative territory defense with neighboring blue males that are genetically similar (Sinervo and Clobert 2003). Yellow-throated males are sneakers that do not establish a territory but mimic females and steal copulations from females on another male's territory (Zamudio and Sinervo 2000). Female side-blotched lizards exhibit one of two alternative reproductive strategies that are genetically correlated with the male strategies (Sinervo and Zamudio 2001; Sinervo et al. 2001). Orange females are *r* strategists that produce large clutches of small eggs. In contrast, yellow-throated females produce small clutches of large eggs. Given the central role of maternal effects (e.g., egg size) in female reproductive strategies, we expect progeny dispersal strategies to be affected by genetic effects associated with the throat-color locus (Sinervo 2001; Sinervo and Zamudio 2001; Sinervo et al. 2001) and by condition-dependent effects of egg size (Sinervo et al. 2000*a*).

To address genetic effects arising from the orange-blue-yellow color locus, we studied dispersal of progeny in field pedigrees where maternity was known with certainty and DNA paternity was used to assign sires (Zamudio and Sinervo 2000). In addition to a sire-based genetic analysis of dispersal, an experimental assessment of maternal effects is essential to gain insight into the causes of progeny dispersal arising from natural matings. This is because the dam might adjust progeny behavior depending on the genetic quality of the sire (Alonzo and Sinervo 2001), and thus, natural variation in maternal effects might be con-

founded by sire genotype. This is especially likely in the case of female side-blotched lizards in which the two female morphs have distinct egg size strategies associated with density-dependent progeny survival (Sinervo et al. 2000*b*, 2001). We used two complementary manipulations of progeny size: experimental miniaturization via yolk removal from freshly laid eggs and experimental gigantization via ablation of follicles on the female's developing ovary. Effects of egg size manipulations on dispersal should be complementary if progeny dispersal changes monotonically with egg size (Sinervo 1990). However, the timing of the gigantization with respect to the female reproductive cycle (e.g., midvitellogenesis) allows the dam to adjust yolk components other than size (Sinervo and DeNardo 1996). No adjustment by dams is possible in the case of yolk removal, which occurs after eggs are laid. Thus, if an asymmetry in the effect of giants and miniatures on dispersal is detected (see Sinervo and Huey 1990), we can infer that additional maternal effects of yolk composition other than yolk volume might govern progeny dispersal.

We augmented the inferences on dispersal from the natural pedigree with a second experiment on dispersal in which progeny were produced from laboratory crosses where sire and dam genotypes were known with certainty. Rather than use the maternal effects of egg size produced in the laboratory as a covariate for dispersal, we studied the effects of female genotypes relative to sire genotypes to disentangle maternal versus paternal contributions to dispersal. Differences in the direction of effect of sire versus dam alleles (e.g., parent of origin effects) on progeny dispersal imply the existence of maternal effects.

Our measures of progeny dispersal are coupled to the survival of progeny to maturity. Thus, our study addresses how effective dispersal, progeny size, and the morph locus synergistically affect survival of the morphs (Sinervo et al. 2001). We focus our predictions on theory of dispersal in the context of kin competition (Hamilton and May 1977). In this regard, mate defense by genetically similar blue males is a key piece of information in formulating predictions for dispersal of male morphs. Territorial male neighbors of high genetic similarity and a similar blue throat enhance the fitness of blue males; however, these males are in fact unrelated (Sinervo and Clobert 2003). In contrast, territorial male neighbors of high genetic similarity regardless of throat color depress the fitness of orange males. Fitness of yellow males is neutral with respect to genetically similar neighbors (Sinervo and Clobert 2003). We predict that orange sons should be the most dispersive, while yellow sons should be the most philopatric, given the striking differences in the potential for kin competition of these two morphs (i.e., strong negative effects in orange but neutral in yellow). However, dispersal of blue sons should depend on the likelihood of locating a genetically similar male as a territorial partner, which implies that intermediate dispersal distance may be favored in blue, given that they must seek out and settle next to an unrelated but genetically similar male to obtain high fitness.

## Methods

### Assigning Parentage

Side-blotched lizards (*Uta stansburiana*) were studied in a population located on a 250-m-long outcropping of sandstone adjacent to Billy Wright Road, Merced County, California (~2 km east of Los Baños Creek). We genotyped nine microsatellite loci (Zamudio and Sinervo 2000) for progeny ($N = 458, 160, 212, 99$), dams ($N = 68, 96, 40, 34$), and sires ($N = 124, 56, 44, 69$), and assigned paternity to 71%, 75%, 64%, and 57% of progeny collected in 1992, 1996, 1998, and 1999, respectively. Sampling was distributed across the male morph cycle, and each morph (blue, orange, and yellow) was common in at least one year (**B** in 1996, **O** in 1992, **Y** in 1998, and **B** in 1999). Therefore, we sampled the range of allele frequencies experienced by the species over the entire cycle of color allele frequency (rock-paper-scissors).

Nine microsatellite loci were amplified from extracted DNA via polymerase chain reaction (Zamudio and Sinervo 2000). Length polymorphism was assessed with fluorescently labeled forward primers on an automated DNA sequencer (ABI 377). Paternity was assigned with the program Kinship, which uses a maximum likelihood method that incorporates exclusionary criteria (Goodnight and Queller 1999). A male was accepted as a hatchling's sire if paternity likelihood was significantly different from that expected for unrelated males ($P < .05$). We partitioned paternity analysis with detailed territory maps (see Sinervo and Clobert 2003).

### Sire Color Genotypes

Colors on the throat and flanks of side-blotched lizards are expressed in discrete classes of orange, blue, or yellow. Previous genetic analyses have demonstrated that color has a strong genetic basis in both sexes and segregates like a single Mendelian factor (Sinervo et al. 2000*a*, 2001, 2006; Sinervo and Zamudio 2001). However, the assumption of Mendelian inheritance is not crucial in the following analyses of dispersal in which we assess additive effects of sire color genotypes on progeny dispersal. Additive effects of color alleles will have similar effects regardless of Mendelian or polygenic patterns of inheritance (Fisher 1918; Li 1977; Sinervo and Zamudio 2001). Putative homozygous males have solid throat colors: orange (*oo*), dark blue

(*bb*), or yellow (*yy*). Blue yellow heterozygotes (*by*) have yellow and pale blue stripes, but the blue is markedly lighter than that of *bb* homozygotes. Blue orange heterozygotes (*bo*) have blue and orange stripes on the throat. Blue orange heterozygotes also have light orange flanks. Yellow orange heterozygotes (*yo*) have pale yellow orange throats and light orange flanks. However, orange is lighter on the flanks of both heterozygotes than on the vibrant flanks of orange homozygotes. A three-class score was constructed for color on both an orange axis and a blue axis. A score of 1.0 was assigned to putative homozygotes and 0.5 to putative heterozygotes. Putative homozygotes that did not express the color of a given axis (e.g., orange or blue) were given a score of 0. Yellow color is also incorporated into color scores (*yy* homozygotes received 0.0 on both axes). Orange and blue color axes estimate the probability that progeny carry alleles and is thus referred to as a genotypic value as it reliably predicts progeny color (Sinervo et al. 2001; Sinervo and Svensson 2002; Sinervo and Calsbeek 2003).

In addition to this analysis of the additive genetic effects of sire color, we also collapsed the male genotypes into the three phenotypic strategies of the rock-paper-scissors game (**O** = *oo*, *bo*, *yo*; **B** = *bb*; **Y** = *by*, *yy*). The justification for this is twofold. First, the genetic model among six color phenotypes is more simply represented as three behavioral strategies in which the *o* allele is dominant to *b* and *y*, while the *y* allele is dominant to *b* (Sinervo 2001). Second, the reduction of six phenotypes in sires to three factors allows us to compute factorial (e.g., sire) and covariate (e.g., dam egg mass or experimental manipulation) interactions in analysis of covariance. This greatly simplifies the visualization of higher-order interactions between sire genotype and natural or experimental maternal effects (Sinervo and Calsbeek 2003).

### *Natural Variation in Egg Size and Progeny Size Manipulations*

Details on female husbandry are provided in Sinervo and DeNardo (1996) and Sinervo and Doughty (1996). The same methods have been used across 18 generations (1989–2006). We mark all progeny obtained from known dams on the focal study plots where progeny were released. Females are collected with oviductal eggs in early April to oviposit their first clutch of eggs in the laboratory. Females are returned to their territories after laying eggs and recaptured on second and third clutches. Incubation environment of eggs was carefully controlled in the laboratory to eliminate maternal effects that might otherwise arise from among-dam variation in oviposition sites and territory quality. We released siblings randomly with respect to the sire's and the dam's territories to remove confound-ing influences that would arise from a correlated maturation environment between dams or sires and their progeny. Finally, we performed two key manipulations of egg size, which is a likely maternal effect. When we discovered freshly laid eggs, we removed a portion of the yolk from half of the eggs in a clutch. Yolk was aspirated using a sterile syringe (25 gauge). Hatchlings were miniaturized in proportion to the amount of yolk removed (Sinervo 1990). The remaining control eggs in the clutch were sham-manipulated by inserting a syringe, but no yolk was withdrawn. Eggs were weighed to the nearest 0.01 g before and after manipulations. Approximately 20% of the yolk by mass was removed from eggs (Sinervo et al. 1992). A total of 287 miniature progeny and 566 control progeny that were genotyped to sire were released into nature.

We also induced 83 dams to lay giant eggs by performing a surgical manipulation of the ovary during early vitellogenesis. In late March, we ablated the follicles on one of the female's ovaries, but the remaining follicles were left intact. The incision was sutured with 5.0 Vicryl. The dam reallocated yolk to the remaining follicles and produced eggs that were ~20% larger than normal (Sinervo et al. 1992). All surgeries were conducted on ice (i.e., hypothermic anesthesia), and the female was injected with 0.02% lidocaine at the site of the abdominal incision. As a control for the follicle ablation procedure, we carried out sham surgical manipulation on a separate group of dams in which we made an incision, but no follicles were ablated. The incision was sutured closed with Vicryl. All dams were returned to their territory within a few hours after surgery, and the females carried out vitellogenesis in nature. A total of 98 giant progeny and 59 progeny from sham-manipulated females were released into nature.

Eggs were individually incubated in moist vermiculite ($-200$ kPa) at 28°C, and vermiculite was changed weekly. Laboratory incubation controlled maternal effects due to oviposition site that would otherwise arise in nature. Newly emerged hatchlings were permanently marked with a unique toe clip and released at nest sites based on natural density of female territories (Doughty and Sinervo 1994; Sinervo et al. 2000*a*). We analyzed the effects of log-transformed hatchling mass (hereafter referred to as "mass") on dispersal, a covariate for amount of yolk removed, and a factor for giant eggs.

### *Laboratory Crosses*

Progeny dispersal was also followed for hatchlings obtained from a laboratory breeding experiment (Sinervo et al. 2001). Adult males and virgin females were collected from the field site at Los Baños Grandes, California, during early March 1999. Single sires were placed in breeding terraria with one to three dams ($N = 45$ sires: 17 orange,

16 blue, and 12 yellow; $N = 72$ dams: 19 orange and 53 yellow). All pairwise combinations of dam and sire throat morph were present in the design. We released progeny from these crosses to the outcroppings of sandstone from which parents were removed. Progeny were released in an experiment designed to control frequency and density of progeny. Details on release densities and frequencies can be found in an article by Sinervo et al. (2001), in which we also report on the genetic basis of throat color from the same laboratory crosses. The three populations into which we released progeny were located 1.3 km to the south, 1.1 km to the east, and 5 km to the northeast of the main population, where we studied the free-ranging pedigree.

## Measuring of Dispersal

Progeny survival was censused at maturity the next year, at which point locations of all progeny were mapped. The recapture probability is high on capture episodes for both males (.97 for first episode, with a probability of survival to the first clutch [i.e., second recapture episode] of .65, based on $N = 613$ males, 1993–1999) and females (.98 for the first episode, with a probability of survival to the first clutch of .78, based on $N = 945$ females, 1993–1999). Given that we performed three recaptures (March, April, and May–June), the joint probability of missing a surviving individual was very low ($P = 1/1{,}558 = .00064$, pooled across both sexes; only a single lizard was not caught during the first and second recapture episodes but was caught during the third episode). Furthermore, within the first capture episode, we mapped the locations of all currently marked lizards that were resighted for analysis of territories (Sinervo and Lively 1996; Sinervo and Clobert 2003). On average, a male that is caught is resighted 9.4 times, while a female is resighted 7.4 times over the ensuing 2–3 weeks of our first capture/territory mapping effort. Evidence from extensive metapopulation studies shows that emigration of hatchlings from our focal population does not confound fitness estimates (Sinervo et al. 2000a; Sinervo and Clobert 2003). For the past 18 years, we have censused the adjacent metapopulations in each of the cardinal directions from the focal population where progeny have been released (a map of the main plot is provided in Svensson and Sinervo 2004) with the same intensity as our focal population. Dispersal of progeny between metapopulations separated by more than 200 m is rare ($P <$ .029 in this study). All long-distance dispersal events (e.g., between metapopulations) that we detected and recorded occurred between our focal population and a ring of metapopulations immediately outside of the focal population (from 500 m to 2 km distant). The maximum dispersal event recorded during our 15 years of study is 1.6 km;

however, none of the progeny in the sire-based pedigree traveled this far (maximum was 422 m). In the breeding experiment described below, we recorded one dispersal event from the outer ring into the focal plot (1.4 km) and one dispersal event between metapopulations in the outer ring (1.5 km). Thus, dispersal among metapopulations is rare, but we are likely to detect these events since our capture effort in the metapopulations is of similar intensity to that employed on focal plots. Metapopulation structure of side-blotched lizards provides the exceptional opportunity to record nearly all dispersal events, an extremely rare situation in dispersal studies (Clobert et al. 1994).

Experiments conducted with laboratory crosses were located on the outer ring surrounding the focal population. These experimental outcrops were themselves surrounded by other populations that we monitored (e.g., in Calsbeek and Sinervo 2002, 2004). In this experiment, we detected two long-distance movements of 1.4 and 1.5 km.

The highest point of each metapopulation was mapped with global positioning system (GPS) coordinates and used as a central landmark, which aided in the construction of local maps of each metapopulation. Within each metapopulation, we mapped lizard locations with respect to a polar coordinate system in which the distance (to the nearest 1 m) and angle (to the nearest degree) was measured to previously mapped landmarks (Doughty and Sinervo 1994). Angle was measured with a pocket surveyor's transit (Brunton). Distance was measured with either a hip chain (distances $\geq 50$ m) or an electronic rangefinder (distances $<50$ m). The GPS coordinate surveys of large-scale metapopulations were transformed to magnetic north longitude and latitude coordinates, given that polar coordinates of local landmarks and lizard locations were based on magnetic north. We define progeny dispersal as the Euclidean distance moved from the progeny release site (i.e., nest) to the location of progeny at maturity the following season. Progeny dispersal distance was normalized with Neperian logarithmic transformation. Thus, the relationship between mass (i.e., ln[hatchling mass]) and ln(dispersal) reflects an allometric slope.

We measured the distance that surviving progeny moved. Multiple surviving offspring from a single sire might inflate the degrees of freedom in our statistical analyses. Accordingly, we performed a preliminary analysis of sire effects in which ln(dispersal) of all progeny from a given sire were averaged. This analysis revealed significant effects of both orange and blue sire color scales on dispersal ($o$: $F = 5.64$, df $= 1, 96$, $P = .02$; $b$: $F = 5.61$, df $= 1, 96$, $P = .02$); thus, the key genetic effects of sire remain significant in the reduced data set. Furthermore, in our paternity analysis, we recovered 21 pairs of progeny (male and female) that came from the same maternal clutch. However, all of these progeny had a different sire (i.e.,

they were half-sibs). Finally, those progeny surviving from the same maternal parent (e.g., full sibs through dam) had treatment (miniaturization) or served as controls. Thus, we included all progeny in our ANOVAs because the key sire genotype and egg treatment interaction effects are not unduly influenced by an overrepresentation of any given family (e.g., either of maternal or paternal origin).

## Results

### Genetic Effects of Sire Color Genotypes in the Field Pedigree

Dispersal distance in the 4-year sample ranged from 1.7 to 422 m, with an average of $63.4 \pm 4.87$ m (SEM). We recovered a total of $N = 170$ progeny from the 1,010 progeny released during 1992, 1996, 1998, and 1999. Of these, we were able to genotype a total of $N = 138$ (81%) to sires with 95% confidence of an individual sire-progeny match. Recoveries were distributed among sire genotypes as follows: 52 *bb*, 30 *by*, 33 *yy*, 12 *bo*, seven *yo*, and four *oo*. The effect of sire morph, partitioned by the three male strategies ($\mathbf{O} = oo$, *bo*, *yo*; $\mathbf{B} = bb$; $\mathbf{Y} = by$, *yy*; Sinervo and Lively 1996; Sinervo et al. 2000*b*), on dispersal distance was significant ($F = 3.43$, df $= 2, 131$, $P = .036$), along with a factor for progeny sex ($F = 5.78$, df $= 1, 129$, $P = .018$). Sons dispersed 1.53 times farther than daughters. The effect of year was not significant ($F = 1.066$, df $= 3, 129$, $P = .37$). Progeny from yellow sires were the most philopatric, progeny from blue sires dispersed intermediate distances, and progeny from orange sires were the most dispersive (fig. 1).

### Interaction between Genetic and Maternal Effects of Size in the Field Pedigree

We tested for significant interactions between sire genotypes and natural and experimental effects of egg size. We considered the effects of sires with two basic ANCOVA models: additive sire effects on the orangeness and blueness scales (see Sinervo et al. 2001) and sire effects pooled into the three male strategies originally described in an article by Sinervo and Lively (1996).

Orangeness ($F = 4.58$, df $= 1, 123$, $P = .038$) and blueness of sires ($F = 4.67$, df $= 1, 123$, $P = .033$) interacted significantly with mass of the progeny. The factors for progeny sex ($F = 7.84$, df $= 1, 123$, $P = .006$) and clutch were significant ($F = 4.19$, df $= 2, 125$, $P = .045$), but the effect of year was not significant ($F = 1.55$, df $= 3, 125$, $P = .21$).

We tested for the joint effects of progeny size and the egg size manipulations in a more complex model that also included covariates for progeny mass and amount of yolk
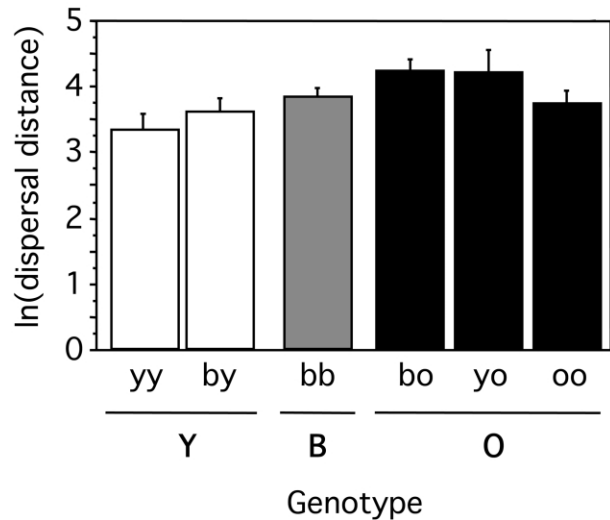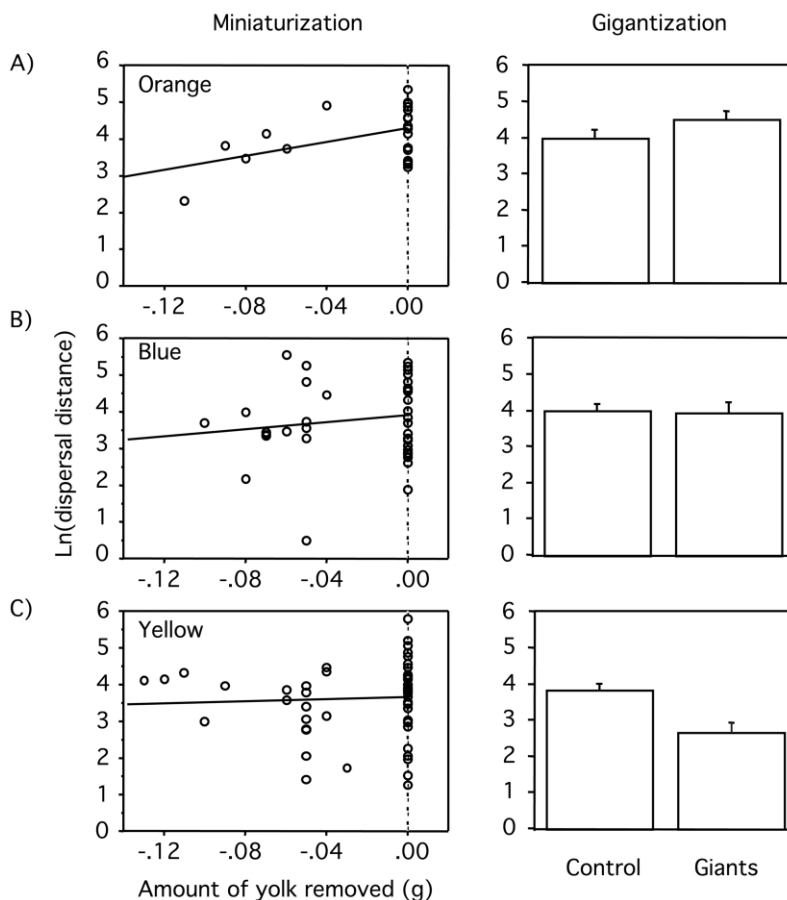


**Figure 1:** Mean effective dispersal distance (Neperian logarithm, ln[m]) of progeny sired by males with a yellow (*yy* and *by* genotypes), blue (*bb*), or orange (*bo*, *yo*, and *oo* genotypes) phenotype.

removed during miniaturization and a factor for giants. As above, we included factors for clutch, year, and sex. Dispersal was not affected by gigantization ($F = 2.41$, df $= 1, 123$, $P = .12$) or miniaturization ($F = 2.18$, df $= 1, 123$, $P = .13$), other than the effect that manipulations had on hatchling size. Similarly, interactions between the factor for gigantization and the covariates for orangeness ($F = 1.32$, df $= 1, 119$, $P = .25$) and blueness ($F = 1.92$, df $= 1, 119$, $P = .17$) were not significant in a more complicated ANCOVA model with two-way interactions. Similarly, interactions between the factor for miniaturization and covariates for orangeness ($F = 1.32$, df $= 1, 119$, $P = .25$) and blueness ($F = 1.32$, df $= 1, 119$, $P = .25$) were not significant. Therefore, the absence of any higher-order interactions of experimental treatment implies that the interactions between natural variation in progeny mass per se and sire genotype are causally associated with size (Sinervo 1990; Sinervo and Huey 1990; Sinervo and Doughty 1996). The effect of female surgery on progeny dispersal was explored in ANOVA models tested on a subset of the data. Sham surgical manipulation did not have a significant effect on progeny dispersal ($F = 0.24$, df $= 1, 89$, $P = .63$).

The effects of higher-order interactions involving progeny sex were also tested with two- and three-way interactions. Progeny sex was not involved in two-way (e.g., sex × mass: $F = 0.86$, df $= 1, 122$, $P = .63$; sex × orangeness: $F = 1.93$, df $= 1, 122$, $P = .15$; sex × blueness: $F = 0.57$, df $= 1, 122$, $P = .45$) or three-way interactions (sex × mass × orangeness: $F = 2.08$,

**Figure 2:** Mean effective dispersal distance (Neperian logarithm, ln[m]) of progeny sired by males according to egg size manipulation and sire color phenotype. *A*, *B*, and *C* panels on the left describe the relationship between dispersal distance (ln[m]) and the amount of yolk removed for the miniaturization experiment (see text for more details) for orange, blue, and yellow males. *A*, *B*, and *C* panels on the right present the mean dispersal distance for control and gigantized eggs for orange, blue, and yellow males.

df = 1, 122, $P$ = .15; sex × mass × blueness: $F$ = 0.55, df = 1, 129, $P$ = .46).

We also considered a second set of ANCOVA models in which sire genotype was included as a simple three-morph factor by pooling the six genotypes into the three alternative strategies that were noted above (e.g., **O**, **B**, and **Y**). We found that the interaction between male strategy (OBY) and progeny mass was again significant ($F$ = 3.92, df = 1, 125, $P$ = .023), along with factors for progeny sex ($F$ = 6.75, df = 1, 125, $P$ = .010) and clutch number ($F$ = 3.43, df = 2, 125, $P$ = .040). Higher-order interactions of progeny sex were not significant (sex × mass: $F$ = 0.63, df = 1, 120, $P$ = .43; sex × OBY: $F$ = 1.74, df = 1, 120, $P$ = .18; sex × mass × OBY: $F$ = 1.60, df = 1, 120, $P$ = .21). The interaction effect between sire strategy (OBY) and mass remained significant in all of these more complex ANCOVA models that were considered (e.g., $F$ = 3.92, df = 1, 120, $P$ = .022). Thus, a con-

sistent sire genotype × maternal allocation interaction was seen across both sexes of progeny.

### Impact of Experimentally Induced Variation in the Field Pedigree

The interaction effects of experimental manipulations and genotype of the sire on dispersal provides evidence of causation associated with progeny size (see the introduction to this article and Sinervo 1990). We partitioned the analysis of each sire morph (**O**, **B**, and **Y**) into miniature progeny and their controls and giant progeny and their controls to investigate these effects further. Within **O** sires, the effects of miniaturization and gigantization were complementary; miniaturizing **O** progeny made them more philopatric ($F$ = 5.08, df = 1, 20, $P$ = .03; fig. 2*A*; effect of sex: $F$ = 1.48, df = 1, 20, $P$ = .24), while gigantizing **O** progeny made them more dispersive ($F$ = 14.50,

df = 1, 20, P = .005; fig. 2A; effect of sex: F = 39.86, df = 1, 20, P = .0002). Within **B** sires, there was no significant effect of either gigantization (F = 0.01, df = 1, 33, P = .95; fig. 2B; effect of sex: F = 5.20, df = 1, 33, P = .03) or miniaturization (F = 0.66, df = 1, 33, P = .42; fig. 2A; effect of sex: F = 2.67, df = 1, 3, P = .11). Within **Y** sires, gigantizing progeny made them more philopatric (F = 10.18, df = 1, 41, P = .003; fig. 2C; effect of sex: F = 4.81, df = 1, 41, P = .03), but miniaturizing the progeny did not affect dispersal (F = 0.015, df = 1, 50, P = .90; fig. 2A; effect of sex: F = 6.31, df = 1, 50, P = .02).

There was also clear evidence of an asymmetry in the effects of gigantization and miniaturization when we simultaneously tested the interaction between sire genotype and the manipulations. The effect of the interaction between the factor for **O**, **B**, and **Y** sire genotypes and experimental gigantization was significant (F = 4.22, df = 2, 90, P = .017; sex: F = 7.77, df = 1, 90, P = .0008). In contrast, the interaction between the factor for **O**, **B**, and **Y** sire genotypes and experimental miniaturization was not significant (F = 0.78, df = 2, 107, P = .46; effect of sex: F = 12.43, df = 1, 90, P = .0006). Enlarged egg size made orange progeny more dispersive but made yellow progeny more philopatric. Miniaturization did not affect dispersal. Therefore, the asymmetry in response between the two types of manipulations suggests that progeny enlargement might also allow the female to allocate additional factors to their eggs, not merely additional yolk.

### Impact of Genotypes from Laboratory Crosses on Progeny Dispersal

We recovered 40 progeny at maturity from the controlled laboratory crosses for which we had dispersal data (24 females, 16 males). In all analyses that follow progeny, size had no effect on dispersal (F = 0.11, df = 1, 39, P < .73), which is not surprising in that eggs were yolked in the laboratory. Thus, analysis of maternal effects is best restricted to the impact of maternal alleles on dispersal, which includes both genetic and maternal effects. ANCOVA indicated that differences in dispersal of sons versus daughters were significant for *o* alleles from both sires and dams (sex × sire *o*: F = 5.01, df = 1, 30, P = .03, sex × dam *o*: F = 5.50, df = 1, 30, P = .03) but only marginally significant for *b* alleles from dams (sex × sire *b*: F = 1.48, df = 1, 30, P = .23, sex × dam *b*: F = 3.48, df = 1, 30, P = .07).

We also partitioned analyses by progeny sex to further investigate interactions. We found that *o* sire alleles (slope = 1.60 ± 0.46, F = 11.97, df = 1, 11, P = .005) and *b* sire alleles (slope = 0.73 ± 0.36, F = 3.95, df = 1, 11, P = .07) had dispersive effects on sons, relative to *y*

sire alleles, while *o* dam alleles (slope = −1.48 ± 0.37, F = 15.40, df = 1, 11, P = .03) and *b* dam alleles (slope = −1.35 ± 56, F = 5.80, df = 1, 11, P = .07) had philopatric effects on sons, relative to *y* dam alleles. There were no significant effects of either dam or sire alleles on daughters in these models (sire *o*: slope = −0.34 ± 0.61, F = 0.53, df = 1, 18, P = .07; sire *b*: slope = −0.21 ± 0.60, F = 0.12, df = 1, 18, P = .73; dam *o*: slope = 0.12 ± 0.52, F = 0.23, df = 1, 18, P = .63; dam *b*: slope = 0.73 ± 0.79, F = 0.88, df = 1, 18, P = .35). Note that the signs of the effects of sire and dam alleles on male versus female progeny are reversed in each case, which drives the significance of the ANCOVA for the progeny sex × sire and progeny sex × dam effects on progeny dispersal noted above.

We also assessed the effect of lay date on dispersal of sons and daughters. While there was no effect of lay date on sons (F = 0.17, df = 1, 9, P = .68), the effect of lay date on daughters was highly significant (slope = 0.013 ± 0.0078, F = 16.19, df = 1, 16, P = .001) and also included a quadratic effect (quadratic term = −0.00080 ± 0.00030, F = 6.78, df = 1, 16, P = .02, lower levels of dispersal earlier and later). Furthermore, controlling for lay date effects resulted in significant effects of covariates for sire and dam alleles on dispersal of daughters (sire *o*: slope = −1.16 ± 0.38, F = 6.50, df = 1, 16, P = .008; sire *b*: slope = −1.10 ± 0.39, F = 6.44, df = 1, 16, P = .02; dam *o*: slope = 0.88 ± 0.35, F = 5.80, df = 1, 16, P = .63; dam *b*: slope = 1.62 ± 0.50, F = 0.88, df = 1, 16, P = .35). The effects of alleles on daughters remained opposite to those observed in sons.

### Discussion

We have demonstrated that male genotype influences dispersal for progeny in a field pedigree and for progeny released into nature from controlled laboratory crosses. Maternal effects, as measured by egg mass, also interacted with effects of sire genotype in the free-ranging pedigree. We found that progeny from orange sires dispersed the farthest, while progeny from yellow sires were most philopatric. Progeny from blue sires were intermediate in this regard. The only effect of progeny gender was an additive effect on dispersal distance across all genotypes. For progeny released from laboratory crosses, the effects of sire alleles on male progeny were parallel to those observed in the field pedigree. Effects of maternal genotype in the crosses opposed the effects of sire alleles in sons, implying a parent-of-origin effect such as a maternal effect. In daughters from laboratory crosses, effect of sire and dam alleles on dispersal in the wild were opposite in sign to those observed in sons. It is important to realize that dispersal in our study, as with any dispersal study in nature,

is linked to fitness in that dispersers must survive to maturity to be censused. Thus, effective dispersal is best viewed as a synergism between morph genotype and dispersal strategy that has cascading effects on survival selection. Below, we discuss the adaptive value of the genotypic patterns of effective dispersal.

Experimental manipulation of egg mass resulted in a modification of dispersal distance in accordance with our prediction, but it was significant only for gigantization. The lack of a consistent dispersal effect for egg miniaturization suggests that the effects of gigantization arise from factors correlated with yolk volume during oogenesis but not yolk volume per se. If we had detected purely complementary effects of the two manipulations, which were also in accord with natural egg size variation, we could conclude that yolk volume governed the maternal interaction with sire genotype (Sinervo 1990). This was not the case. Other sources of maternal effects (e.g., yolk steroids) are discussed below. In the laboratory crosses, size per se did not affect dispersal (not surprising, as we reared females in the lab to control such effects), but maternal genotype had strong effects on dispersal of sons and daughters. In addition, dispersal of daughters was affected by lay date. The experimental manipulation of size in the context of a field pedigree reflects the first causal demonstration of an interaction between genotype and maternal effects on progeny dispersal (Clobert et al. 2004). The laboratory crosses indicate that dispersal is likewise affected by a complex interaction between sire and maternal genotypes.

### Genetic Determination of Dispersal

Besides studies of genetically based morphological traits that are related to dispersal and comparative studies of dispersal among species, there is no firm demonstration that dispersal, when measured in natural conditions, is genetically mediated, based on results from laboratory crosses of parents (however, see Dingemanse et al. 2003). Attempts to demonstrate genetic control have failed in part because dispersal is an omnibus response to many different types of problems and will have a complex determination. Indeed, maternal and environmental effects plague dispersal analysis based on parent-offspring regression (and paternal effects for species with biparental care). In our study, we successfully measured dispersal in the context of genetically determined alternative strategies, which compartmentalizes variance in dispersal behavior to the genetic factors controlling morph development.

We found a strong effect of male genotype (color morph) on offspring dispersal. Evidence that this is a genetic effect stems from the following: first, throat color is determined by a single genetic factor (Sinervo 2001; Si-

nervo and Zamudio 2001; Sinervo et al. 2001); second, there is no parental care in this species (and therefore no paternal effect expected); third, environmental effects have been removed by randomly releasing offspring in the field with respect to sire and dam territory; and fourth, we explicitly tested for egg size maternal effects on dispersal (see below). However, because offspring are not the result of a half-sib-full-sib breeding design, we cannot rule out the possibility that females either actively chose a mate or that they alter allocation to progeny according to the male genotype. Females actively engage in cryptic mate choice (Calsbeek and Sinervo 2002, 2004), and coercive male mating strategies result in high levels of multiple paternity (81%; Zamudio and Sinervo 2000). Many offspring of different sire morph origin experienced the same maternal conditions, thereby reducing the probability that our results reflect a maternal effect. Furthermore, in our sample from the field pedigree, none of the surviving pairs of progeny from a single female parent had the same sire (e.g., 21 sib pairs); thus, multiple paternity was ubiquitous.

The laboratory crosses allowed us to resolve more clean genotypic effects of sire, not confounded by multiple paternity. However, the relevance of maternal egg size in the laboratory is of dubious value with regard to progeny dispersal in the wild; thus, effect of maternal genotype was used to estimate the maternal contribution, which includes both genetic and induced maternal effect contributions. The laboratory environment, however, controls many salient effects that otherwise would arise in nature. In this regard, the consistent effects of sire alleles in the laboratory and field pedigree on dispersal of sons imply a genetic origin of dispersal in sons. More complex maternal effects on both sons and daughters and the opposing sign detected for dam versus sire alleles on dispersal imply that the female parent also modulates progeny dispersal with maternal effects. A complete treatment of maternal effects in the field is forthcoming for the entire 18-generation pedigree, including induced density interactions with yolk volume and induced effects of the stress hormone corticosterone as a function of female density cycles.

### Egg Mass and Dispersal

Mounting evidence suggests that in addition to species with a well-differentiated dispersing morph (most often found in plants and insects, but see the naked mole-rat; O'Riain et al. 1996), many species still show variation in life-history traits of dispersing versus philopatric individuals (Bélichon et al. 1996; Murren et al. 2001). Most reported cases treat life-history traits such as survival or fecundity. However, the role of investment in dispersing versus philopatric offspring remains to be demonstrated. Reported differences in morphology, physiology, or con-

dition between dispersive and philopatric individuals at birth are rare and sometimes contradictory (Bélichon et al. 1996; Murren et al. 2001). These contradictory results might be better understood when the causes of dispersal are considered.

In the common lizard *Lacerta vivipara*, parent-offspring competition seems to drive dispersal (Ronce et al. 1998; Le Galliard et al. 2003). For example, dispersing offspring have been shown to be in better condition compared with philopatric offspring when dispersal was induced by the presence of a surviving mother (e.g., a high likelihood of parent-offspring interaction; Léna et al. 1998; Meylan et al. 2004). Such a result is biologically reasonable in cases where intensity of kin selection renders dispersal beneficial, even if fitness of the disperser is reduced. In the case of a mother influencing dispersal of progeny, the female parent is resolving parent-offspring conflict. The net gains of the mother surviving and inducing dispersal in her progeny outweigh survival costs of dispersal for the progeny. In this situation, any reduction of this cost is likely to be under strong selection (Murren et al. 2001).

We have demonstrated in previous articles that dispersal in *Uta stansburiana* was also strongly related to genetic similarity (genetic similarity was assessed by the correlation of multilocus microsatellite genotypes; Sinervo and Clobert 2003; Sinervo et al. 2006). However, detailed natural pedigrees indicate that none of the males with enhanced fitness through territorial cooperation were kin. Genetic similarity within morphs arises from strong correlation selection observed in *Uta* (Sinervo and Calsbeek 2003). Furthermore, the selective benefit of genetic similarity was found to strongly depend on male color morph (Sinervo and Clobert 2003). Blue male fitness was high in the presence of genetically similar blue males, orange male fitness was low in the presence of genetically similar males, regardless of throat color, and yellow male fitness was unaffected by genetic similarity of neighbors. If the results of Léna et al. (1998) and Meylan et al. (2004) are general, we should also observe a significant relationship between offspring dispersal and condition as measured by egg mass and an interaction between dispersal and male throat-color morph. Indeed, sires with more blue alleles tended to produce more philopatric offspring, while sires with more orange alleles produced more dispersers. When analyses included egg mass, dispersal was positively related to offspring condition (egg mass) if orange males sired them, but negatively related to offspring condition if yellow males sired them. No effect of offspring condition was observed if blue males sired the offspring.

Manipulations of offspring size confirm the causality of this relationship. Gigantization increased dispersal for orange male offspring, while it decreased dispersal for yellow male offspring. Miniaturization did not influence dis-

persal. The timing of gigantization with respect to ovarian development might allow the female to increase energy allocation as well as nonenergetically related components (Sinervo and DeNardo 1996). For example, females may alter hormone levels in the egg, and hormones have been demonstrated to play a role in offspring dispersal (de Fraipont et al. 2000; Dufty and Belthoff 2001; Dufty et al. 2002). In *Uta*, levels of yolk testosterone and yolk estrogen vary among female color morphs (e.g., **O** versus **Y**; L. Lancaster, J. Wingfield, and B. Sinervo, unpublished data). Manipulations of egg size thus provide evidence of a link between offspring condition and dispersal in the context of kin interaction. It is perhaps not surprising that the only other reported case of a dispersing morph (enlarged body) in a vertebrate concerns a mammal living in close kin colonies (the naked mole-rat; O'Riain et al. 1996).

We suggest that differences in dispersal among male progeny reflect genetic causality in dispersal strategies. Although it may be argued that results are also due to maternal allocation, we controlled for this potential effect by experimentally manipulating resources in the egg. Furthermore, all experiments, including those performed in the laboratory, will show a form of covariance between maternal allocation and sire genotype. Covariance arises because the female gains direct knowledge of the sire's identity during mating. Females may then alter allocation strategies to match the genotypes of her progeny (Calsbeek and Sinervo 2002). Thus, the covariance will always be present, even in controlled lab mating, except in cases where fertilizations are performed in vitro. Even in such cases, cryptic female choice may still allow the female to alter progeny allocation as a function of sire genotype, if she can determine the genotype of her progeny (e.g., sex and morph; Calsbeek and Sinervo 2002, 2004; Sinervo and Calsbeek 2003). Indeed, the results of our laboratory crosses and the different effects of sire and dam alleles on the dispersal of sons and daughters strongly imply the existence of such covariance between sire genotype and maternal effects arising from the dam. Nevertheless, we observed very consistent effects of sire genotypes on the dispersal induction of sons in both the field pedigree and the crossing study implying a very strong and consistent effect of sire genotype on dispersal of sons.

Evidence from experimental manipulations of territory quality suggests that alternative dispersal strategies are also adaptive for progeny, at least for sons. We have shown elsewhere (Calsbeek et al. 2002) that orange male progeny employ a usurping strategy whereby they assess territory quality over large spatial scales and target the highest quality areas for takeover. The philopatric strategy of blue males specializes in territory defense; thus, blue males are not expected to disperse far. Furthermore, neutral effects of egg size manipulations reflect the marginal importance

of dispersal to blue males in which finding a genetically suitable partner plays a major role. Finally, adult yellow males do not actively defend territories and thus should do well by adopting a philopatric strategy, which might also minimize mortality during the juvenile stage. Furthermore, the cryptic nonterritorial strategy may allow juvenile yellow males and females to avoid cannibalism by adults (Wilson 1975; B. Sinervo, unpublished observations) that are still present on the outcrop when hatchlings from the first clutch emerge.

## Acknowledgments

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