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Nonadditive Genetic Effects in Animal Behavior

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ABSTRACT: Heritabilities, commonly used to predict evolutionary potential, are notoriously low for behaviors. Apart from strong contributions of environmental variance in reducing heritabilities, the additive genetic components can be very low, especially when they are camouflaged by nonadditive genetic effects. We first report the heritabilities of courtship traits in founder-flush and control populations of the housefly (*Musca domestica* L.). We estimated the heritability of each male and female display through the regression of the courtships involving daughters and sons (with randomly selected mates) onto the "midparental" courtship values of their parents. Overall, the average heritability was significantly ($P = .012$) higher for the parent-daughter assays than for the parent-son assays. We attributed the low (even negative) heritabilities to genotype-by-environment interactions whereby the male's behavior is influenced by the "environment" of his mating partner's preferences for the display, generating epistasis through indirect genetic effects. Moreover, bottlenecked lines had up to 800% of the heritability of the controls, suggesting "conversion" of additive genetic variance from nonadditive components. Second, we used line-cross assays on separate populations that had been selected for divergence in mating behavior to identify dominance and epistasis through heterosis and outbreeding depression in courtship. Finally, our literature review confirms the prevalence of such low heritabilities (i.e., a conservative mean of 0.38) and nonadditive genetics in other behavioral repertoires (64% of the studies). We conclude that animal behavior is especially prone to the gamut of quantitative genetic complexities that can result in negative heritabilities, negative selection responses, inbreeding depression, conversion, heterosis, and outbreeding depression.

Keywords: dominance, epistasis, genotype-by-environment interactions, indirect genetic effects, inbreeding depression, outbreeding depression.

The notoriously low heritabilities of animal behaviors pose special challenges to quantitative genetic efforts to measure

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levels of genetic variance and to predict evolutionary potential. Abiotic sources of noise, such as temperature, commonly reduce within-individual repeatabilities, resulting in low (or undetectable) heritabilities (e.g., Boake 1994; Hedrick 1994). Physiological processes, such as age and stress, also generate experimental noise in behavior assays (e.g., Boake 1994; Garland 1994). Often these effects can be controlled to minimize the extent to which the environmental variance components dilute the heritabilities (e.g., Boake 1994).

More important, behaviors themselves often have low heritabilities because of low additive genetic variance components. Behaviors usually have strong correlations with overall fitness, with nonadditive genetic effects, such as dominance and epistasis, concealing additive genetic variance (e.g., see Aspi 2000). Natural selection is expected to deplete additive genetic variance for fitness traits until it is opposed by counterbalancing forces (Fisher 1958; see Aspi 2000). Ritchie and Kyriacou (1994), for example, attributed the nonsignificant heritabilities for aspects of *Drosophila melanogaster* courtship song to historical selection pressure on reproductive success (sensu Fisher 1958). They further suggested that nonadditive genetic processes were masking the additive genetic effects (Ritchie and Kyriacou 1994).

Traditionally, dominance and epistasis have been treated as noise, or residual, effects (e.g., see Falconer 1989; Wang et al. 1999), but nonadditive effects have important evolutionary ramifications. Traits structured by dominance and some forms of epistasis are subject to inbreeding depression (Falconer 1989; Charlesworth 1998). Outbreeding depression, resulting from the breakdown of epistatic complexes, can drive the evolution of reproductive isolation and, potentially, the formation of new species (Lynch 1991; Parker 1992; Aspi 2000). Importantly, dominance and epistasis cause the genetic backgrounds of traits to shift under inbreeding or selection (Goodnight 1988; Cheverud and Routman 1996; Hansen and Wagner 2001). In particular, additive genetic variance can increase with inbreeding when dominance and epistatic components are "converted" to additive variance (Willis and Orr 1993; Cheverud and Routman 1996; see Meffert 1999, 2000 for reviews). Such conversion can alter the genetic covariance-correlation structure across

Table 1: Description of housefly behaviors expressed during courtship

Behavior	Code	Description
Mount	mt	The male mounts the female and attempts copulation
Close	cl	The male stands still next to the female, close enough that he can touch her without moving further forward
Creep	cr	The male makes creeping movements as he comes near the female
Touch	to	The male touches the female with his forelegs
Buzz	bz	The male buzzes his wings while mounting the female
Lunge	lg	While mounting the female, the male lunges forward over the female's head
Hold	hd	The male stops his wing buzzing (bz) and holds his wings over the female's head
Lift	lf	While in the lunge (lg) position, the male lifts the female's forelegs with his own forelegs
Female	fm	Before mounting, the female touches the male with her forelegs or middle legs
Wing out	wo	During the mounting by the male, the female hikes her wings out perpendicular to her body so that she can kick at him from behind

traits (Bryant and Meffert 1988; Shaw et al. 1995). Thus, the ability to forecast evolutionary potential is seriously compromised by such nonadditive effects.

Behaviors are also especially prone to the influences of social environment. These effects range from rather primitive interactions, such as the influence of larval density on *Drosophila simulans* pupation height (Ringo and Wood 1983), to direct cultural inheritance, as with ground squirrel foraging behavior (Ritchie 1991) and countless cases of bird song (e.g., Darwin's finches; Grant and Grant 1995). Ritchie (1991), for example, claimed that the culturally inherited maternal effects in squirrel foraging were "uncontrollable" in heritability assays. Importantly, such influences of social environment can produce genotype-by-environment interactions (i.e., Meffert 1995; Moore et al. 1997) in the form of indirect genetic effects (sensu Wolf et al. 1998; Wolf et al. 1999). In such social interactions, the "environment" is the interacting conspecific, creating genotype-by-genotype interactions as a special form of epistasis (Boake and Hoikkala 1995; Meffert 1995; Wolf et al. 1998; Brodie 2000; Wolf 2000). Consequently, these interactions do not just simply contribute to the environmental variance term of the heritability but also have causal effects on nonadditive genetic architecture and can obscure evolutionary projections (Via and Lande 1985, 1987). In particular, genotype-by-environment interactions can generate negative heritability estimates and selection responses (Meffert 1995). In other scenarios, however, genotype-by-environment effects can inflate heritabilities (Gromko 1987; Moore 1990).

In this study, we examine the variation in heritability assays and the nonadditive genetic structure of courtship traits in the housefly (*Musca domestica* L.). In particular, we assayed the heritabilities of 10 courtship traits in bottlenecked (two pair, founder-flush) and nonbottlenecked lines. We also present analyses on line-crosses (P_1, P_2, F_1, F_2, and backcrosses) between lines subjected to artificial selection for multivariate divergence in five courtship elements. Finally, we summarize quantitative genetic literature on the

prevalence of nonadditive genetic effects in animal behavior. We find that dominance, epistasis, genotype-by-environment interactions, and genotype-by-genotype interactions strongly influence the genetic structure of housefly mating behavior as well as the behaviors of other animals. These processes complicate evolutionary projections, resulting in conversion (increased additive genetic variance with inbreeding), inbreeding depression, negative selection responses, heterosis, and outbreeding depression.

Methods

Bottleneck Experiment

We started this project with a population of houseflies that had been in the laboratory for three generations. We derived each of six bottlenecked lines by pooling the progeny from two isolated, random male-female pairs of founders. Over the course of three generations in the laboratory, the bottlenecked populations flushed to the standard husbandry size of ∼2,000 individuals. In the same generation as the founder events, we split the stock control population into two replicate control lines and held them at the standard husbandry size for three generations. We then spent the next six generations of the experimental protocol videotaping the courtship repertoire (for descriptions of the behaviors, see table 1 and Meffert 1995) of a total of 805 families (1,610 courtships) among the eight lines.

In conducting the parent-offspring regressions, we treated the courtship repertoire of a set of parents as the "midparental" (see, e.g., Falconer 1989) value of interacting traits (see, e.g., Brodie 2000), such as the male display and the associated female preference for the male's performance. We assayed the courtship of a single daughter or son from this family in the next generation as they mated with a randomly chosen partner. We first performed the parent-son analyses (over two generations) followed by the parent-daughter tapings (over two generations) and

finished with a combination of parent-daughter and parent-son assays. We thus obtained heritabilities for the eight male displays and the two female displays (see table 1) on the basis of the regressions of the matings observed in daughters and sons onto the courtships of their parents. Note that we interpret a parent-daughter regression for a male display (i.e., using the covariance of the display of a daughter's random partner with the display that her father had performed for her mother) as a measure of the heritability for female preferences for the male's performance (see below). In particular, male houseflies apparently use serial courtship attempts to accommodate female preferences for their displays (Meffert 1995; Aragaki and Meffert 1998; Meffert and Regan 2002). This protocol yielded a mean of 50.3 and SD of 4.4 for the number of families in the parent-offspring (parent-son or parent-daughter) regressions per strain (for more detail, see Meffert 1995).

For these videotapings (this bottleneck experiment) and the videotapings of the line crosses (the selection experiment described below), we employed the following measures to control for experimental noise: we controlled for the body size of the adults by rearing the larvae at standard densities (approximately 80 eggs/18 g of Chemical Specialities Manufacturer's Association medium). We minimized the effects of anesthesia by sexing the emerging adults under light CO_2 within 24 h of eclosion and transporting the virgins for videotaping without any anesthesia (using glass tubes). We controlled for age effects by videotaping the flies at the age of peak sexual activity (7 and 8 d posteclosion for the bottleneck and selection experiments, respectively). Additionally, we screened out incompatible pairs by setting a cutoff point for the initiation of copulation (40 and 30 min for the bottleneck and selection experiments, respectively). Finally, we analyzed only those courtships that resulted in copulation (ostensibly, the courtship that satisfied the female preferences and thus induced her to copulate).

Selection Experiment

At the beginning of the selection experiment, we videotaped the courtships of 160 virgin male-female pairs taken from a population that had been in the laboratory for 11 generations (from a different sample from the same field site that was used for the bottleneck experiment). We placed each pair in an isolated cage and collected their eggs as isolated family cultures. During the 2-wk period of the larval and pupal stages, we collected data from the videotapes to determine the principal component scores (along the first principal component for five courtship traits; see table A1) for each set of parents. Because of the logistical challenges of the experiment, we streamlined the

assays to only five postmounting behaviors (buzz, lunge, hold, lift, and wing out; see tables 1 and A1).

We then established four populations for undergoing selection for divergence along the first principal component (table A1). Specifically, we established two replicate lines for both selection trajectories (i.e., selection for either the positive or negative trajectory on the first principal component; see table A1). For each trajectory, the two replicate lines were composed from the pooled offspring of the 30 male-female pairs from the base population that showed the most extreme scores in the desired evolutionary direction. We established the ultimate degree of selection pressure as a compromise between minimizing inbreeding effects and maximizing selection pressure, given the logistical constraints of husbandry. In the next two generations of selection (i.e., after establishment of the lines), we allowed the 30 most deviant parents to contribute offspring to the next generation, from a mean number of 37.4 and SD of 3.2 families per population, per generation. Realizing that the logistics were resulting in rather weak selection pressure, we intensified the selection pressure in the last five generations. In this part of the protocol, we allowed only the 25 most deviant parents to contribute to the next generation, from a mean of 36.9 and SD of 3.0 per population per generation. A total of 1,299 courtships were analyzed in this part of the protocol.

After the eight generations of selection, we performed line crosses (P_1, P_2, F_1, F_2, and the two backcrosses; see Lynch and Walsh 1998; Bradshaw and Holzapfel 2000) between lines that had been selected for opposite evolutionary trajectories (i.e., females from a positive trajectory line mating with males from a negative trajectory line and visa versa for the other two replicates). We videotaped the parental (pure) lines in the same generation as the F_1 hybrids. The F_2's and backcrosses were assayed in the generation thereafter. We thus analyzed a total of 283 courtships for the line-cross assays ($\overline{X} = 23.6$, SD $= 2.4$, per parental line assay or cross).

Analytical Considerations for the Bottleneck and Selection Experiments

In both studies, we used event-recording software (Noldus 1990) to collect the data from the videotapes. We then used our own software (using Interactive Matrix Language; SAS Insititute 1988) to express each behavior as a proportion of time spent in its execution (i.e., the total amount of time spent in the behavior divided by the total observation period). Where necessary, we transformed the data for conformation to assumptions of normality (SAS Institute 1988; for more detail, see Meffert 1995).

For the bottleneck experiment, we estimated heritabilities through parent-offspring regressions, using the resid-

uals from the block means to remove potential intergenerational block effects. Again, we interpret the net courtship display for any male-female pair as involving interactions between sexually dimorphic traits (e.g., male performance and the associated female preference for his performance; Meffert 1995; see Moore et al. 1997). Thus, we treated the net performance in the parents as a "midparental" value (e.g., Falconer 1989) for estimating the heritability by regressing the courtship performance in a son's or daughter's mating with a randomly selected mate onto that of their parents. The heritability estimates on the pooled data conformed to the assumptions of normality (SAS Institute 1988), justifying parametric tests.

For the selection experiment, we employed joint-scaling tests (Hayman 1960; Hard et al. 1993; Lynch and Walsh 1998; Bradshaw and Holzapfel 2000) to identify the influences of dominance and epistasis. For these analyses, the six means (P_1, P_2, F_1, F_2, and the two backcrosses) were tested for goodness of fit with the expected line means. These expectations were derived from the parameter estimates (e.g., grand mean, additivity, dominance, and additive-by-additive epistasis), on the basis of the components of the design matrix and the line means and variances (see Bryant and Meffert 1995; Lynch and Walsh 1998). The figures thus depict the tests of the three hierarchical models: purely additive, additive with dominance, and additive with both dominance and additive-by-additive epistasis. A significant deviation from the model (tested by χ^2) indicates rejection in favor of the next model in the hierarchy.

Literature Review

We surveyed the quantitative genetic animal behavior literature (see table B1) for heritability estimates (and genetic variances) and additional evidence of nonadditive genetic effects (i.e., dominance, epistasis, genotype-by-environment interactions, and genotype-by-genotype interactions). In compiling the heritability data (see table B1), we used the upper bound when there was a range of assays given in the study. In order to make a concerted effort to find nonadditive effects, we also used the following keywords in the search: backcross, diallel, female choice, heterosis, inbreeding, line cross, and nonadditive. In identifying nonadditive effects, we used the conclusions given by the authors (see table B1). In rare cases, we report our own conclusions when we felt the article had rather indisputable evidence of nonadditivity (or straightforward second-party heritability calculations in one case). These second-party conclusions are identified in table B1. In general, we summarized each article as a single study (e.g., taking the range of heritabilities when more than one behavior was analyzed). Some citations, however, occur more than once in the term for "number of studies" ($N = 73$)

because the research evaluated more than one behavioral repertoire (e.g., Boake and Konigsberg [1998] analyzed aggression and courtship components of *Drosophila silvestris*). A few studies were pooled when they were clearly subsets of a larger study (e.g., Brandes 1988, 1991).

Results

Bottleneck Experiment

Figure 1 depicts the heritabilities of the 10 courtship behaviors (see table 1), on the basis of the parent-son and parent-daughter regressions in the six bottlenecked populations and two controls (nonbottlenecked populations). We used the pooled data (i.e., pooled across strains and behaviors) for the 99% confidence intervals (CI) for heritabilities having a significant deviation from 0 (fig. 1). Both the parent-son (fig. 1*a*) and parent-daughter heritabilities (fig. 1*b*) have significant ($P < .01$) deviations from 0 in both directions (i.e., for positive and negative values). Overall, the average heritability among all traits and lines was significantly ($P = .012$) higher for the parent-daughter regressions as compared with that for the parent-son assays ($\overline{X} = 0.07$ and 0.02, respectively). There was a wide range in the heritabilities among lines. In the parent-son regressions, the greatest range was between control and bottlenecked lines for the male wing display, hold (hd, ranging from -0.21 to 0.43, respectively, table 1; fig. 1*a*). In the parent-daughter regressions, the greatest range was between two bottlenecked populations for the male leg movement lift (lf, ranging from -0.30 to 0.41, respectively, table 1; fig. 1*b*).

The average heritability among all traits and lines (within bottlenecked and nonbottlenecked treatments) was higher for the bottlenecked lines, but not significantly so ($P = .87$; fig. 1). There is no numerical bias for the bottlenecked lines to have higher or lower heritabilities than the mean of the controls. In particular, the χ^2 tests for a 50% : 50% distribution around the control means yield 1.7 ($P = .19$) and 2.4 ($P = .12$) for the parent-son and parent-daughter assays, respectively. To examine the variation within traits, we derived 95% CIs based on the SEs of the line means within each trait. Importantly, every trait had at least one bottleneck line with a significant ($P < .05$) deviation from the mean of the controls (fig. 1). In the parent-son assays, the greatest deviation was a 4.3-fold increase in the heritability of the male hold display (hd, using a conservative estimate of 0 for the -0.06 value in the mean control, table 1; fig. 1*a*). The greatest deviation in the parent-daughter assays was a 7.9-fold increase for the male lift display (i.e., female preference for the male's lift, lf, keeping the 0.05 value of the mean control, table 1; fig. 1*b*).
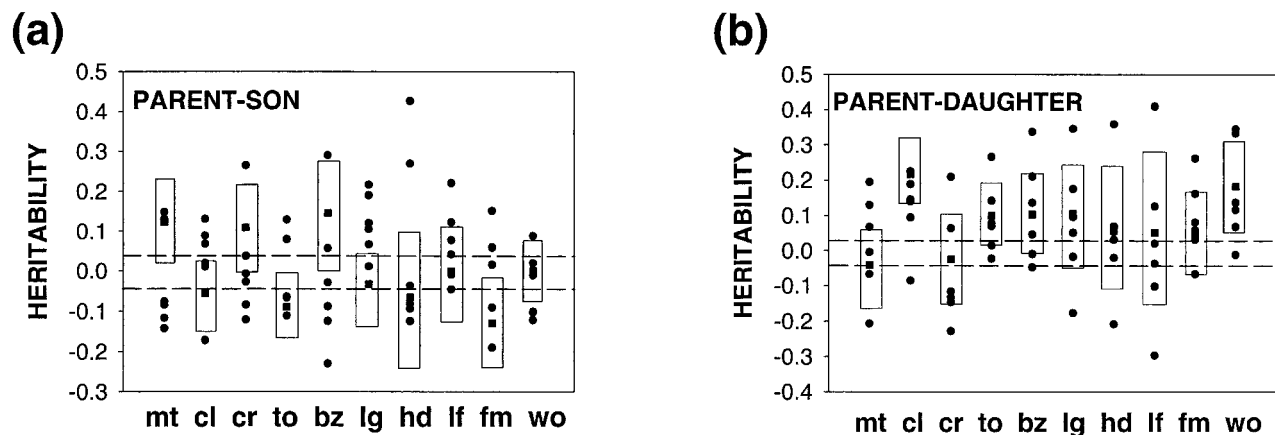
Figure 1: The heritabilities of 10 housefly courtship behaviors, on the basis of (*a*) parent-son and (*b*) parent-daughter regressions in six bottlenecked and two nonbottlenecked (control) populations. For the regressions, we treat the parental courtship value as a "midparental" result from the interactions between sexually dimorphic behaviors (e.g., the indirect genetic effects of female preferences onto the expression of a male's display; see Meffert 1995; Moore et al. 1997; Brodie 2000; Wolf 2000). The courtships of sons or daughters (with randomly selected partners) are thus regressed onto their parent's values for each heritability estimate. See table 1 for descriptions of the behaviors and their abbreviations. The dashed lines indicate the 99% confidence intervals for significant deviations from 0 (on the basis of data pooled across strains and across traits). The average heritability among all traits and lines is significantly ($P = .012$) higher for the parent-daughter regressions than for the parent-son assays. The boxes indicate 95% confidence bounds for significant deviations from the means of the controls (*squares*). The average heritability among all traits and lines (within bottlenecked and control treatments) is higher for the bottlenecked treatment, but not significantly so ($P = .87$).

For testing the differences in the heritabilities for the bottlenecked and control treatments, neutral expectation holds that the bottlenecked lines should, on average, have a decrease to 87.5% of the heritability of the controls (e.g., $1/2N$, where $N = 4$; Falconer 1989). In this study, however, the presence of negative heritabilities suggests that the assumptions for neutral expectation are violated. Thus, we are reporting more conservative tests for deviations from the controls.

Selection Experiment

Figure 2 depicts the data from the line crosses (with 95% CIs), along with their expectations for pure additivity (fig. 2a–2e; see Stevens 1994). Both blocks of line crosses (i.e., replicates) for the buzz assays (fig. 2a) conform to additive expectations. However, the model of additivity with both dominance and additive-by-additive epistasis is rejected for lunge, hold, lift, and wing out in the second block of

line crosses (fig. 2b–2e), suggesting even higher-order epistasis (i.e., dominance-by-additive and/or dominance-by-dominance epistasis). The influence of dominance and at least additive-by-additive epistasis is also apparent in lunge, lift, and wing out (fig. 2b, 2d–2e) in the first block. Heterosis (i.e., the F_1 mean lying outside of the parental phenotypes; see Falconer 1989) is indicated for lunge and wing out (second block of fig. 2b, 2e). Outbreeding depression (i.e., breakdown in the F_2 or backcrosses) is apparent in lunge (both blocks of fig. 2b), hold (second block of fig. 2c), lift (both blocks of fig. 2d), and wing out (both blocks of fig. 2e).

Literature Review

Figure 3 summarizes the quantitative genetic literature review of heritability estimates and nonadditive genetic effects in animal behavior. Of the 73 records (see table B1), 64% indicated at least one nonadditive effect and 40%

Figure 2: Line-cross assays for strains subjected to artificial selection for divergence in courtship. Separate panels are shown for the five postmounting courtship traits, with each panel depicting the two replicate blocks. The *X*-axis represents the genomic representation for each line mean (i.e., 0 and 1 for the parental lines, 0.5 for the F_1 and F_2 hybrids, and 0.25 and 0.75 for the appropriate backcrosses). The *Y*-axis represents the trait value for the intensity of the display (see table 1 for descriptions of the behaviors). The open circles indicate the F_2 means. The straight lines identify the expected means based on pure additivity, and the error bars represent the 95% confidence intervals for the means. Each panel also provides the χ^2 significance values for the hierarchical fits to the diallel models: (*a*) additivity, (*b*) additivity with dominance, and (*c*) additivity with dominance and additive-by-additive epistasis. A significant deviation calls for rejection of the model in favor of the next one in the hierarchy. Significance values are given as follows: one asterisk, $P < .05$; two asterisks, $P < .01$; and three asterisks, $P < .001$.

a

b

c

d

e
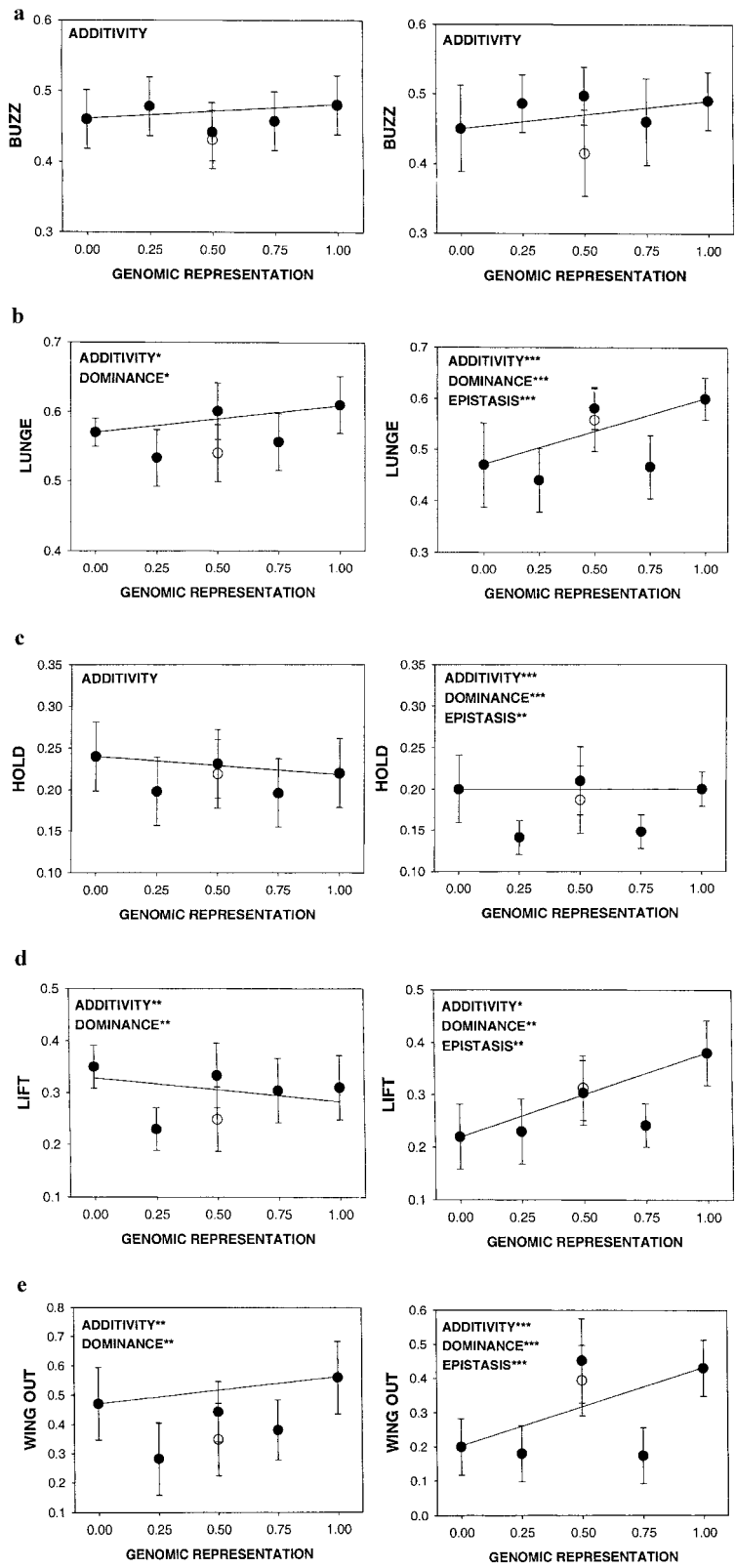
demonstrated dominance, with 37% having two or more nonadditive processes. Of the 57 studies with heritability values, the mean heritability was 0.38, with 54% having nonadditive genetic effects. There is no trend for low-heritability traits to have more or fewer nonadditive genetic effects (i.e., ∼50% of the studies in each heritability category or pooled categories for high vs. low values have nonadditive genetic effects).

Discussion

As would be expected, the heritabilities of housefly courtship traits are generally low (fig. 1). Heritabilities for behaviors are commonly lower than those of morphological traits (Roff and Mousseau 1987; Moore 1990; Lynch 1994; Boake and Konigsberg 1998; Meffert 2000). In our experiments, the mean heritability among bottlenecked and control populations was 0.04 (fig. 1). Our literature search (fig. 3) yielded a mean of 0.38, which is in good agreement with Roff and Mousseau (1987). Note that our estimate in the literature review is biased toward higher heritabilities because we conservatively used the upper limit heritability for studies that examined more than one behavior. We further suggest that publication biases in rejecting (or not submitting) statistically nonsignificant low heritabilities artificially inflate global estimates of the heritabilities of behaviors. Indeed, only a handful of experimental systems have had as much success as ours in achieving statistical significance with such low heritabilities (e.g., the 0.05 heritabilities for weevil oviposition and housefly assortative mating; Tanaka 2000; Regan et al. in press, respectively). Actually, the logistical scale necessary for these estimates can exceed population sizes in nature. Nevertheless, behaviors can have high heritabilities. For example, Garland (1994) detailed why the garter snake behaviors, ostensibly under strong selection, should exhibit heritabilities as high as 0.70 (for treadmill endurance), even higher than the morphometric heritabilities. He discounted the potential for evolutionary trade-offs while acknowledging the potential inflation by maternal effects, dominance, and epistasis (Garland 1994) in his full-sib heritability analyses (see Falconer 1989).

There was extremely high variation among our sub-populations in the heritability estimates (fig. 1). Similarly, Brandes (1988) reported very different heritabilities for learning among honeybee populations. Lynch (1988) described how one should expect high variation among heritability estimates, even for ostensible replicates. Thus, much of the variation we observed can be attributed to the statistical caveats of estimating genetic variance components (Lynch 1988). For example, error terms are essentially squared, thus amplifying contributions from experimental noise. We expect, however, that at least some

of the increases in the heritabilities in the bottleneck lines result from the conversion of additive genetic variance from the nonadditive components (see Meffert 1999, 2000). In particular, bottlenecked lines had up to 800% of the heritability of the mean control (fig. 1b). Even without conversion, these data attest to the radical unpredictability of the heritabilities among subsets of a single population.

Moreover, we were using a conservative approach to identify significant increases in the heritabilities caused by the bottlenecks. We tested simply for deviations in the bottlenecked populations from the controls, yet the additive genetic variance of the bottlenecked lines was expected to decrease by 12.5% ($1/2N$, where N = the number of founders = 4; Falconer 1989) under a purely additive model. Thus, the effects of dominance and epistasis found in the selection experiment (fig. 2) are likely to have operated in the bottleneck experiment (albeit derived from a separate sample from the field), causing conversion of additive genetic variance from the nonadditive components (e.g., Meffert 1999, 2000). It is important to note that much of the increased genetic variance would have negative fitness consequences through inbreeding depression (relieved by line crosses; see fig. 2; see Willis and Orr 1993; Charlesworth 1998). However, the unique evidence for outbreeding depression presented here (see fig. 2 and below) suggests more complex processes than simply the inflated frequencies of deleterious recessive alleles.

We found appreciable numbers of negative heritability estimates (that were significantly different from 0, fig. 1; Meffert 1995). Likewise, Gromko (1989) and Boake and Konigsberg (1998) reported negative heritabilities for courtship traits, although the estimates were not statistically significant. Nevertheless, Dohm et al. (1996) found significant negative heritability estimates in some trials of house mouse sprint speed. For our housefly courtship traits, a model of genotype-by-environment interactions (where the environment is the mating partner; see Meffert 1995) can account for negative heritabilities. These kinds of indirect genetic effects have been modeled extensively (Moore et al. 1997; Wolf et al. 1998; Brodie 2000). In prior simulations of such effects in housefly courtship, negative parent-offspring covariances arose when a population's distribution of females' preferences was more disjunctive (i.e., less overlapping) with the distribution of the males' ability to perform the behavior (Meffert 1995). This scenario should be unstable and thus drive the evolution of compatible female preferences and male competence, depending on the amount of additive genetic variance available (Meffert 1995; see Brodie 2000).

In general, negative heritabilities can translate to negative selection responses (e.g., with *Drosophila melanogaster* learning; Hewitt et al. 1983; see Gromko 1989) or non-
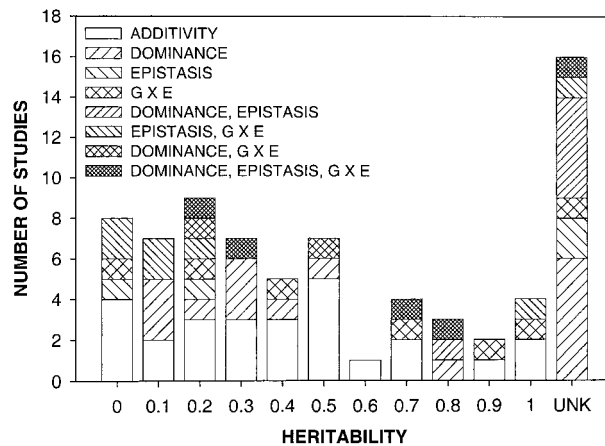
Figure 3: Summary of a literature search on heritability assays and nonadditive genetic effects in animal behavior. The *x*-axis denotes the heritability, with UNK (unknown) representing studies without heritability estimates. The *y*-axis identifies the number of studies (see table B1 for more detail). The effects of additivity, dominance, epistasis (with genotype-by-genotype interactions), and genotype-by-environment interactions are identified in the key. The mean heritability is 0.38 (based on 57 studies with heritabilities). Overall, nonadditive effects were found in 64% of the studies (total $N = 73$).

significant computations of realized heritabilities, despite significant selection responses (Ritchie and Kyriacou 1994; L. M. Meffert, J. Regan, S. Hicks, N. Mukana, S. Day, J. Bersola, and S. Gupta, unpublished data). Prior housefly experiments (Meffert and Regan 2002; L. M. Meffert, J. Regan, S. Hicks, N. Mukana, S. Day, J. Bersola, and S. Gupta, unpublished data) revealed negative heritabilities and selection responses in mating behavior, ostensibly because of the pleiotropic effects of inbreeding depression on overall mating propensity. In general, loci that influence behaviors commonly exhibit strong pleiotropic effects. For example, mating propensity in flies is influenced by loci involved with ambulatory activity and sensory capabilities, along with the genetic underpinnings of basic metabolic and neurological requirements for performing courtship (Faugeres et al. 1971; Taylor 1975; Markow 1981; Sharp 1984; Meffert and Bryant 1991). Other experimental systems have found pleiotropic-correlated responses to selection, such as larval feeding rate being correlated to locomotor activity in *D. melanogaster* (Sewell et al. 1975) and food consumption evolving along with nest building in mice (Bult and Lynch 2000). The prevalence of behavioral intercorrelations resulting from pleiotropic effects (e.g., Roff and Mousseau 1987) thus impinges on the ability to make evolutionary predictions about independent traits.

There were strong differences in the heritability estimates within populations, depending on the gender of the offspring in the assay (fig. 1), such that the parent-daughter regressions were significantly higher than the parent-son estimates. Interestingly, eight out of the 10 courtship traits

that yielded these results are displays performed by the male (all but female and wing out; see table 1). We suggest that the significant parent-daughter heritabilities for male displays identify genetic variance for female preferences for male courtship performance. In particular, indirect genetic effects (Brodie 2000; Wolf 2000) occur when the male housefly modulates his behavior (through serial courtships) to meet the female's preferences for his display (Meffert 1995; Aragaki and Meffert 1998; Meffert and Regan 2002). The females, however, are less plastic in the way that they manipulate the male displays (through their preferences for the male's expression of his display) or in the execution of their own movements. This asymmetry in courtship control thus yields especially low parent-son heritabilities. Gromko (1989) also reported strong differences between father-son and mother-daughter heritabilities for copulation duration in *D. melanogaster,* with the mother-daughter estimates being negative (but not significantly so). Moreover, he found no significant genetic correlations across the sexes, as assayed through mother-son covariances (Gromko 1989). His comparisons thus suggest that the male is more influential in determining copulation duration in this species. Similarly, Mackay et al. (1996) found no evidence for genetic correlations across the sexes for olfaction traits in *D. melanogaster,* ostensibly because of the different roles that olfaction plays in the life histories of the two sexes. They concluded that genotype-by-environment effects (where the environment is sexual determination) were important in the maintenance of genetic variation for olfaction. Thus, sexual dimorphisms in behavior, while often more cryptic than mor-

phological traits, critically influence genetic structure and evolutionary potential, often in counterintuitive ways.

Our line-cross assays revealed appreciable levels of heterosis and outbreeding depression (fig. 2*b*–2*e*). Perhaps the most intriguing finding was that such effects were manifested even in crosses between parental lines that were not significantly different from each other (fig. 2*c*). These data thus depict the essence of epistasis. That is, two populations can arrive at the same phenotypes evolutionarily with materially different genetic solutions, with the resulting genetic architectures being incompatible with each other. To our knowledge, only Ewing's (1967) research on *D. melanogaster* locomotion produced comparable results. Nevertheless, Aspi (2000) also found inbreeding and outbreeding depression in line-cross assays of the courtship songs of divergent *Drosophila montana* populations. Similarly, line crosses have revealed dominance for knockdown resistance (Cohan et al. 1989) and larval feeding rate (Sewell et al. 1975) in *D. melanogaster*. Dominance has also been detected through heterosis (hybrid vigor) in mouse nest building (Bult and Lynch 2000) and wheel running (Bruell 1964; Dohm et al. 1996), as well as in learning in *D. melanogaster* (Hewitt et al. 1983). Learning in blowflies exhibits both heterosis and epistasis (McGuire and Tully 1987). As in our study, the unpredictability of such line-cross assays on behavior could confound efforts to conduct quantitative trait locus (QTL) investigations (e.g., see McGuire and Tully 1987). Indeed, analyses of digenic epistasis and hybrid breakdown have long been part of the QTL analyses (e.g., see Li et al. 1997*a*, 1997*b*), but the theoretical complications of QTL analyses with nonadditive effects are only recently being appreciated (Wang et al. 1999).

Most of the studies in our literature review involved arthropods, with the vast majority involving *D. melanogaster* and its congeners (table B1). Our review cannot be considered exhaustive but should represent a fairly reasonable sample. As noted before, there is a bias to overestimate global heritabilities because of the numerous confounds in obtaining statistical significance in behavioral quantitative genetics. A potential bias in gauging the prevalence of nonadditive genetic effects, however, is less clear. The studies that focused only on identifying nonadditivity without estimating heritabilities (i.e., the "unknown" category in fig. 3) naturally yield 100% nonadditive effects because that was the focus of each manuscript. Still, the absence of data on nonadditive effects in the other studies could result from the inability (or disinterest) to address the issue while performing heritability assays. In our search, we found only four studies that yielded direct negative evidence of nonadditive effects (Cohan et al. 1989;

Brandes 1991; Pereira and Sokolowski 1993; Bult and Lynch 2000), while 47 reported nonadditivity (see table B1). Moreover, three of the four studies that refuted nonadditive effects could not discount nonadditivity altogether (i.e., Cohan et al. 1989; Pereira and Sokolowski 1993; Bult and Lynch 2000; see table B1). For example, Lynch's (1994) work on mouse wheel running, while negating the effects of epistasis, still supported the influences of dominance and genotype-by-environment interactions. Finally, this literature search does not include the abundant evidence in support of founder-flush theory, which implicates, albeit indirectly, nonadditive genetic effects in behavior (for a review, see Meffert 1999). We conclude that our experimental system is not peculiar in exhibiting the strong influences of nonadditive genetic effects (i.e., negative heritabilities, inbreeding depression, conversion, heterosis, and outbreeding depression). In general, at least 50% of behavioral systems are prone to these intriguing evolutionary complications.

In conclusion, behaviors are well known for having strong environmental influences, such as ambient temperature effects on locomotor traits (e.g., Sokal et al. 1960; Arnold and Bennett 1984; Garland 1994; Claireaux et al. 1995; Passek and Gillingham 1997; Weetman et al. 1998) and courtship song (Hedrick 1994; Ritchie and Kyriacou 1994; Sanborn 1997). Moreover, physiological processes such as nutritional or age effects on mating behavior commonly generate experimental noise in behavior assays (Meffert 1988; Mair and Blackwell 1998; Papadopoulos et al. 1998; Belmain et al. 2000; Bertram 2000). Often such abiotic and physiological effects can be controlled to minimize the dilution of heritability estimates by strong environmental variance components (Hedrick 1994; Ritchie and Kyriacou 1994; Meffert 1995; Aspi 2000). Nevertheless, we suggest that estimations of behavioral heritabilities are also especially subject to the confounds of nonadditive and indirect genetic effects, such as dominance, epistasis, genotype-by-environment interactions, and genotype-by-genotype interactions (indirect genetic effects). These factors are not merely nuisance factors but, rather, can catalyze complex evolutionary dynamics for animal behavior.

APPENDIX A

Table A1: Multivariate intercorrelation structure of five courtship traits in the housefly

Trait	PC1
Buzz	.116
Lunge	.614
Hold	.173
Lift	.573
Wing out	.501
Variance explained (%)	40.8

Note: Correlations of the courtship traits with the first principal component (PC1) are given, on the basis of 160 courtships in the base population (from which the selection lines were derived). See table 1 for descriptions of the behaviors.

APPENDIX B

Table B1: Sources of literature in the search for additional heritability estimates and evidence of nonadditive genetic effects

Behavior: animal	h^2	Dom	Epis	$G \times E$	$G \times G$	Source
Aggression:						
Drosophila silvestris	.00			(+)		Boake and Konigsberg 1998
Japanese quail	.09–1.95			+	+	Nol et al. 1996
Assortative mating:						
Housefly	.05					Regan et al., in press
Cannibalism:						
Flour beetle	<.75	+		+	+	Stevens 1994
Copulation duration:						
Drosophila						
melanogaster	.23–.46					Gromko 1987, 1989
Courtship:						
Crickets	.72					Hedrick 1994
D. melanogaster	.00					Ritchie and Kyriacou 1994
Drosophila montana	−.23 to .80	+	+	+		Aspi and Hoikkala 1993; Aspi 2000
Drosophila littoralis	−.33 to .18			+		Aspi and Hoikkala 1993
Cockroach	.33–1.07					Moore 1990
D. silvestris				+	(+)	Boake and Hoikkala 1995
D. silvestris	.00			(+)	(+)	Boake and Konigsberg 1998
Guppy		+	(+)			Farr 1983; Farr and Peters 1984
Housefly	−.01 to .25			+	+	Meffert and Regan 2002
Housefly	.06–.10			+	+	Aragaki and Meffert 1998
Housefly	.20	+	+		+	Meffert 2000
Molly	.84–1.38			+		Travis 1994
Moth	.18–.45			+		Collins et al. 1999; Jia et al. 2000
Defense:						
Garter snake	.37–.45					Arnold and Bennett 1984
Garter snake	.41					Garland 1994
Honeybee		+				Hunt et al. 1998
Foraging:						
D. melanogaster	.11–.21	+	+	+	(+)	Sewell et al. 1975
D. melanogaster	.02–.04					Wallin 1988
Garter snake	−.05 to .82	+				Arnold 1981*a*, 1981*b*
Zebra finch	.35					Lemon 1993

Table B1 (*Continued*)

Behavior: animal	h^2	Dom	Epis	$G \times E$	$G \times G$	Source
Geotaxis:						
D. melanogaster	.10–.31					Markow 1979
Drosophila persimilis	.07	+				Polivanov 1975
Drosophila simulans	.00			+		Ringo and Wood 1983
Grooming:						
Japanese quail	.16–.23					Gerken and Petersen 1992
Knockdown resistance:						
D. melanogaster	.17	+	−			Cohan et al. 1989
Learning:						
Blowfly		+	+			McGuire and Tully 1987
D. melanogaster	.28–.42	+				Hewitt et al. 1983
Honeybee	(.39–.54)	−				Brandes 1988, 1991
House mouse	.21	+		+		Henderson 1968*a*, 1968*b*
House mouse	.40–.50	+				Oliverio 1971; Oliverio et al. 1972
Pig	.45					Willham et al. 1963
Rat	.56					Bignami 1965
Locomotion:						
Caenorhabditi elegans		+	(+)			Park and Horvitz 1986
D. melanogaster	.51					Connolly 1966
D. melanogaster	.10					van Dijken and Scharloo 1979
D. melanogaster		−		+		Pereira and Sokolowski 1993
D. melanogaster		+				Weber 1996
Garter snake	.58–.70					Garland 1994
House mouse		+				Bruell 1964
House mouse	.14–.28					Swallow et al. 1998
House mouse	.17–.33	+				Dohm et al. 1996
Racehorse	.24					Buttram et al. 1988
Racehorse	.36					Gaffney and Cunningham 1988
Mate recognition:						
D. melanogaster			+			Finley et al. 1997
Mating propensity:						
D. melanogaster		+	+	+	+	Casares et al. 1993; Carracedo et al. 1995
D. melanogaster		+				Fulker 1966
D. melanogaster	−.17 to .25	+				Kessler 1969
D. melanogaster	.30	+				Manning 1961
D. melanogaster	.0					Gromko 1987
D. melanogaster		+				Sharp 1984
Housefly	−.03 to .10	+				L. M. Meffert et al., unpublished data
Migration:						
Armyworm moth	.71–.88			+		Gatehouse 1986; Dingle 1994
Milkweed bug	.20–.41			+		Caldwell and Hegmann 1969; Dingle 1994
Mite	.22					Li and Margolis 1993
Vole		+				Rasmuson et al. 1977; Dingle 1994
Warbler	.58–.87					Berthold et al. 1990
Nest building:						
House mouse	.07–.53	+	−	+		Lynch 1994; Bult and Lynch 2000
Olfaction:						
D. melanogaster		+	+			Fedorowicz et al. 1998
D. melanogaster	.08–.13		(+)	+		Mackay et al. 1996
Oviposition:						

Table B1 (*Continued*)

Behavior: animal	h^2	Dom	Epis	$G \times E$	$G \times G$	Source
Seed beetle	.15–.32					Messina 1993
Weevil	.05					Tanaka 2000
Phonotaxis:						
Moth	.21				(+)	Jang and Greenfield 2000
Photoperiodism:						
Mosquito	.15–.79	+	+			Hard et al. 1993
Phototaxis:						
Drosophila ananassa	.05–08					Markow and Smith 1979
D. persimilis	.07	+				Polivanov 1975
Reactivity:						
Paradise fish	.06–.98					Gervai and Csányi 1985
Territoriality:						
D. melanogaster	−.04 to .06			+	+	Hoffman 1994

Note: For figure 3, the general type of behavior is given, along with the study organism. Ranges of heritabilities (h^2) are presented (separated by dashes), along with authors' conclusions about the presence of nonadditive genetic effects (present = +, absent = −). The second-hand conclusions here in this article are set off by parentheses. The nonadditive effects are coded as follows: dominance (Dom), epistasis (Epis), genotype-by-environment interaction ($G \times E$), and genotype-by-genotype interaction ($G \times G$).

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