

ENVIRONMENTAL COMPONENTS OF PHENOTYPIC VARIATION: DIETARY AND  
TRANS-GENERATIONAL EFFECTS ON BEHAVIOR

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**Title**

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The Supervisory Committee certifies that this *disquisition* complies with North Dakota State University's regulations and meets the accepted standards for the degree of

**MASTER OF SCIENCE**

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## **ABSTRACT**

Phenotypic variation, or the total variation in a trait, and its components are of great importance in the fields of evolutionary and behavioral ecology. Phenotypic variation can be broken down into both environmental and genetic influences on that particular trait. However, due to an increasing trend of quantitative genetics in behavioral studies, researchers have begun to consider lesser studied components of phenotypic variation in addition to the commonly studied direct environmental and genetic influences. Some of these lesser studied components include maternal and paternal effects, or the effect that parental phenotype has on their offspring's phenotype. In Chapter 1, I examine the impacts of direct environmental manipulation on cricket song production. For Chapter 2 however, instead of examining the direct environmental influence at the individual level, I examine, through meta-analysis, how the indirect environmental influences that occur at both the maternal and paternal level impact offspring phenotype across taxa.

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## **DEDICATION**

To Neil for his unwavering support, for his love and for making me believe that I could do this. I

could not have finished this thesis without him.

To my parents for their support. Without their love and encouragement, I could not have even

considered pursuing this career path.

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## LIST OF SYMBOLS

$\tau$  ..... Repeatability of a trait, calculated by the proportion of among-individual variance relative to the total phenotypic variance

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## INTRODUCTION

Phenotypic variation, the total variation in a trait ( $V_P$ ), combines the total genetic ( $V_G$ ) and environmental influence ( $V_E$ ) on that particular trait (Falconer, 1996). This phenotypic variation and its components are of great importance in the fields of evolutionary and behavioral ecology, as selection on phenotypic variation will cause changes in a population's average trait value *if* there is heritable variation (Boake, 1989). This change in a population's average trait value can have large impacts on the population as a whole. While the two main components of phenotypic variation,  $V_G$  and  $V_E$ , have been well defined and studied in the past (Falconer, 1996), an increased application of a quantitative genetics framework to behavioral studies (Dingemanse & Dochtermann, 2014) has led researchers to consider an expanding number of components of phenotypic variation (Lynch & Walsh, 1998; Mousseau & Fox, 1998).

$V_E$  and  $V_G$  can be further expanded into a number of less studied components that can determine a phenotype of an individual. Lynch and Walsh (1998) proposed a path diagram that shows three major components that determine an individual's phenotype ( $z_x$ , Figure A1). The first component,  $E_{ox}$ , represents the direct environmental effects experienced by an individual. For example, if an individual is exposed to a poor diet or declining temperatures, that would have an influence on their phenotype as is the case when a male variable field cricket (*Gryllus lineaticeps*), is exposed to a high quality food regime. A male exposed to higher quality food will call more frequently compared to males that were exposed to a low quality diet (Wagner & Hoback, 1999). The second component,  $G_{ox}$ , or the direct genetic effects on an individual, also impacts an individual's phenotype. For example, in a nested half-sibling breeding design in guppies, overall responsiveness to any male encountered showed significant additive genetic variance (the effects that genes have on a phenotype) (Brooks & Endler, 2001). Both  $E_{ox}$  and  $G_{ox}$

act directly at the individual level. However, growing evidence suggests that indirect effects must also be considered when examining phenotype determination.

An additional component of a phenotype is the maternal effect ( $M_x$ ), or the effect that a maternal phenotype has on their offspring's phenotype through means other than direct genetic effects on a trait (Lynch & Walsh, 1998). These maternal effects can also be broken down into both genotypic and environmental components ( $G_{mw}$  and  $E_{mw}$ , respectively) (Lynch & Walsh, 1998; Wolf & Wade, 2016).  $G_{mw}$  represents the indirect genetic effects from the mother that influence an offspring's phenotype while  $E_{mw}$  represents the indirect effect of the mother's environment on offspring phenotype. An example of both genetic and environmental maternal influences has been previously seen in Canada goldenrod (*Solidago altissima* L.). Germination probability and seedling (offspring) mass were significantly affected by both the genetics ( $G_{mw}$ ) and soil environment ( $E_{mw}$ ) of the mother (Schmid & Dolt, 1994). While only maternal effects were initially considered as a component for phenotypic variation, increasing evidence has shown that fathers also play a role in offspring phenotypic variation (Qvarnstrom & Price, 2001; Wolf, Brodie, & Moore, 1999). For example, in the dung beetle (*Onthophagus Taurus*), provisioning tactics of fathers determine whether or not offspring males will develop horns (Hunt & Simmons, 2000). Due to the suggested importance of both paternal effects ( $P_x$ ) and maternal effects ( $M_x$ ), the originally proposed figure by Lynch and Walsh (1998) has been adapted here (Figure A1) to show that both maternal and paternal effects are major environmental influences that aid in determining an offspring's phenotype with  $P_x$  representing the paternal effect and  $M_x$  representing the maternal effect. Similar to  $M_x$  being comprised of both genetic and environmental components,  $P_x$  is also broken down into  $G_{pv}$  (the indirect genetic

effects from the father on offspring phenotype) and  $E_{pv}$  (the indirect effect of the father's environment on offspring phenotype).

In Chapter 1, I examine the direct environmental influence component ( $E_{ox}$ , Figure A1) of phenotypic variation by testing how dietary manipulation at both developmental and post-developmental stages influences call structure in the *Acheta domesticus*.

Various organisms employ different types of signals to achieve desired outcomes. For example, a cricket uses a long-distance signal to attract a female to his territory. While these long-distance advertisement calls have been shown to be impacted by differing environments like dietary manipulation (Holzer, Jacot, & Brinkhof, 2003; Wagner & Hoback, 1999), there has been little research examining how *lifetime* dietary conditions impact other types of signals (e.g. courtship and aggressive) production. I investigated how resource quality over a lifetime affects the production of all call types in *A. domesticus*. In addition to testing for dietary effects on calling, I tested for modularity in all three cricket call types using structural equation modeling and testing various calling hypotheses present in the literature.

In Chapter 1 I examined the importance of direct environmental influences (diet manipulation) on offspring behavior. For Chapter 2 I was interested in the indirect environmental influences that occur at both the maternal ( $E_{mw}$ ) and paternal level ( $E_{pv}$ , Figure A1). To do this, I performed a meta-analysis that examined how both maternal and paternal environmental manipulations influence offspring behavior across taxa. Non-genetic influence of parents on offspring phenotypes, i.e. trans-generational effects (TGEs), have been of increasing interest in behavioral ecology over the past 15 years due to their potential to alter fitness of both parents and offspring. In other areas of evolutionary ecology, the overall strength of these effects has been assessed via meta-analysis for other classes of traits but behavior has not been

quantitatively reviewed. I asked the question: What is the magnitude of TGEs on offspring behavior?

Chapter 1  
Chapter 2

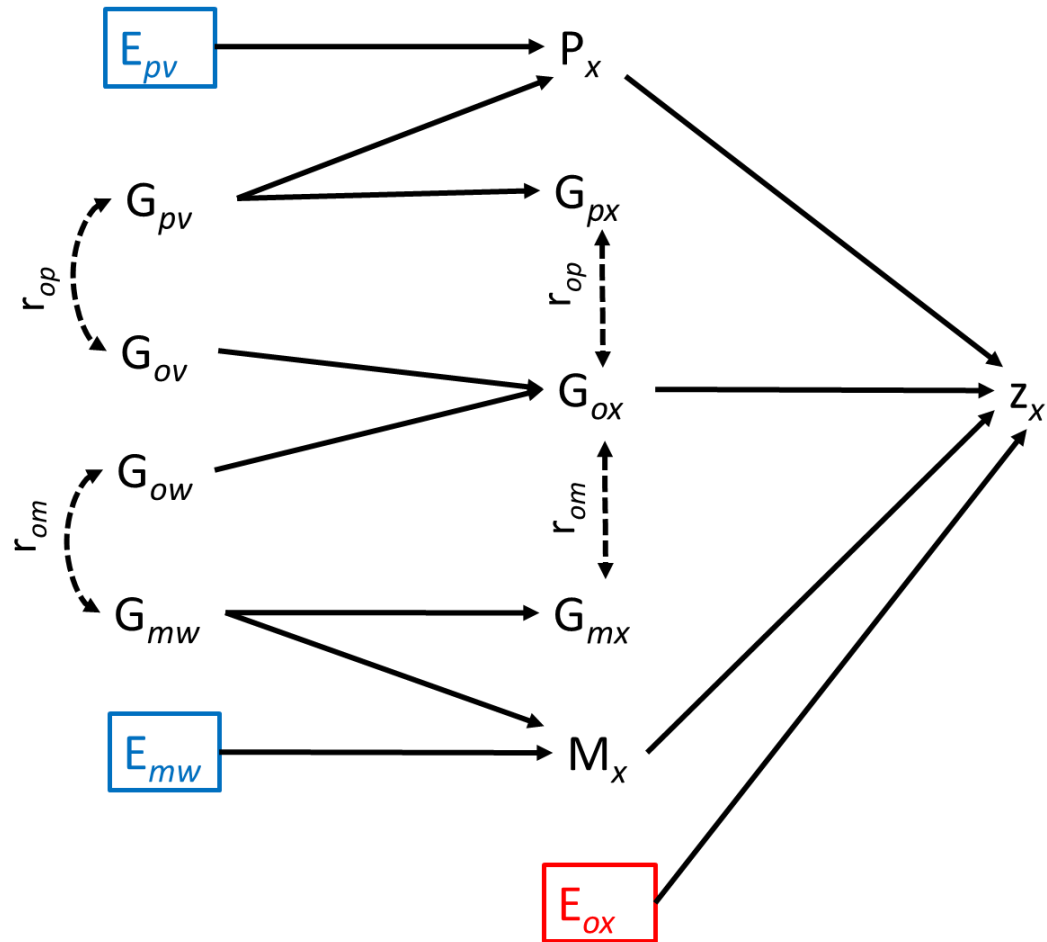


Figure 1.1. Path diagram adapted from Lynch and Walsh (1998) representing the determination of an individual's phenotype ( $z_x$ ) by direct environmental effects ( $E_{ox}$ ), direct genetic effects ( $G_{ox}$ ), maternal effects ( $M_x$ ) and paternal effects ( $P_x$ ). The mother of  $x$  is denoted by  $w$  and the father of  $x$  is denoted by  $v$ .  $r_{om}$  and  $r_{op}$  represent the genetic correlations between direct and parental effects. Chapter 1 examines the direct environmental effects ( $E_{ox}$ ) on behavior by manipulating diet of crickets. Chapter 2 is a meta-analysis that examines the influence of maternal and paternal environmental manipulation ( $E_{mw}$  and  $E_{pv}$ ) on offspring behavior across taxa



# CHAPTER 1: INTEGRATION OF SIGNALS USED IN INTRA- AND INTER-SEXUAL SELECTION

## Abstract

Dietary conditions are known to impact long-distance signaling for mates in many species, although little research has examined how lifetime dietary conditions impact short-range signaling. Male *Acheta domesticus* employ three types of calls: a long-distance advertisement call, a courtship call, and an aggression call. Courtship call production in *A. domesticus* has a high energetic cost, suggesting honest signaling due to energetic constraints. We investigated how resource quality over a lifetime affects the production of all call types in *A. domesticus*. We provided crickets with a high-quality diet (3.35 cal/g and 45% protein content) or a low-quality diet (1.12 cal/g and 15% protein content) during development and then either maintained or switched an individual's diet at maturation. In addition to testing for dietary effects on calling, we tested for modularity and integration in all three cricket call types using structural equation modeling and testing various calling hypotheses. The effects of diet quality on male calling effort did not vary by call type, suggesting that the three call types are not condition-dependent in *Acheta domesticus*, at least insofar as we manipulated condition. However, we did find evidence for integrated calling in *Acheta domesticus* suggestive of signal redundancy.

## Introduction

Sexual selection results in differing reproductive success based on among-individual variation in traits. Traits most typically shaped by sexual selection include male and female genitalia morphology, male ornamentation, and sexual signaling (Andersson & Simmons, 2006). Sexual signaling is particularly important for many species of birds, insects and amphibians, (Harrison, Thomson, Grant, & Bertram, 2013; Moreno-Gomez, Bacigalupe, Silva-Escobar, &

Soto-Gamboa, 2015). For example, both Common Starling (*Sturnus vulgaris*) and Zebra Finch (*Taeniopygia guttata*) females have been shown to select males that produce more complex calls (Buchanan, Spencer, Goldsmith, & Catchpole, 2003; Spencer, Buchanan, Goldsmith, & Catchpole, 2003; Woodgate, Mariette, Bennett, Griffith, & Buchanan, 2012), leading to the evolution of increasing call complexity over time. Because sexual selection has been shown to act on specific components of a signal (Buchanan et al., 2003; A. Hedrick & Weber, 1998; A. V. Hedrick, 1986; Spencer et al., 2003; Woodgate et al., 2012), studying call structure and call production can provide valuable insights regarding the function of complex signals and the action of sexual selection.

Calls convey a variety of information to the listener, and therefore, it may be beneficial for an individual to “lie” about its condition or other information. If a signal is indeed “honest” then it will accurately communicate the condition of a male to a listening female (Smith, 1991). If a signal is condition-dependent then body condition and signal structure should be related (Wagner & Hoback, 1999). Condition can generally be broken down into the direct and indirect benefits that a male can provide a female (Wagner & Hoback, 1999). Because of these benefits, females can be expected to select males on the basis of condition; in turn, manipulating condition can provide valuable information on how signals reflect current male state and the general operation of sexual selection. One of the most well documented ways to alter an organism’s overall quality is to manipulate that organism’s diet. Therefore, differing nutrition regimes should impact signals. Past studies have shown that long-distance mate attraction calls in many organisms are often state-dependent (Buchanan, Catchpole, Lewis, & Lodge, 1999; Buchanan et al., 2003; Holzer et al., 2003; Hunt et al., 2004; Spencer et al., 2003; Wagner & Hoback, 1999)

and thus honest. However, there is little research examining how lifetime dietary conditions impact other types of signals (e.g. short range courtship calls).

In addition to courtship calls, house crickets (*Acheta domesticus*) have two other call types that could also be condition dependent. Calls of house crickets can be categorized as one of three types: a long-range advertisement call, a short-range courtship call, and an aggressive call (Gray & Eckhardt, 2001) (Figure 1.1). Aggressive calls are used by males to inform rival males about fighting ability and thus are likely under inter-sexual selection. However, there is little known about the specific information conveyed by aggressive calls in crickets (Brown, Smith, Moskalik, & Gabriel, 2006). The two types of calling behavior involved in inter-sexual selection and essential for mating success in crickets (and many other insects) are advertisement and courtship calls. Advertisement calls are used by males to attract females and convey information about male quality to those females (Gray, 1997). Courtship calls are produced once males come into contact with females and are usually required for organisms to mate (Harrison et al., 2013). Courtship call has been determined to be twice as energetically costly as advertisement call production in *Acheta domesticus* (Hack, 1998), suggesting that courtship call is likely an honest signal based on an energetic handicap.

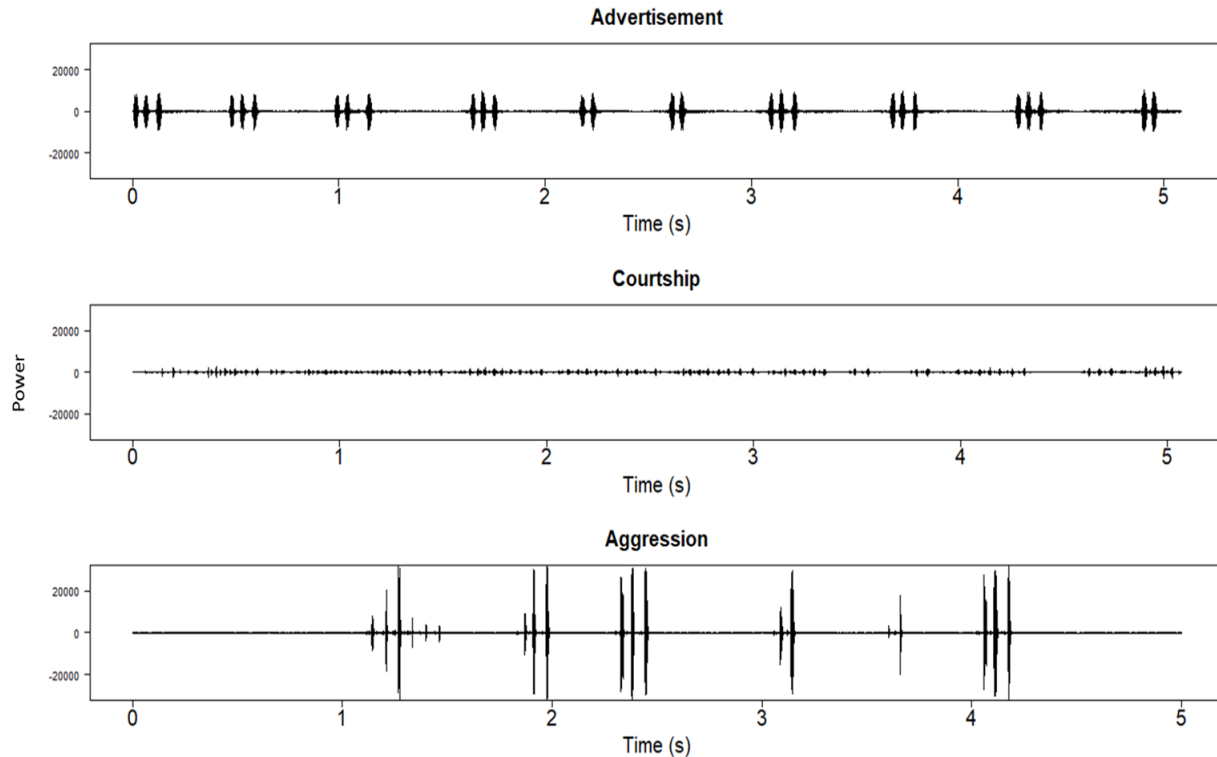


Figure 1.2. Waveform structures of five seconds of advertisement, courtship and aggression call from the same cricket. The y-axis represents the amplitude of the call

The impacts of diet and condition dependency on advertisement call have been extensively studied in Gryllid species (including *Acheta domesticus*). Nutritional content and diet quality have been shown to affect many different call components (chirp rate, frequency etc.) specifically in insects (Holzer et al., 2003; Hunt et al., 2004; Wagner & Hoback, 1999). In contrast to research on the effects of diet on advertisement call, there are only a handful of studies that have looked at the effect of diet on courtship call in different species of crickets, both of which found it is *not* condition-dependent (Gray & Eckhardt, 2001; Wagner & Reiser, 2000). This is in surprising contrast to the condition-dependent nature of advertisement call and suggests that the calls might be providing independent but complementary information about males to listening females. Since advertisement call has been found to be condition dependent in *A. domesticus* (Gray, 1997), it follows that the more energetically costly courtship call will also

be condition-dependent. Further, while previous studies have looked at diet effects of both advertisement and courtship call at different life stages, there are inconsistencies regarding exactly how diet impacts advertisement and courtship call. These discrepancies could be attributed to the life stages over which diet was manipulated. In most cases, diet is changed only when adulthood is reached and there are few studies looking at the effects of diet during development. This might have led to the lack of condition-dependence that was found in previous studies examining courtship call in other species of crickets.

With most studies focusing on a single call type or manipulation during a single life stage (e.g. Harrison et al., 2013; Wagner & Hoback, 1999), the overall effects of diet across life-stages and across call types are poorly understood. Further, no previous studies have looked at how nutritional content of diet during **both** the developmental and post-developmental stages impact advertisement, aggression, and courtship call in *A. domesticus*. By considering the developmental diet, the adult diet, and all three call types simultaneously, a better understanding can be had of whether call structure is condition-dependent and whether any of the calls function as honest signals. Moreover, the relationships among these different types of calls, and their constituent components, is poorly understood.

The relationships among the call types, i.e. the pattern of phenotypic integration (Pigliucci, 2003), has important implications for how calls might be interpreted by receivers. For example, high integration among call types would also suggest high degree of redundancy in the information provided by each call type and explain a form of signal redundancy. Alternatively, if call types show low patterns of integration, this suggest that each call type provides the receiver with different information on the emitter and would explain a form of the multiple-message hypothesis (Moller & Pomiankowski, 1993). A number of hypotheses examining how various

call types or call components (i.e. aggressive calls versus advertisement calls) might be related can be proposed. For example, the “multiple message” hypothesis states that each signal — advertisement, aggression, or courtship — reflects unique aspects of a male’s quality (Moller & Pomiankowski, 1993). If two signals are uncorrelated, this would lend support to the “multiple message” hypothesis since the uncorrelated signals would be providing separate measurements of one’s quality. Another signaling hypothesis, the “redundant signal” hypothesis, states that signals convey redundant, shared information to the receiver (Johnstone, 1996). As a modification of the redundant signal hypothesis, individuals might have a general calling phenotype which causally influences each of the three call types. Moreover, this general calling phenotype may represent an honest signal, providing accurate information about condition (e.g. mass) to a receiver (Berglund, Bisazza, & Pilastro, 1996; Schluter & Price, 1993; Zahavi, 1975). Given that advertisement, aggression, and courtship calls have generally been studied in isolation, which of these—or other—hypotheses describing phenotypic integration and modularity of calling has not been previously tested.

Here, we tested the following questions:

- 1) How does diet manipulation during both the developmental and adult life stages impact advertisement, courtship and aggression call structure in *Acheta domesticus*?
- 2) How do components of advertising, courtship and aggression calls vary among individuals?
- 3) Do advertising, courtship and aggression call types and their components covary such that they’re providing multiple, redundant, or otherwise structured information?

## Methods

### Diet and Rearing

Male nymph *A. domesticus* (obtained from Fluker's Cricket Farm, Louisiana) were reared on one of two different diet treatments: either a high (HQ, 46% Protein, 11% Lipid, 23% Carbohydrate and 3% non-nutritive cellulose, with 1.12 cal/g) or low (LQ, 15.33% Protein, 3.66% Lipid, 7.66% Carbohydrate and 65% non-nutritive cellulose with 3.35 cal/g) quality diet. The high percentage of non-nutritive cellulose in the low-quality diet should have imposed a gut limitation on individual crickets such that they should not have been able to overcome the relative energy differences by simply eating more (Royaute & Dochtermann, 2017). Upon reaching sexual maturity, individuals were either switched to the other diet type or maintained on the same diet. This resulted in a  $2 \times 2$  factorial design crossing life-stage (immature or mature) and diet type (low or high quality) with 39 individuals in the HQHQ, 30 individuals in HQLQ, 29 individuals in LQHQ, and 29 in LQLQ.

Immature crickets were reared in plastic containers with each plastic container (34.6 x 21 x 12.4 cm) containing around 10 nymphal crickets with a 12:12 hr light cycle and maintained at 32° C. Juvenile crickets were provided with egg carton housing and food and water *ad libitum*. Once crickets reached maturity, they were moved into individual containers (0.71-L) and fed their assigned diet and water *ad libitum*. Mature crickets were kept at a 12:12 hr light cycle at 25° C

### Call Recording

For each mature individual cricket, we measured advertisement, courtship and aggression call (Table A1), with a total of 930 calling trials. For the 127 total crickets, most individuals were

recorded repeatedly on each of the three call types though, due to natural mortality, some call types were recorded more frequently than others (Table A1).

To record advertisement calls, housing containers were surrounded by acoustic foam and USB audio recorders were placed in each individual container for 2 hours. Because females are not necessary to elicit advertisement calls (personal observation), males called over this period without a female cricket in the container. We attempted to measure each individual's advertisement call 3 separate times.

To record courtship calls, a female cricket must be present with the male. Following Zuk et al. (2008), male crickets were introduced into a container the same size as those used for housing but only containing a USB audio recorder and a random live female. The females used in courtship trials were raised on a generic chick feed diet and were obtained from our laboratory stock collection, so mating status was unknown. Courtship call was then recorded for a period of 5-10 minutes. If a male failed to call within the first 5 minutes of the trial, the trial was stopped and the male was removed and recorded as not calling. If a female attempted to copulate with (mounted) the focal male during the trial, recording was also stopped and mating was not allowed to be completed to avoid carryover effects of successful matings. All courtship calls were conducted at least 48 hours after the final advertisement calls had been recorded since potential contact with a female could alter the male's long range calling effort.

To record aggressive calls, we followed a similar procedure to the courtship trials. Focal males were placed in a novel container with a random male (muted by having its forewings removed). A pilot study showed that *A. domesticus* will aggressively call towards the rival male without a female present as a stimulus, so females were not used to elicit aggressive calls. Aggressive calls were recorded for 5-10 minutes. Trials were ended when there was a clear



winner or one cricket retreated. If a male failed to call within the first 5 minutes of the trial, the trial was stopped and the male was removed and recorded as not calling and tested again at a later date.

### **Call Analysis**

We characterized call structure according to the following 7 components: the total time spent calling within a trial (s), the call's amplitude (m) and peak frequency (kHz), the rate and duration of chirps (s), and the rate and number of pulses per chirp. Peak frequency, defined as the frequency of the peak of greatest amplitude within the call was calculated using the call amplitude spectra (Grace & Anderson, 2015). Sound analysis was performed using Audacity and Avisoft and all measurements were averaged in order to return a single value per call component within a trial. We expect each of these components to scale positively with energy expenditure. Therefore, if these call components are representative of an "honest signal", higher values for any of these components should be indicative of males of higher quality (i.e. higher body mass).

For advertisement calls, we used the aforementioned software to analyze the middle forty-five minutes of each recording. Courtship calls were more difficult to analyze, as males would randomly produce advertisement calls during courtship. To properly analyze courtship call, only sections of the courtship trial recordings that were exclusively courtship were analyzed. There is a visible difference in call type structure between courtship and advertisement calls (Figure 1.2). A similar issue was encountered with aggression call, but aggression call is easily distinguished based on call waveforms (Figure 1.2).

## **Statistical Analysis**

### ***Effects of Diet on Call Components***

To analyze how diet treatment affected each call component, we used univariate linear mixed models for all 21 extracted call components using the lme4 package for mixed effect models (Bates, Machler, Bolker, & Walker, 2015) in the R statistical language. Diet treatment (developmental diet, adult diet and the interaction between the two), temperature, repetition number, batch, time of recording, and day since diet switch were included as fixed explanatory variables. Focal male identity along with developmental box ID (the box used in the growth chamber) were included as random factors for all call types (Dingemanse & Dochtermann, 2013). For the analysis of advertisement call components, the chamber in which the male was recorded was also included as a random factor. For the analysis of courtship and aggressive call components, the female receiver ID or male opponent ID were added as random factors.

### ***Repeatability by Call Type***

We estimated both adjusted and unadjusted repeatabilities as well as the variation due to all random and fixed effects for each call component using the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017) in the R statistical language. Adjusted repeatability is calculated as the proportion of among individual variation ( $V_I$ ) over the variation at the among and within-individual level ( $V_I + V_W$ ). Unadjusted repeatability is calculated as the proportion of among individual variation ( $V_I$ ) over the variation at the among and within-individual level ( $V_I + V_W$ ) including the variation due to fixed effects ( $V_{\text{Fixed}}$ ).

### ***Tests of Phenotypic Integration***

To test competing hypotheses of phenotypic integration we first estimated among- and within-individual covariance/correlation matrices with a multi-response mixed effects model

(Dingemanse, Dochtermann, & Nakagawa, 2012) for the 9 call components that exhibited the highest repeatabilities (and commonly used in calling literature) from our univariate models (Table A3) along with mass. Diet treatment (developmental diet, adult diet and the interaction between the two), temperature, repetition number, batch, time of recording, and day since diet switch were included as explanatory variables and focal male identity was included as a random factor. The 10 response variables were mean and variance standardized to facilitate model fitting. The multi-response mixed effect model was fit using the MCMCglmm package (Hadfield, 2010) in the R statistical language. The model was fit with an MCMC chain with  $1.3 \times 10^6$  iterations, a 300000 burn-in period, and a thinning interval of 1000 and a prior that was flat for correlations. “Significance” of any particular correlation was based on whether its 95% credibility interval overlapped zero.

The estimated among-individual correlation matrix was then used to test the fit of structural equation models (SEMs) to the data (the MCMC analyses produced 1000 estimates of the correlation matrix). SEMs combined with Akaike Information Criteria (AIC) based model comparison approaches allow the testing of specific hypothesis of trait integration (Araya-Ajoy & Dingemanse, 2014; Dingemanse, Dochtermann, & Wright, 2010; Dochtermann & Jenkins, 2007). Here nine *a priori* structural equation models of trait integration were compared (Figure 1.3):

*Model 1.* Silly Null, all call components are uncorrelated.

*Models 2-3.* Two versions of the “Redundant Signal Hypothesis” wherein signals are providing equivalent information to the listener. In Model 2, Advertisement and Courtship signals are providing females with redundant information about size and quality and Advertisement and Aggression calls are providing males with redundant information about size

and quality (Figure 1.3B, paths a and b are active). In Model 3, Courtship and Aggression call are also providing redundant information to the listener (Bertram & Rook, 2012) (Figure 1.3B, paths a, b and c are active).

*Model 4. Multiple-Messages Hypothesis:* all three call types are providing different but complementary information to listening conspecifics (Harrison et al., 2013; Moller & Pomiankowski, 1993). The three call types are uncorrelated in this model (Figure 1.3B, no paths active).

*Model 5. Short Range Calling:* both courtship and aggression will be correlated due to the short range that each call travels (Figure 1.3B, path c is active).

*Model 6. Honest Signaling:* All three call types causally stem from an underlying calling syndrome or phenotype, implying some signal redundancy. However, each call type still exhibits modularity (e.g. components of aggression calls are more closely related to other components of aggression calls than to components of advertisement calls (Holzer et al., 2003; Wagner & Hoback, 1999)). This underlying calling structure is causally affected by mass (Figure 1.3C, path a is active) and so downstream call components are honest signals of mass.

*Model 7. Calling Syndrome:* All three call types causally stem from an underlying calling structure a larger calling syndrome or phenotype. However, mass does not affect calling structure (Figure 1.3C, path a is not active), i.e. calls do not honestly signal mass.

*Models 8. Full Integration:* All of the calling components stem from a single underlying calling phenotype, with no modularity within the three call types (Figure 1.3D, no paths active).

*Models 9. Full Integration with Honest Signaling:* All of the calling components stem from a single underlying calling phenotype which is causally affected by mass (Figure 1.3D, path a is active).

The among-individual correlations were fit to these *a priori* models using the lavaan package in R and the ability of each model to explain the pattern of correlations compared based on differences of AIC values among models ( $\Delta\text{AIC}$ ) (Dingemanse et al., 2010; Dochtermann & Jenkins, 2007). Because we estimated among-individual correlations using a Markov Chain Monte Carlo approach, we had 1000 estimates of the correlation matrix. Following Araya-Ajoy and Dingemanse (2014) the SEM models were fit to each of the 1000 estimated correlation matrices and so we also had 1000 estimates of the AIC and  $\Delta\text{AIC}$  values of each model. Therefore, the model with a  $\Delta\text{AIC}$  whose posterior mode was closest to zero was ranked as the overall best model. Because there was also an estimated uncertainty around these  $\Delta\text{AIC}$  values we also considered how often a particular model was ranked as best (i.e.  $\Delta\text{AIC} = 0$ ) or could not be distinguished from the best model (i.e.  $\Delta\text{AIC} \leq 2$ ). “Significance” of any particular correlation was based on whether its 95% credibility interval overlapped zero.

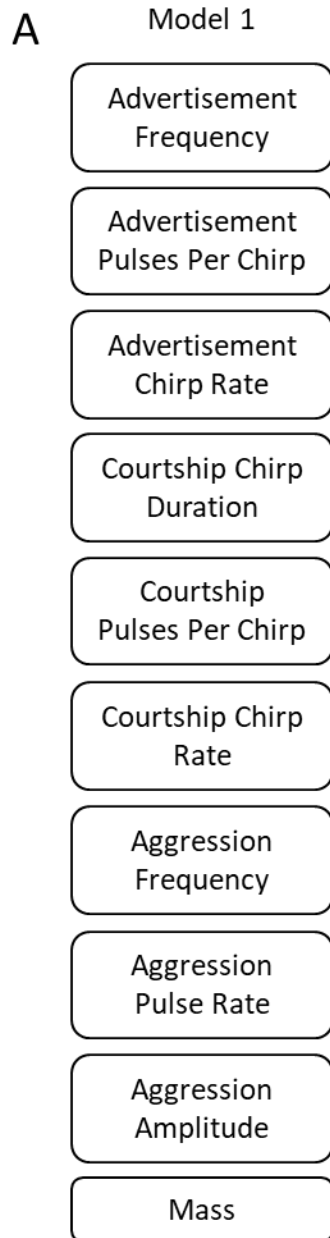


Figure 1.3. Visual representations of the Models 1-9. Models are described in the text. Model comparison results are given in Table 3. Single arrows represent causal relationships between a latent variable and call components. Bidirectional arrows represent an undefined correlation between call components. Paths 'a' and 'b' are active in Model 2. Paths 'a', 'b' and 'c' are active in Model 3; Path 'c' is active in Model 5; Path 'a' is active in Models 6 and 9.

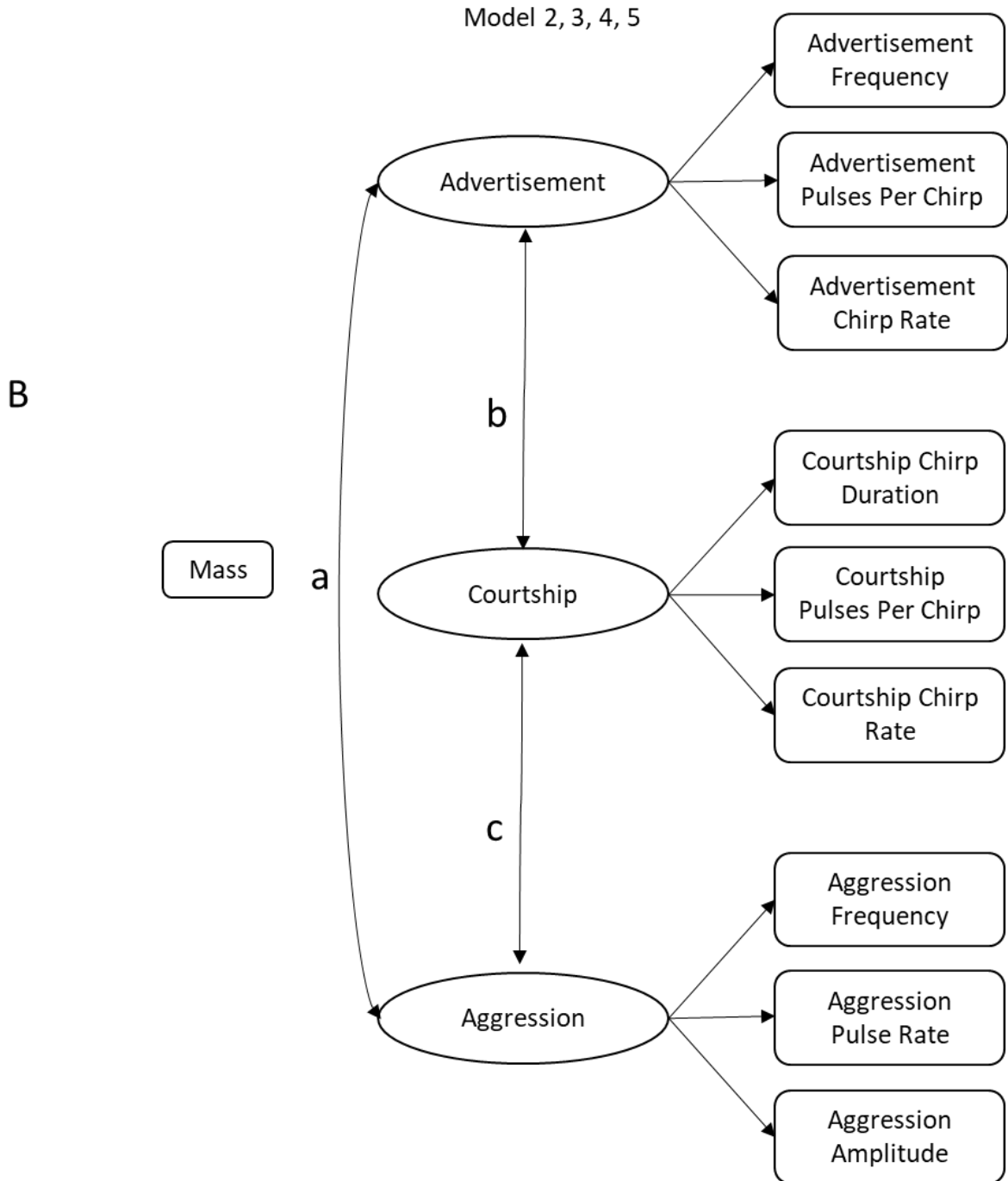


Figure 1.3. Visual representations of the Models 1-9 (continued). Models are described in the text. Model comparison results are given in Table 3. Single arrows represent causal relationships between a latent variable and call components. Bidirectional arrows represent an undefined correlation between call components. Paths 'a' and 'b' are active in Model 2. Paths 'a', 'b' and 'c' are active in Model 3; Path 'c' is active in Model 5; Path 'a' is active in Models 6 and 9.

C

Model 6, 7

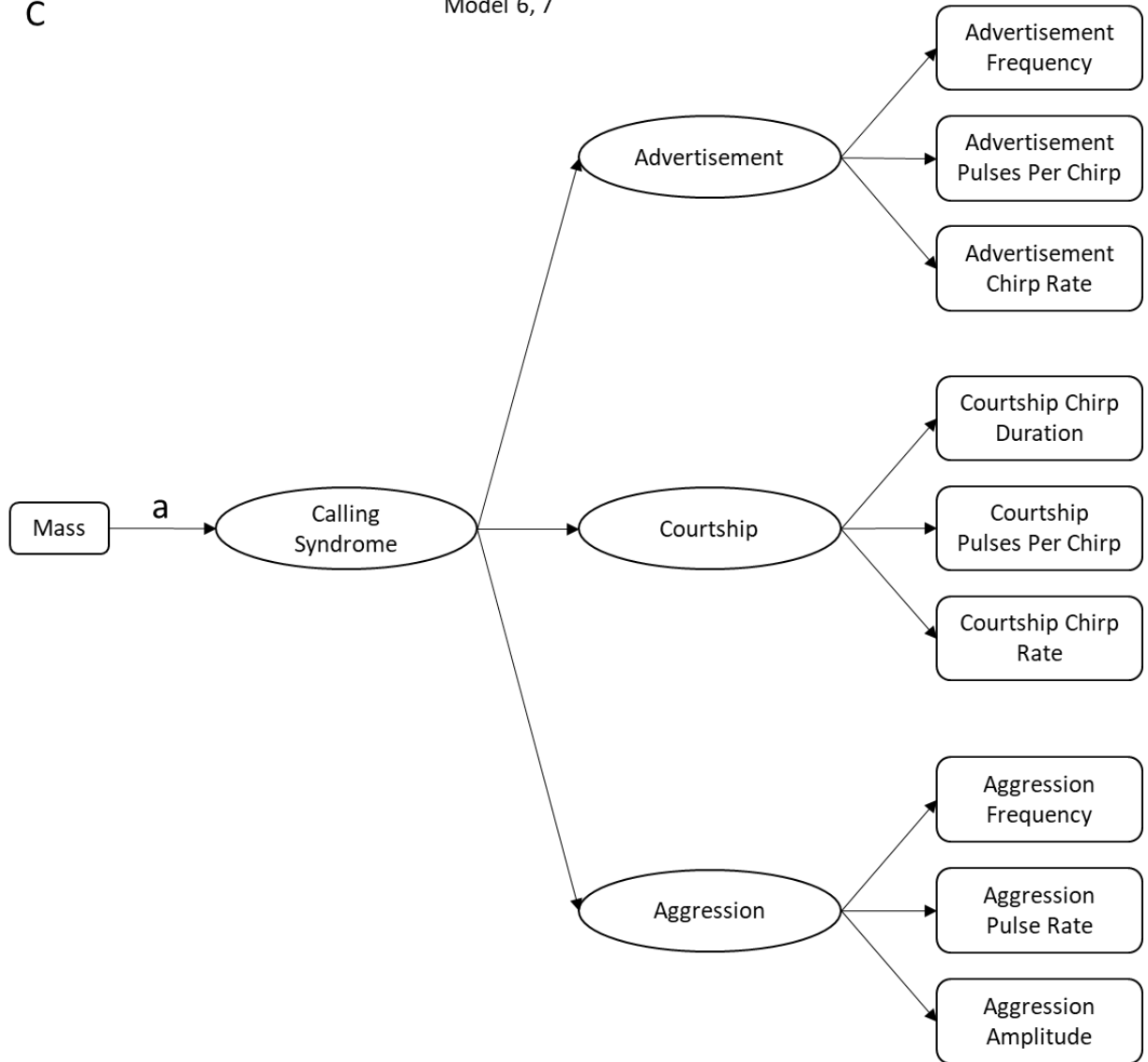


Figure 1.3. Visual representations of the Models 1-9 (continued). Models are described in the text. Model comparison results are given in Table 3. Single arrows represent causal relationships between a latent variable and call components. Bidirectional arrows represent an undefined correlation between call components. Paths 'a' and 'b' are active in Model 2. Paths 'a', 'b' and 'c' are active in Model 3; Path 'c' is active in Model 5; Path 'a' is active in Models 6 and 9.



D

Model 8, 9

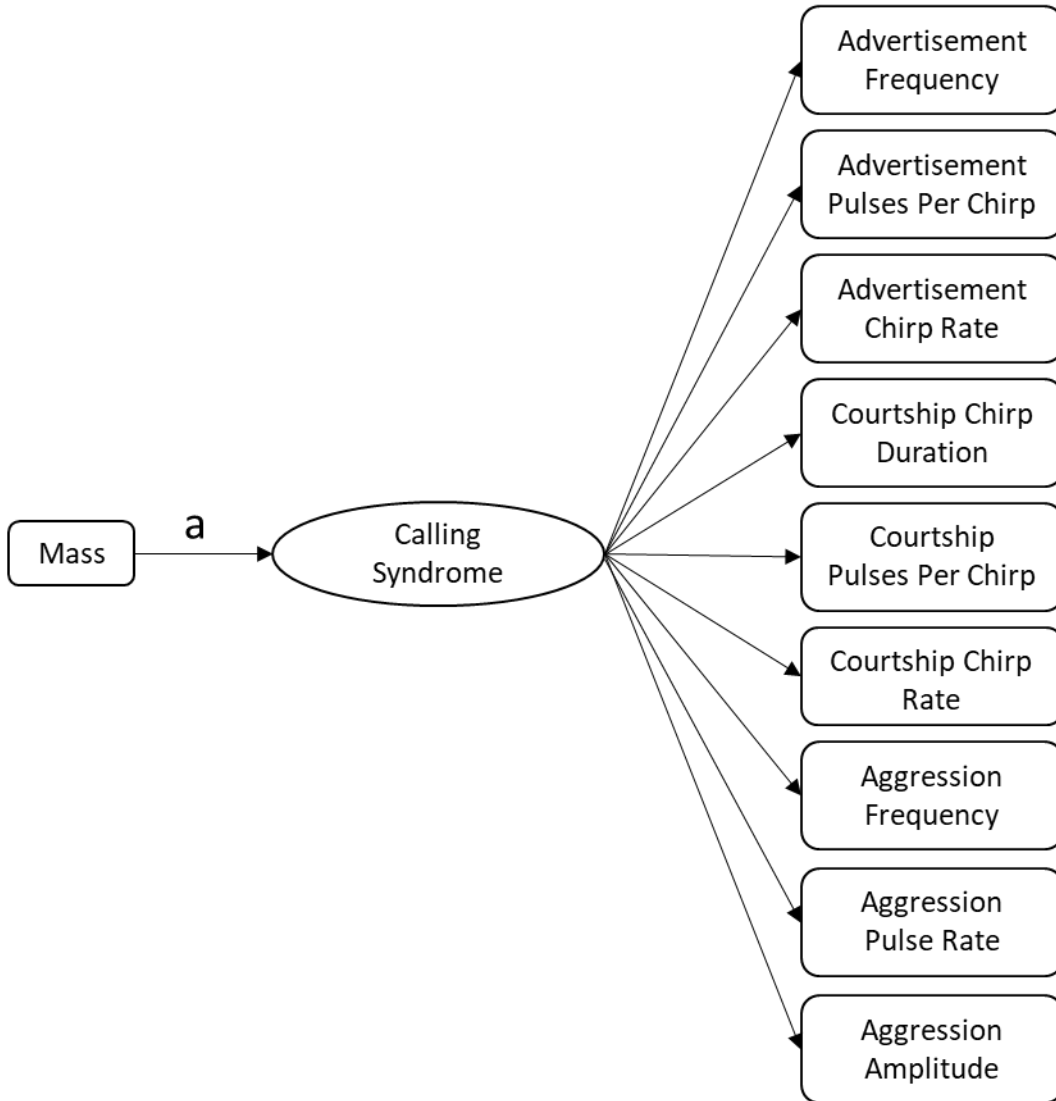


Figure 1.3. Visual representations of the Models 1-9 (continued). Models are described in the text. Model comparison results are given in Table 3. Single arrows represent causal relationships between a latent variable and call components. Bidirectional arrows represent an undefined correlation between call components. Paths 'a' and 'b' are active in Model 2. Paths 'a', 'b' and 'c' are active in Model 3; Path 'c' is active in Model 5; Path 'a' is active in Models 6 and 9

## Results

### Effects of Diet on Call Components

Average mass at adult emergence for the low-quality developmental diet males was not significantly different from that of the high-quality developmental diet males ( $t = 1.036$ ,  $df =$

117.7,  $p = 0.305$ ) (Figure A1A). However, individuals from the low-quality developmental diet matured more slowly compared to individuals from the high-quality developmental diets ( $t = -2.152$ ,  $df = 115.6$ ,  $p = 0.03$ ) (Figure A1B).

Developmental diet, adult diet, or the interaction of the two diets, rarely affected the call structure or production of any call type, apart from advertisement chirp rate ( $F_{1,82.1}=5.05$ ,  $p=0.03$ ) and advertisement amplitude ( $F_{1,86.3}=4.23$ ,  $p=0.04$ ) (Table A2). However, due to the total number of effects analyzed, these two instances were no longer significant after correcting for multiple testing. While temperature and batch number often and significantly influenced call components, most fixed effects did not have a detectable impact on the measured call components (Table A2).

### **Repeatability by Call Type**

All advertisement call components were moderately to highly repeatable with peak frequency having the highest repeatability ( $\tau = 0.58$ ) (Table 1.1). Aggression calls were moderately repeatable as well with peak frequency once again having the highest repeatability ( $\tau = 0.48$ ) (Table 1.1). Contrary to advertisement and aggression call components, courtship call components were generally low to moderately repeatable, with only pulses per chirp ( $\tau = 0.30$ ), chirp duration ( $\tau = 0.30$ ) and chirp rate ( $\tau = 0.38$ ), exhibiting repeatabilities above 0.1 (Table A3). The call components used for the subsequent analysis for each call type were: Advertisement – frequency, pulses per chirp and chirp rate, Aggression – frequency, pulse rate, amplitude, Courtship – pulses per chirp, chirp duration and chirp rate (Table 1.1). Neither Chamber or Box contributed substantial variation to any of the call components measured (Table A3). Female identity also did not explain a large proportion of the variation present in courtship call components, never explaining more than seven percent of the variation present (Table A3). In

contrast to courtship call, the rival male present did explain a modest proportion of the variation present in aggression call components (Table A3).

### **Structural Equation Models**

Courtship calls had a higher number of significant among-individual correlations compared to the other call types (Table 1.2). Significant within-individual correlations were present across all three call types (Table 1.2).

The best fit model corresponded to an Honest Signals hypothesis (Model 6), with the Calling Syndrome hypothesis (Model 7) also showing a fit within 2 AIC values of the model over a third of the time (Table 1.3, Figure 1.4). The only difference between Model 6 and 7 lies in whether size has a causal effect on call structure, as expected according to the honest signaling hypothesis. Overall, the strengths of the paths from the overarching syndrome structure to the latent variables for all call types were very similar in each model. In both models, all components of advertisement and courtship call had high loadings on their respective latent variable. In contrast, aggression call structure was mostly explained by call frequency with little additional information provided by pulse rate and call amplitude. In addition, the path coefficient for courtship call on the overall calling syndrome latent variable was substantially weaker than for advertisement and aggression calls. This suggests that courtship calls provide additional information not shared by either advertisement or aggression calls (Figure 1.4).

While the general structure of the Honest Signals model was most well supported (Table 1.3), it is particularly noteworthy that the relationship between mass and the underlying “Calling Syndrome” was negative (estimate = -0.245, se = 0.119, ci = (-0.477, -0.012)) (Figure 1.4). As a result, the relationship between mass and, for example, advertisement and aggression frequencies

were likewise negative (Figure 1.4). This is consistent with the pattern observed for among-individual correlations (Table 1.2).

Table 1.1. Repeatabilities from univariate models for the traits chosen for the multi-response mixed-effects model with 95% confidence intervals

	$\tau_1^a$	$\tau_2^b$
<b>Advert Frequency</b>	0.58 (0.45, 0.7)	0.38 (0.25, 0.50)
<b>Advert Pulses per Chirp</b>	0.46 (0.29, 0.60)	0.39 (0.24, 0.52)
<b>Advert Chirp Rate</b>	0.42 (0.27, 0.59)	0.36 (0.22, 0.49)
<b>Aggression Frequency</b>	0.39 (0.23, 0.54)	0.28 (0.15, 0.41)
<b>Aggression Pulse Rate</b>	0.31 (0.16, 0.50)	0.28 (0.14, 0.44)
<b>Aggression Amplitude</b>	0.22 (0.09, 0.42)	0.17 (0.07, 0.31)
<b>Courtship Pulses per Chirp</b>	0.32 (0.13, 0.55)	0.29 (0.10, 0.48)
<b>Courtship Chirp Duration</b>	0.32 (0.13, 0.55)	0.29 (0.10, 0.48)
<b>Courtship Chirp Rate</b>	0.29 (0.1, 0.53)	0.27 (0.07, 0.47)

a – adjusted repeatability, calculated as  $V_I/V_I + V_W$ ; b – unadjusted repeatability, calculated by  $V_I/V_I + V_W + V_{Fixed}$

Table 1.2. Among and within-individual correlations, along with repeatabilities, as estimated by a multi-response mixed effects model. Among-individual correlations are above the diagonal, within-individual correlations are below the diagonal, with repeatabilities (calculated from the multi-response model rather than the univariate models of Table 1.1) shown on the diagonal. Shaded within-individual correlations are inestimable and overlap with zero. 95% credibility intervals for repeatabilities are reported along the diagonal. Bold values are the among- and within-individual correlations whose 95% credibility intervals did not overlap zero.

	Advert_FQ	Advert_PC	Advert_CR	Court_CD	Court_PC	Court_CR	Agg_FQ	Agg_PR	Agg_Amp	Mass
Advert_FQ	0.64 (0.53-0.73)	-0.09	0.09	-0.09	-0.13	0.14	<b>0.41</b>	0.00	-0.12	-0.18
Advert_PC	0.12	0.50 (0.39-0.62)	<b>-0.58</b>	0.24	0.16	-0.23	-0.08	-0.06	0.21	0.09
Advert_CR	<b>-0.17</b>	<b>-0.71</b>	0.58 (0.42-0.73)	-0.20	-0.22	<b>0.30</b>	0.21	0.25	-0.28	-0.21
Court_CD				0.47 (0.32-0.60)	<b>0.62</b>	<b>-0.48</b>	-0.03	<b>-0.33</b>	0.21	0.15
Court_PC				<b>0.81</b>	0.48 (0.34-0.61)	<b>-0.41</b>	0.00	-0.27	0.22	0.08
Court_CR				<b>-0.54</b>	<b>-0.49</b>	0.48 (0.34-0.63)	0.10	0.18	-0.14	-0.19
Agg_FQ							0.53 (0.39-0.63)	-0.09	0.05	-0.13

Table 1.2. Among and within-individual correlations, along with repeatabilities, as estimated by a multi-response mixed effects model (continued). Among-individual correlations are above the diagonal, within-individual correlations are below the diagonal, with repeatabilities (calculated from the multi-response model rather than the univariate models of Table 1.1) shown on the diagonal. Shaded within-individual correlations are inestimable and overlap with zero. 95% credibility intervals for repeatabilities are reported along the diagonal. Bold values are the among- and within-individual correlations whose 95% credibility intervals did not overlap zero.

	Advert_FQ	Advert_PC	Advert_CR	Court_CD	Court_PC	Court_CR	Agg_FQ	Agg_PR	Agg_Amp	Mass
Agg_PR							<b>-0.24</b>	0.45 (0.35- 0.62)	-0.29	-0.11
Agg_Amp							<b>0.42</b>	<b>-0.27</b>	0.45 (0.32- 0.55)	0.20
Mass										0.48 (0.35- 0.68)

FQ - frequency, PC – pulses per chirp, CR – chirp rate, CD – chirp duration, PR – pulse rate, Amp - amplitude

Table 1.3. Posterior modal estimates for AIC and  $\Delta$ AIC values for each model and the number of MCMC posterior samples for which a particular model was the best fitting ( $\Delta$ AIC = 0) and or within  $\Delta$ AIC  $\leq$  2 from the best fitting model.

Model	Model Rank	AIC	$\Delta$ AIC	AIC = 0	AIC $\leq$ 2
Silly Null (Model 1)	9	2848	148	0	0
Redundant Signals (Model 2)	5	2725	25	50	84
Redundant Signals 2 (Model 3)	3	2718	18	129	224
Multiple-Messages (Model 4)	6	2733	33	8	15
Short Range Calling (Model 5)	4	2721	21	62	107
<b>Honest Signals (Model 6)</b>	<b>1</b>	<b>2704</b>	<b>3</b>	<b>545</b>	<b>775</b>
Calling Syndrome (Model 7)	2	2709	9	186	363
Full Integration (Model 8)	7	2734	34	11	30
Full Integration 2 (Model 9)	8	2735	35	9	29

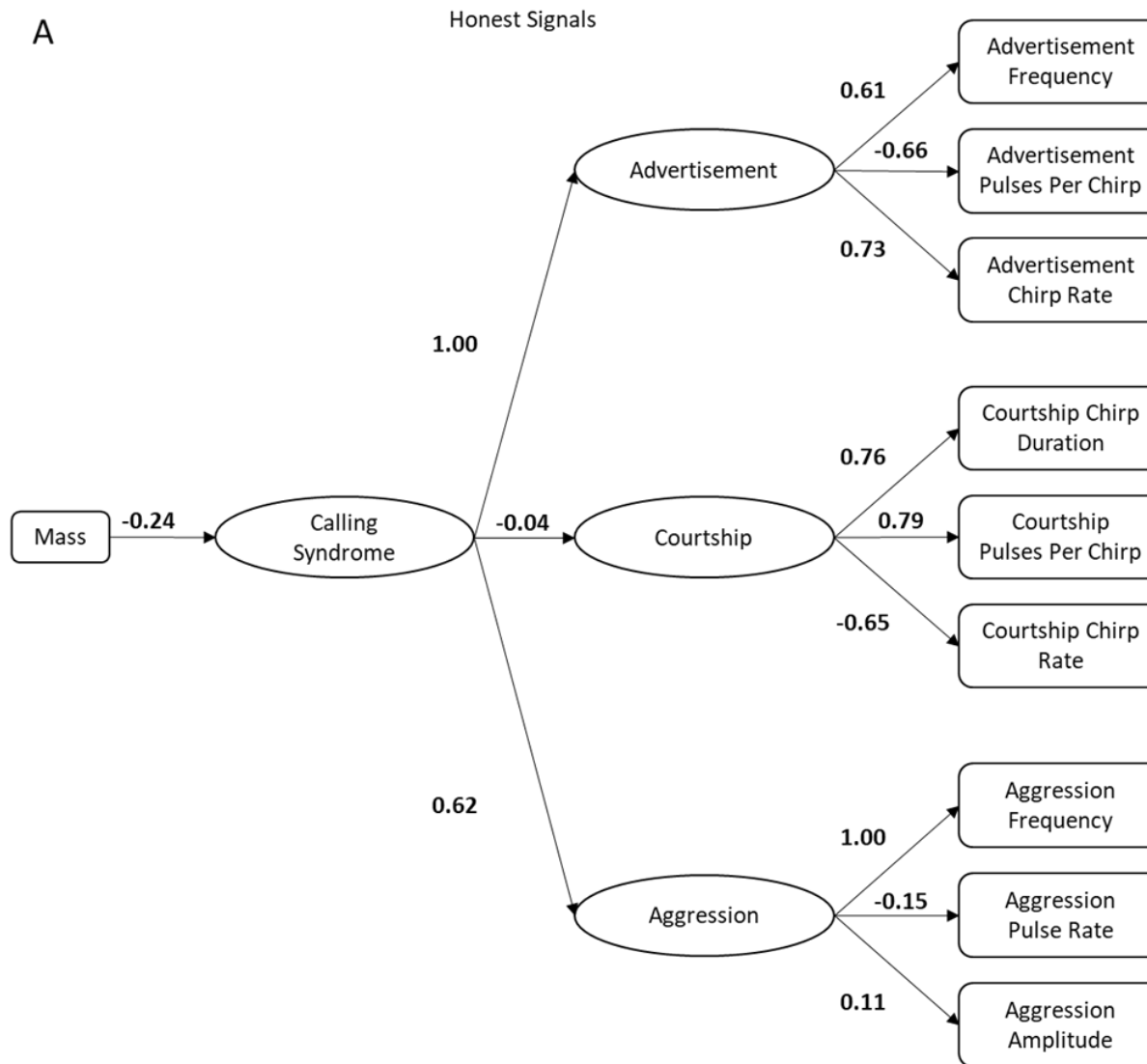


Figure 1.4. Structural equation model parameter estimates of the Honest Signals Model and the Calling Syndrome Model.



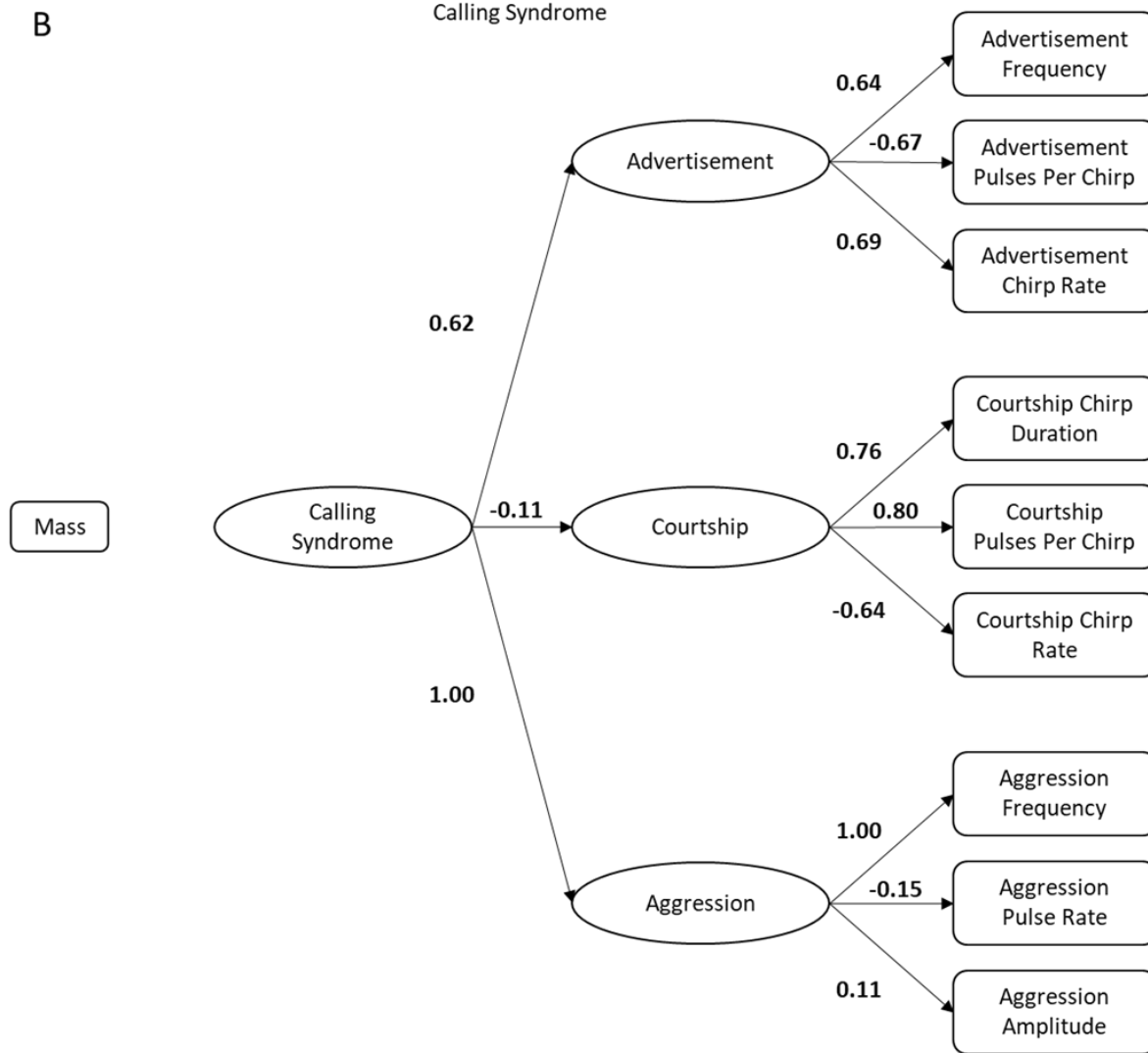


Figure 1.4. Structural equation model parameter estimates of the Honest Signals Model and the Calling Syndrome Model (continued).

## Discussion

In contrast to previous studies (Holzer et al., 2003; Hunt et al., 2004; Wagner & Hoback, 1999), we found that advertisement calls in *Acheta domesticus* did not seem to be condition dependent in that they were not affected by diet treatment. Similar to what was found by Harrison et al. (2013), courtship call was also not affected by diet treatment and so perhaps condition independent. Larger mass has previously been shown to be preferred by females (Gray, 1997) and one of the main predictors of male quality (Bertram & Rook, 2012; Hack, 1998; Harrison et al., 2013). Since our developmental treatments did not produce significantly different weights at maturity (Figure A2), our experimental males may have ultimately been equal in quality, explaining the lack of dietary effects on call components even if calls were honestly signaling quality. Despite the lack of differences in adult mass (Figure A2), males in the low-quality diet took, on average, 2 days longer to mature compared to the high-quality individuals (Figure A2). This potentially suggests compensatory growth, and low-quality diet crickets should still have had less energy to invest in calling. The lack of a difference among treatments in mass as adults is surprising as these experimental diets have previously been shown to affect growth trajectories of *A. domesticus* nymphs (Royaute & Dochtermann, 2017). Nonetheless, since our experimental males did not significantly differ in size, the absence of diet effects on call components is perhaps not surprising.

Many of the call components exhibited repeatabilities greater than the average reported for behaviors ( $\tau = 0.37$ , (Bell, Hankison, & Laskowski, 2009)). In particular, much of the variance in advertisement call was explained by individual identity, implying that advertisement call is a reliable indicator of caller identity (Tables 1.1 and A3). Interestingly, courtship call components were not substantially influenced by female receiver identity (Table A3). In other

words, male calling behavior was not affected by the identity of the female being courted.

Within-individual variation was high for all courtship call components (Table A3) which, along with the findings of Harrison et al. (2013), suggests that we still know little about what courtship is communicating to females and suggests that further exploration is needed regarding other signaling hypotheses.

In contrast to what was observed for female receiver identity during courtship calls, for aggression call components rival male substantially influenced the variation of aggression call type for both aggression amplitude and aggression frequency (Table A3). This makes intuitive sense: a higher quality opponent may deter a lower quality male from producing a strong call. These findings also align with previous research of indirect genetic effects on aggression in other gryllid species (Santostefano, Wilson, Araya-Ajoy, & Dingemanse, 2016; Santostefano, Wilson, Niemela, & Dingemanse, 2017).

Including the causal effect of mass (Model 6) on calling syndrome led to the best fit of all models (Table 1.3, Figure 1.3A). However, this was not the effect that was expected if the overarching call structure is honest, as mass seems to be negatively influencing call components.

While the only difference in the two best fit models (Models 6 and 7) lies in whether or not mass has a causal effect on overall structure, we can say (regardless of the inclusion of mass), that our results are indicative of an overarching calling syndrome from which the three individual call types stem, as suggested previously (Bertram & Rook, 2012; Holzer et al., 2003; Wagner & Hoback, 1999). The presence of an overall calling syndrome also suggests that all three call types are part of a redundant signal strategy for *Acheta domesticus* (Bertram & Rook, 2012; Harrison et al., 2013), i.e. one call type will provide the similar information to a listener as will another call type. The strong link between advertisement and aggression to the overall

Calling Syndrome in the two best fit models (Figure 1.3) indicates that advertisement and aggression are indeed providing similar information about males (Bertram & Rook, 2012). The overall tested structure suggests support for signal redundancy but that the particular components of a call type are more strongly related to each other than across call types. Meanwhile the call types differ in the strength of association with the calling syndrome and thus level of integration (courtship being the least integrated). As discussed by Royauté et al (2015), phenotypic integration can occur in a module capacity, or integration can exist within modularity, due to shared developmental pathways or functions (Royauté et al., 2015). A high level of integration means selection on one trait will also have repercussion on all other traits. For example, our high levels of integration between advertisement and aggression calls would suggest that selection on advertisement frequency would influence all other components of both advertisement and aggression calls. Alternatively, a more modular structure means that each call component is capable of independent evolutionary trajectories. The lack of association with courtship calls and the overarching calling syndrome may suggest that the call components measured for courtship calls are capable of evolving differently (Royauté et al., 2015).

This study found little treatment effects on any call components, but further investigation of call integration suggest that all three call types are best explained as stemming from an overarching calling syndrome, suggesting that there is redundant signaling in *Acheta domesticus*. This overarching syndrome is also influenced by mass, but not as would be expected under honest signaling. While diet quality along with the stage the diet was manipulated did not alter call structure for any call type, the information provided by the structural equation models gives us valuable insight regarding sexual signals in *Acheta domesticus*.

## **CHAPTER 2: PARENTS DO KNOW BEST: EVIDENCE FOR TRANS- GENERATIONAL EFFECTS ON OFFSPRING BEHAVIOR**

### **Abstract**

The non-genetic influence of parents on offspring phenotypes, i.e. trans-generational effects (TGEs), have been of increasing interest in behavioral ecology over the past 15 years due to their potential to alter fitness of both parents and offspring. In other areas of evolutionary ecology, the overall strength of these effects has been assessed via meta-analysis for other classes of traits but behavior has not been quantitatively reviewed. Here, we asked the question: What is the magnitude of TGEs on offspring behavior? We conducted a meta-analysis of 61 articles and 327 estimates testing the effect of parental manipulation on offspring behavior. Overall, TGEs on behavior were found to be of large strength (Hedge's  $g = 0.64$  SE=0.10). Besides identifying a large overall effect size, we also found a significantly greater effect of TGEs on the behavior of female versus male offspring ( $F_{2,183} = 10.01$ ,  $p < 0.001$ ). While we found evidence for a large effect of TGEs on offspring behavior, the magnitude of TGEs was surprisingly homogenous across biological categories with fixed effects explaining only 8% of the variation in the dataset. Neither taxonomic class nor any other included biological factor substantively influenced the strength of TGEs, however, our results suggest that behavior is similarly influenced by TGEs compared to other offspring traits.

### **Introduction**

Altering phenotypes in response to environmental conditions or information, i.e. phenotypic plasticity, changes and produces variation in fitness (Ghalambor, McKay, Carroll, & Reznick, 2007; Stearns, 1989). In variable environments parents might gain a fitness benefit by providing offspring with information about their future environment if this information alters the

offspring's phenotype (Marshall & Uller, 2007; Mousseau & Fox, 1998). A trans-generational effect (TGE), or the influence that parental environmental conditions have on offspring phenotypes, is therefore parentally induced plasticity in offspring that can lead to variation in fitness for both parents and offspring (Mousseau & Fox, 1998). Because of these fitness effects and their role as a source of non-genetic inheritance, TGEs are of increasing interest to evolutionary ecologists and their quantification has been a key goal of research over the last 15 years.

TGEs can be broadly categorized into the following four classes (following Marshall and Uller (2007)):

- 1) Anticipatory TGEs, where parents increase their fitness by increasing offspring fitness. Specifically, parents adjust offspring phenotypes based on their current conditions, typically under temporal or spatial heterogeneity. Examples of anticipatory TGEs include inducing resource preferences in offspring (Bentz, Navara, & Siefferman, 2013) or priming offspring to increase responsiveness to cues of predator presence when mothers have previously been attacked (Storm & Lima, 2010).
- 2) Selfish TGEs, where parents increase their fitness at the expense of their offspring's fitness. Parents will trade offspring quality or performance for quantity (Marshall & Uller, 2007). These types of effects often occur when mothers can reproduce repeatedly or the mother could potentially have more successful future reproduction attempts (Marshall & Uller, 2007). An example of this class of TGE would be when a parent reduces the size of offspring when mating with lower quality mates (Uller, Nakagawa, & English, 2013).

- 3) Bet-hedging TGEs, where parents reduce the variation in their fitness by producing a range of offspring phenotypes, and this usually occurs when the environment is unpredictable. If the future environment is unpredictable, producing a variety in offspring sizes compared to one offspring size may give the parent a higher likelihood of success (Marshall & Uller, 2007).
- 4) Transmissive TGEs, reduce both parental and offspring fitness, and occurs when some sort of environmental variation negatively impacts both offspring and parent, even though there is no benefit to either the parent or offspring (Marshall & Uller, 2007).

Transmissive TGEs include when parents transmit pathogens to offspring and there is a low likelihood of survival (Marshall & Uller, 2007).

Due to the fitness-affecting potential and adaptive significance of TGEs (Bentz et al., 2013; Marshall & Uller, 2007; Mousseau & Fox, 1998) it is not surprising that many previous studies have examined how various traits are influenced by TGEs (Champagne & Meaney, 2008; Forstmeier, Coltman, & Birkhead, 2004; Krist, 2011; Lagisz et al., 2015; Reinhold, 2002; Uller et al., 2013). Generally, TGEs on non-behavioral traits have a weak effect on offspring fitness (Uller et al., 2013). However, this conclusion is based on testing one specific anticipatory trans-generational effect hypothesis: whether offspring perform better when their environment matched that of their parents versus environmental mismatch (altering the environment “predictability” for the parent). Besides the narrowness of this question, the general absence of behavior from previous meta-analyses represents an important gap in our understanding of TGEs. This is particularly true given that many fitness-affecting behaviors have previously been shown to be influenced by TGEs (e.g. Champagne & Meaney, 2008; Curley, Davidson, Bateson, & Champagne, 2009; Storm & Lima, 2010).

Given the scope of previous meta-analyses, it has been unclear whether behavior is generally influenced by TGEs and, if so, to what degree. To address this gap, we asked the following questions:

- 1) What is the magnitude of TGEs on offspring behavior?
- 2) Do mammals exhibit stronger TGEs relative to other classes?
- 3) Are maternal or paternal TGEs stronger?
- 4) Does the type of organism (endotherm versus ectotherm, vertebrate vs invertebrate) influence overall effect sizes?
- 5) Does offspring sex influence overall effect sizes?
- 6) Does the strength of a TGE diminish over multiple generations?
- 7) Does behavioral test category influence overall effect sizes?
- 8) Does the current literature appropriately report TGEs?
- 9) Is the magnitude of TGEs on behavior similar to that of other traits?

Overall, we expected to find a weak influence of TGEs on behavior due to previous meta-analyses on other traits (Uller et al., 2013). We also expected that mammals would exhibit higher TGEs compared to other taxa on behavior due to viviparity and generally prolonged parental care (Reinhold, 2002) and that maternal TGEs would be stronger than paternal TGEs due to required maternal investment (Bonduriansky & Head, 2007; Mousseau & Fox, 1998). We predicted that endotherms and ectotherms would exhibit similar strengths of TGEs based on previously published studies on ectotherms (Feiner et al., 2016; Pagel, Bekkevold, Pohlmeier, Wolter, & Arlinghaus, 2015). Finally, due to contradicting results of several key studies on TGEs (Lagisz et al., 2015; Uller et al., 2013), we expected that we would find an indication of publication bias or skewed reporting of effect sizes. While we did not have explicit predictions regarding how TGEs



would differ between offspring sex, vertebrate versus invertebrate, offspring generation or behavioral test category (defined in Table A3), these factors were also considered to provide an inclusive picture of TGEs and how they impact offspring behavior.

## **Methods**

### **Data Collection**

We searched all years of the Web of Science core collection database in August and September of 2016. We searched by topic using search terms that excluded humans but covered the range of topics falling under TGEs (e.g. maternal and paternal effects; Table A4 and A5), yielding a total of 1616 records (Figure 2.1, Table A6).

These 1616 papers were screened according to the following criteria: First, studies had to measure the effect of varying parental condition (i.e. stressed versus unstressed parent) on the behavior of offspring in non-human animals (not including effects of addictive substances). Second, to be included, studies that used hormonal manipulations had to use levels that were within the physiological range for an organism. Based on eligibility and whether sufficient design and statistical information was provided, the final dataset included 61 articles and 327 effect size estimates (Figure 2.1). For comparisons of effect sizes for behavior to physiology, life-history, and morphology, we also extracted 663 estimates provided in supplemental materials from Uller et al. (Uller et al., 2013).

### **Data Analysis**

To determine overall strength of TGEs on behavior we calculated standardized mean differences, Cohen's  $d$ , according to standard formulas (Lipsey & Wilson, 2011; Nakagawa & Cuthill, 2007) for each eligible estimate. To accurately and confidently compare the magnitude of TGEs to that of other previously studied traits, we converted our Cohen's  $d$  estimates to

Hedge's  $g$  using an online converter. We then used Hedge's  $g$  for all subsequent analyses. Because we were not interested in the direction of the effect sizes, but the magnitude of the effect, we used the absolute value of Hedge's  $g$ . It is important to note that although "informal meta-analyses" (Morrissey, 2016) that use absolute values can lead to biased estimates, Hedge's  $g$  incorporates estimation error in its calculation and therefore should be unbiased in this regard. Both the unadjusted and adjusted (absolute) values of Cohen's  $d$  and Hedge's  $g$  are included in the supplementary material. We then used a mixed-effects model with only an intercept as well as article and taxonomic class included as random effects (Hadfield & Nakagawa, 2010; Santos & Nakagawa, 2012). Because we lacked a complete phylogeny and had poor replication within orders, the inclusion of class as a random factor best addressed the evolutionary non-independence among estimates. All analyses were conducted in R version 3.31 using the lme4 package for mixed effect models (Bates et al., 2015) and confidence intervals around estimates calculated using likelihood profiles or, for fixed effects, assuming normally distributed error.

To determine if the strength of TGEs differed according to various selected biological factors we used a mixed-effects model with offspring sex, generation (one, F1, or two, F2, generations removed from parental manipulation), parental effect type (maternal or paternal), thermoregulation type (ectotherm vs endotherm), invertebrate versus vertebrate, and behavioral test category (Table A4) as fixed effects. Article number and taxonomic class were again included as random effects. To determine if estimates of TGEs were reported uniformly and properly, we fit the previous mixed-effects model but included journal as an additional fixed effect and assessed publication bias via funnel plot. We also calculated the proportion of variation in TGE estimates that was explained by our fixed and random effects (Nakagawa & Schielzeth, 2013).

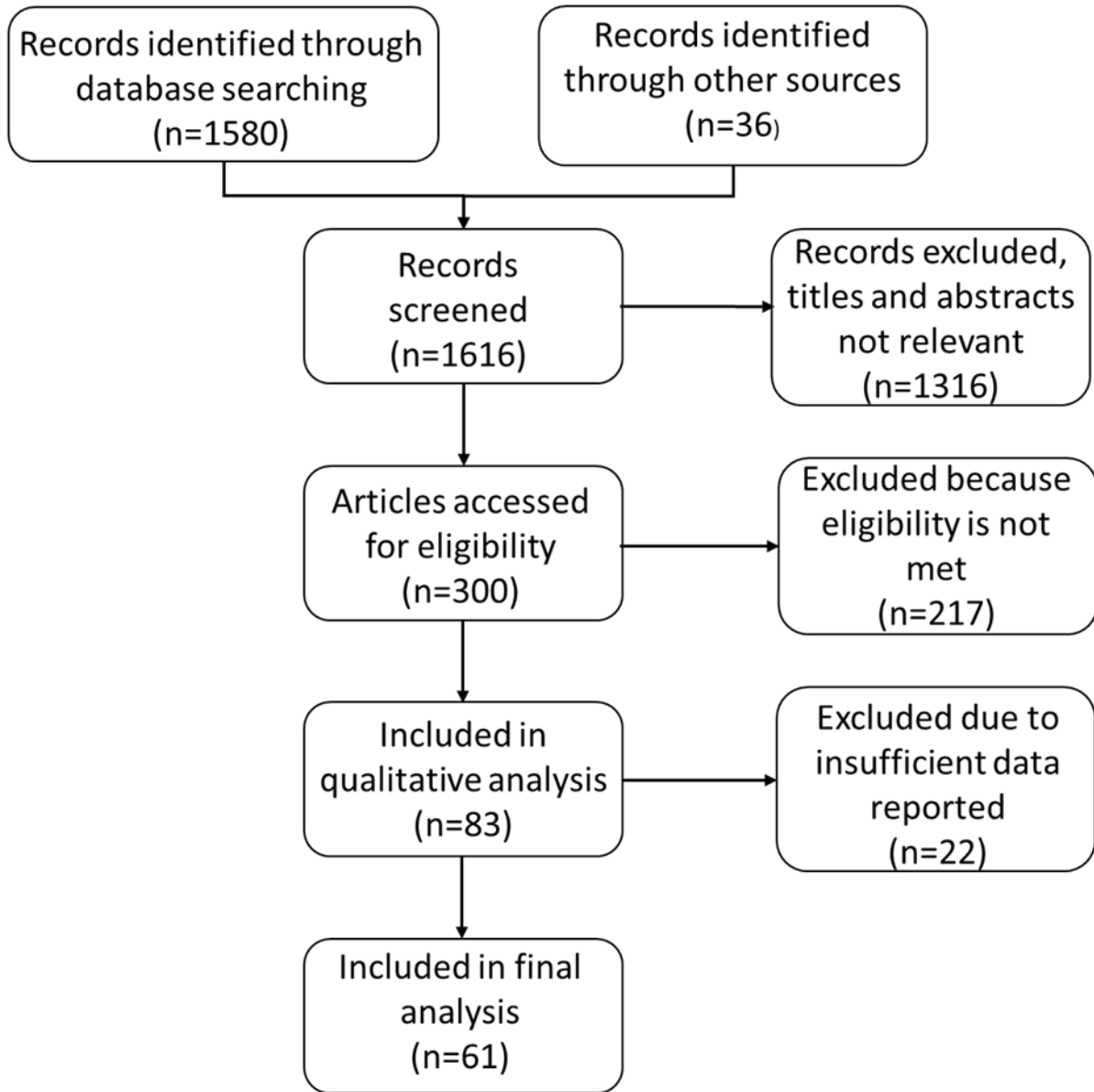


Figure 2.1. Preferred Reporting Items for Systemic Reviews and Meta-Analyses (PRISMA ) Flow Diagram for the number of articles included in subsequent analyses

## Results

The global effect size (Hedge's  $g$ ) of TGEs on behavior was 0.643 (SE = 0.103) (Figure 2.2, Table A7). This suggests that TGEs are common for behavior and that parental environment has a strong effect on offspring behavior (Cohen, 1988).

Generation, parental effect type, invertebrate versus vertebrate, and behavioral test category did not significantly influence the strength of TGEs (Figure 2.3, Table A8) while male offspring exhibited significantly lower TGE strength ( $F_{2,183} = 10.01$ ,  $p < 0.001$ , Figure 2.3, Table A8). Thermoregulation type (ectotherm versus endotherm) approached significance ( $F_{1,64} = 3.81$ ,  $p = 0.055$ ) with endotherms tending to exhibit higher TGEs (Figure 2.3, Table A8). Overall, TGEs on offspring behavior appeared to be uniformly reported in the literature (Figure A3) with no indication of publication bias (Figure 2.4).

Article number accounted for most of the observed variation in estimates (64%), with no detected influence of class (0%) and only a minimal combined influence of any of the above fixed effects (8%) (Table 2.1).

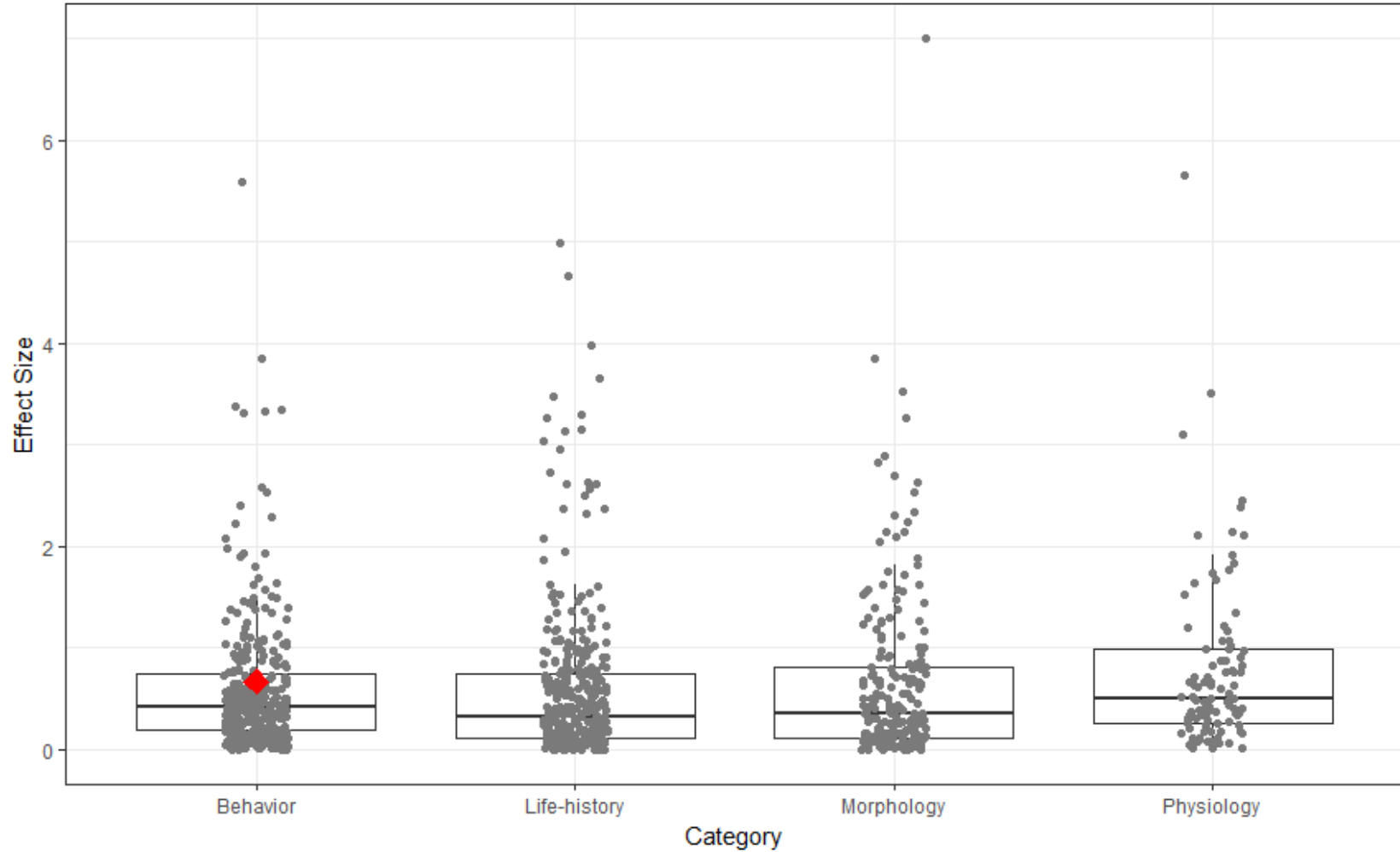


Figure 2.2. Distribution of adjusted effect sizes for trans-generational effects across various categories with life-history, morphology and physiology estimates calculated from Uller et al. 2013. Behavioral estimates were calculated using Hedge's  $g$ . The red diamond represents the result from the mixed-effects model.

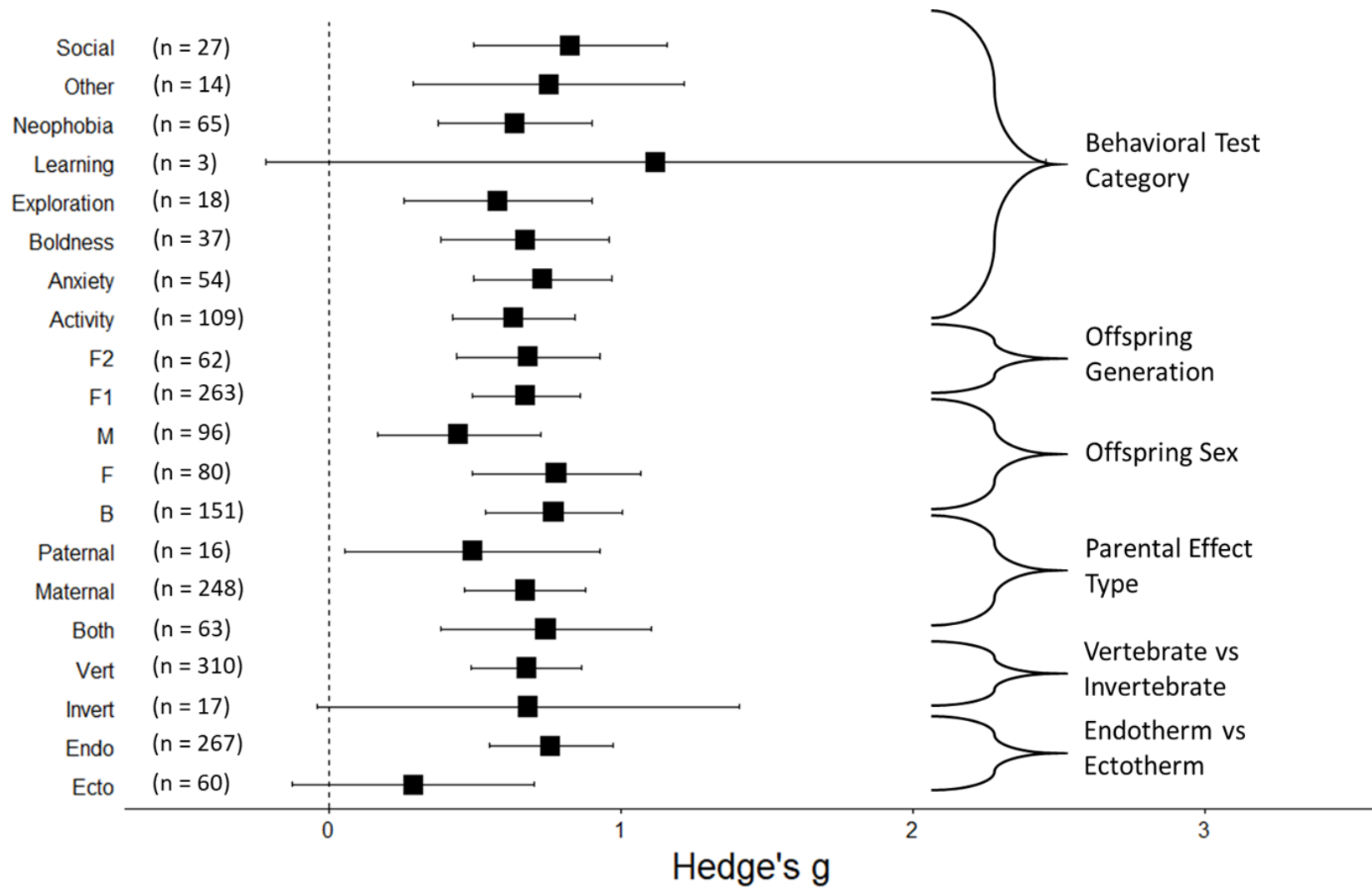


Figure 2.3. Effect size compared across fixed effects. Squares indicate the value of the effect size for each type of effect. The error bars represent the 95 percent confidence intervals for the estimates

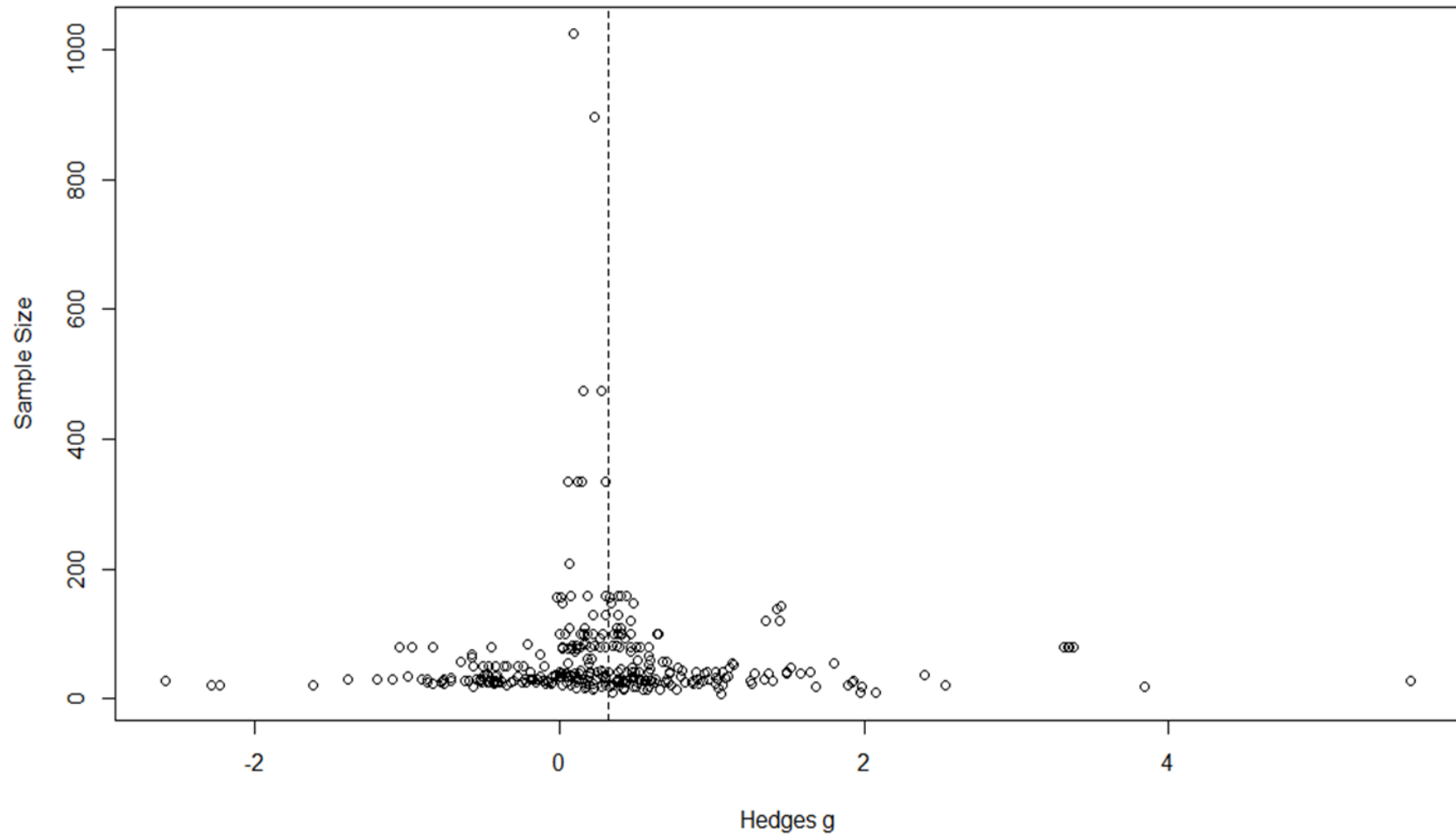


Figure 2.4. Hedge's  $g$  estimates by sample size. The dotted line represents the mean unadjusted effect size from all studies. There was no indication of publication bias

Table 2.1. Proportion of variation explained by random and fixed effects from the full model which included offspring sex, life stage, parental effect type, thermoregulation type (ectotherm vs. endotherm), invertebrate vs. vertebrate, and behavioral category

Category	Variance Explained
<i>Fixed Effects</i>	0.08
<i>Random Effects</i>	0.64
Article id	0.64
Class	0.00
<i>Residual</i>	0.28

## Discussion

Overall, the magnitude of TGEs on offspring behavior was large (Cohen, 1988), indicative of a strong effect of TGEs on offspring behavior. When we ignored direction of effect, and examined the raw estimates of TGEs from other studies, we also found that behavior exhibited similar magnitudes of effect sizes compared to other categories of traits (Figure 2.2). For life-history, physiological, and morphological traits Uller et al. (Uller et al., 2013) reported average effect size magnitudes of 0.59, 0.78, and 0.65 respectively while the effect size magnitude for behavior was 0.64 (Figure 2.2). From this, we suggest that behavior is similarly influenced by TGEs compared to other traits, as evident in overlap of the four categories (Figure 2.2). Interestingly, heritability of behavior is also of similar magnitude as that of physiology and life-history (Mousseau & Roff, 1987; Stirling, Reale, & Roff, 2002). These combined findings suggest that both the genetic and non-genetic inheritance for behavior is the same, on average, as for other labile traits.



One important caveat to our findings is that we did not split studies into the broader categories of anticipatory, selfish, bet-hedging, or transmissive TGEs (Marshall & Uller, 2007). We did not do so because these categories were not necessarily considered by the authors of individual studies and multiple categories of TGEs might have been at play in each study. Nonetheless, an informal examination of the included papers suggests that many focused on anticipatory TGEs. However, due to the potential of multiple TGE mechanisms in each study, we cannot explicitly test if any of the four categories of TGEs acts more strongly on offspring traits. Testing the strength of the different types of TGEs represents a future avenue of research as each has different evolutionary and ecological impacts.

Besides the overall mean effect, the impact of specific biological factors on the strength of TGEs produced several surprising results: First, male offspring were significantly less affected by TGEs compared to both female offspring and when offspring sex was not identified (Figure 2.3). Because we used standardized effect sizes it is not clear whether the analyzed TGEs had positive or negative effects on offspring fitness. However, most manipulations used in the analyzed studies induced stress in the parental generation. Thus, despite previously discussing TGEs from the perspective of inducing adaptive plasticity in offspring, it is possible that the decreased TGEs observed in male offspring could be due to parental buffering of environmental effects, consistent with studies that have shown differential investment between male and female offspring (Sheldon & West, 2004; Zizzari, van Straalen, & Ellers, 2016). Unfortunately, our data do not allow us to critically assess this possibility, suggesting it is an important topic for future research.

Second, contrary to our expectations, we observed no measurable effect of taxonomic class on TGEs (Table 2.1). This result was surprising given that viviparity and lactation

(Reinhold, 2002) led us to predict stronger TGEs for mammals. This leads us to our third, and again surprising, result: the general lack of effect of any of our a priori or exploratory biological categories on TGEs. Despite the significant effect of offspring sex and thermoregulation type approaching significance, fixed effects explained only 8% of the variation in the dataset. Therefore, neither taxonomic class nor any other included biological factor substantively influenced the strength of TGEs. Instead, the strongest effect on variation in TGEs was due to the article from which an estimate was drawn. This high explanatory power of article ID (Table 2.1) suggests that specific methodological approaches may produce stronger TGEs, and that these specifics are conflated with article ID. A potential limitation of our analysis stems from unequal research effort into TGEs. Specifically, effects on males were less frequently studied or not independently studied (Figure 2.3). Likewise, paternal effects, invertebrates and ectotherms were understudied. This poor representation of invertebrates and ectotherms is consistent with the general taxonomic bias present in the behavioral literature, a bias which threatens the generality of most of the field's findings (Rosenthal, Gertler, Hamilton, Prasad, & Andrade, 2017). Finally, despite many studies being identified in our initial search, a large number of otherwise eligible studies had to be excluded due to lack of statistical information (e.g. no sample sizes, no test values, no model outputs) (Figure 2.1).

While we found that the influence of TGEs on behaviors was large, we did not consider support for specific hypotheses of TGEs. Previous testing of specific hypotheses, such as the silver-spoon or environmental matching hypotheses for anticipatory effects (Engqvist & Reinhold, 2016; Monaghan, 2008), have found weak evidence for these hypotheses (Uller et al., 2013). It is worth noting, however, that when ignoring direction of effect, and focusing on magnitude of effect size, the estimates of TGEs that we found were very similar to the estimates

found by Uller et al for physiology, life history and morphology (Uller et al., 2013). The testing of specific TGE hypotheses, and our general finding of differences between male and female offspring in how strongly their behaviors are affected by TGEs, warrant further exploration. However, with these caveats in mind, we suggest that offspring behavior is indeed influenced by TGEs, comparable to other categories of traits, and note that behavior should be considered in addition to life-history, morphology and physiology when studying trans-generational effects.

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## APPENDIX

Table A1. Number of individuals who went through each repetition of recording for each call type.

<b>Rep</b>	<b>Advertisement</b>	<b>Aggression</b>	<b>Courtship</b>	<b>Total</b>
<b>1</b>	127	91	105	323
<b>2</b>	122	87	101	310
<b>3</b>	107	85	100	292
<b>4</b>	5			5

Table A2. Strength and significance of fixed effects on advertisement, courtship and aggression call parameters as calculated using univariate linear mixed models. Significant fixed effects are bolded.

<i>Call Type</i>	Frequency			Pulses Per Chirp			Total Time Calling			
Fixed Effect	df	F	p	df	F	p	df	F	p	
<i>Advertisement</i>										
Develop_Diet	1, 12.5	3.94	0.07	1, 100.6	0.44	0.51	1, 96.3	0.02	0.89	
Adult_Diet	1, 92.5	0.72	0.40	1, 97.4	2.23	0.14	1, 91.8	0.76	0.38	
Temperature	1, 158	<b>10.75</b>	<b>0.00</b>	1, 172.2	0.02	0.90	1, 199.6	0.13	0.72	
Rep	1,186	0.00	0.96	1, 161.2	0.32	0.57	1, 124.5	1.94	0.17	
Batch	3, 113	<b>4.20</b>	<b>0.01</b>	3, 111.7	<b>2.77</b>	<b>0.04</b>	3, 92.6	2.54	0.06	
Time	1, 183	0.00	0.98	1, 200.2	0.00	0.95	1, 217.4	2.21	0.14	
Day Since Diet Switch	1, 189	0.00	0.99	1, 165.2	0.00	0.97	1, 129.3	1.22	0.27	
Develop_Diet*Adult_Diet	1, 89.5	0.01	0.94	1, 94.01	1.73	0.19	1, 87.2	1.77	0.19	
<i>Courtship</i>										
Develop_Diet	1, 35.9	0.06	0.81	1,56.41	1.22	0.27	1, 9.6	0.17	0.69	
Adult_Diet	1, 40.8	0.13	0.72	1, 59.93	1.1	0.3	1, 104.2	0.58	0.45	
Temperature	1, 132.5	0	0.95	1, 133.83	0.25	0.62	1, 135.8	3.48	0.06	
Rep	1, 125.5	0.03	0.86	1, 135.53	0.38	0.54	1, 138	1.6	0.21	
Batch	3, 42.5	<b>8.91</b>	<b>0</b>	3, 46.7	<b>4.63</b>	<b>0.01</b>	3, 32.8	1.43	0.25	
Time	1, 130.1	0.03	0.86	1, 119.06	0.56	0.45	1, 136.3	0.4	0.53	
Day Since Diet Switch	1, 77.8	0.8	0.37	1, 108.33	1	0.32	1, 129.5	0.86	0.36	
Develop_Diet*Adult_Diet	1, 35.8	0.01	0.92	1, 55.8	1.01	0.32	1, 123.6	2.74	0.1	
<i>Aggression</i>										
Develop_Diet	1, 81.6	1.06	0.31	1, 77.8	1.07	0.30	1, 11.4	0.01	0.92	
Adult_Diet	1, 78.8	0.23	0.63	1, 74.2	2.59	0.11	1, 183.4	2.77	0.10	



Table A2. Strength and significance of fixed effects on advertisement, courtship and aggression call parameters as calculated using univariate linear mixed models. Significant fixed effects are bolded (continued).

<i>Call Type</i>	Frequency				Pulses Per Chirp				Total Time Calling		
Fixed Effect	df	F	p		df	F	p		df	F	p
<i>Aggression</i>											
Temperature	1, 142.6	0.08	0.78		1, 160.2	1.32	0.25		1, 183.8	1.64	0.20
Rep	1, 177.4	0.26	0.61		1, 147.5	<b>4.73</b>	<b>0.03</b>		1, 182	1.43	0.23
Batch	3, 36.5	<b>6.16</b>	<b>0.00</b>		3, 23.9	1.61	0.21		3, 35.2	0.14	0.94
Time	1, 135.1	1.26	0.26		1, 151.1	0.00	0.95		1, 181.4	<b>6.97</b>	<b>0.01</b>
Day Since Diet Switch	1, 111.2	0.29	0.59		1, 93	1.70	0.19		1, 172.7	0.09	0.77
Develop_Diet*Adult_Diet	1, 79.2	1.67	0.20		1, 74.1	2.56	0.11		1, 181.9	1.51	0.22

Table A2. Strength and significance of fixed effects on advertisement, courtship and aggression call parameters as calculated using univariate linear mixed models. Significant fixed effects are bolded (continued).

<i>Call Type</i>	Chirp Duration				Chirp Rate				Pulse Rate		
Fixed Effect	df	F	p		df	F	p		df	F	p
<i>Advertisement</i>											
Develop_Diet	1, 97.7	0.60	0.44		1, 11.7	2.77	0.12		1, 86.8	0.96	0.33
Adult_Diet	1, 94.7	2.85	0.09		1, 82.1	<b>5.05</b>	<b>0.03</b>		1, 83.9	2.65	0.11
Temperature	1, 170.8	<b>6.48</b>	<b>0.01</b>		1, 157.5	1.38	0.24		1, 173.7	<b>56.35</b>	<b>0.00</b>
Rep	1, 159.3	1.27	0.26		1, 152.9	0.06	0.80		1, 135.8	1.39	0.24
Batch	3, 109.5	2.32	0.08		3, 100.9	1.27	0.29		3, 88.9	2.33	0.08
Time	1, 198.8	0.82	0.37		1, 190.9	0.24	0.63		1, 200.5	<b>6.27</b>	<b>0.01</b>
Day Since Diet Switch	1, 163.4	0.26	0.61		1, 157.2	0.47	0.49		1, 140.5	0.50	0.48
Develop_Diet*Adult_Diet	1, 91.3	1.28	0.26		1, 78	1.50	0.22		1, 80.5	0.87	0.36
<i>Courtship</i>											
Develop_Diet	1, 55.4	0.82	0.37		1, 8.8	0	0.96		1, 62.5	0.54	0.47
Adult_Diet	1, 57.5	1.13	0.29		1, 51.6	0	0.96		1, 67.4	0.17	0.68
Temperature	1, 134.5	0.02	0.88		1, 133.4	0.21	0.64		1, 131.1	0.03	0.86
Rep	1, 135.2	0.93	0.34		1, 136.6	2.76	0.1		1, 134.5	0.04	0.83
Batch	3, 46.2	2.68	0.06		3, 59.8	2.32	0.08		3, 71.8	<b>4.86</b>	<b>0</b>
Time	1, 120	1.21	0.27		1, 119.4	1.24	0.27		1, 139.9	0.53	0.47

Table A2. Strength and significance of fixed effects on advertisement, courtship and aggression call parameters as calculated using univariate linear mixed models. Significant fixed effects are bolded (continued).

<i>Call Type</i>	Chirp Duration			Chirp Rate			Pulse Rate		
Fixed Effect	df	F	p	df	F	p	df	F	p
Day Since Diet Switch	1, 109.5	1.41	0.24	1, 110.8	3.11	0.08	1, 107.8	0.13	0.72
Develop_Diet*Adult_Diet	1, 55.7	0.17	0.68	1, 52.5	0	0.98	1, 66.7	0.56	0.46
<i>Aggression</i>									
Develop_Diet	1, 14.7	0.84	0.37	1, 15	1.22	0.29	1, 9.4	0.96	0.35
Adult_Diet	1, 72.9	1.77	0.19	1, 68.3	1.35	0.25	1, 56.1	1.80	0.19
Temperature	1, 159.6	0.73	0.39	1, 164.1	0.71	0.40	1, 144.7	0.26	0.61
Rep	1, 176.4	3.32	0.07	1, 176	1.78	0.18	1, 176.2	0.01	0.92
Batch	3, 25.6	1.10	0.37	3, 22.7	0.50	0.69	3, 33	1.92	0.14
Time	1, 150.2	0.24	0.63	1, 153.2	0.06	0.81	1, 131.33	0.73	0.39
Day Since Diet Switch	1, 100	1.22	0.27	1, 93.5	2.27	0.14	1, 84	0.01	0.94
Develop_Diet*Adult_Diet	1, 73.2	2.81	0.10	1, 68.3	2.46	0.12	1, 56.5	0.24	0.63

Table A2. Strength and significance of fixed effects on advertisement, courtship and aggression call parameters as calculated using univariate linear mixed models. Significant fixed effects are bolded (continued).

<i>Call Type</i>	Amplitude		
Fixed Effect	df	F	p
<i>Advertisement</i>			
Develop_Diet	1, 14.8	0.00	0.96
Adult_Diet	1, 89.6	0.53	0.47
Temperature	1, 180.6	0.47	0.50
Rep	1, 144.5	0.00	0.97
Batch	3, 112.8	1.74	0.16
Time	1, 210.2	1.31	0.25
Day Since Diet Switch	1, 148.9	0.09	0.76
Develop_Diet*Adult_Diet	1, 86.3	<b>4.23</b>	<b>0.04</b>
<i>Courtship</i>			
Develop_Diet	1, 61.8	1.32	0.26

Table A2. Strength and significance of fixed effects on advertisement, courtship and aggression call parameters as calculated using univariate linear mixed models. Significant fixed effects are bolded (continued)

<i>Call Type</i>	Amplitude		
Fixed Effect	df	F	p
Adult_Diet	1, 66.7	0.04	0.84
Temperature	1, 130.9	0.66	0.42
Rep	1, 134.4	0.53	0.47
Batch	3, 71	<b>4.44</b>	<b>0.01</b>
Time	1, 139.9	0.6	0.44
Day Since Diet Switch	1, 107.2	0.33	0.57
Develop_Diet*Adult_Diet	1, 66	1.95	0.17
<i>Aggression</i>			
Develop_Diet	1, 13.2	1.81	0.20
Adult_Diet	1, 71.9	1.00	0.32
Temperature	1, 153.1	<b>4.25</b>	<b>0.04</b>
Rep	1, 173.2	0.53	0.47
Batch	3, 31.6	<b>3.90</b>	<b>0.02</b>
Time	1, 144.2	0.67	0.41
Day Since Diet Switch	1, 96.6	1.04	0.31
Develop_Diet*Adult_Diet	1, 72.1	0.11	0.75

Table A3. Repeatabilities and variances at the among- and within-individual levels as well as the fixed and random effects for each call parameter calculated using the rptR package with 95% confidence intervals. The bolded call components represent those chosen for the condensed multi-response MCMCglmm model

	$\tau_1^a$	$\tau_2^b$	$V_I^c$	$V_W^d$
<b>Advert Frequency</b>	0.58 (0.45, 0.7)	0.38 (0.25-0.50)	0.41 (0.28 -0.62)	0.29 (0.22-0.35)
<b>Advert Pulses per Chirp</b>	0.46 (0.29, 0.60)	0.39 (0.24, 0.52)	0.40 (0.23, 0.64)	0.48 (0.35, 0.57)
Advert Total Time Calling	0.12 (0, 0.30)	0.11 (0, 0.26)	0.11 (0, 0.30)	0.79 (0.57, 0.94)
Advert Chirp Duration	0.45 (0.31, 0.60)	0.36 (0.22, 0.48)	0.37 (0.23, 0.56)	0.43 (0.32, 0.52)
<b>Advert Chirp Rate</b>	0.42 (0.27, 0.59)	0.36 (0.22, 0.49)	0.41 (0.24, 0.65)	0.49 (0.36, 0.59)
Advert Pulse Rate	0.33 (0.17, 0.49)	0.18 (0.10, 0.28)	0.19 (0.09, 0.33)	0.37 (0.28, 0.45)
Advert Amplitude	0.28 (0.13, 0.45)	0.24 (0.10, 0.39)	0.25 (0.12, 0.45)	0.58 (0.42, 0.71)
<b>Aggression Frequency</b>	0.39 (0.23, 0.54)	0.28 (0.15, 0.41)	0.33 (0.17, 0.55)	0.39 (0.27, 0.47)
Aggression Pulses per Chirp	0.21 (0.07, 0.40)	0.19 (0.05, 0.34)	0.20 (0.05, 0.43)	0.61 (0.43, 0.76)
Aggression Total Time Calling	0 (0, 0.21)	0 (0, 0.18)	0 (0, 0.22)	0.91 (0.65, 1.07)
Aggression Chirp Duration	0.26 (0.09, 0.46)	0.24 (0.09, 0.40)	0.25 (0.11, 0.49)	0.61 (0.43, 0.75)
Aggression Chirp Rate	0.21 (0.06, 0.42)	0.19 (0.04, 0.37)	0.20 (0.06, 0.45)	0.65 (0.45, 0.81)
<b>Aggression Pulse Rate</b>	0.31 (0.16, 0.50)	0.28 (0.14, 0.44)	0.32 (0.14, 0.59)	0.6 (0.42, 0.72)
<b>Aggression Amplitude</b>	0.22 (0.09, 0.42)	0.17 (0.07, 0.31)	0.19 (0.07, 0.38)	0.43 (0.30, 0.53)
Courtship Frequency	0.14 (0, 0.38)	0.08 (0, 0.23)	0.09 (0, 0.30)	0.49 (0.32, 0.63)
<b>Courtship Pulses per Chirp</b>	0.32 (0.12, 0.54)	0.26 (0.09, 0.44)	0.29 (0.10, 0.62)	0.55 (0.34, 0.71)
Courtship Total Time Calling	0 (0, 0.25)	0 (0, 0.23)	0 (0, 0.31)	0.92 (0.58, 1.10)
<b>Courtship Chirp Duration</b>	0.32 (0.13, 0.55)	0.29 (0.10, 0.48)	0.33 (0.12, 0.68)	0.64 (0.38, 0.81)
<b>Courtship Chirp Rate</b>	0.29 (0.1, 0.53)	0.27 (0.07, 0.47)	0.31 (0.09, 0.66)	0.67 (0.43, 0.82)
Courtship Pulse Rate	0.04 (0, 0.32)	0.04 (0, 0.25)	0.04 (0, 0.32)	0.86 (0.56, 1.03)
Courtship Amplitude	0.04 (0, 0.30)	0.04 (0, 0.25)	0.04 (0, 0.29)	0.89 (0.57, 1.05)

Table A3. Repeatabilities and variances at the among- and within-individual levels as well as the fixed and random effects for each call parameter calculated using the rptR package with 95% confidence intervals (continued). The bolded call components represent those chosen for the condensed multi-response MCMCglmm model

	$V_{\text{Conspecific}}^e$	$V_{\text{Chamber}}^f$	$V_{\text{Box}}^g$	$V_{\text{Fixed}}^h$
<b>Advert Frequency</b>	NA	0 (0, 0.04)	0.01 (0, 0.10)	0.38 (0.25, 0.63)
<b>Advert Pulses per Chirp</b>	NA	0.004 (0, 0.06)	0 (0, 0.03)	0.14 (0.09, 0.33)
Advert Total Time Calling	NA	0.04 (0, 0.15)	0 (0, 0.07)	0.10 (0.06, 0.25)
Advert Chirp Duration	NA	0.01 (0, 0.07)	0 (0, 0.08)	0.22 (0.15, 0.42)
<b>Advert Chirp Rate</b>	NA	0.001 (0,0.06)	0.08 (0, 0.26)	0.16 (0.11, 0.39)
Advert Pulse Rate	NA	0.02 (0, 0.07)	0 (0, 0.05)	0.47 (0.36, 0.66)
Advert Amplitude	NA	0 (0, 0.07)	0.07 (0, 0.22)	0.14 (0.09, 0.33)
<b>Aggression Frequency</b>	0.13 (0.02, 0.30)	NA	0 (0, 0.12)	0.33 (0.18, 0.68)
Aggression Pulses per Chirp	0.14 (0.01, 0.35)	NA	0 (0, 0.09)	0.12 (0.08, 0.38)
Aggression Total Time Calling	0.05 (0, 0.20)	NA	0.02 (0, 0.11)	0.08 (0.06, 0.24)
Aggression Chirp Duration	0.09 (0, 0.27)	NA	0.02 (0, 0.14)	0.09 (0.06, 0.31)
Aggression Chirp Rate	0.06 (0, 0.21)	NA	0.05 (0, 0.19)	0.11 (0.06, 0.35)
<b>Aggression Pulse Rate</b>	0.10 (0, 0.31)	NA	0.02 (0, 0.14)	0.1 (0.06, 0.38)
<b>Aggression Amplitude</b>	0.20 (0.06, 0.44)	NA	0.03 (0, 0.15)	0.26 (0.11, 0.64)
Courtship Frequency	0.06 (0, 0.21)	NA	0 (0, 0.09)	0.44 (0.27, 0.74)
<b>Courtship Pulses per Chirp</b>	0.06 (0, 0.24)	NA	0 (0, 0.14)	0.19 (0.11, 0.50)
Courtship Total Time Calling	0.07 (0, 0.28)	NA	0.06 (0, 0.20)	0.06 (0.05, 0.28)
<b>Courtship Chirp Duration</b>	0.05 (0, 0.23)	NA	0 (0, 0.18)	0.11 (0.08, 0.36)
<b>Courtship Chirp Rate</b>	0 (0, 0.14)	NA	0.07 (0, 0.31)	0.08 (0.06, 0.33)
Courtship Pulse Rate	0 (0, 0.14)	NA	0 (0, 0.11)	0.16 (0.10, 0.38)
Courtship Amplitude	0 (0, 0.15)	NA	0 (0, 0.11)	0.13 (0.09, 0.35)

a – unadjusted repeatability, calculated as  $V_I/V_I + V_W$ ; b – adjusted repeatability, calculated by  $V_I/V_I + V_W + V_{\text{Fixed}}$ ; c – estimated among-individual variance, d – estimated within-individual variance, e – estimated variance due to conspecific id, f – estimated variance due to chamber, g – estimated variance due to developmental box, h - estimated variances due to fixed effects including batch, temperature, rep and diet treatments

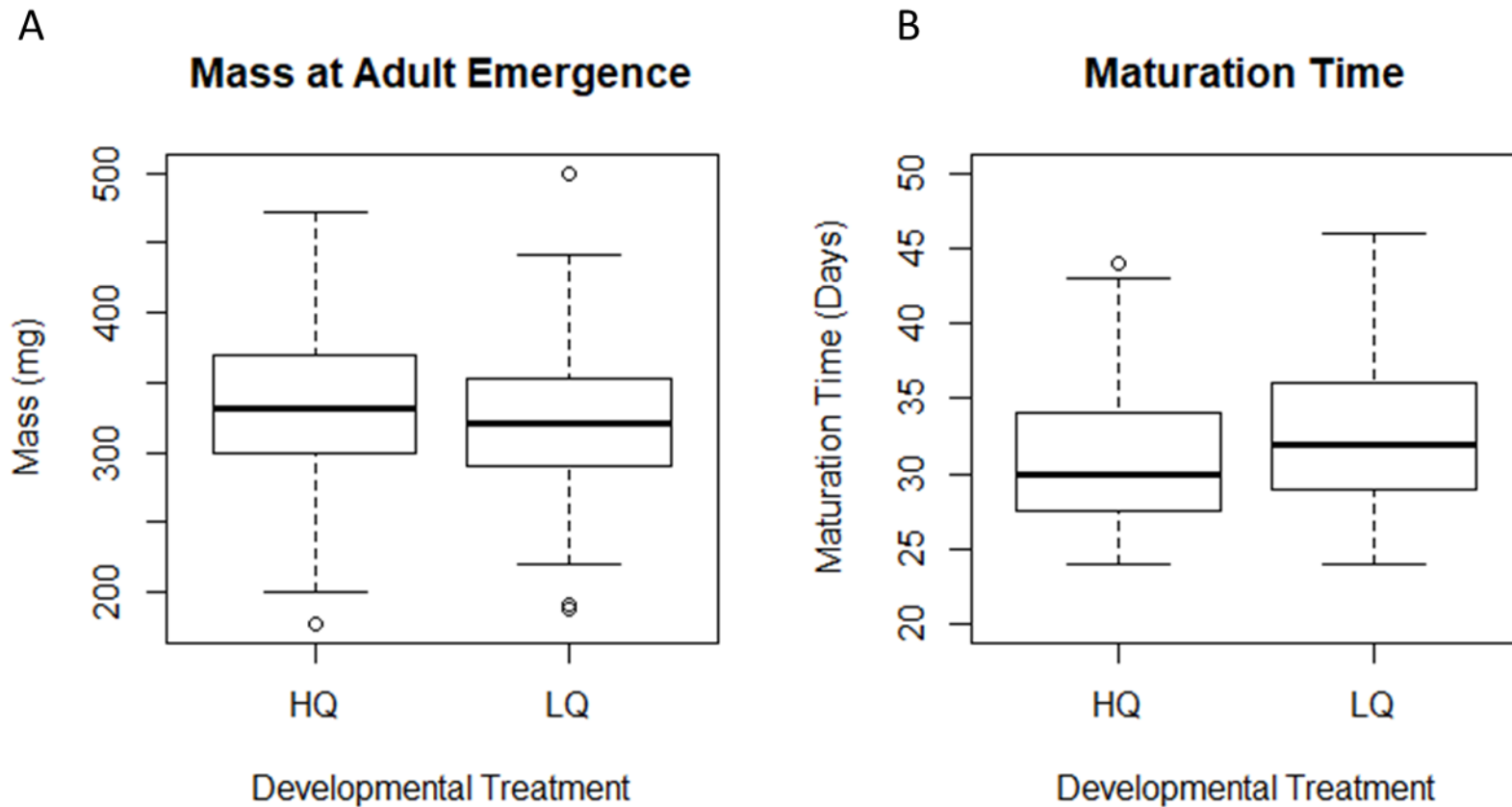


Figure A1. Box plots showing mass at adult emergence (A) and maturation time (B) for the two developmental diet treatments. There was no significant difference in mass at adult emergence between the two diet treatments ( $t = 1.036$ ,  $df = 117.7$ ,  $p = 0.305$ ). LQ developmental diet individuals matured significantly slower compared to the HQ developmental diet individuals ( $t = -2.152$ ,  $df = 115.6$ ,  $p = 0.03$ )



Table A4. Behavioral test categories and definitions

Category	Definition
Activity	Movement during trial
Boldness	Tendency to take risks
Social	Interactions with conspecifics
Learning	Ability to learn layout of maze
Exploration	Percent of area explored in given span of time
Anxiety	Behavior when exposed to aversive event or situation (i.e. elevated space, forced swim test)
Neophobia	Aversions to novel situations
Other	

Table A5. Search terms used in literature review

Search term
parental effect* behav* AND animal NOT human
maternal effect* behav* AND animal NOT human OR adult
paternal effect* behav* AND animal NOT human OR adult
trans-generational effect* behav* AND animal NOT human OR adult
transgenerational effect* behav* AND animal NOT human OR adult
'silver spoon' behav* AND animal NOT human OR adult
'environment-matching' behav* AND animal NOT human OR adult
transgenerational effects on behavior NOT human
parental effects on animal personality

Table A6. List of articles included in final analysis.

Authors	Year	Journal
Ericsson et al.	2016	PLOS One
Possenti et al.	2016	Hormones and Behavior
Sopinka et al.	2015	Animal Behaviour
Hsu	2016	Animal Behaviour
Freinschlaq & Schausberger	2016	Experimental and Applied Acarology
Donelan & Trussell	2015	Ecology
Volkova et al.	2015	General and Comparative Endocrinology
Volkova et al.	2015	Hormones and Behavior
Zaidan & Gaisler-Salomon	2015	Psychoneuroendocrinology
Attisano & Kilner	2015	Animal Behaviour
Schweitzer et al.	2014	Animal Behaviour
Allan et al.	2014	Proceedings of the Royal Society B
Soares et al.	2013	Neuroscience Letters
Saavedra-Rodriguez & Feig	2013	Biological psychiatry
Backus et al.	2015	Applied Animal Behaviour Science
Guibert et al.	2013	Proceedings of the Royal Society B
Itonaga et al.	2012	Physiological and Biochem Zoology
Guibert et al.	2011	Applied Animal Behaviour Science
Smith et al.	2009	PLOS One
Emack et al.	2008	Hormones and Behavior
Malcolm et al.	2006	Biology of Reproduction
Kaiser et al.	2000	Physiology and Behavior
Welch et al.	2014	Nature Climate
Kraus & Naguib	2014	Evolutionary Ecology
Giesing et al.	2010	Proceedings of the Royal Society B
Bennett & Murray	2014	Proceedings of the Royal Society B
McGhee et al.	2012	Functional Ecology
Wisenden et al.	2011	Behaviour
Roche et al.	2012	Biology letters
Storm & Lima	2010	The American Naturalist
Dias & Ressler	2014	Nature neuroscience

Table A6. List of articles included in final analysis (continued).

Authors	Year	Journal
Stein & Bell	2014	Animal Behaviour
Guenther et al.	2014	Behavioral ecology and sociobiology
Curley et al.	2009	Frontiers in behavioral neuroscience
Curley et al.	2008	Animal Behaviour
Masis-Calvo et al.	2013	Physiology and Behavior
Malkesman et al.	2008	Pharmacology Biochemistry and Behavior
Riber et al.	2007	Applied Animal Behaviour Science
Carratu et al.	2006	Neuroscience
Dimatelis et al.	2012	Brain research
Houdelier et al.	2011	PLOS One
de Margerie et al.	2013	Developmental Psychobiology
Khoury et al.	2006	Progress in Neuro-Psychopharmacology and Biological Psychiatry
Riedstra et al.	2013	Animal Behaviour
Bouet et al.	2011	Neuroscience Letters
Liang et al.	2007	Zoology
Tschirren et al.	2006	The American Naturalist
Friske & Gammie	2005	Physiology and Behavior
Eising & Groothuis	2003	Animal Behaviour
Meek et al.	2000	Physiology and Behavior
Sevi et al.	1999	Applied Animal Behaviour Science
Berchard & Lewis	2016	Behavioural Brain Research
Vignet et al.	2015	Science and Pollution
Johnson et al.	2014	Animal Behaviour
Curno et al.	2011	Proceedings of the Royal Society B
Fuentes et al.	2014	Frontiers in behavioral neuroscience
Baldo et al.	2014	Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology
Blaney et al.	2013	Behavioural Brain Research
Llorente et al.	2007	Psychoneuroendocrinology
Otten et al.	2007	Livestock Science
Nordgreen et al.	2006	Animal Behaviour

Table A7. Global effect size (intercept) for trans-generational effects on offspring behavior calculated using a linear mixed model with only an intercept as a fixed effect. Confidence intervals were estimated via likelihood profile.

<b>Effect</b>	<b>Estimate</b>	<b>Lower CI</b>	<b>Upper CI</b>
<b>Fixed Effect</b>	<b>Mean estimate (SE)</b>		
(Intercept)	0.643 (0.103)	0.38	0.871
<b>Random Effects</b>	<b>Variiances</b>		
Article ID	0.391	0.530	0.804
Class	0.011	0.00	0.412
Residual	0.183	0.410	0.489

Table A8. Trans-generational effects on offspring behavior by different fixed effects, calculated using a linear mixed model.

Fixed Effect	F	df	p	Subcategory	Hedge's g	lower CI	upper CI
Parental Effect Type	0.829	2, 139	0.439				
				Both	0.744	0.383	1.105
				Maternal	0.672	0.464	0.881
				Paternal	0.494	0.057	0.931
Offspring Sex	10.01	2, 183	< 0.001				
				Both	0.771	0.537	1.006
				Female	0.780	0.493	1.068
				Male	0.446	0.168	0.725
Behavioral Test Category	0.483	7, 174	0.846				
				Activity	0.633	0.424	0.843
				Anxiety	0.732	0.496	0.969
				Boldness	0.673	0.384	0.962
				Exploration	0.579	0.258	0.901
				Learning	1.121	-0.213	2.455
				Neophobia	0.637	0.373	0.901
				Social	0.823	0.495	1.159
				Other	0.754	0.289	1.218
Offspring Generation	0.008	1, 285	0.928				
				F1	0.676	0.490	0.862
				F2	0.684	0.438	0.930
Endotherm vs Ectotherm	3.808	1, 64	0.055				
				Ectotherm	0.291	-0.123	0.704
				Endotherm	0.762	0.548	0.975
Vertebrate vs Invertebrate	0.0003	1, 61	0.985				
				Invertebrate	0.684	-0.038	1.406
				Vertebrate	0.677	0.488	0.867

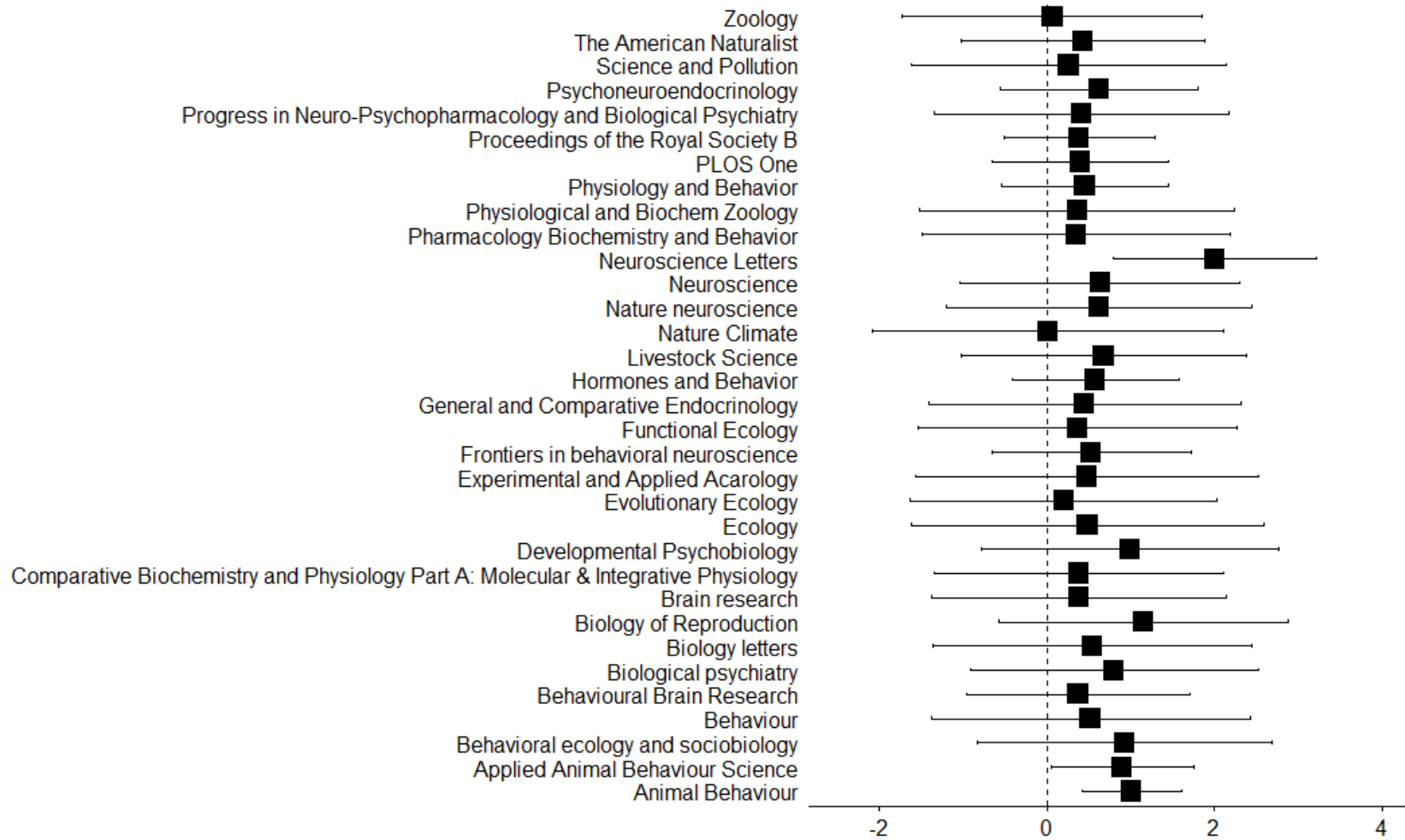


Figure A2. Effect size compared across different journals. Squares indicate the value of the effect size for each journal and the bars represent the 95% confidence intervals for each estimate