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## Individual plasticity in fecundity varies among populations of a globally-distributed songbird

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## 1 Summary

- 2 1. Plasticity in life history characteristics can influence multiple ecological and evolutionary  
3 phenomena, including how invading organisms interact with novel conditions in new  
4 locations or how environmental change affects organisms in native locations. Variation in  
5 reaction norm attributes is a critical element to understanding plasticity in life history, yet  
6 we know relatively little about the ways in which reaction norms vary within and among  
7 populations.
- 8 2. We amassed data on clutch size from marked females in 8 populations of house sparrows  
9 (*Passer domesticus*) from North America and Europe. House sparrows produce multiple  
10 clutches per season and some individuals live for several seasons. We exploited repeated  
11 measures of clutch size to assess the extent of within-individual phenotypic plasticity and  
12 among-individual variation in clutch size and to test predictions arising from a model of  
13 optimal clutch size reaction norms (Rowe, Ludwig & Schluter 1994).
- 14 3. Worldwide, females of this multi-brooded species altered their clutch size with respect to  
15 date, attempt order, and the interaction of date and order. However, we found significant  
16 differences between populations in the response to date and the date by attempt order  
17 interaction.
- 18 4. We tested the prediction that the relationship with date should be increasingly negative as  
19 breeding season becomes shorter and found steeper declines in clutch size with date in  
20 populations with longer seasons, contrary to the prediction. Populations also differed in  
21 the level of among-individual variation in reaction norm intercept, but we found no  
22 evidence of among-individual variation in reaction norm slope.

1        5. We show that complex reaction norms in life history characters exhibit within and among  
2            population variance. The nature of this variance is only partially consistent with current  
3            life history theory and stimulates expansions of such theory to accommodate  
4            complexities in adaptive life history.

5

6    Keywords: adaptation, clutch size, life history, phenology of breeding, phenotypic plasticity,  
7    trade-offs, within-individual variance

8

For Review Only

## 1 Introduction

2 Many organisms exhibit labile traits—behavioral, physiological, or morphological characters  
3 that differ in expression during an individual's lifetime. Labile traits are examples of phenotypic  
4 plasticity, broadly defined as the effect of an environmental factor on the phenotypic expression  
5 of a genotype (Stearns 1989; Scheiner 1993). Because individual organisms can express labile  
6 traits multiple times, they can be described in terms of a function relating phenotype to  
7 environment, or a reaction norm (Woltereck 1909; Bradshaw 1965; Gomulkiewicz & Kirkpatrick  
8 1992; Nussey, Wilson & Brommer 2007). For linear reaction norms, both the elevation (the  
9 individual's mean phenotype in the average environment, or intercept) and the slope (the change  
10 in the individual's phenotype in different environments) could vary among individuals. Because  
11 the shape of a reaction norm has often been hypothesized to have evolved through natural  
12 selection (e.g., Gotthard & Nylin 1995; Pigliucci 2001; Ghalambor, Angeloni & Carroll 2010),  
13 the nature of variation in reaction norm parameters is essential for both selection and, to the  
14 extent that this variation has a genetic basis, the evolutionary response to selection (e.g., Lande  
15 2009). Despite a growing number of studies measuring reaction norm parameters in natural  
16 populations (e.g., Dingemanse & Wolf 2013), many important aspects of reaction norms and the  
17 way they vary within and among populations remain poorly understood (e.g., Husby et al. 2010).

18 Consider the number of eggs laid by birds per breeding attempt, or clutch size, which is an  
19 important component of life history that varies substantially both between and within species  
20 (e.g., Lack 1947; Martin 1987; Crick, Gibbons & Magrath 1993; Bennett & Owens 2002). There  
21 is growing evidence that this trait is phenotypically plastic—individuals within a population  
22 produce different clutch sizes in different breeding attempts (van Noordwijk 1989; Postma & van  
23 Noordwijk 2005; Westneat, Stewart & Hatch 2009; Husby et al. 2010) or in response to

1 manipulated environmental conditions (e.g., Boutin 1990; Nager, Rueger & van Noordwijk  
2 1997; Clifford & Anderson 2001). This plasticity appears adaptive because females usually alter  
3 the size of their clutch in the direction expected to maximize the number of surviving offspring  
4 (Perrins 1965; Drent & Daan 1980).

5 As an example, clutch size in many bird species declines with clutch initiation date (Klomp  
6 1970; Drent & Daan 1980; Murphy 1986; Brommer, Pietiäinen & Kokko 2002). Declining clutch  
7 size with date could be a result of among-individual variation in condition; individuals in good  
8 condition can breed early and also produce large clutches whereas those in poor condition breed  
9 later and produce small clutches (Rowe, Ludwig & Schluter 1994; Verhulst & Nilsson 2008).  
10 Alternatively, such declines could reflect phenotypic plasticity if individuals adjust clutch size in  
11 response to time of season (Drent & Daan 1980; Verhulst & Nilsson 2008). Such plasticity could  
12 be adaptive for two different reasons. First, resources needed for producing eggs and raising  
13 offspring may deteriorate late in the season. Second, in many bird populations offspring that are  
14 produced late in the season recruit less often into the breeding population than offspring  
15 produced earlier (Perrins 1970, Drent & Daan 1980), perhaps because they are insufficiently  
16 developed to deal with stressful conditions such as the onset of winter. This effect of a time  
17 horizon on the production of offspring could interact with differences in female quality to  
18 produce the relationships between female breeding date and clutch size. The results from  
19 correlational and experimental studies suggest that both between-individual differences in quality  
20 and within-individual flexibility in the face of changes in environment may influence seasonal  
21 patterns of clutch size variation (e.g. Verhulst & Nilsson 2008).

22 Rowe, Ludwig & Schluter (1994) made predictions about plasticity in clutch size and timing  
23 of breeding from a model incorporating the time horizon hypothesis. Two studies have tested

1 some of these predictions. First, Brommer, Pietiäinen & Kokko (2002) showed that in Ural owls  
2 (*Strix uralensis*), differences in food supply altered the effect of date on recruitment rate of  
3 offspring. The Rowe et al. model predicts that when recruitment rate declines faster with date, so  
4 should the relationship between date and clutch size. However, Brommer, Pietiäinen & Kokko  
5 (2002) found the opposite pattern.

6 Rowe et al. presented a modified set of predictions for organisms that have multiple breeding  
7 attempts within a season. Westneat, Stewart & Hatch (2009) tested these predictions using a  
8 long-term dataset from house sparrows (*Passer domesticus*). Using a mixed model approach,  
9 Westneat, Stewart & Hatch (2009) found that, as Rowe et al. had predicted, clutch size declined  
10 with date, increased with attempt order within a season after controlling for date, and the effect  
11 of date became more negative as attempt order increased. Their analysis also showed that other  
12 factors, not included in the Rowe et al. model, also predicted clutch size. These included a  
13 negative quadratic effect of date (expected if seasonal resource levels at first increase and then  
14 decrease), a positive effect of female age, and a persistent effect of female identity. If these  
15 attributes of the clutch size reaction norm are widespread, then additional parameters would need  
16 to be incorporated into a general model of the timing of breeding and clutch size.

17 The house sparrow has a nearly global distribution, with long-established populations in  
18 western Asia and throughout Europe and variably-established introduced populations in North  
19 America, South America, Africa, and Australia. The species also breeds from the equator to just  
20 south of the Arctic circle and just north of the Antarctic Circle in both mainland and island  
21 locales (Anderson 2006). This wide distribution and the habit of producing multiple clutches per  
22 season offer an unusual opportunity to compare multiple populations to assess several  
23 predictions about the evolution of reaction norms in general and the forces affecting plasticity of

1 clutch size in particular. First, to be under selection, reaction norms must exhibit within-  
2 population variation in slope (e.g., Postma & van Noordwijk 2005; Nussey, Wilson & Brommer  
3 2007). Second, if selection on plasticity is driven by general features of the life history of the  
4 organism, then regardless of population, the multidimensional reaction norm uncovered in a  
5 single population by Westneat, Stewart & Hatch (2009) should be present in all populations.  
6 Third, if plasticity is driven by ecological conditions affecting either the amount of food  
7 available to raise offspring or a time horizon for their recruitment, populations differing in  
8 ecology should exhibit predictably different reaction norms, possibly in both elevation and slope.  
9 In particular, because the work of Rowe, Ludwig & Schluter (1994) was focused on the idea that  
10 if offspring fitness and thus the reproductive value of an egg declines as lay date approaches the  
11 end of the season, clutch sizes in populations with shorter seasons should display a steeper  
12 decline with date and a stronger interaction with attempt order. The alternative hypothesis, that  
13 clutch size decreases because food resources necessary to produce eggs or raise young increase  
14 early in the season and decrease late (e.g., Lack 1947), predicts that populations with different  
15 seasonality would differ in the quadratic effect of date. Finally, the distribution of house  
16 sparrows worldwide is a mix of populations that are either native or introduced as well as insular  
17 or continental. We asked if the magnitude of among-individual variation differed among  
18 populations, which might suggest differences in genetic structure or the presence of additional  
19 environmental variables affecting the plasticity of clutch size.

## 20 Methods

### 21 Data set

22 We analyzed data on clutch size from individually marked or otherwise known female house  
23 sparrows from 8 multi-year studies distributed in North America and Europe (Table 1): Chizé



1 (France), Helgeland (Norway), Hoedic (France), Kentucky (USA), Lundy Island (UK),  
2 Nottingham (UK), Oklahoma (USA), and Veszprém (Hungary). At all sites, females were  
3 individually marked with either a numbered metal band, a unique combination of color bands on  
4 their legs, or both. Females were captured using seed-baited traps (Kentucky: Westneat, Stewart  
5 & Hatch 2009), mist-nets (Helgeland: Jensen et al. 2008; Veszprém: Bókonyi et al. 2008), or  
6 some combination of methods (Chizé: Chastel & Kersten 2002, Lendvai & Chastel 2010;  
7 Hoedic: Bichet et al. submitted; Lundy Island: Cleasby et al. 2010; Nottingham: Burke 1984;  
8 Oklahoma: Schwagmeyer, Mock & Parker 2002). In 7 of the 8 populations, females bred in  
9 artificial nest boxes but in the Helgeland population females nested in cavities and crevices in  
10 farm buildings and other man-made structures. In all populations, nests were checked at least  
11 once per week beginning in early spring continuing all summer. Clutch completion and final  
12 clutch size was indicated by the same number of eggs on two successive checks or information  
13 (such as the timing of hatching) that indicated a check occurred in the middle of incubation  
14 (sparrows incubate for 10-11 days following clutch completion, Anderson 2006). The Hoedic  
15 population was followed through the first two attempts but not through the end of breeding, so it  
16 was removed from some analyses. For 7 of the 8 populations, females were assigned to nest  
17 attempts based on them being observed repeatedly entering or standing on the nest box during  
18 incubation or nestling provisioning, or being captured in the box. In some cases in each  
19 population, the female was not observed at a particular clutch, but was assigned that clutch based  
20 on the fact that she nested there during the previous or subsequent attempt (or both), and there  
21 were no unusual disruptions or long intervals between attempts to suggest there had been a  
22 change in ownership. In the Helgeland population, females were assigned to nests by use of  
23 microsatellite analysis of DNA collected from females and nestlings (Jensen et al. 2008).

1 Clutches at Helgeland that failed to hatch therefore could not be assigned except if they were at  
2 the same site and timed in between two other clutches of the same female.

3 All clutches were assigned an attempt order, referring to their position in the series of  
4 clutches produced by a known female in that season. For nearly all clutches in all populations,  
5 we also determined the date that the first egg of the clutch was laid. For clutches checked during  
6 laying, this was deduced from the fact that house sparrows lay 1 egg per day (Anderson 2006).  
7 For successful clutches that were not checked until laying had been completed, we inferred the  
8 date the first egg was laid based upon the date they hatched, assuming an 11-day incubation  
9 period between the laying on the penultimate egg and hatching (Anderson 2006). For clutches  
10 that never hatched but had been checked at least twice during incubation, we estimated date of  
11 first egg as the midpoint of the period between the earliest and latest possible date of first egg.  
12 Breeding season was estimated as the range in days between the first egg date of the first clutch  
13 and that of the last clutch in that season.

14

#### 15 Statistical analysis

16 Each clutch laid by each female was considered an observation and in total we amassed data on  
17 4871 breeding attempts, with 42 attempts omitted because of unknown clutch sizes due to gaps  
18 in egg-laying or nest failure before a final clutch size could be determined. We analyzed the  
19 variation in clutch size using linear mixed-effects models with restricted maximum likelihood  
20 estimation and a Gaussian error structure (clutch size does not arise from a Poisson process, is  
21 not distributed as a Poisson variable, and so is not appropriately modeled as a Poisson despite  
22 being a count variable). We checked the distribution of residual error in the global model and

1 found it to fit well with expectation of normality. Over 80% of the residuals behaved as  
 2 expected, with only a slight excess of small residuals (Figure S1).

3 The initial model of the  $i^{\text{th}}$  clutch ( $Y_{ijk_g}$ ) included three random intercept effects  
 4 representing the hierarchical nature of the data, and so is useful to understand at what levels key  
 5 parameters affecting variation in clutch size may act. The three random intercepts included  
 6 effects of the  $g^{\text{th}}$  population ( $pop_{0g}$ ), the  $k^{\text{th}}$  year nested within population ( $year_{0kg}$ ) and the  $j^{\text{th}}$   
 7 individual nested within population ( $ind_{0jg}$ ):

$$8 \quad Y_{ijk_g} = (\beta_0 + pop_{0g} + year_{0kg} + ind_{0jg}) + e_{0ijk_g} \quad (1)$$

9 where  $e_{0ijk_g}$  is the residual clutch size (within-individual) for the  $i^{\text{th}}$  clutch, and  $pop_{0g}$ ,  $year_{0kg}$   
 10 and  $ind_{0jg}$  are all normally distributed with mean 0 and variance  $\sigma^2$ ,  $\sigma_{pop}^2$ ,  $\sigma_{year}^2$  and  $\sigma_{ind}^2$ ,  
 11 respectively. The statistical significance of a random effect was tested using the likelihood ratio  
 12 test (LRT) in which twice the difference in log-likelihood (-2dLL) between a model with the  
 13 random effect and a model lacking that term is distributed as a chi-square with 1 df (Pinheiro and  
 14 Bates 2000). We also tested for a difference between populations in the random effect of  
 15 individual by estimating the individual term for each population (e.g.,  $ind_{0j[g]}$ ). This required  
 16 estimating among-individual variance for all 8 populations (or 7 if we omit Hoedic from the  
 17 analysis) and so was tested using an LRT with 7 (or 6) df.

18 We tested for the effect of clutch initiation date and attempt order on the variation in  
 19 clutch size. Although clutch initiation date could be considered a second phenotype (e.g., Husby  
 20 et al. 2010), we treated it as an environmental variable because after the first clutch of the season,  
 21 subsequent clutch initiation dates are affected by an array of new variables that complicate a  
 22 multivariate analysis. We created two variables for each of these factors allowing us to assess

1 between- and within-individual differences in initiation date and attempt order (e.g., van de Pol  
 2 and Wright 2009). To assess among-individual variance in both variables, we calculated the  
 3 mean clutch initiation date and mean attempt order over all clutches produced by each female.  
 4 We centered these values (so that intercepts would be estimated at the mean) by subtracting the  
 5 yearly population mean date and attempt order from each value (mean-centered-between, or B).  
 6 To assess within-individual variance, we subtracted the female's mean date and attempt order  
 7 from that of each of her clutches (mean-centered-within or W). These variables allowed us to  
 8 assess clutch size plasticity in response to clutch initiation date, attempt order, and their  
 9 interaction, and control for between-individual biases in both variables, as depicted in the  
 10 following model:

$$\begin{aligned}
 Y_{ijk g} = & \beta_0 + pop_{0kg} + year_{0kg} + ind_{0jg} + \\
 & \beta_1 \cdot dateB_{jk g} + \beta_2 \cdot attemptB_{jk g} + \beta_3 \cdot dateW_{ijk g} + \beta_4 \cdot attemptW_{ijk g} + \\
 & \beta_{12} \cdot dateB_{jk g} attemptB_{jk g} + \beta_{13} \cdot dateB_{jk g} dateW_{ijk g} + \\
 & \beta_{24} \cdot attemptB_{jk g} attemptW_{ijk g} + \beta_{34} \cdot dateW_{ijk g} attemptW_{ijk g} + \\
 & \beta_{44} \cdot dateW_{ijk g} dateW_{ijk g} + e_{0ijk g} \quad (2)
 \end{aligned}$$

12 The variables of within-female date (*dateW*) and within-female attempt order (*attemptW*)  
 13 were strongly positively correlated ( $r = 0.87$ ). This raised concerns that collinearity would  
 14 produce spurious results in the analysis. We assessed this by running maximum likelihood  
 15 models omitting one or the other of those variables and comparing AIC values. Removing either  
 16 within-female date or within-female attempt produced substantially larger AIC values ( $\Delta AIC >$   
 17  $2$ ), indicating that including both improved model fit despite the strong correlation between  
 18 them. We proceeded to analyze both terms together with their interactions, but we also checked

1 AIC values of models lacking the within-individual date or attempt order to ensure their  
2 contribution was not influenced by this correlation.

3 To test the idea that population might influence specific dimensions of the reaction norm,  
4 model 2 was modified to include population as a fixed effect, where both the main effect of  
5 population as well as interaction terms with all three within-individual terms (within-individual  
6 mean centered date, attempt order, and their interaction) were added. To test specific differences  
7 between populations in characteristics (e.g., season length) we altered model 2 by adding season  
8 length and its interactions with within-individual date and attempt order as fixed effects.

9 All analyses were conducted in SAS 9.2 (SAS Institute 2008). Fixed effects were tested  
10 using F-tests with denominator degrees of freedom estimated with the Kenward-Roger method.

11

## 12 Results

### 13 Patterns of variance

14 The 4829 clutches averaged 4.6 eggs and the variance in clutch size over the entire dataset was  
15 0.85. Clutch size, dates of first egg, and number of attempts per season and per female varied  
16 among the 8 populations (Table 1). A model partitioning the variance in clutch size into that  
17 among populations, among years within populations, and among individuals within populations  
18 revealed significant variance of all three random effects (Model 1, Table 2).

19

### 20 Reaction norm for clutch size

21 Linear mixed model analysis confirmed the basic multi-dimensional reaction norm reported for  
22 Kentucky sparrows by Westneat, Stewart & Hatch (2009). In the full dataset of all 8 populations,

1 clutch size declined linearly within females with date, also showed a negative quadratic with  
2 date, independently increased with attempt order, and the decline in date was more negative as  
3 attempt order increased (Table 3). We assessed whether these patterns were driven by the KY  
4 data by testing the model without them. However, the results were qualitatively the same as  
5 those from the full analysis (i.e., all effects were in the same direction and remained statistically  
6 significant; results not shown).

7 We also controlled for individual differences within populations in mean number of  
8 attempts and dates of clutch initiation. Females with a larger average attempt order (more  
9 attempts per season) produced larger clutches (*attemptB*, Table 3), and those with a later average  
10 date of clutch initiation produced smaller clutches (*dateB*, Table 3). Individual females with a  
11 later average date of clutch initiation also showed a steeper decline in clutch size as within-  
12 individual date progressed (*dateB* by *dateW*; Table 3).

#### 14 Population differences in reaction norm

15 Populations differed in several elements of the reaction norm. Because the Hoedic population  
16 was not fully studied through the entire breeding season, we omitted it from these analyses.

17 Populations had significantly different mean clutch sizes ( $F_{6,60.9} = 18.0$ ,  $P < 0.0001$ , Table S1) and  
18 differed significantly in the relationship between date and clutch size within females (Table S1,  
19 Figure 1; *dateW* by population interaction:  $F_{6,3537} = 10.8$ ,  $P < 0.0001$ ). In five of the seven  
20 populations, clutch size decreased significantly with date within females (Table S1). Both  
21 Helgeland and Nottingham exhibited a non-significant positive association between clutch size  
22 and date within females. Population identity did not affect the magnitude of the effect of attempt  
23 order ( $F_{6,3790} = 1.4$ ,  $P = 0.21$ , Table S1), which was positive in all populations. The interaction

1 between date and attempt order was negative in all but one population (Chizé) but did not differ  
2 among populations ( $F_{6,4574} = 1.6$ ,  $P = 0.13$ ). The non-linear effect of within-individual variation in  
3 date was negative in 5 of 7 populations (positive in Helgeland and Veszprém) but also did not  
4 differ significantly among populations ( $DateW^2$ ;  $F_{6,4521} = 1.3$ ,  $P = 0.22$ ).

5 We tested whether variation in the length of the breeding season influenced elements of  
6 the clutch size reaction norm. We altered the model presented in Table 3 in three ways and ran  
7 the modified model to test this idea. First, we dropped all fixed effects terms that were not  
8 significant. Second, we added season length for each year within each population as a continuous  
9 covariate. Finally, we added a season length by within-individual date interaction term. This  
10 analysis thus tested the impact of variation in season length, combining both within and between  
11 population effects on the term whose impact varied significantly among populations.

12 We found no main effect of season length on clutch size ( $-0.001 \pm 0.003$ ,  $F_{1,55.9} = 0.3$ ,  $P =$   
13  $0.58$ ). However, we found that the negative impact of within-individual date was significantly  
14 more negative as season length increased (Season length by date:  $-0.00009 \pm 0.00002$ ,  $F_{1,3586} =$   
15  $23.9$ ,  $P < 0.0001$ ), a result that is hinted at in Figure 1 (which shows only between-population  
16 differences in season length). While adding season length had little qualitative effect on most  
17 other terms (fixed and random) in the model shown in Table 3, two fixed terms were  
18 substantially different. The significantly negative effect of within-individual date entirely  
19 disappeared ( $0.003 \pm 0.003$ ,  $F_{1,3611} = 1.2$ ,  $P = 0.28$ ) and the significant negative effect of the  
20 interaction between within-individual date and attempt order became non-significant ( $-0.002 \pm$   
21  $0.003$ ,  $F_{1,4239} = 0.6$ ,  $P = 0.45$ ).

22

23 Among-individual variance in reaction norm parameters

1 As was found in Westneat, Stewart & Hatch (2009), female identity explained a significant  
2 portion of the variance in clutch size (Table 2) and this persisted regardless of the fixed effects  
3 included in the models. In contrast to Westneat, Stewart & Hatch (2009), here we controlled for  
4 potential biases due to individual females producing clutches at different times in the season or  
5 having different numbers of attempts. Both individual mean date of clutch initiation and  
6 individual mean attempt order had significant effects on clutch size (Table 3), but both had  
7 roughly similar effect sizes as within-female date and attempt order, suggesting that they may  
8 arise from the same underlying reaction norm. Despite this, female identity (random effect of  
9 individual in model shown in Table 3) continued to have a significant effect on variance in clutch  
10 size, accounting for 14% (0.12) of the total variance (0.85) in clutch size.

11 We tested if among-individual variance in clutch size differed between populations by  
12 comparing a modification of the model in Table 3 (population omitted as a random effect,  
13 included as a fixed effect along with population by *dateW*) with one in which the random effect  
14 of female identity was split into separate estimates from each of the 8 populations (Figure 2). A  
15 likelihood ratio test revealed that the model with the separate population estimates was a  
16 significantly better fit than one with a single estimate of among-female variation ( $-2\text{dLL} = 23.3$ ,  
17  $\text{df} = 7$ ,  $P = 0.0006$ ), indicating that populations differed in among-female variance in clutch size  
18 after controlling for within-individual plasticity and between-individual differences in timing.  
19 The model could not estimate variance in the Nottingham population (Figure 2), possibly due to  
20 small samples sizes for both the number of individuals and the number of clutches per individual.

21 We also assessed potential among-individual variance in slopes with respect to both date  
22 and attempt order by adding a random slope term to the model. We found no evidence for  
23 differences in individual slope with respect to date (mean-centered within; estimate =  $0.00006 \pm$



1 0.00005,  $-2dLL = 2.4$ ,  $df = 2$ ,  $P = 0.30$ ). We also found no evidence that the multidimensionality  
2 of the reaction norm due to the interaction between date and attempt order varied among  
3 individuals ( $-2dLL = 0.3$ ,  $df = 2$ ,  $P = 0.86$ ). By contrast, we found significant between-individual  
4 differences in slope with respect to within-individual attempt order ( $0.014 \pm 0.006$ ,  $-2dLL = 9.3$ ,  
5  $df = 2$ ,  $P = 0.01$ ), with the estimated covariance between slope and intercept slightly negative ( $-$   
6  $0.004 \pm 0.007$ ). Estimating the individual random slope term for each population did not  
7 significantly improve the fit of the model ( $-2dLL = 6.8$ ,  $df = 6$ ,  $P = 0.34$ ).

## 8 9 Discussion

10 Our results from multiple populations confirm that clutch size in house sparrows exhibits a  
11 complex form of phenotypic plasticity in which the reaction norm is a warped plane in  
12 multidimensional environmental space. This reaction norm varies among populations but not in  
13 the way predicted by either of two hypothesized forces thought to drive selection on the shape of  
14 the optimal reaction norm. Populations also differed in the nature of individual variation in  
15 reaction norm parameters, and, if this variation had a genetic basis, these differences could affect  
16 the ways in which reaction norms could respond to selective pressures acting within those  
17 locales. Thus our results have implications for understanding the evolution of reaction norms in  
18 general and the specific forces potentially acting on plasticity in clutch size in birds. We explore  
19 these implications in more detail.

## 20 Comparative analyses of reaction norms

21 The clutch size reaction norm, as measured across 8 populations of house sparrows,  
22 exhibits several intriguing properties. Perhaps not surprisingly from either a life history or

1 statistical perspective, populations differed in intercept (elevation) and there was significant  
2 repeatability of elevation within individuals across all populations after controlling for some  
3 potential biases due to plasticity. Elevation represents the mean clutch size at the intersection of  
4 the mean environments included in the model. Not only are differences in means easier to detect  
5 statistically than are slopes, but populations may differ more in mean aspects of food availability  
6 and climate than in their timing, and these factors may have a clearer effect on means than on  
7 slopes.

8 We also found that the level of repeatability in clutch size differed between populations.  
9 Because within-population, among-individual variation affects the nature of selection and could  
10 reflect the level of underlying genetic variation (Nussey, Wilson & Brommer 2007), differences  
11 in repeatability can affect evolutionary potential. Between-individual differences in any  
12 phenotypic trait could arise from two sources: genetic variation or unaccounted phenotypic  
13 plasticity. The characteristics of populations showing high among-individual variance support  
14 the latter hypothesis over the former for two main reasons. First, North American (introduced)  
15 populations of house sparrows have somewhat lower levels of genetic diversity (as measured at  
16 presumably neutral microsatellite loci) than do European populations (Schrey et al. 2011).  
17 However, Kentucky has the second highest among-individual variance in clutch size, whereas  
18 Oklahoma is intermediate, suggesting that reduced level of neutral genetic variation is not  
19 associated with reduced individual differences in clutch size. Assuming that variation at neutral  
20 loci reflects variation at loci affecting clutch size (supported by recent data from one of the  
21 studied populations, Hagen et al. in press), this would argue against a genetic explanation for  
22 differences in repeatability. Island populations also generally have lower levels of genetic  
23 variation than mainland populations in many species (e.g., Frankham 1997). However, we found

1 that the Helgeland population, located on an island, had the highest level of among-individual  
2 variation. The other two smaller (in area) islands (Lundy Island and Hoedic) had intermediate  
3 levels of among-individual variation, similar to the mainland populations of Oklahoma,  
4 Veszprém, and Chizé.

5 A second reason for suspecting that population-level differences in between-individual  
6 variation may be due to unaccounted plasticity is that populations differed in several variables  
7 that contributed to phenotypic plasticity in clutch size. For example, based on the number of  
8 years bred, populations might vary in their age distributions (Table 1). For example, in  
9 Kentucky, females bred for 1-6 years, whereas in Nottingham the maximum was 2 years. It is  
10 likely the differences in ranges reflect the length of the study, but it is nevertheless possible that  
11 age distributions varied among the populations. Clutch size increased with number of years  
12 present in our data set (model as in Table 3 with addition of female years and the Nottingham  
13 population omitted;  $F_{1,3472} = 42.8$ ,  $P < 0.0001$ ), but this did not eliminate the differences between  
14 populations in among-female variance ( $-2dLL = 15.1$ ,  $df = 5$ ,  $P < 0.01$ ). Nevertheless, females in  
15 some locations could be experiencing a wider range of other environmental conditions. Because  
16 we have not accounted for all environmental factors in our analysis, it seems likely that  
17 differences in environmental variance may be the cause of population differences in between-  
18 individual variance.

19 The evolution of plasticity requires variation in reaction norm slope, and our results  
20 suggest complexity in patterns of variation in slopes. An especially interesting element of the  
21 sparrow clutch size reaction norm is the interaction between date and attempt order. In most  
22 populations this is negative (although it is significantly so in only two, Table S1), meaning that  
23 as females have produced more prior clutches, the greater the negative effect of date. This

1 interaction term produces the non-additive feature of the multidimensional reaction norm and is a  
2 unique prediction of the Rowe, Ludwig & Schluter (1994) model of optimal clutch size. To  
3 evolve, there must be within-population variation in this interaction, but we found no support for  
4 individuals differing in this parameter of the reaction norm. We strongly suspect this is an issue  
5 of statistical power rather than of biology; while we have data on a total of 1512 females, for  
6 only 107 females did we have 3 or more clutches (sufficient to measure slope with some residual  
7 variance) for each of 3 attempt orders. To reduce the impact of sampling variance on the residual  
8 variance, we would need even more clutches per attempt order, and consequently sample size  
9 drops considerably. Power to detect among-individual variation in this parameter of the reaction  
10 norm is thus likely to be quite low (e.g. van de Pol 2012).

11 Our power to detect variance among individuals in univariate slopes is considerably  
12 greater and our results from these analyses raise some interesting questions regarding the  
13 evolution of plasticity. First, we found that populations differed significantly in the average slope  
14 of clutch size with date. Divergence in slope is expected if plasticity is under different selection  
15 pressures in different populations. Divergent selection and an evolutionary response are only  
16 possible if there are individual, heritable, differences in slope, yet we failed to detect significant  
17 among-individual variation in this slope. We did uncover significant among-individual variation  
18 in slope with respect to attempt order, but found no evidence of among population variance in  
19 slope. Thus our results seem to indicate a paradoxical situation; for the parameter of the clutch  
20 size reaction norm (slope with respect to date) that appears to have diverged between  
21 populations, there is no evidence of the individual variation within populations that is necessary  
22 for selection to lead to such divergence. Conversely, for the parameter of the reaction norm

1 (slope with respect to attempt order) that exhibits the necessary variance among individuals, no  
2 divergence between populations has apparently occurred.

3         There are many possible explanations for this situation, but we focus on two that seem  
4 especially interesting. One is that slope with respect to attempt order is under little or no  
5 selection in all populations, thereby retaining individual variation and limiting divergence,  
6 whereas slope with respect to date is under strong stabilizing selection with some directional  
7 selection and the combination has eliminated present sources of individual variation but lead to  
8 divergence. Testing this would require data on selection and heritability (additive genetic  
9 variance) of clutch size from each population, which we do not have at present. Another  
10 hypothesis that deserves more attention in cases of plasticity is the action of additional,  
11 unaccounted environmental variables. Most studies of reaction norms assess slopes in only a  
12 single environmental axis (Pigliucci 2001; Brommer, Pietiäinen & Kokko 2002; Postma & van  
13 Noordwijk 2005; Nussey, Wilson & Brommer 2007). We explicitly analyzed the clutch size  
14 reaction norm as a plane in bivariate environmental space. Westneat, Stewart & Hatch (2009)  
15 considered additional environmental variables (e.g., precipitation) but found no phenotypic  
16 association. It is conceivable, however, that clutch size responds to variables that are not  
17 captured by either date or attempt order. If these differ among populations in ways that generate  
18 both differences between individuals within populations and average effects that differ between  
19 populations, then n-dimensional plasticity could explain the patterns of variation we observed.  
20 Testing this idea would require a more detailed understanding of the ecology of clutch size and  
21 within-population plasticity to identify this unknown variable (or variables) and measurements of  
22 them within and among populations.

23 The life history of fecundity

1           Our results raise new questions about the life history of fecundity. We tested if the  
2 differences between populations in reaction norm slopes with respect to date (Table 3, Figure 1)  
3 might support the Rowe, Ludwig & Schluter (1994) model of optimal fecundity. We reasoned  
4 they would be consistent with Rowe et al. if the more negative influence of date occurred in  
5 populations with shorter breeding seasons. We found the opposite; the steeper decline in clutch  
6 size occurred in populations with longer breeding seasons. This result raises questions about the  
7 decline in offspring fitness with date, the assumption underlying the structure of the Rowe et al.  
8 model. Data on recruitment rate have been published for two of the populations studied; in  
9 Helgeland, Ringsby et al. (2002) found that recruitment probability increased initially and then  
10 declined with hatch date (Husby et al. 2006). In Oklahoma, recruitment rate strongly declines  
11 with date (Schwagmeyer & Mock 2008). This is an intriguing coincidence given the  
12 relationships between clutch size and date in the two populations (Figure 1), with Helgeland  
13 having a flat relationships and Oklahoma steeply negative.

14           Our results lead us to re-evaluate the underlying biology of the Rowe et al. model. One  
15 possibility is that Lack's (1947) classic hypothesis for clutch size, that parents match clutch size  
16 to the number of offspring they can expect to raise based on projected food supply, is more  
17 influential than effects of a time horizon. For most bird populations, the amount of food available  
18 for nestlings (primarily insects) likely begins to increase in early spring then decreases in late  
19 summer, and so the size of clutches that females produce is expected to parallel this change. Our  
20 data lend only partial support to this idea. First, the expected negative quadratic relationship  
21 between date and clutch size existed across all populations. However, there was no evidence the  
22 quadratic relationship varied among the populations, despite the apparently large differences in

1 the season lengths and climate. Thus the Lack hypothesis also appears inadequate to explain the  
2 differences among populations in reaction norm.

3 Alternatively, the key relationship modeled in the Rowe et al model may be more  
4 complex than they assumed. Brommer, Pietiäinen & Kokko (2002) noted that relatively subtle  
5 differences in the relationship of offspring fitness with date could have large effects on the  
6 outcome of the Rowe, Ludwig & Schluter (1994) model. The model can be simplified to the  
7 following equation, which is the condition that must be met for the optimal time-clutch  
8 combination:

$$9 \quad \frac{C'(t)}{C(t)} = \frac{V'(t)}{V(t)} \quad (3)$$

10 where  $C(t)$  is the clutch size at time  $t$  and  $V(t)$  is the recruitment probability at time  $t$ , and  $C'$   
11 and  $V'$  are the rates of change in clutch size or recruitment probability with  $t$ . In our analysis of  
12 variation in breeding season length and clutch size, we assumed that  $V(t) = 0$  at the end of the  
13 breeding season and that peak recruitment ( $\max V(t)$ ) was the same in all populations; thus  
14 season length would be collinear with  $V'(t)$ . Brommer, Pietiäinen & Kokko (2002) noted in their  
15 study that differences in  $\max V(t)$  alone could create differences in  $C'(t)$ . This could affect our  
16 results as well. However, Rowe, Ludwig & Schluter (1994) assumed that parents stop breeding  
17 when  $V(t) = 0$ . We suggest that this assumption may be invalid because other factors may  
18 influence when parents stop breeding, ensuring that  $V(t)$  does not equal zero and altering the  
19 relationship between  $V'(t)$  and season length. For example, if independent offspring must have  
20 time to acquire skills at finding food (seeds) before peak times of food stress (e.g., Loman 1982,  
21 Hochachka 1990), then it is possible the decline in offspring fitness over the breeding season  
22 depends on when this food stress occurs relative to the end of the breeding season. If the insect

1 food fed to nestlings declines early such that parents cease breeding long before the period of  
2 food stress that juveniles might experience, then breeding date may have little impact on clutch  
3 size. The relative timing and rate of declines in insect food and periods of food stress could  
4 produce complex differences in reaction norms for clutch size between populations.

5 Alternatively but similarly, house sparrows molt once per year in autumn (Anderson 2006). Late-  
6 hatched juveniles might experience increased mortality if their molt is delayed into increasingly  
7 colder weather or if they have to molt quickly and produce poorer feathers as a result. As with  
8 the first hypothesis, differences between populations in when breeding ceases and when molt is  
9 optimal could create selection favoring a different decline in clutch size with date.

10 Other possibilities exist, although all of them would require more detailed information on  
11 the underlying basis of presumed seasonal declines in recruitment. Such data are not presently  
12 available for the populations in this study. Moreover, the details are likely to be complex.

13 Consider the Oklahoma population, the southernmost locale in our analysis. Females there  
14 started breeding early in the season, but also ceased breeding early (Table 1). Breeding in this  
15 population typically stalls in early July, possibly because the hot and dry conditions of late July  
16 and August in Oklahoma limit suitable insect food for nestlings. Because of its southern location  
17 however, there is a long delay between breeding and cold weather. Because of this delay, we  
18 would expect that late-hatched juveniles should be in less of a time-crunch and so should have  
19 similar survival to early-hatched juveniles. The Rowe et al. model would thus predict that date  
20 would have little effect on clutch size in Oklahoma, but in fact the Oklahoma birds have the  
21 steepest decline with date. This implies that either our presumption about the timing of stressful  
22 conditions for juveniles (e.g., when cold weather arrives) is incorrect, or that other processes  
23 linked to date are affecting clutch size.



1 A mitigating factor in our analyses is that clutch size is likely to be part of an integrated  
2 phenotype (Pigliucci 2003) that includes when a female begins breeding within each season and  
3 how many attempts she has. In our analyses, we treated attempt and date as environmental  
4 factors, but some of their variation is likely due to variation in female phenotype. For example,  
5 the timing of a female's first attempt of the season also exhibits phenotypic plasticity and shows  
6 among-individual variance in plasticity (e.g., Brommer et al. 2005; Brommer, Rattiste & Wilson  
7 2007; Husby et al. 2010), which sometimes has a genetic basis (e.g., Charmantier et al. 2008).  
8 Earlier breeding in a multi-brooded species such as the house sparrow is typically associated  
9 with more attempts and earlier initiation dates for each attempt (Anderson 2006). Both date and  
10 attempt order in house sparrows are themselves traits that could also be sensitive to  
11 environmental conditions. Thus phenotypic integration of date of first breeding is likely to exist.  
12 If so, then among-individual variation in plasticity associated with date of first breeding (e.g.,  
13 spring temperature) could exist. Selection acting on the decision to start breeding may influence  
14 reaction norm shape for clutch size during later attempts. A looming challenge then is to assess  
15 the level of phenotypic integration within and among populations simultaneously with  
16 independent effects of environment on a trait like clutch size.

17

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For Review Only

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1 Table 1. Summary statistics on location, study duration, timing of breeding, and key variables  
 2 relevant to analysis of clutch size for 8 populations of house sparrows. Means  $\pm$  1 SD and ranges  
 3 given as appropriate (KY=Kentucky, OK=Oklahoma).

4

Variable	Population							
	Chizé	Helgeland	Hoedic <sup>2</sup>	KY	Lundy	Nottingham <sup>1</sup>	OK	Veszprém
Latitude	46N 8' 50"	66N 32' 16"	47N 20' 24"	38N 6' 42"	51N 9' 53"	52N 56' 51"	35N 23' 00"	47N 05' 32"
Longitude	0W 25' 29"	12E 50' 58"	2W 52' 42"	84W 29' 51"	4W 39' 44"	1W 05' 45"	97W 45' 00"	17E 53' 43"
Years	2005-2007	2003-2008	2008-2010	1992-2011	2000-2012	1980-1982	2000-2006	2005-2009
Clutches	250	286	81	2125	1220	172	527	168
Clutch size	4.9 $\pm$ 0.8	5.0 $\pm$ 1.0	4.5 $\pm$ 0.8	4.9 $\pm$ 0.9	4.2 $\pm$ 0.8	4.2 $\pm$ 0.7	4.4 $\pm$ 0.8	4.7 $\pm$ 0.8
Date of first egg (Julian)	138 $\pm$ 24 96-199	154 $\pm$ 25 107-212	139 $\pm$ 19 112-176	141 $\pm$ 37 60-220	155 $\pm$ 31 88-224	150 $\pm$ 29 102-222	139 $\pm$ 31 80-207	142 $\pm$ 30 90-210
Attempts per female per season	1.6 $\pm$ 0.6 1-3	1.8 $\pm$ 0.7 1-4	1.5 $\pm$ 0.5 1-2	2.7 $\pm$ 1.2 1-6	2.3 $\pm$ 0.9 1-6	1.2 $\pm$ 0.5 1-3	1.9 $\pm$ 0.9 1-4	2.2 $\pm$ 0.9 1-4
Total attempts known per female	3.0 $\pm$ 1.5 1-6	3.7 $\pm$ 2.7 1-11	2.4 $\pm$ 1.4 1-6	7.3 $\pm$ 5.2 1-26	6.4 $\pm$ 3.9 1-17	1.2 $\pm$ 0.8 1-4	4.7 $\pm$ 3.5 1-14	2.8 $\pm$ 1.9 1-9
Years female bred	1.7 $\pm$ 0.7 1-3	1.9 $\pm$ 1.3 1-5	1.4 $\pm$ 0.6 1-3	2.3 $\pm$ 1.3 1-6	2.5 $\pm$ 1.3 1-6	1.1 $\pm$ 0.4 1-2	1.9 $\pm$ 1.1 1-5	1.3 $\pm$ 0.7 1-4

5 <sup>1</sup>Nottingham study occurred on 2 sites located 40 km apart in Nottinghamshire, England.

6 Coordinates are the midpoint between them.

7 <sup>2</sup>Hoedic population was not followed through the end of breeding in most years.

8

- 1 Table 2. Partitioning of variance in clutch size into components for 4829 clutches in 8  
 2 populations of house sparrows from a REML mixed model with 3 random intercepts and no  
 3 fixed effects (Model 1 in main text).

Variance component	Estimate $\pm$ SE	Likelihood ratio test*	P-value
Population	0.09 $\pm$ 0.05	55.7	<0.0001
Year (within Population)	0.01 $\pm$ 0.005	25.5	<0.0001
Individual (within Population)	0.11 $\pm$ 0.01	156.0	<0.0001
Residual (within individuals)	0.64 $\pm$ 0.02	-	-

- 4 \*Calculated from the fit of the complete model (log-likelihood = -6104) and a model lacking the  
 5 focal term (df = 1)

6

1 Table 3. Results of REML linear mixed model of clutch size from 4829 clutches produced by  
 2 1512 female house sparrows from 8 populations (Model 2 in text). Population, year within  
 3 population, and individual within population were included as random effects. Fixed effects were  
 4 mean-centered between-individual date (*DateB*) and attempt number (*AttemptB*) and their  
 5 interaction, mean-centered within-individual date and attempt (*DateW* and *AttemptW*,  
 6 respectively) and their interaction, the quadratic of *DateW*, and interactions of within- and  
 7 between-individual date and attempt order.

Factor	Effect $\pm$ SE	F-Statistic	df	P-value
Global intercept ( $\beta_0$ )	4.7 $\pm$ 0.01	-	-	-
<i>AttemptB</i>	0.25 $\pm$ 0.03	52.8	1, 1093	< 0.0001
<i>DateB</i>	-0.007 $\pm$ 0.001	48.2	1, 2080	< 0.0001
<i>DateB*AttemptB</i>	-0.001 $\pm$ 0.001	0.9	1, 2625	0.35
<i>AttemptW</i>	0.12 $\pm$ 0.03	13.8	1, 3820	0.0002
<i>DateW</i>	-0.009 $\pm$ 0.0008	111.9	1, 3806	< 0.0001
<i>DateW*AttemptW</i>	-0.003 $\pm$ 0.0008	13.2	1, 4341	0.0003
<i>DateW*DateW</i>	-0.00009 $\pm$ 0.00002	19.8	1, 4512	<0.0001
<i>DateB*DateW</i>	-0.0003 $\pm$ 0.00004	53.8	1, 3567	< 0.0001
<i>AttemptB*AttemptW</i>	0.008 $\pm$ 0.03	0.08	1, 3560	0.77

1 Figure Legends

2 Figure 1. Population average reaction norms of clutch size with respect to nest initiation date  
3 (mean centered within individual) for the 8 populations of house sparrows studied. Lines are  
4 plotted over the range of dates experienced by individuals in each population. Slopes are  
5 unadjusted for the influence of other variables and estimated slopes from LMM analysis differ  
6 slightly (see Table S1).

7

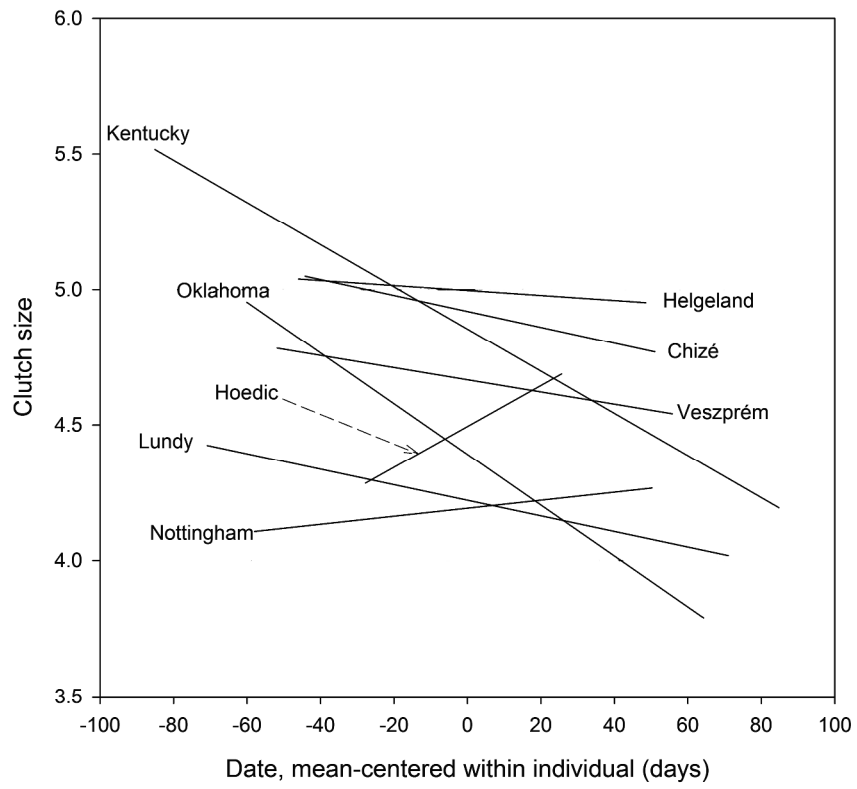
8 Figure 2. Estimates of population-specific among-individual variance in clutch size from the full  
9 REML mixed model including both within- and among-individual fixed effects (date and attempt  
10 order and their interaction; Table 3). Error bars are estimated standard errors.

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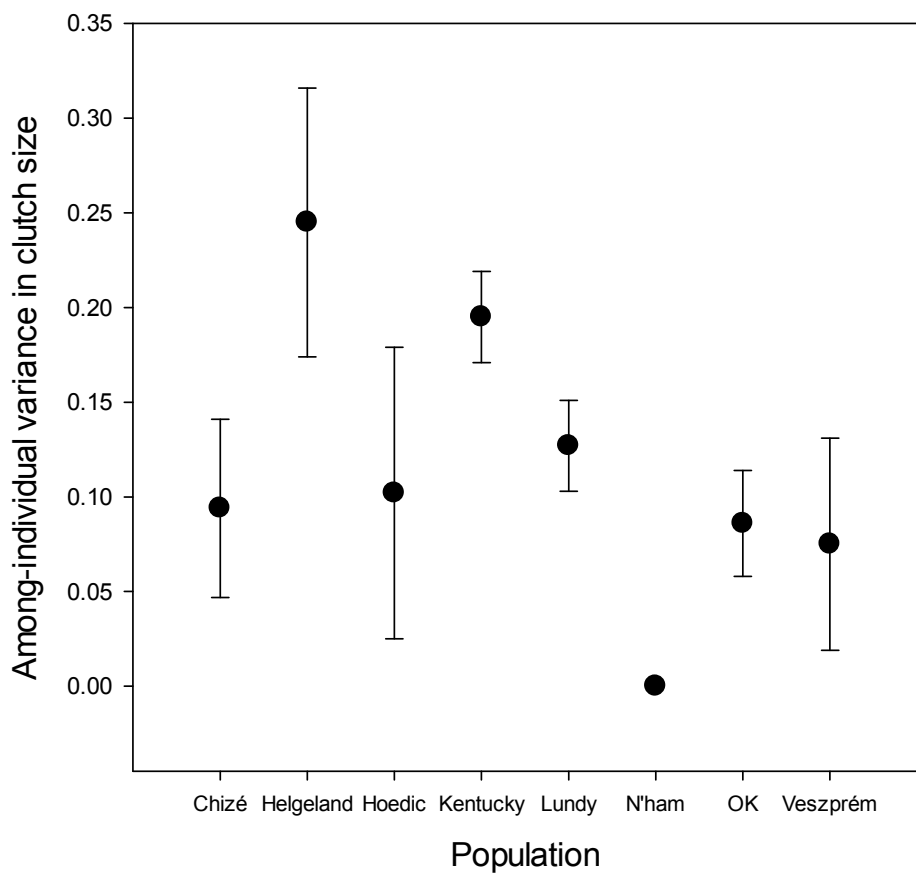
1 Figure 1



2

3

1 Figure 2



2