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1 **Heritability of gonad size varies across season in a wild song bird**

2  
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17  
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22 **Abstract**

23 Many organisms advance their seasonal reproduction in response to global warming. In  
24 birds, which regress their gonads to a non-functional state each winter, these shifts are  
25 ultimately constrained by the time required for gonadal development in spring. Gonadal  
26 development is photoperiodically-controlled and shows limited phenotypic plasticity in  
27 relation to environmental factors, such as e.g. temperature. Heritable variation in the time  
28 required for full gonadal maturation to be completed, based on both onset and speed of  
29 development, is thus a crucial prerequisite for an adaptive advancement of seasonal  
30 reproduction in response to changing temperatures. We measured gonadal seasonal  
31 development in climate-controlled aviaries for 144 great tit (*Parus major*) pairs, which  
32 consisted of siblings obtained as whole broods from the wild. We show that the extent of  
33 ovarian follicle development (follicle size) in early spring is highly heritable ( $h^2=0.73$ ) in  
34 females, but found no heritability of the extent of testis development in males. The heritability  
35 in females decreased as spring advanced, caused by increasing environmental variance and  
36 a decrease in additive genetic variation. Heritable variation in a physiological mechanism  
37 underlying reproductive timing may enable genetic adaptation to climate change, a key  
38 insight as this great tit population is currently under directional selection for advanced egg  
39 laying.

40

## 41 **Introduction**

42 The natural world is changing at an unprecedented rate in response to climate change  
43 (Parmesan & Yohe, 2003, Root et al., 2003, Walther et al., 2002), and global warming has  
44 led many organisms, most notably amphibians and birds, to reproduce earlier in the season  
45 (Beebee, 1995, Brown et al., 1999, Charmantier et al., 2008, Crick et al., 1997,  
46 Forchhammer et al., 1998, Visser et al., 1998). Small songbirds, which aim to time egg-laying  
47 such that the time of maximum nestling growth coincides with maximum food availability in  
48 their environment (Rowan, 1926, Lack, 1968), currently face the problem of an increasing  
49 mismatch of their breeding season with the short period of high food abundance in spring  
50 required to feed their young (Visser et al., 1998). This phenological mismatch may result in a  
51 disruption of population dynamics with wider implications for ecosystem functioning (Both et  
52 al., 2006, Møller et al., 2008, Jones & Cresswell, 2010, but see Reed et al., 2013).

53

54 Timing of egg-laying in birds of the temperate zone is affected by the developmental time of  
55 their reproductive physiology, as egg-laying can only occur following full gonadal maturation.  
56 Outside of the breeding season both male and female reproductive organs of so-called  
57 'seasonal' birds are fully regressed, presumably mainly as an energy saving strategy. This  
58 requires a subsequent period of slow gonadal growth that takes several months, typically  
59 starting in winter (e.g. Dawson, 2003, Dawson, 2005, Visser et al., 2011, Schaper et al.,  
60 2012b). Avian testes increase in size several hundred fold during this period of slow gonadal  
61 growth (Dawson et al., 2001). Seasonal birds use the annual cycle in photoperiod as a  
62 predictive cue to time gonadal growth (Dawson et al., 2001), culminating in full maturation in  
63 time for laying. In later developmental stages, other environmental cues may be used to  
64 determine the exact time of egg-laying (Schaper et al., 2012b, Dawson, 2008, Wingfield &  
65 Kenagy, 1991, Wingfield et al., 1992). Earlier egg-laying in warmer springs may suggest that  
66 temperature has an effect on the rate of gonadal maturation. However, this is not the case; in  
67 studies on starlings (*Sturnus vulgaris*, Dawson, 2005) and great tits (*Parus major*, Schaper et  
68 al., 2012b, Visser et al., 2011) exposed to a simulated natural increase in photoperiod during

69 spring, ambient temperature had no effect on the timing or rate of gonadal maturation. The  
70 observed temperature-related advancement of egg-laying itself has hence to be due to  
71 physiological processes or behavioural decisions taking place after full gonadal maturation.

72

73 With the more rapid warming of spring climate predicted by the Intergovernmental Panel for  
74 Climate Change (IPCC Core Writing Team, 2007), the fixed response of reproductive  
75 physiology to photoperiod might ultimately constrain the ability of birds to advance laying  
76 dates to compensate for the earlier appearance in food resources. In response to warming  
77 spring temperatures, egg-laying dates have already advanced by about two weeks compared  
78 to the situation in 1980 in a closely monitored population of great tits (Visser & Holleman,  
79 2001, Visser et al., 2006), yet this advancement is still not sufficient to fully compensate for  
80 the phenological shift in the environment and birds lay their eggs too late compared to the  
81 peak in their food resources (Visser & Holleman, 2001, Visser et al., 2006). As a  
82 consequence, timing of reproduction is currently under directional selection in this population  
83 (Reed et al., 2013, Husby et al., 2010). Spring is predicted to commence even earlier in  
84 coming decades, which would require egg laying at a time when at present gonadal growth is  
85 not yet completed. Genetic differences in the timing of full gonadal size, i.e. in either  
86 seasonal onset of gonadal maturation or in growth rate, are crucial to facilitate micro-  
87 evolutionary changes in egg-laying date which would allow a sufficient tracking of food  
88 phenology under a future climate change scenario.

89

90 If the seasonal timing of egg-laying is constrained by reproductive physiology, adaptation in  
91 egg-laying date can only occur if there is heritable variation in physiological responses to  
92 photoperiod. Quantitative genetic analyses have shown that the date that the first egg is laid  
93 is phenotypically plastic and fine-tuned in response to increasing spring temperatures, that  
94 individual females differ in their plasticity, and that this variation is heritable (Husby et al.,  
95 2011), but see (Brommer & Rattiste, 2008, Husby et al., 2010). However, we currently do not  
96 know which part of the process underlying egg-laying date is genetically variable. If genetic

97 variation is only present at the later stages after gonadal development, an evolutionary  
98 advancement of egg-laying dates would be constrained by the date of full gonadal  
99 maturation, which results from both onset and rate of gonadal development. While the ability  
100 to advance egg laying date within the time-window after full gonadal maturation is predicted  
101 to increase in the population, little is known about the potential to accommodate a necessary  
102 advancement of gonadal growth itself. Furthermore, the extent of gonadal development in  
103 late spring is currently only predicting a small part of the laying date variation (Schaper et al.,  
104 2012a). An analysis of the variation, plasticity and heritability of the reproductive physiology  
105 underlying timing of egg laying is currently lacking.

106

107 In this study, we aimed to measure variation and heritability in the extent of gonadal  
108 maturation (gonad size) in captive great tits of wild origins in response to photoperiod.  
109 Between 2007 and 2010, four separate experiments were carried out under controlled  
110 conditions to investigate the effects of different temperature regimes on the timing of full  
111 gonadal development and on gonadal growth rate. By applying a between-sibling  
112 comparison we demonstrate heritable variability in the extent of ovarian follicle growth in  
113 early spring in this songbird.

114

115

## 116 **Material and Methods**

117

### 118 **Birds**

119 In total, we used 144 one-year old great tit pairs in these experiments over four years. The  
120 birds were the offspring of 40 wild pairs (10 broods each year) from a long-term studied  
121 population that we chose for having either early or late laying dates (see scheme in Fig. 1).  
122 We selected parental pairs with known ancestors and large clutches of a balanced sex ratio.  
123 Paternity by the social father was verified (Saladin et al., 2003) before the chicks were hand-

124 raised under a standardized protocol from 10 days of age onwards (Drent et al., 2003), thus  
125 limiting an inflated heritability measure due to common environment effects. We thus  
126 assessed full-sibling family resemblance by measuring reproductive timing, as state of  
127 gonadal development, in sisters and brothers raised and kept under standardized conditions,  
128 after being exposed to the same early nest environment. We formed non-sibling pairs within  
129 a pool of offspring from five early or five late laying families per year. The parents' laying  
130 dates did not affect the offspring's gonadal development (Schaper et al., 2012b), implying  
131 that under current natural conditions the (heritable) adjustments of the laying date were not  
132 the result of (potentially heritable) adjustments of the timing of gonadal growth.

133

#### 134 **Housing conditions**

135 Breeding pairs were housed in 36 separate climate-controlled aviaries (2 x 2 x 2.25 m). They  
136 received an artificial light regime mimicking the natural photoperiod, with step changes twice  
137 weekly. Light sources were three high frequency fluorescent light tubes, complemented with  
138 a 8 W bulb providing an additional half hour of light at dawn and dusk. A shaft from the roof,  
139 whose opening was synchronized with the light schedule, allowed for supplementary  
140 daylight. The birds were fed *ad libitum* with a constant daily amount of food (Schaper et al.,  
141 2012b, Visser et al., 2011) and water for drinking and bathing. We provided nesting material  
142 from March onwards.

143

144 We exposed the breeding pairs to experimental temperature treatments which varied over  
145 years, but did not affect gonadal development (for details and rationale see Schaper et al.,  
146 2012b, Visser et al., 2011). In 2007, we divided the 36 pairs into two groups differing in the  
147 ambient temperature to which they were exposed, with the cold temperature treatment 4°C  
148 lower than the warm temperature. From December to March temperatures were kept  
149 constant at 4 and 8°C, respectively, after which we gradually increased temperatures by  
150 0.65°C per week until July, reaching 15 and 19°C, respectively. In 2008, we divided the pairs

151 into four groups, all of which were exposed to a constant temperature of 15°C from  
152 December onwards. In three groups, this temperature was lowered to 7°C in February,  
153 March or April for a month, before being increased to 15°C again. In 2009, there was no  
154 seasonal temperature pattern, but we changed temperature over the day. Each treatment  
155 was composed of a high or low mean with either a high or low day-night amplitude. The two  
156 warm treatments fluctuated around 14°C (11-17°C or 13-15°C), the two cold treatments  
157 around 8°C (5-11°C or 7-9°C). In 2010, we kept all birds at 6°C until February. On 8<sup>th</sup>  
158 February, two groups experienced a linear increase in temperature from 6 to 16°C over the  
159 course of two weeks, and were then kept at 16°C for three or five weeks, after which  
160 temperature was increased to 20°C. Starting on 22<sup>nd</sup> February, we exposed the other two  
161 groups to an increase from 6 to 11°C over the course of two weeks. They were then kept at  
162 11°C for one or three weeks, after which we increased temperatures to 15°C.

163

#### 164 **Data collection**

165 We measured the size of the testis or largest ovarian follicle monthly via laparotomy, except  
166 in January 2010 and for females in April 2009. We omitted January samplings in 2010  
167 because we were in that year mostly interested in the late gonadal growth phase. We did not  
168 sample females in April once to test if a laparotomy that close to egg laying would delay the  
169 onset of laying (which was, however, not the case, see Schaper et al., 2012). Birds were  
170 unilaterally laparotomized under isoflurane anaesthesia (Forene, Abbott, Hoofddorp, The  
171 Netherlands). Left testis dimensions and diameter of the largest follicle in the ovary were  
172 measured to the nearest 0.1 mm, using a scale engraved in the ocular of a binocular  
173 microscope. We calculated testis volume as:  $V = 4/3 \pi a^2 b$ , where a is width/2 and b is  
174 length/2, and follicle volume as:  $V = 4/3 \pi a^3$ , where a is width/2. We did not sample all birds  
175 successfully monthly, leading to varying sample sizes (Table 1).

176

#### 177 **Statistical analyses**



178 Quantitative genetic analyses were done using an 'animal model' (Wilson et al., 2010) with  
179 pedigrees including up to the grandparental generation. In calculating heritabilities, we log-  
180 transformed gonad volumes and analyzed them separately for each sex and month.  
181 Significance of narrow-sense heritability ( $h^2$ ) was tested by comparing models with and  
182 without the additive genetic effect fitted using a likelihood-ratio test with one degree of  
183 freedom. Only families with at least two siblings of the measured sex in a month were  
184 included (range: two to six). To test whether additive genetic variance varied among months  
185 we chose not to use a random regression animal model, which would test whether individual  
186 slopes differ genetically, because the assumption of linear slopes may not be satisfied. We  
187 aimed to test the interaction between month and the additive genetic effect within a  
188 multivariate animal model framework, but these models were too complex and did not  
189 converge. We therefore tested the interaction between month, as a fixed factor, and family,  
190 as a random effect, in a standard mixed model. Since there were few pedigree links between  
191 parents of sib-groups, our pedigree structure resembled a full-sib breeding design and  
192 consequently a sib-model yields very similar results to an animal model including the  
193 complete pedigree, while being computationally far less complex. As a variance-covariance  
194 matrix was fitted, i.e. correlations of the family-effect among months were not constrained, a  
195 likelihood-ratio test with nine degrees of freedom was used. Due to repeated measurements,  
196 individual was fitted as a random effect. We included tarsus length to correct for body size.  
197 By fitting a fixed year effect, we avoided introducing bias due to variation in environmental  
198 conditions between birth years, variation in the timing of monthly measurements or  
199 experimental temperatures between years. All models were run with ASReml 3 (VSN  
200 International).

201

## 202 **Results**

203 From January to April, the size of the largest ovarian follicles and testis sizes increased  
204 exponentially with naturally lengthening photoperiod (Fig. 2 a,b). This photoinduced gonadal

205 maturation was not affected by temperature (Schaper et al., 2012). In female great tits,  
206 heritable variation in the extent of photoinduced maturation of the largest ovarian follicles  
207 (follicle volume) accounted for more than 70% of the phenotypic variation in this trait in  
208 January, but decreased progressively between February and April (Table 1, Fig. 3a). The  
209 differences in genetic variation were statistically significant in females ( $\chi^2=22.0$ ,  $df=9$ ,  
210  $p=0.009$ ). In contrast, the extent of testis development (testis volume) in males showed no  
211 statistically significant genetic variation (Table 1, Fig. 3b).

212

213

## 214 **Discussion**

215 We identified early gonadal growth in females as a heritable avian reproductive trait. We  
216 show, for the first time to our knowledge, that physiological mechanisms underlying the  
217 reproductive timing are heritable and that genetic variation in this varies throughout the  
218 season. This strongly suggests that the shared genetic element does not lie in the speed of  
219 gonadal development, because this would lead to higher resemblance between related  
220 females at later, rather than earlier, stages. Decreasing heritability was partly caused by  
221 increased residual variance being possibly the result of accumulated environmental effects  
222 on growth rate. Additionally, genetic variance decreased significantly from January until April.  
223 In males, variation in testis development, corrected for body size, could be the result of slight  
224 differences in body condition.

225

226 Our estimates of heritability are possibly inflated by dominance, maternal and common  
227 environment effects during early development. This problem cannot be overcome, since at  
228 minimum the egg environment is shaped by the mother and is hard to manipulate. Some  
229 caution is therefore needed in the interpretation of heritability estimates reported here, but  
230 most quantitative genetic studies in wild populations suffer from similar limitations in the data.  
231 However, due to our standardized rearing protocol, including a standardized diet and

232 housing, we decrease the influence of this effect from an age of 10 days onwards. Therefore,  
233 our measure is in this respect, and also in terms of family sample sizes, superior to  
234 heritability estimates derived from wild birds.

235

236 Due to their heritability, reproductive processes, such as gonadal growth in females, can  
237 respond to selection by micro-evolution. Selective forces can operate via the need to  
238 advance egg laying towards the time period when, at least under current conditions, gonadal  
239 growth is not yet completed. Such micro-evolution is needed as recent climate warming  
240 currently favours an advance in the mean onset of laying of about two weeks (0.25 days a  
241 year in a period between 1973-2010 Schaper, 2012). This may be achieved by plasticity in  
242 the final rapid gonadal maturation phase. However, if the trend for an earlier onset of laying  
243 continues, the observed variation in the extent of ovarian growth, likely caused by different  
244 onsets, will become more important in accommodating this trend, and may eventually limit it.  
245 This limitation will mostly arise through the females, as males generally develop their gonads  
246 in advance of the females (Caro et al., 2009).

247

248 Even though the heritability of gonadal size in late spring is low, under natural conditions an  
249 early gonadal maturation, which is – as shown here – highly heritable, would be a selective  
250 advantage and thus would favour offspring of birds with this trait. So far we have too little  
251 knowledge to speculate about the selective forces acting on gonadal growth in early spring  
252 that could counteract these benefits. In early spring, food resources are low and thus  
253 energetic constraints could counteract the benefits of an early onset of gonadal maturation,  
254 therefore hampering an advancement of gonadal growth and possibly early egg laying (te  
255 Marvelde et al., 2012). Only genetic shifts in the time of gonadal development can further a  
256 shift in egg laying date beyond the advancement currently observable, which is restricted to  
257 the period after gonadal maturation is finished.

258

259 Our results have implications for understanding genetic variation in key life-history traits,  
260 such as timing of avian egg laying, mammalian rut and parturition or moult and migration,  
261 which are changing in response to climate warming in different ecosystems worldwide  
262 (Parmesan & Yohe, 2003, Forchhammer et al., 1998, Visser et al., 1998, Hughes, 2000,  
263 Barbraud & Weimerskirch, 2006). These changes are at least partly based on selection of  
264 underlying physiological mechanisms rather than selection of the life-history trait itself.  
265 Components of the mechanism can show variation, but may not be phenotypically plastic or  
266 heritable, thereby restricting an adaptive change in the trait value in response to climate  
267 change (Visser, 2008). Integration of quantitative genetics and developmental physiology, in  
268 combination with an ecological understanding of natural selection pressures, is needed to  
269 develop predictive models of the responses of animal populations to climate change.

270

271

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282

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380 **Figure legends**

381

382 **Figure 1: Origins and housing conditions of captive birds**

383 Scheme of the origins and history of housing conditions of the experimental breeding pairs in  
384 the aviary setup. The setup was repeated over four years from 2007 to 2010, so that gonadal  
385 growth from 144 female and 144 male captive great tits from 40 families was measured in  
386 total.

387

388 **Figure 2: Growth of the largest ovarian follicle (a) or left testis (b) before the start of**  
389 **seasonal reproduction in great tits in 2007-2010.**

390 Females and males were measured from January to April in 2007 (open circles), 2008 (light  
391 grey circles), 2009 (dark grey circles) and 2010 (closed circles). Gonad volume was not  
392 measured in January 2010 and in females in April 2009. Data are log-transformed. Means ( $\pm$   
393 1 SE) are given.

394

395 **Figure 3: Heritabilities of the largest ovarian follicle volume (a) and testis volume (b)**  
396 **before the start of seasonal reproduction in great tits.**

397 Heritabilities ( $\pm$  1 SE) of follicle volume decreased from January to April ( $\chi^2=22.0$ ,  $df=9$ ,  
398  $p=0.009$ ) and differed from zero in January ( $h^2=0.73$ ,  $df=1$ ,  $p=0.006$ ) and February ( $h^2=0.52$ ,  
399  $df=1$ ,  $p=0.001$ ), but not any more in March ( $h^2=0.33$ ,  $df=1$ ,  $p=0.06$ ). Heritabilities of testis  
400 volume were not different from zero (all  $p>0.05$ ).

401

402 **Table 1: Results from animal model analyses**  
 403

month	Follicle volume (log) females				Testis volume (log) males			
	January	February	March	April	January	February	March	April
$V_P$	0.807 (0.144)	1.118 (0.155)	1.011 (0.135)	1.208 (0.189)	0.116 (0.018)	0.236 (0.032)	0.672 (0.089)	0.280 (0.036)
$V_A$	0.588 (0.287)	0.577 (0.282)	0.335 (0.229)	0.175 (0.319)	0.015 (0.030)	0.074 (0.056)	0.163 (0.143)	0.021 (0.054)
$h^2$	0.729 (0.274)	0.516 (0.216)	0.332 (0.210)	0.145 (0.259)	0.131 (0.254)	0.313 (0.222)	0.243 (0.204)	0.076 (0.193)
n (individuals)	85	127	127	89	90	122	126	127
n (families)	27	38	37	25	28	38	39	40
$\chi^2$	7.58	10.56	3.54	0.32	0.27	2.6	1.96	0.17
p	0.006	0.001	0.06	0.57	0.61	0.11	0.16	0.68

404  
 405 Variance components, heritabilities and sample sizes (n) from animal model analyses of  
 406 logged gonad size of great tits kept in climatized aviaries, separated by sex and month.  $V_P$  is  
 407 the total phenotypic variance and  $V_A$  the additive genetic component. The heritability ( $h^2$ ) is  
 408 the proportion of the variance explained by the additive genetic effect ( $V_A/V_P$ ). Estimates are  
 409 followed by their standard errors, in brackets.  $\chi^2$  values and significances refer to  $V_A$ .

410

411





**Figure 1**

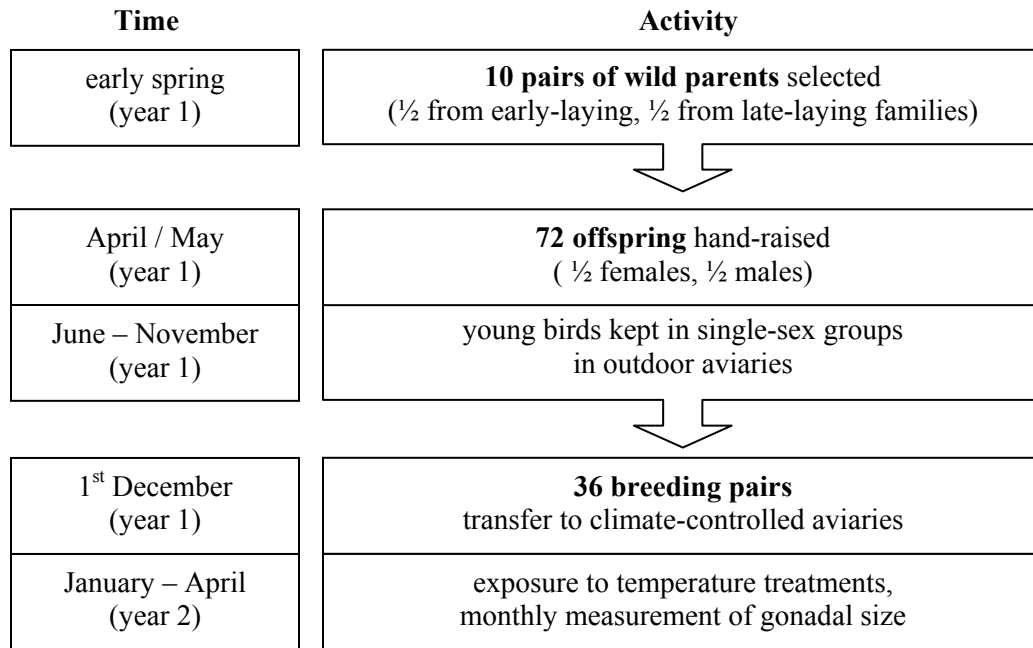


Figure 2

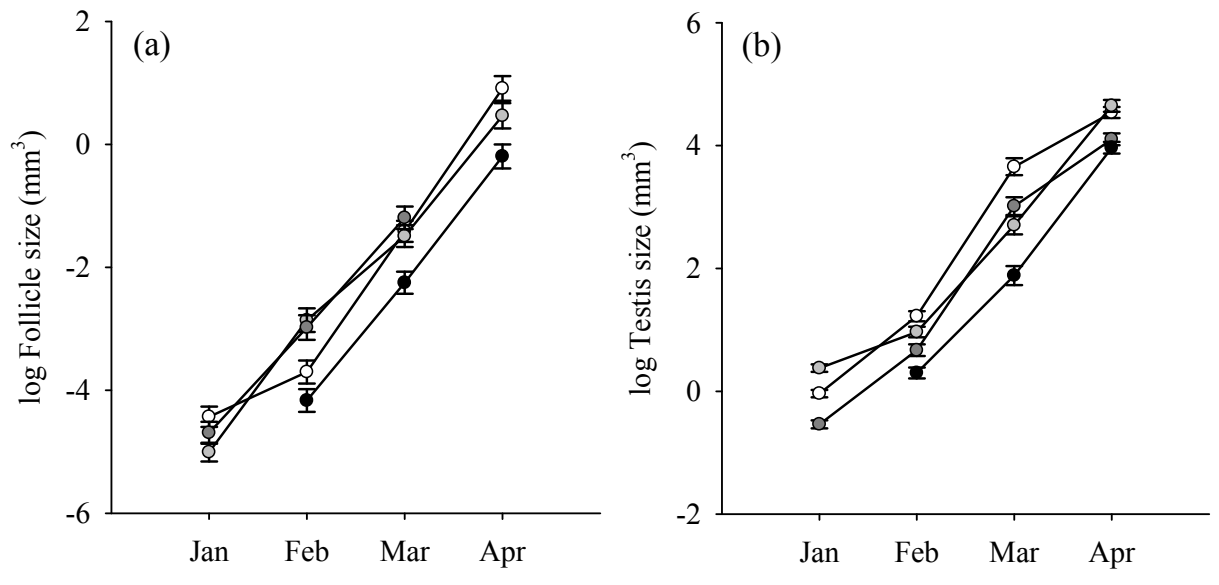


Figure 3

