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1 **Seasonal clutch size decline and individual variation in the timing of breeding are related to**  
2 **female body condition in a non-migratory species, the Upland Goose *Chloephaga picta leucoptera***

3

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14

15 **ABSTRACT**

16 Several studies have shown that waterfowl females in good condition lay larger clutches and  
17 start egg-laying earlier in a breeding season. However, most of these studies lack corresponding data  
18 on individual condition and timing of breeding in different years. We analysed data on clutch size, egg  
19 size, hatching date and female body condition of a non-migratory species, the Upland Goose  
20 *Chloephaga picta leucoptera*, recorded in three seasons on New Island, Falkand Islands. We found a  
21 strong seasonal decline in both egg and clutch size. Egg size increased with clutch size. The mean egg  
22 volume and total clutch volume increased with female body condition and hatching date was earlier  
23 for females in higher body condition. Chicks hatched from nests with higher mean egg volume had  
24 higher early body condition. We also compared individual females between different study years and  
25 found that individual body condition showed a significant repeatability between years, whereas  
26 hatching date did not. While female aging did not systematically affect hatching date, females  
27 produced clutches that hatched earlier in years of higher body condition. We could thus show for the  
28 first time that the frequently reported negative relationship between female condition and hatching

29 date also holds true on an individual basis. To our knowledge, this is the first study on seasonal clutch  
30 size decline in sheldgeese and one of a few in waterfowl comparing condition and timing of breeding  
31 within individuals between different years.

32  
33 *Keywords:* clutch size decline, egg size, waterfowl, Tadornini, Upland Goose, *Chloephaga picta*  
34 *leucoptera*, reproductive investment, body condition

35

## 36 INTRODUCTION

37         There are numerous studies on seasonal variation in reproductive success in birds, one of the  
38 most common patterns being a seasonal decline in clutch size (Klomp 1970). Early-nesting birds often  
39 lay bigger clutches; their offspring grow more rapidly and have a higher chance of survival and  
40 recruitment than late-nesting birds (Blums et al. 2002; Drent and Daan 1980; Hochachka 1990;  
41 Sockman et al. 2006), which results in a decrease in offspring value within a season. In precocial birds  
42 such as waterfowl young receive parental care in the form of vigilance, social support and defence  
43 against predators (e.g. Lamprecht 1985; Owen and Black 1990; Schindler and Lamprecht 1987;  
44 Winkler and Walters 1983). Parents also lead their offspring to good feeding sites and enable chicks to  
45 gain access to these sites when competitors are present (Lepage *et al.* 1999; Winkler and Walters  
46 1983). However, chicks do not depend on parental feeding, a component that is correlated with clutch  
47 size in altricial species (Lack 1968). Instead, the investment into clutch formation plays an important  
48 role for precocial chick survival. Most hypotheses concerning clutch size in waterfowl have implied  
49 that the condition of the female prior to laying is a determinant for reproductive success (Bengston  
50 1971; Johnsgard 1973; Lack 1968; Ryder 1970; Winkler and Walters 1983). The body condition of  
51 individuals can vary according to individual quality and experience, leading to increased foraging  
52 efficiency, as well as the food resources available in the territory. Thus, high-quality individuals in  
53 high-quality territories may gain condition more rapidly after the winter and would therefore be the  
54 first to start laying in the breeding season, while low quality individuals in lower quality territories or  
55 individuals facing less favourable feeding conditions would lay later (Rowe *et al.* 1994; Sockman *et*  
56 *al.* 2006). Drent and Daan (1980) suggested that the conflict between early breeding (high offspring  
57 value) and late breeding (higher accumulated condition and potential clutch size) results in the

58 observed timing of laying and clutch size. From a graphical model Drent and Daan (1980) concluded  
59 that birds in poorer condition might have more to gain from a delay than birds in good condition. Field  
60 studies have shown that in most species females in good condition lay larger clutches and earlier in the  
61 season (Klomp 1970; Sockman *et al.* 2006). Experiments manipulating parental condition by  
62 supplementary feeding prior to egg laying resulted in earlier laying and increased clutch sizes (Karell  
63 *et al.* 2008; Meijer *et al.* 1988; Meijer *et al.* 1990; Rowe *et al.* 1994).

64 However, most of the studies on the relationship between body condition and hatching date  
65 have been conducted either using data on population-level (e.g. Bety *et al.* 2003; Dalhaug *et al.* 1996;  
66 e.g. Devries *et al.* 2008; Sjoberg 1994) or, if conducted on an individual basis, then only on repeated  
67 observations of clutch size and hatching date without collecting corresponding data on individual  
68 condition (e.g. Hamann and Cooke 1987; Petersen 1992). To our knowledge there is but one study that  
69 compares individual females between different years, finding a positive relation between Common  
70 Eider *Somateria mollissima* clutch size and female mass, but no relation with hatching date (Erikstad  
71 *et al.* 1993).

72 Egg size is another important component of parental effort in birds and several studies have  
73 shown a positive relationship between egg size and offspring fitness, in altricial as well as precocial  
74 birds. Larger eggs may enhance offspring fitness by increasing survival prospects in the first days after  
75 hatching and competitive power through a larger offspring size and the possession of more resources  
76 to survive adverse conditions (Amundsen and Stokland 1990; Anderson and Alisauskas 2002; Ankney  
77 1980; Christians 2002; Dawson and Clark 2000; Goth and Evans 2004; Magrath 1992; Potti 1999;  
78 Rutkowska and Cichon 2005). Increased egg size through food supplementation could be linked to  
79 improved hatchability of the egg, increased size at hatching, early growth and survival during the  
80 nestling stage (reviewed in Williams 1994; Christians 2002, see also Grindstaff, Demas & Ketterson  
81 2005).

82 We studied seasonal egg and clutch size decline and their relation to female body condition in  
83 a non-migratory waterfowl species, the Upland Goose *Chloephaga picta leucoptera*. Upland Geese  
84 belong to the order of the sheldgeese (Tadornini), a group that physically resembles true geese  
85 (Anserinae) and shows similar habits but is more closely related to shelducks and ducks. The smaller

86 (migratory) sub-species *C. picta picta* breeds on the South American mainland, whereas the slightly  
87 larger one (*C. picta leucoptera*) is restricted to the Falkland Islands. Their basic breeding biology and  
88 life-cycle has been studied in the Falklands from 1977 to 1980 (Summers 1983). Upland geese are  
89 highly territorial and socially monogamous, usually returning to the same territory with the same mate  
90 every year. Territories are taken up from August onwards and eggs laid between late September and  
91 end of October. The mean clutch comprises 6 eggs (Summers and McAdam 1993). Hatching mainly  
92 takes place between mid-October and mid-November and fledging starts with about 70 days of age.  
93 Family groups then stay together for the austral summer and winter (Summers 1983) and during the  
94 breeding season no creching occurs.

95         Additionally to the general analysis of the relationship of clutch size, hatching date and body  
96 condition in this non-migratory waterfowl species, we were able to compare data from individual  
97 females captured in subsequent years in the same territories. To our knowledge, this is the first study  
98 on seasonal clutch size decline in sheldgeese and one of a few comparing condition and timing of  
99 breeding within individuals between different years in waterfowl.

100         We tested the following hypotheses:

- 101         1. Egg and clutch size decrease with increasing hatching date.
- 102         2. Egg size, clutch size and hatching date is related to female body condition.
- 103         3. Individual variation in hatching dates is related to individual variation in body condition.
- 104         4. Chicks hatched from larger eggs are in a better condition than chicks from smaller eggs.

105

## 106 **MATERIALS AND METHODS**

107         The study was carried out in the New Island Nature Reserve, Falkland Islands (51°43'S,  
108 61°17'W) from October to December in 2005, 2007 and 2008. New Island has an estimated 84km of  
109 coastline embracing some 2,300 ha. The island has been established as a nature reserve in 1970 when  
110 all livestock was removed from the island. This led to an increase in the density of Upland Geese,  
111 which is now with approximately 0.8 pairs ha<sup>-1</sup> one of the highest in the Falkland Islands (Quillfeldt et  
112 al. 2005).

113 For the study of seasonal decline, a total of 84 nests were included in the analysis (29 from  
114 2005, 25 from 2007 and 30 from 2008). At the start of each field season we mapped nests using GPS.  
115 Females left their nests at varying distances when approached, eggs were covered with down after  
116 measurements and all females returned to their nests afterwards. For each nest, we determined clutch  
117 size, measured length (L, expressed in cm) and width (B, expressed in cm) of each egg to the nearest  
118 0.1 mm using callipers and weighed each egg to the nearest 0.1 g using a digital balance. Egg volume  
119 (V; in cm<sup>3</sup>) was calculated as  $V = (L \times B^2 \times 0.507)$  following Furness and Furness (1981). We defined  
120 total clutch volume as the sum of the volumes of each egg in the clutch. Avian eggs decrease in  
121 density with increasing length of incubation mainly due to water loss. In 2005, a subsample of eggs  
122 was reweighed at a later date to estimate the density loss. Eggs lost an average of  $0.0063 \pm 0.0005$  SE  
123 g/cm<sup>3</sup> per day. We determined expected hatching date as follows: (1) we calculated egg density (D)  
124 from egg mass M (expressed in g) and V. (2) Our 2005 data showed that hatching occurred at a mean  
125 egg density of  $0.89\text{g/cm}^3 \pm 0.01\text{g/cm}^3$  SE (n=14 eggs). (3) Thus, the number of days to hatching T was  
126 estimated as  $T = (D - 0.89\text{g/cm}^3) / 0.0063\text{g/cm}^3$ . We then visited nests again at least once a day,  
127 starting at the estimated hatching date. All eggs hatched within 0-2 days of the estimated hatch date.

128 We caught adults during the period when they attended their brood (mean chick age:  
129  $14.8 \pm 4.1$  days) using a 3 x 5 m whoosh net. One person herded the family of geese slowly to the  
130 catching area, and when they arrived directly in front of the furled net, the other researcher pulled the  
131 trigger. Adults were marked with an individual metal ring on one leg and a plastic ring readable from a  
132 distance on the other and weighed to the nearest 10g using a digital spring balance. Head length,  
133 culmen length, and tarsus length were measured to the nearest 0.1 mm using callipers; wing length  
134 (maximum flattened chord) was measured to the nearest 1 mm using a foot rule. Chicks were marked  
135 individually using web-tags placed in the footwebs. We left enough space for the foot web to grow and  
136 did not observe any adverse effects on gosling growth. Chicks were weighed to the nearest 1g using a  
137 spring balance (<300g) or to the nearest 10g using a digital spring balance (> 300g). We measured  
138 head length, culmen length, wing length and tarsus length ( $\pm 0.1$  mm) using callipers. Chick age was  
139 determined from a growth curve for head and tarsus lengths established from chicks of known age in  
140 2005. For each clutch, the mean chick age and thereby mean hatching date were calculated. As

141 hatching dates could not be determined from egg density for all individual females, we used this  
142 estimated hatching date for further analyses. Estimated hatching dates from egg measures and chick  
143 measures were highly correlated ( $R = 0.973$ ,  $P < 0.001$ ,  $n = 41$ ).

144 The body condition of females then was determined accounting for structural size and chick  
145 age, as we did not catch females during the prelaying period and captured females had goslings of  
146 different age. Females lose weight during incubation, and regain weight after hatching of the chicks  
147 (Summers and McAdam 1993). We estimated an expected body mass for each individual based on a  
148 multiple linear regression of body mass on the first principal component (PC1) of measurements of  
149 wing, head, bill and tarsus and chick age. Body condition was calculated as the ratio of the observed  
150 body mass to the derived expected body mass, according to female size and chick age. For the analysis  
151 of the effect of mean egg volume on chick body condition we only included clutches with chicks  $\leq 20$   
152 days of age as until then no sex-specific growth was observed (A.Gladbach, unpublished data). Chick  
153 body condition was expressed as the ratio of observed to expected body mass. To avoid using the same  
154 data to determine chick body condition and chick age (see above), in this case we used the estimated  
155 hatching date determined from egg density data. Expected body mass was the population mean of  
156 chicks of the same age (based on body mass data of a total of 553 chicks), following Quillfeldt (2002).  
157 Using this method, age is included indirectly into the model and hence controlled for. As a result, body  
158 condition is by definition uncorrelated (orthogonal) to age. For each clutch, we calculated a mean  
159 body condition of chicks.

160

## 161 **Statistical analysis**

162 Statistical tests were performed in SPSS 11.0 and R 2.9.1 (R Development Core Team 2009,  
163 [www.r-project.org](http://www.r-project.org)). Normality was tested with Kolmogorov-Smirnov tests and data were transformed,  
164 if necessary. Means are given with standard errors. We assessed significance using Pearson  
165 correlations or F-statistics in General Linear Models (GLM), based on Type III Sum of Squares. To  
166 indicate the direction (positive or negative) of the correlation to the covariable, we included t values,  
167 and as a measure of effect sizes, we included partial eta-squared values ( $\eta^2$ ) (i.e. the proportion of the  
168 effect + error variance that is attributable to the effect). The sums of the partial eta-squared values are

169 not additive (e.g. [http://web.uccs.edu/lbecker/SPSS/glm\\_effectsize.htm](http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm)). To analyse the dependency  
170 of mean egg volume on clutch size, we used a non-parametric Spearman correlation.

171 For the analysis of individual data from different years we used a linear mixed effects model  
172 (lme) in R 2.9.1. with hatching date as the response variable, body condition and year (as ordered  
173 fixed factor) as explanatory variables and female identity as a random effect. Thereby we could  
174 simultaneously test whether hatching date on an individual basis depended on body condition or if  
175 there was a relation with increasing age (year). In the final model, “year” was excluded based on the  
176 stepwise AIC function, an information-theoretical approach (Burnham and Anderson 2004). We here  
177 present results of this final model.

178 Statistical repeatabilities of variables in different years were calculated by the method of  
179 Lessells and Boag (1987). Significance level was set to  $p < 0.05$ . Some territories were not visited  
180 before chicks hatched and hence some data on clutch size and egg volumes were missing, resulting in  
181 different sample sizes for the respective tests.

182

## 183 **RESULTS**

184

### 185 *Egg and clutch size decline*

186 Clutch size and mean egg volume were significantly higher in clutches with earlier hatching  
187 date (Fig. 1, Table 1). Mean egg volume increased significantly with increasing clutch size (Pearson  
188 correlation,  $R = 0.377$ ,  $P < 0.001$ ). This correlation remained significant when controlling for female  
189 structural size ( $R = 0.373$ ,  $P = 0.018$ ), but not when controlling for female mass ( $R = 0.221$ ,  $P = 0.171$ )  
190 or body condition ( $R = 0.238$ ,  $P = 0.139$ ).

191

### 192 *Female body condition and hatching date, clutch size and mean egg volume*

193 Hatching date and female post-hatching body condition were positively related, with females  
194 in a better body condition having earlier clutches (Fig. 2, Table xy).

195 We compared data of 28 recaptured individuals (5 captured in all three study years, 4 in 2005  
196 and 2008, 4 in 2005 and 2007 and 15 individuals in 2007 and 2008). Body condition data showed



197 significant repeatability ( $r = 0.308$ ,  $F_{27,60} = 1.969$ ,  $P = 0.032$ ), whereas repeatability of hatching date  
198 was non-significant ( $r = -0.171$ ,  $F_{27,60} = 0.683$ ,  $P = 0.844$ ). Hatching date was significantly negatively  
199 related to body condition within individuals (lme in R; body condition:  $F_{1,32} = 18.80$ ,  $t = -4.336$ ,  
200  $P = <0.001$ ), while changes in year (i.e. female age) did not systematically affect hatching date as it  
201 was dropped from the full model (see “Statistical analysis”).

202 Clutch size and mean egg volume were higher in females in better post-hatching body  
203 condition and this relationship was independent of the sample year (Fig. 3, Table xy).

204

#### 205 *Egg volume and chick body condition*

206 Chick body condition was positively related to mean egg volume and negatively to hatching  
207 date, i.e. chicks hatched from nests with higher mean egg volume and earlier clutches had significantly  
208 higher early body condition (Table 3, Fig. 4). Clutch size had no effect on chick early body condition  
209 (Table 3). Mean body condition of chicks from females with high body condition was higher  
210 compared to chicks of low body condition females (Table 3).

211

## 212 **DISCUSSION**

213 In our present study on Upland Geese we found that:

- 214 1. Clutch size and egg size decreased with later hatching date.
- 215 2. Clutch size variables and hatching date were related to female post-hatching body  
216 condition.
- 217 3. Individual variation in hatching dates was related to individual variation in body condition.
- 218 4. Egg size had a direct and positive effect on chick body condition in the first weeks after  
219 hatching.

220 We found the observed seasonal decline of clutch and egg size on the population level in Upland  
221 Geese to be mainly caused by the early onset of reproduction by females in good body condition. We  
222 could show, to our knowledge for the first time, that the commonly observed positive relation between  
223 female condition and hatching date also holds true on an individual basis. Annual variation in  
224 individual body condition had a direct effect on the onset of reproduction, with females in an

225 individually better condition having earlier hatching dates. The significant repeatability of post-  
226 hatching body condition indicates that differences in quality between individuals remain stable over  
227 several years, but that despite this stability small individual changes in body condition affect timing of  
228 reproduction. However, as we did not measure female pre-breeding condition we are aware that our  
229 results must be treated cautiously as it must not necessarily be linked to her post-hatching condition,  
230 an assumption that still needs to be tested in Upland Geese.

231         Differences in body condition between individuals may arise due to differences in the inherent  
232 quality of individual birds (e.g. Jensen et al. 2003; e.g. Merila et al. 2001), which is supported by the  
233 significant repeatability of body condition in our study. As Upland Geese return to the same territories  
234 every year, also differences in territory quality may affect female body condition. Differences in  
235 individual body condition could have more immediate causes such as differences in weather, food  
236 availability, health state etc.. That small differences in condition affect the timing of the onset of  
237 reproduction supports the idea that a) egg laying starts when a certain individual threshold body  
238 condition is reached and that b) the investment into egg size and number decreases as the season  
239 advances, as expected offspring value is assumed to decline during a breeding season. Alternatively, if  
240 female-post-hatching condition is closely linked to her pre-laying condition, the investment into more  
241 and heavier eggs could also be explained by this better body condition. In contrast to previous studies  
242 that found an age effect with earlier hatching dates in older age classes to be the main cause for inter-  
243 individual variation in hatching dates (Blums *et al.* 2002; Finney and Cooke 1978; Hamann and Cooke  
244 1987; Hamann and Cooke 1989) we did not observe a decline in hatching date within individual  
245 females over the study years. Upland Geese have an average adult life expectancy of about five years  
246 (Summers and McAdam 1993), our study period thus covered a considerable amount of this expected  
247 lifespan. However, the small sample size of individuals sampled in three different years (N=5) may  
248 also explain why we could not detect an age effect in our study. One hint for the possibility of an age  
249 effect at the very end of an individual life span is one female found dead at the end of the last study  
250 year which had hatched chicks 30 days earlier in 2008 than in 2005 and 2007.

251         In precocial species like waterfowl, where the young feed for themselves after hatching, the  
252 role of the parents and their effect on offspring performance is harder to detect than in altricial species.

253 Parental quality may not only be reflected in the effect of social factors like predator  
254 avoidance/defence and social competence for variation of reproductive success. High quality parents  
255 may also be able to produce larger clutches and to accumulate more resources and more rapidly than  
256 low quality individuals which would allow an earlier nesting (Drent and Daan 1980) and thereby  
257 providing better growing conditions for the offspring (Hoekman *et al.* 2004; Lepage *et al.* 1999;  
258 Lepage *et al.* 1998). Female egg investment may play an important role in determining survival  
259 prospects of offspring (Amat *et al.* 2001) and thereby increasing individual fitness. We here show that  
260 early chick body condition increased with increasing egg size. This is line with other studies on  
261 waterfowl, where chick body size was also found to be related to egg size (e.g. Christians 2002,  
262 Ankney 1980, Anderson and Alisauskas 2002).

263         Interestingly, we found that egg size increased with increasing clutch size. Other studies on  
264 waterfowl already have shown that the theoretical trade-off between size and number of offspring as  
265 proposed by Lack (1968) can be observed on an interspecific level (Figuerola and Green 2006), but is  
266 not always present on an intraspecific level (Christians 2000; see Christians 2002 for a review). The  
267 intraspecific relationship does not show a consistent pattern, as there was no correlation between egg  
268 size and clutch size in some species but a positive correlation in others (see Christians 2002 for a  
269 review). Hōrak *et al.* (2008) pointed out that the absence of a trade-off between egg size and number  
270 may be explained by the lower quality of young hatched from larger clutches, i.e. the trade-off  
271 occurring between egg number and hatchling quality. We found no evidence that this is true for  
272 Upland Geese, as clutch size had no influence on chick body condition.

273         Flint *et al.* (1996) suggested that in waterfowl which rely on endogenous reserves for egg  
274 production, large-bodied birds may tend to lay larger clutches of larger eggs than do small-bodied  
275 birds. Our results show, that in Upland Geese body size is no proxy for egg size as we failed to detect  
276 a relationship between structural size and either egg or clutch size. In contrast, the availability of  
277 endogenous reserves (reflected in body mass and body condition) was an important source for  
278 variation in egg and clutch size between female Upland Geese. This supports the idea that high-quality  
279 females are able to produce more eggs and larger eggs than low-quality females, although we could  
280 not distinguish whether the higher body condition of these females was caused by higher foraging

281 efficiency, or indirectly by defending a high-quality territory. Assessing the body condition during the  
282 non-breeding season, when Upland Geese gather in large groups around ponds, could shed further  
283 light on the importance of the breeding territory or winter condition for the differences in body  
284 condition during the breeding season. In addition a comparison of individual clutch and egg size  
285 measures in relation to body condition over several years, which was not possible in this study, could  
286 further deepen our understanding of optimal investment.

287

## 288 **Zusammenfassung**

289

290

291 **Saisonaler Rückgang der Gelegegröße und individuelle Variation des Brutbeginns sind bei der**  
292 **nicht-ziehenden Magellangans *Chloephaga picta leucoptera* von der weiblichen Körperkondition**  
293 **abhängig**

294

295 Viele Studien an Wasservögeln haben gezeigt, dass Weibchen in guter Kondition größere Gelege  
296 haben und früher in der Brutsaison mit der Eiablage beginnen. Allerdings fehlen in diesen Studien  
297 parallele Daten über individuelle Kondition und Brutbeginn in verschiedenen Jahren. Wir haben Daten  
298 über die Gelege- und Eigröße, das Schlupfdatum und die Körperkondition der Weibchen bei der  
299 Magellangans *Chloephaga picta leucoptera* während dreier Brutsaisons auf New Island,  
300 Falklandinseln, aufgenommen und untersucht, inwieweit Variabilität von Reproduktionsparametern  
301 und Körperkondition sowohl innerhalb als auch zwischen Weibchen zusammenhängen.

302 Wir fanden eine starke saisonale Abnahme von sowohl Ei- als auch Gelegegröße auf  
303 Populationsebene. Ei- und Gelegegröße nahmen mit steigender Weibchenkondition zu und Weibchen  
304 in besserer Körperkondition hatten frühere Gelege. Küken aus Gelegen mit größeren Eiern waren in  
305 einer besseren Körperkondition. Der Vergleich individueller Daten aus verschiedenen Jahren ergab  
306 dass die Körperkondition zwischen den Jahren signifikant wiederholbar war, das Schlupfdatum jedoch  
307 nicht. Während Unterschiede im Alter der Weibchen keinen Effekt auf das Schlupfdatum hatten, ging  
308 eine individuelle Verbesserung der Kondition mit einem früheren Schlupfdatum einher. Wir konnten  
309 damit zum ersten Mal zeigen, dass der bekannte allgemeine Zusammenhang von Körperkondition der

310 Weibchen und Reproduktionszeitpunkt auch auf individueller Ebene Gültigkeit besitzt. Unserem  
311 Wissen nach ist dies die erste Studie zu saisonaler Gelegeverkleinerung bei Halbgänsen und eine von  
312 wenigen an Wasservögeln die Körperkondition und Reproduktionszeitpunkt innerhalb von Individuen  
313 und zwischen verschiedenen Jahren vergleicht.

314

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325

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486           **FIGURES**

487

488   **Figure 1.** Seasonal decline of clutch size (a), and mean egg volume (b) in Upland Geese on New  
489   Island.

490

491   **Figure 2.** Negative relationship between female body condition and hatching date in Upland Geese.

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493   **Figure 3.** Positive relationship between female body condition and clutch size (a), and mean egg  
494   volume (b) in Upland Geese on New Island.

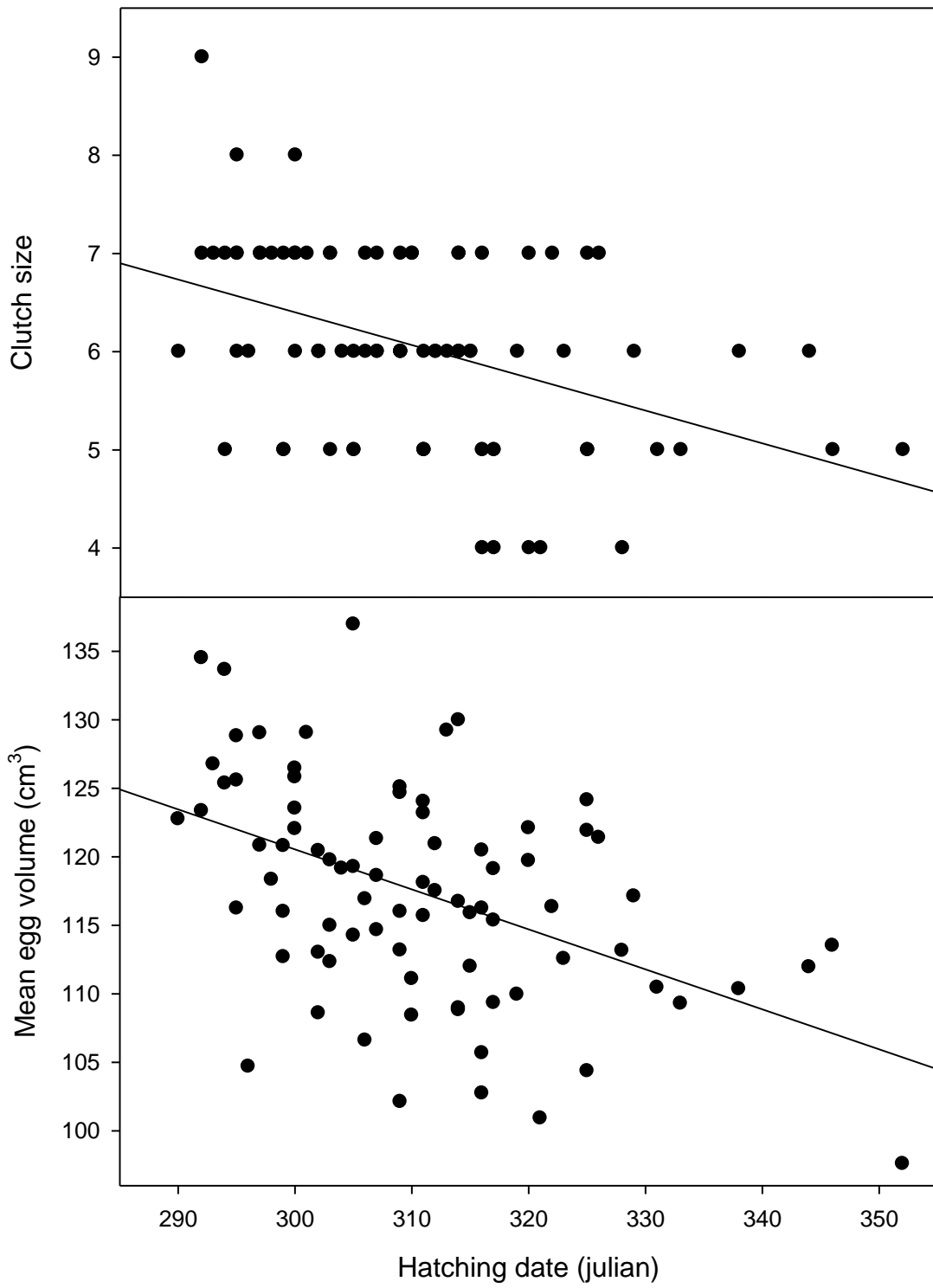
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496   **Figure 4.** Relationship between chick body condition, hatching date and mean egg volume in Upland  
497   Geese.

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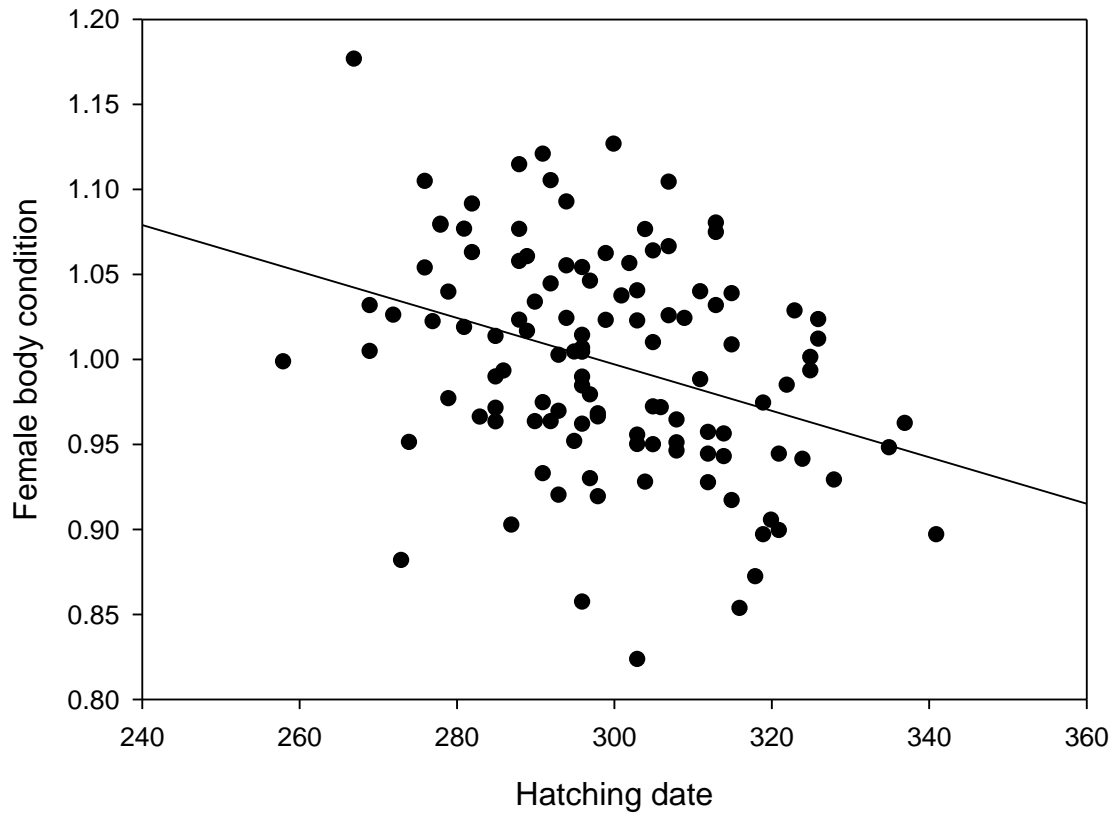
500 **Figure 1.**  
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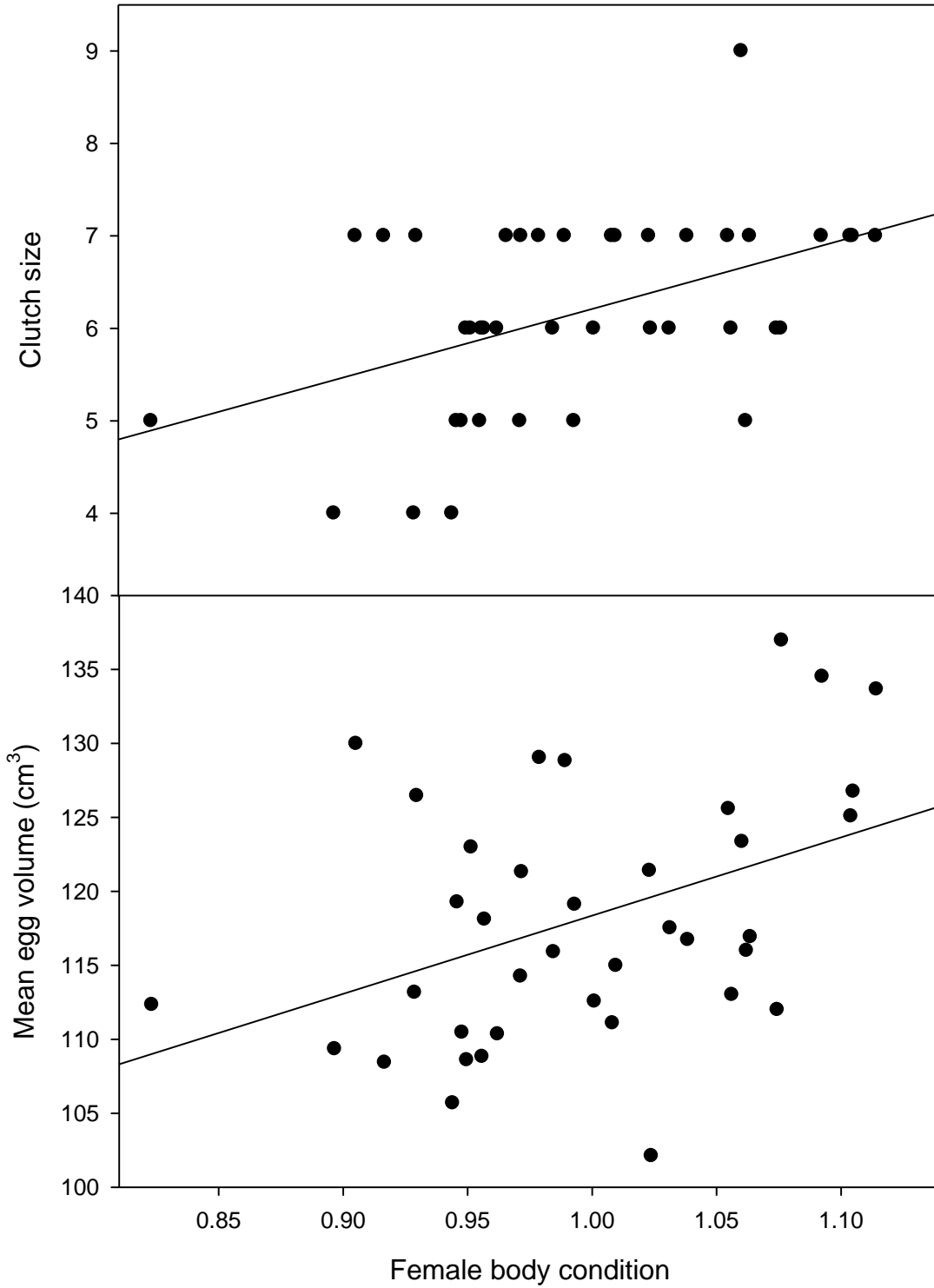
505 **Figure 2.**

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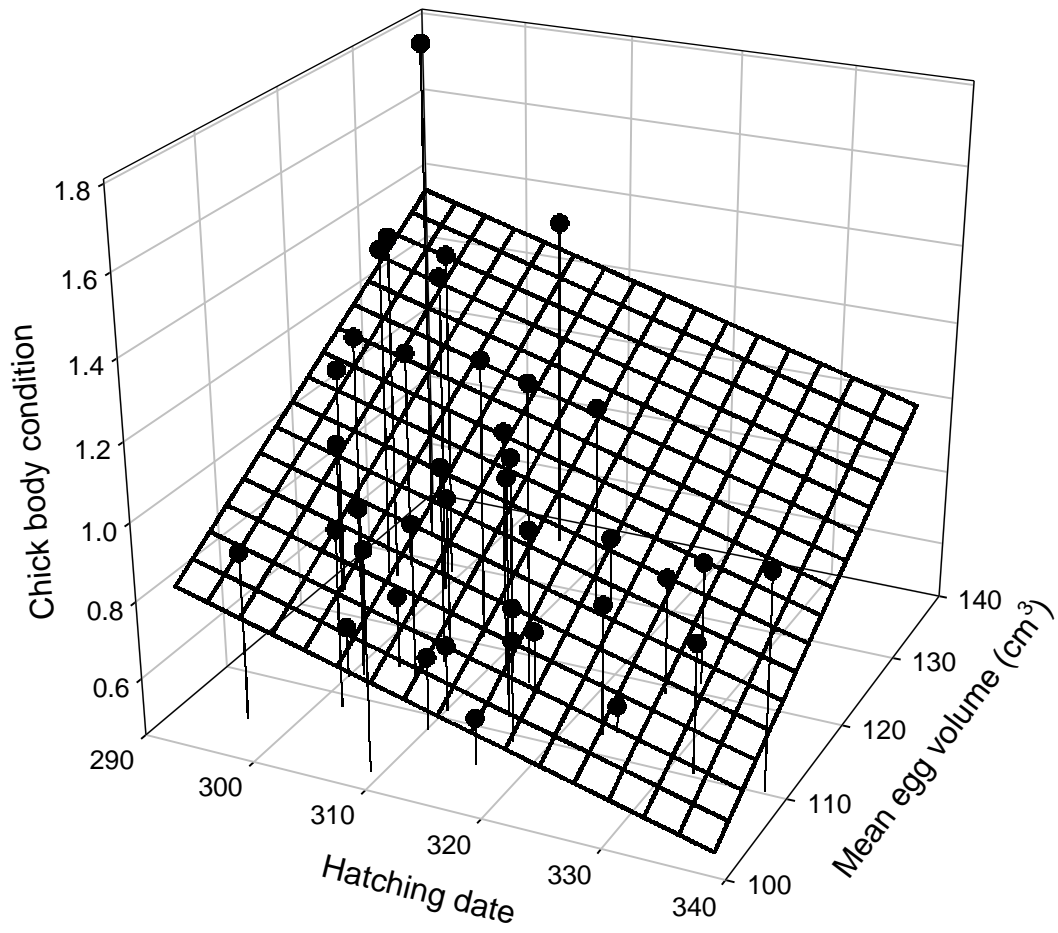
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509 **Figure 3.**  
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514 **Figure 4.**  
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519 **Table 1** Results of General Linear Models (GLM) showing the effects of year and hatching date on clutch size and mean egg volume in adult female Upland  
 520 Geese. Clutch size or mean egg volume were used as dependent, year as a fixed factor and hatching date as covariate.  $\eta^2$  was included to indicate the effect size  
 521 and t-values to indicate the direction (positive or negative) of the correlation to the covariable.

Parameter	year	hatching date (hd)	interaction (year*hd)
clutch size	$F_{2,84} = 0.469, P = 0.628, \eta^2 = 0.012$	$F_{1,84} = 13.213, \mathbf{P} < \mathbf{0.001}, \eta^2 = 0.145, t = -1.300$	$F_{2,84} = 0.434, P = 0.649, \eta^2 = 0.011$
mean egg volume	$F_{2,84} = 1.505, P = 0.228, \eta^2 = 0.037$	$F_{1,84} = 20.183, \mathbf{P} < \mathbf{0.001}, \eta^2 = 0.206, t = -1.273$	$F_{2,84} = 1.528, P = 0.223, \eta^2 = 0.038$

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524

525 **Table 2** Results of General Linear Models (GLM) showing the effects of year and body condition on hatching date, clutch size and mean egg volume in adult  
 526 female Upland Geese. Hatching date, clutch size or mean egg volume were used as dependent, year as a fixed factor and hatching date as covariate.  $\eta^2$  was  
 527 included to indicate the effect size and t-values to indicate the direction (positive or negative) of the correlation to the covariable.

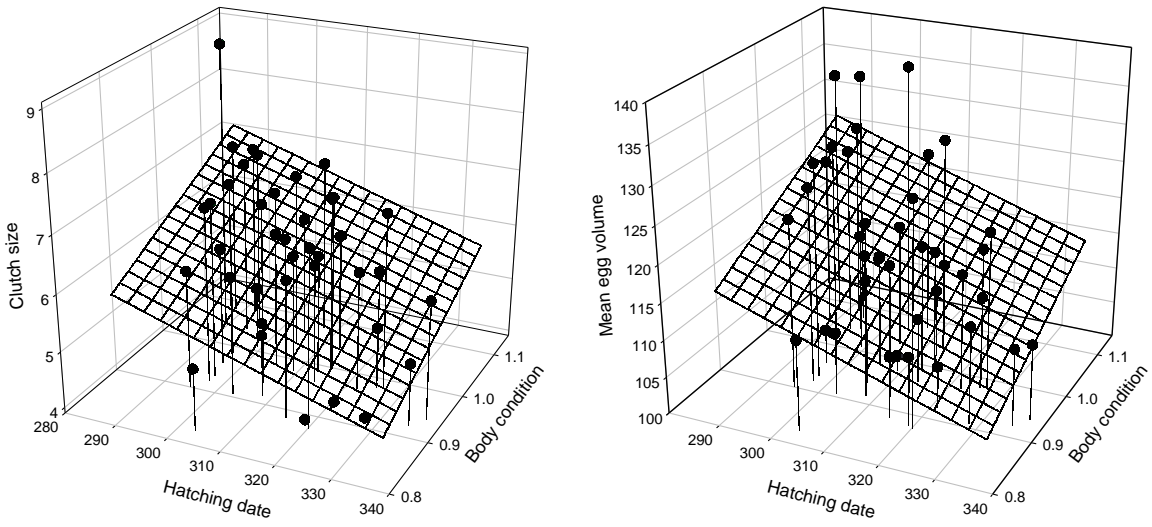
Parameter	year	body condition (bc)	interaction (year*bc)
hatching date	$F_{2,83} = 0.301, P = 0.741, \eta^2 = 0.008$	$F_{1,83} = 10.138, \mathbf{P} = \mathbf{0.002}, \eta^2 = 0.116, t = -1.199$	$F_{2,83} = 0.303, P = 0.739, \eta^2 = 0.008$
clutch size	$F_{2,41} = 1.314, P = 0.282, \eta^2 = 0.070$	$F_{1,41} = 10.741, \mathbf{P} = \mathbf{0.002}, \eta^2 = 0.235, t = 3.174$	$F_{2,41} = 1.119, P = 0.338, \eta^2 = 0.060$
mean egg volume	$F_{2,39} = 0.356, P = 0.703, \eta^2 = 0.021$	$F_{1,39} = 15.366, \mathbf{P} < \mathbf{0.001}, \eta^2 = 0.318, t = 2.085$	$F_{2,39} = 0.503, P = 0.609, \eta^2 = 0.030$

528

529 **Table 3** Results of General Linear Models (GLM) showing the effects of year, hatching date and (a)  
 530 mean egg volume, (b) clutch size and (c) female body condition on early chick body condition in  
 531 Upland Geese. Chick body condition was used as dependent, year as a fixed factor and hatching date  
 532 and mean egg volume, clutch size or female body condition as covariates.  $\eta^2$  was included to indicate  
 533 the effect size and t-values to indicate the direction (positive or negative) of the correlation to the  
 534 covariable.

<b>a</b>	year	$F_{2,39} = 0.844, P = 0.439, \eta^2 = 0.047$
	hatching date	$F_{1,39} = 4.582, \mathbf{P} = \mathbf{0.040}, \eta^2 = 0.119, t = -2.141$
	mean egg volume	$F_{1,39} = 12.904, \mathbf{P} = \mathbf{0.001}, \eta^2 = 0.275, t = 3.592$
<b>b</b>	year	$F_{2,39} = 0.022, P = 0.978, \eta^2 = 0.001$
	hatching date	$F_{1,39} = 5.547, \mathbf{P} = \mathbf{0.024}, \eta^2 = 0.140, t = -2.355$
	clutch size	$F_{1,39} = 4.023, P = 0.053, \eta^2 = 0.106, t = 2.006$
<b>c</b>	year	$F_{2,39} = 2.802, P = 0.075, \eta^2 = 0.141$
	hatching date	$F_{1,39} = 3.531, P = 0.069, \eta^2 = 0.094, t = -1.879$
	female body condition	$F_{1,39} = 2.597, \mathbf{P} < \mathbf{0.001}, \eta^2 = 0.420, t = 4.960$

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540 **Figure 5.** Relation of female body condition, hatching date and clutch size (left) and egg size (right) in

541 Upland Geese derived from multiple linear regression.

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