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**A spring cold snap is followed by an extreme
reproductive failure event in a mountain
population of pied flycatchers *Ficedula
hypoleuca***

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24 **Capsule** Very low and anomalous temperatures in early spring of 2010 were followed
25 by the only massive reproductive failure event recorded in 24 years in a population of
26 pied flycatchers *Ficedula hypoleuca* breeding at 1200 m altitude at Valsaín, central
27 Spain.

28 **Aim** To estimate the effects of an extreme climatic event on reproductive success in a
29 montane population of a long-distance migratory bird.

30 **Methods** To compare nestling growth and mortality in nests of different brood sizes in
31 the context of a brood manipulation experiment.

32 **Results** Total failure affected 36% of the broods and only 2.5 nestlings on average
33 were raised to fledging age. Most mortality affected broods in the second week of
34 nestling life. Fledglings attained very low values for mass and wing length compared
35 with long-term averages. Subsequent local recruitment was the lowest for any cohort in
36 24 years. The typical date-dependent decrease in breeding success in the population
37 was inverted.

38 **Conclusion** Breeding success was markedly affected by a weather event happening
39 one month before hatching and lasting only a few days. An increased frequency of
40 extreme weather events as predicted by some climate change scenarios may
41 dramatically affect insectivorous avian populations in the future.

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43

44 Climate change has been predicted to lead to higher rates of extreme climatic events
45 (Rind *et al.* 1989, Liang *et al.* 1995, Easterling *et al.* 2000). Thus, cyclones (King *et al.*
46 1992), droughts (Fletcher & Koford 2004), heat waves (Salzman 1982) and cold
47 springs (Wiggins *et al.* 1994) have been reported as inducing mass reproductive failure
48 in birds (reviewed in Moreno & Møller 2011). The literature on adaptation to climate
49 change primarily involves research into effects of climate trends, not extreme events
50 (Jentsch *et al.* 2007). Incorporating responses to extreme events may give a more
51 balanced view on the potential impacts of climate on populations. Thus, extreme
52 weather conditions may have stronger effects on population dynamics than average
53 climate (Knopf & Sedgwick 1987, Franklin *et al.* 1992, Hellman 2002, Saunders *et al.*
54 2011). Animal populations may suffer important set-backs after extreme climatic
55 events for which recovery time may exceed intervals between such events if their
56 frequency increases in a climate change scenario.

57 The winter of 2009/2010 was extreme throughout the northern hemisphere
58 (Wang *et al.* 2010). The record-breaking cold temperatures from North America to
59 Europe and Asia that winter were linked with extremely negative values of the North
60 Atlantic Oscillation (NAO) index. Low NAO values in winter are normally associated
61 with warm and humid conditions in Southwest Europe. Although the months of
62 January-March 2010 were extremely wet in Spain as expected from low NAO values,
63 this normal precipitation pattern was accompanied by very low temperatures in central
64 and northern Spain during January-March (Spanish Meteorological Agency AEMET,
65 annual reports). In marked contrast, April temperatures were 2 °C higher than normal.
66 In the first days of May, a cold snap in central Spain led to record-breaking low
67 temperatures directly following mild conditions (Spanish Meteorological Agency AEMET,
68 annual reports). Freezing temperatures especially affected mountain areas.

69 While plant phenology was delayed by 10-15 days in central Spain at the
70 beginning of April 2010, this consequence of the previous harsh winter conditions had

71 been erased by the end of the month (AEMET, phenology reports). Oak buds start to
72 open in the first days of May in the pied-de-mont forests of the central Spanish
73 mountain system as is usual following mild April temperatures (Sanz *et al.* 2003). The
74 dramatic cold snap in the first days of May implied that minima reached freezing over
75 large areas (AEMET annual report), a long-term record for that time of year. Own
76 observations at 1200 m above sea level (asl) showed that buds of early-budding oaks
77 were instantly killed by the cold snap while their opening was abruptly stopped in other
78 trees. Moreover, oak budding was considerably delayed at higher altitudes. Here we
79 show that these anomalous spring conditions were followed by the only mass
80 reproductive failure recorded in 24 years (1991-2015) of research on a mountain
81 population of Iberian pied flycatchers *Ficedula hypoleuca iberiae*. A brood manipulation
82 experiment planned for a year without mass failure was conducted in 2010 and
83 associated with detailed nestling mortality checks at the nests. What was to be a
84 manipulative experiment on brood size was conducted in what became an anomalous
85 year and the results thus provided insight into the effects of sudden climatic extremes
86 on breeding success of an insectivorous passerine.

87

88 **METHODS**

89 **General methods**

90 Since 1991 we have studied a population of Iberian pied flycatchers breeding in nest-
91 boxes in a montane oak (*Quercus pyrenaica*) forest at 1200 m.asl in Valsaín, Segovia,
92 central Spain (40° 54'N, 04° 01'W) (see Sanz et al. 2003 for a description of the study
93 area and population). All nest-boxes (approximately 300) are repeatedly inspected
94 each spring and occupation by pied flycatchers recorded (50-125 are occupied by
95 Iberian pied flycatchers). We have collected breeding data from all pied flycatcher
96 nests between 1991 and 2014 by visiting the nest-boxes every 2-3 days from early May

97 (birds arrive during the second half of April) to end of June. The mean clutch size in the
98 population is 5.60 ± 0.04 (n=24 years) and the mean brood size is 4.64 ± 0.08 (24 years)
99 nestlings. Nestlings fledge with 16 days and cannot be handled after day 13 without
100 inducing premature fledging. Hatching date is obtained through daily inspections when
101 full clutches have been incubated for 12 days (duration of incubation is 13-15 days).
102 The first observation of a nestling is then established as hatching date. We have thus
103 obtained information on laying date, hatching date and the number of nestlings alive at
104 13 days (hatching date = day 1). We have obtained the biometrical measurements of
105 all nestlings when 13 days old. We have ringed adults and nestlings with numbered
106 aluminium rings, measured their tarsus length with a digital calliper to the nearest 0.01
107 mm and weighed them with a Pesola® spring balance (precision of 0.25 g). Folded
108 wing length has been measured since 2002 with a stopped ruler to the nearest mm. As
109 we have conducted different field experiments on this population throughout the long-
110 term study, only non-experimental nests have been included in long-term comparisons.
111 Hatching success is calculated as the number of hatched eggs divided by clutch size.
112 Fledging success is calculated as the number of fledged young divided by the number
113 of hatched nestlings. The death of complete broods has been noted without
114 confirmation if some parent was still provisioning the brood when the death of the last
115 nestling occurred or if the brood had been deserted.

116 Local climatic information was provided by the Spanish Meteorological Agency
117 (AEMET). The weather station (Segovia, station no. 2465, coordinates: 40° 56' 43" N,
118 4° 7' 35" O) is located 9 km from the study area and at the same altitude.

119

120 **Brood manipulation**

121 This experiment was conducted unawares of the impending dramatic conditions for the
122 population which could not be detected before hatching of the young. The cold snap

123 (see below) happened before the beginning of egg-laying in the population (no laying
124 occurs in the first week of May). Two days after hatching was detected during daily
125 nest checks, two or one nestling were transferred between simultaneously hatched
126 reduced broods (n=21) and enlarged broods (n=21). A control group of 30 nests with a
127 similar distribution of hatching dates as in the other treatments was left unchanged with
128 respect to brood size, although nestlings were handled at the same age. The number
129 of nestlings transferred depended on brood size at hatching, with broods of 5 and 6
130 hatchlings losing or receiving two nestlings and broods of 4 losing or receiving one
131 nestling (there was only one brood of 7 which was kept as control). Nests were visited
132 at 3, 7, 9, 11 and 13 days of age to check for nestling mortality and stage of total
133 failure.

134

135 **Statistical analyses**

136 Data on breeding success for 2010 were compared with data for control broods in the
137 other years. Results from the brood manipulation experiment included all nests for
138 2010. Treatments have been compared with parametric or non-parametric tests
139 depending on data distributions (Statistica package, STATSOFT). Medians are
140 presented with quartiles for nonparametric distributions and as means with standard
141 errors (SE) for normal distributions.

142

143 **RESULTS**

144 **Climate**

145 In 2010 minimum temperatures during the first week of May in the study area attained
146 very low values including freezing conditions following directly after exceptionally warm
147 weather in the last days of April (Fig. 1). The difference in minima between April 29 and

148 May 6 was 15°C (Fig. 1). On the other hand, mean daily minimum temperatures during
149 June 2010 when broods were being raised were within the 95% confidence interval for
150 other years.

151

152 **Comparison of breeding success with other years**

153 Hatching success (91.6 %) was close to the average for all years (90.3 ± 1.3 %, n=23
154 years). However, fledging success (53.8%) was the lowest for the whole study period
155 and clearly lower than for other years (79.9 ± 1.7 %, range 66-93%, n=23 years). In total
156 26 or more than a third of broods suffered total mortality before the age of 13 days.
157 Total mortality affected less than 12% of broods in other years (average 5.1 ± 0.7 %,
158 range 0-11.2%). While on average 4.6 ± 0.1 (range 3.8-5.3, n=23 years) chicks per nest
159 were raised in other years, only 2.7 ± 0.4 nestlings on average (n=30 control broods)
160 fledged in 2010. Fledglings weighed 1 g less on average (12.6 ± 0.3 g, n=18 control
161 broods with surviving nestlings at 13 days) than the average for other years (13.6 ± 0.1
162 g, range 11.9-14.8, n=23 years). They also showed the shortest mean tarsi (16.8 ± 0.1
163 mm, n=18 broods) recorded (17.39 ± 0.05 mm, range 16.98-17.85 mm, n=23 years).
164 Mean wing length (41.4 ± 0.8 mm, n=18 broods) was also the shortest since 2002
165 (45.8 ± 0.4 mm, range 42.8-47.8, n=12 years).

166

167 **Brood manipulation**

168 Total failure affected 19% of reduced broods, 37% of control broods and 52% of
169 enlarged broods. Frequencies of total failure differed significantly between reduced and
170 enlarged broods ($\chi^2=5.08$, p=0.024), but not in other comparisons between treatments.
171 There was no significant difference between treatments in the number of nestlings
172 fledged in the three experimental treatments (Table 1).

173 There was barely any mortality in the nests before the age of 3 days (Table 1).
174 Absolute mortality (no. of dead chicks) was detectable in control and enlarged broods
175 in the periods 3-7 and 9-11 days and only for enlarged broods in the period 7-9 days
176 (Table 1). However, absolute mortality did not differ between treatments for any period
177 (Table 1). Mortality rate (%) during the first week after hatching was detectable for
178 control and enlarged broods but did not differ between treatments (Table 1). However,
179 mortality rate during the second week was significantly related to treatment (Table 1),
180 with a significant difference between reduced and enlarged broods ($H_{42}=7.2$, $p=0.014$).
181 Total mortality rate increased from reduced to enlarged broods ($H_{42}=9.1$, $p=0.002$), and
182 the median for enlarged broods was total failure (Table 1). More than half of mortality
183 happened in the second week of nestling life and the proportions according to period
184 (1-7 and 7-13 days) did not differ among treatments (Kruskal-Wallis $H_{48}=0.90$,
185 $p=0.6382$).

186 Mass and wing length were significantly affected by treatment, with both
187 measures declining with experimental brood size (Table 1). Nestlings in reduced
188 broods had higher masses than nestlings in other treatments (Post-hoc Fisher LSD
189 tests: reduced-control $p=0.005$, reduced enlarged $p=0.002$). Nestlings in enlarged
190 broods had shorter wings than nestlings in other treatments (Post-hoc Fisher LSD
191 tests: enlarged-control $p=0.032$, enlarged-reduced $p=0.004$). Only in reduced broods
192 did nestlings attain masses before fledging which can be considered normal (Table 1).

193 Strikingly, the number of fledglings raised was positively (Fig. 2a) and second-
194 week mortality negatively related to hatching date for all broods (Fig. 2b). Total failures
195 were more frequent at early nests (Fig. 2). If only considering control broods, the trend
196 was only significant for second-week mortality (Kendall $\tau_{29}=-0.43$, $p<0.01$).

197 Only 6 fledglings from the 2010 cohort recruited to the population, the lowest
198 number for any year in the study period except 1996 when a mass predation event

199 occurred. This amounted to 3.3% of fledged young which is half the average
200 recruitment rate for the rest of the study years ($6.7 \pm 0.01\%$, $n=21$).

201

202 **DISCUSSION**

203 The cold snap at the beginning of May 2010 in central Spain following mild April
204 conditions was associated with dramatic reproductive failure in a population of Iberian
205 pied flycatchers, the only such event witnessed by researchers in the study population
206 in 24 years. The event was characterized by frequent total failures during the second
207 week of life of nestlings, especially between the ages of 9 and 11 days. Moreover,
208 fledged nestlings in non-deserted broods attained very low values for all
209 measurements, especially for mass. There are several lines of evidence linking the
210 event to conditions of extremely low food availability for nestlings and parents. First,
211 broods were massively deserted in the second week of life, especially after the age of 9
212 days, when food demand by broods reaches its peak. Second, only experimentally
213 reduced broods suffered normal levels of mortality and of nestling growth. Third,
214 mortality and total failures hit strongest the early broods which are usually the more
215 successful in the population, an inverted trend which may be linked to low caterpillar
216 availability in the habitat. This leads to the inference that the cold snap with freezing
217 temperatures in the morning during the period when oak buds normally open and
218 folivorous caterpillars start their development, probably killed off the main prey base on
219 which pied flycatchers depend for breeding (Moreno *et al.* 1995). Evidence for areas at
220 higher altitudes (J. Moreno, unpubl. observations), where oaks show a later phenology,
221 indicate that our study population occupied habitats critically affected by the May 2010
222 cold snap in the Spanish central mountain range.

223 Cold spells during the nestling stage have been shown to affect nestling
224 mortality and growth in northern pied flycatcher populations (e.g. Virolainen 1984, Eeva

225 et al. 2002). In our study, the anomalous weather conditions during late April and early
226 May were followed one month later by frequent total failure, high partial mortality and
227 exceptionally poor nestling growth. Moreover, the weather conditions prevailing during
228 the nestling stage of most broods were not exceptional and could not explain mass
229 reproductive failure in our population. Thus we show that weather conditions of short
230 duration can affect food availability one month later. The most plausible explanation for
231 such delayed effects is that folivorous caterpillars failed to develop due to shortage of
232 young leaves to feed on or to effects on reproducing adult moths. Folivorous
233 caterpillars constitute the main prey base of pied flycatchers in the study area (Moreno
234 *et al.* 1995). Freezing temperatures in early May may have completely stopped bud
235 development in montane oak forests at altitudes where it had already started like our
236 study area.

237 The frequency of total failures and nestling mortality were very low before the
238 nestling age of 3 days, increased slightly to the age of 7 days and accelerated just as
239 food demands by nestlings in connection with growth spurts reach their maxima
240 (Lundberg & Alatalo 1992). Total failures were especially frequent between the ages of
241 9 and 11 days. Almost half of the total failures occurring at this stage affected enlarged
242 broods, although not even reduced broods were immune to total failure. Individual
243 nestlings also died with high frequency at this stage, reducing many broods at fledging
244 to only 2 or 3 nestlings. The dramatic effect of brood enlargement on reproductive
245 success is evidence of the cliff-edge effect postulated for clutch size limitation in
246 stochastic environments (Boyce & Perrins 1987, Roff 2002). Clearly, large clutches are
247 heavily penalized in extreme conditions in our population. Moreover, the apparent
248 inability of females to predict future conditions at laying, which occurred after the cold
249 snap, indicates that food availability for nestlings is not predictable several weeks in
250 advance. The study indicates also that there are no efficient brood reduction
251 mechanisms that can avoid total failure in our and possibly other populations. Our

252 experiment unintendedly showed that only in reduced broods did fledglings approach
253 normal values for fledging mass. However, the food situation must have been so critical
254 that even reduced broods suffered total failure. There were very few local recruits to
255 the population from the 2010 cohort, suggesting that postfledging survival was
256 extremely low for chicks raised during the mass failure event. Mean failure rate during
257 normal conditions according to a revision of 14 studies on mass reproductive failures
258 (Moreno & Møller 2011) was 27% but 79% during extreme conditions. Our failure rate
259 of 36% is intermediate but is still extreme considering that it is more than twice as high
260 as in other years. It is also higher than the 23% total failure rate in a Scandinavian
261 population of the collared flycatcher *Ficedula albicollis* elicited by a cold spring
262 (Wiggins *et al.* 1994). Breeding failure may have been linked to decreased adult
263 survival (Moreno & Møller 2011). Unfortunately many adult birds suffered total failure
264 before they could be caught, so we cannot estimate this effect accurately.

265 Early breeders in the population are those normally better adjusting the nestling
266 stage to high availability of caterpillars and attaining a high reproductive success
267 (Morales *et al.* 2007, Moreno *et al.* 2009, Ruiz-de-Castañeda *et al.* 2009). Late
268 breeders provision may provisnestlings with increasing amounts of prey other than
269 caterpillars (J. Moreno, unpubl. data), which are inadequate prey for growing nestlings
270 of forest passerines (Banbura *et al.* 1999, Wilkin *et al.* 2009). In 2010, the typical date-
271 dependent decrease in breeding success was inverted. It was early breeders that
272 suffered the heaviest casualties, presumably because the caterpillar food base failed
273 almost completely while alternative prey were still not available. Inverted date-
274 dependent trends in breeding success may constitute a critical indication of food base
275 failure for breeding insectivorous birds.

276 Published information on mass breeding failures in passerines is scant as most
277 studies deal with seabirds and waders (e.g. Ganter & Boyd 2000, Gaston *et al.* 2002,
278 Viera *et al.* 2006, Yannic *et al.* 2014). However, some studies on forest birds report

279 massive breeding failure linked to long-term drought conditions (Mac Nally *et al.* 2009).
280 We conclude that the mass reproductive failure event detected in 2010 in our
281 population may be a frequent undetected consequence of late cold snaps in
282 Mediterranean mountain habitats as only long-term population studies may be able to
283 register such events. Other populations of the species breeding at higher altitudes were
284 not equally affected by the cold snap (J. Moreno, pers. obs.), indicating that local
285 variation in vegetation and insect phenology may be paramount to explain the
286 geographical distribution of such effects. In any case, an increased frequency of
287 extreme weather events as predicted by some climate change scenarios (Moreno &
288 Møller 2011) may dramatically affect insectivorous avian populations in the future.
289 Increased future frequencies of early spring cold snaps as predicted by some climate
290 change scenarios may have serious repercussions for birds in mountain habitats which
291 depend on folivorous caterpillars.

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293

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306

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392 Table 1. Comparisons between experimental treatments in mortality and reproductive success variables (median and quartiles or mean±SE) with non-
 393 parametric (Kruskal-Wallis, H) or parametric tests (ANOVA, F)

394

395	Reduced	Control	Enlarged	Test	
396	(n=21)	(n=30)	(n=21)		
397					
398	Brood size after manipulation	3 (3-4)	5 (4-6)	7 (7-8)	H=52.9, p<0.001
399					
400	Nestling mortality 1-3 days	0 (0-0)	0 (0-0)	0 (0-0)	H=1.91, p=0.38
401					
402	Nestling mortality 3-7 days	0 (0-0)	0 (0-1)	0 (0-1)	H=4.44, p=0.11
403					
404	Nestling mortality 7-9 days	0 (0-0)	0 (0-0)	0 (0-1)	H=5.04, p=0.08
405					
406	Nestling mortality 9-11 days	0 (0-0)	0 (0-1)	0 (0-1)	H=4.47, P=0.11
407					
408	Nestling mortality 11-13 days	0 (0-0)	0 (0-0)	0 (0-0)	H=2.11, p=0.35
409					
410	% Nestling mortality 1-7 days	0 (0-0)	0 (0-20)	0 (0-20)	H=1.69, p=0.43
411					
412	% Nestling mortality 7-13 days	0 (0-0)	8.3 (0-40)	28.6 (0-100)	H=7.72, p=0.021
413					
414	% Total nestling mortality	0 (0-33)	29.2 (0-100)	100 (28.6-100)	H=20, p<0.001
415					
416	Fledged young	3 (2-3)	3.5 (0-5)	0 (0-5)	H=1.68, p=0.43
417					
418	Fledgling tarsus length (mm)	17.01±0.14	16.78±0.13	16.56±0.18	F=2.06, p=0.14
419					
420	Fledgling mass (g)	13.77±0.28	12.60±0.27	12.22±0.37	F=6.93, p=0.002
421					
422	Fledgling wing length (mm)	42.5±0.8	41.4±0.8	38.4±1.1	F=4.61, p=0.015
423					

424

425

426 **Figure legends**

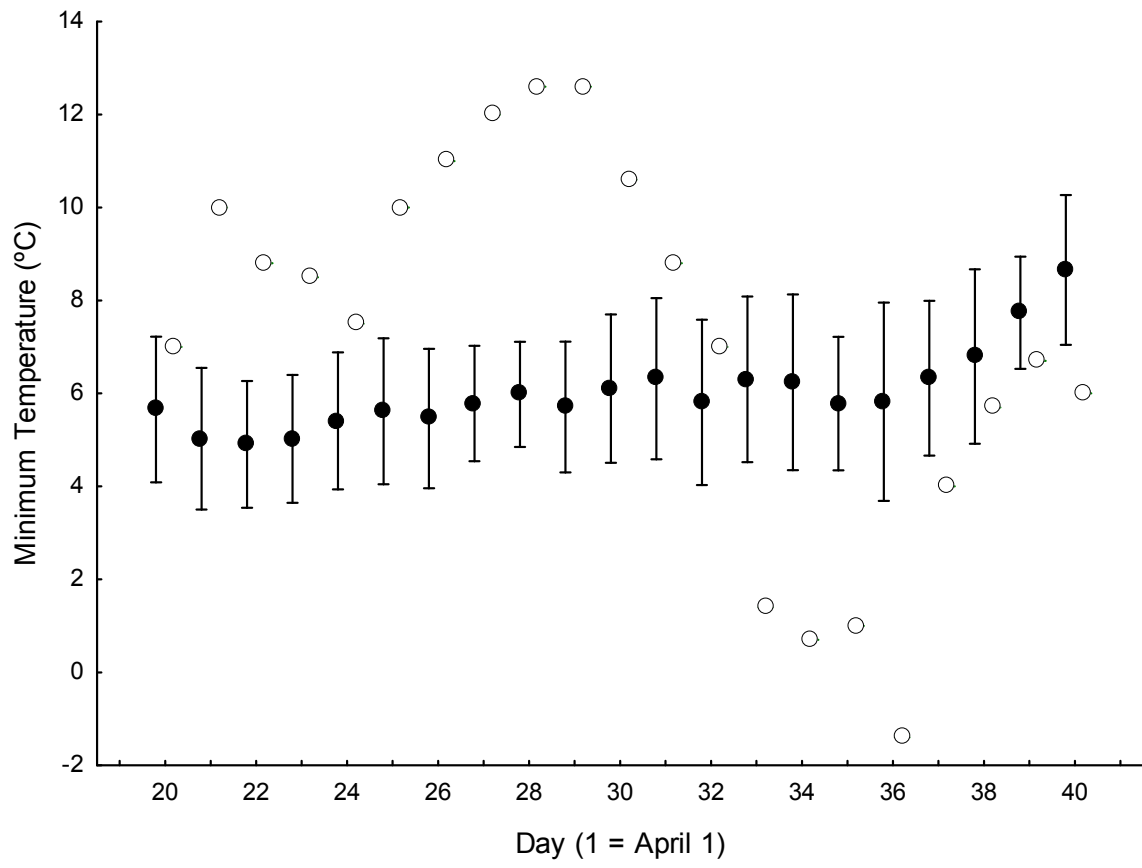
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428 **Figure 1.** Minimum temperatures near the study area for the period 20 April-10 May for
429 2010 (open dots) and for 1991-2014 excluding 2010 (means as filled symbols \pm 95%
430 confidence intervals)

431 **Figure 2.** Correlations between hatching date (April 1=1) and a) number of fledglings
432 (Kendall τ_{71} =0.17, $p<0.05$) and b) nestling mortality in the second week of life (Kendall
433 τ_{71} =-0.30, $p<0.05$)

434

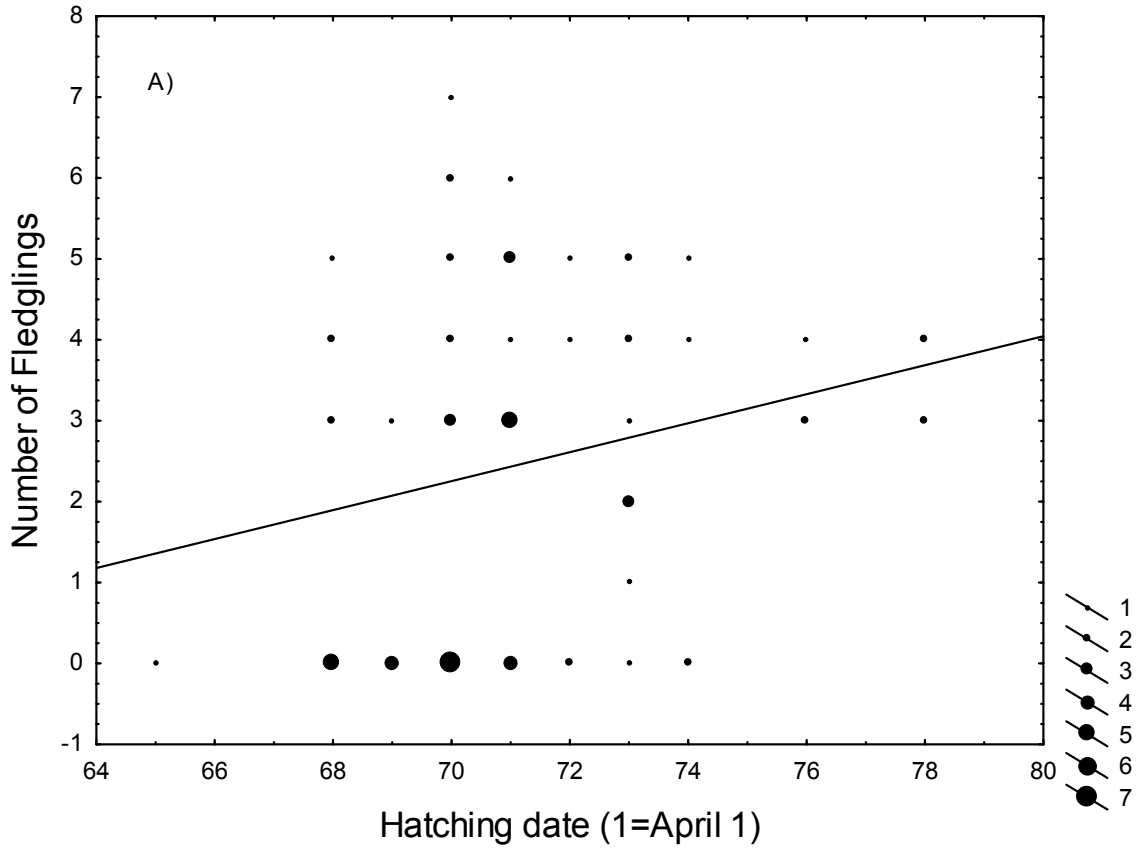
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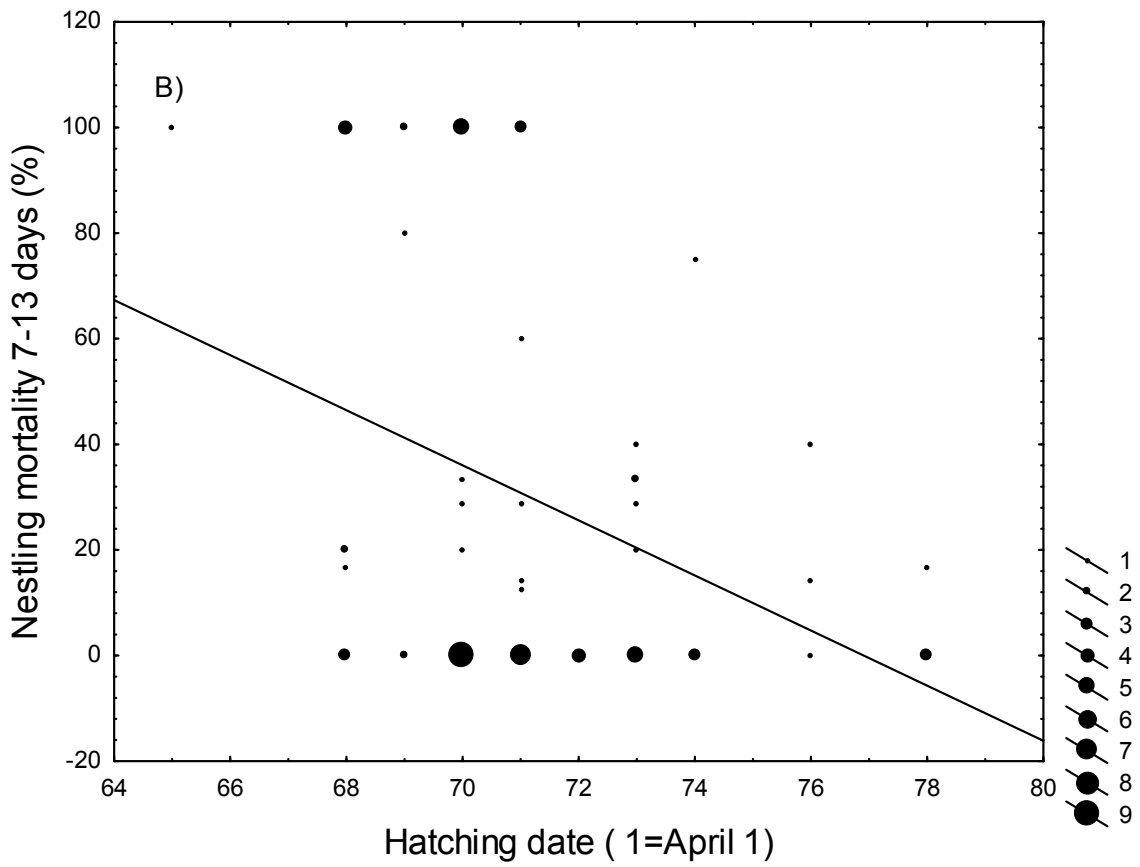
436
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438

439 Figure 1



440
441



442
443

Figure 2