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RH: Temperature and onset of breeding along elevational gradients

Modeling phenological reaction norms over an elevational gradient reveals contrasting strategies of Dusky Flycatchers and Mountain Chickadees in response to early season temperatures

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1 **ABSTRACT**

2 We developed an approach to distinguish among three alternative strategies birds may employ
3 relating the timing of egg-laying across elevations to annual variation in spring temperature
4 (phenological reaction norms), which we applied to analyze breeding phenology of two species
5 over an elevational gradient in the Sierra Nevada, California. In a “simple offset” strategy, birds
6 at different elevations initiate breeding relative to environmental temperature in a consistent
7 manner, in that breeding onset is triggered by a critical temperature regardless of when it occurs
8 in the spring. Elevation-specific reaction norms based on multiple years are offset (high-
9 elevation birds start breeding later) but parallel. In a “delay” strategy, in cooler springs
10 populations at higher elevations that are sensitive to early-season weather-related risks delay
11 laying onset relative to those at lower elevations, yielding a high-elevation reaction norm that
12 diverges from a low-elevation one at cooler temperatures. Conversely, high-elevation
13 populations in cooler springs that are sensitive to the risk of having insufficient time to complete
14 a breeding cycle advance laying onset relative to lower populations (“advance” strategy),
15 yielding a high-elevation reaction norm that converges with a low-elevation one. Both delay
16 and advance strategies imply an elevation-dependent interaction between temperature and date
17 (photoperiod) in influencing laying onset. Examined across three elevation groupings,
18 phenological reaction norms of Mountain Chickadees (*Poecile gambeli*) were essentially
19 parallel, consistent with simple offset, whereas Dusky Flycatchers (*Empidonax oberholseri*)
20 relationships were more complex. In cooler springs, mid-elevation flycatchers bred
21 comparatively late relative to lowest-elevation birds (delay), implying greater sensitivity to early
22 season risks, but still with sufficient time to complete a breeding cycle. However, high-elevation

23 flycatchers bred comparatively early relative to mid-elevation populations (advance); delaying at
24 these highest elevations may not be an option. Our approach revealed differences in risk-
25 sensitivity that were consistent with other ecological differences between the two species.

26

27

28 **Keywords:** Dusky Flycatcher, elevational gradient, lay date, Mountain Chickadee, phenological
29 reaction norms, reproductive phenology, temperature and breeding onset, timing of reproduction

30

31 **LAY SUMMARY**

- 32 • Birds at higher elevations usually begin laying later than those at lower elevations mainly
33 because temperatures that cue breeding occur later at higher elevations. And spring
34 storms that bring rain to lower elevations may produce snow at higher ones, which might
35 favor delaying breeding even longer. However, with shorter breeding seasons at higher
36 elevations, delaying breeding risks running out of time to complete the breeding cycle,
37 favoring relatively earlier laying.
- 38 • Dusky Flycatchers in southern Sierra Nevada demonstrate both responses, depending on
39 elevation: compared to lowest elevations, mid-elevation birds delayed breeding in cooler
40 years, whereas highest-elevation birds advanced lay dates in cooler years compared to
41 mid-elevations; delaying may not be an option.
- 42 • No such risk-sensitivity was observed in Mountain Chickadees, where differences across
43 elevations in first egg dates were constant. Cavity-nesting and other ecological attributes

44 of chickadees likely buffer them from risks to which open cup-nesting flycatchers are
45 more susceptible.

46

47 **INTRODUCTION**

48 The timing of breeding is an important component of life history strategy for organisms because
49 it influences many aspects of reproductive success. In bird species that nest in northern temperate
50 regions, clutch size, fledging success, and/or other fitness components often decline across the
51 breeding season (Perrins and McCleery 1989, Winkler and Allen 1996, Brown and Brown 1999,
52 Verhulst and Nilsson 2008, Wiebe and Gerstmar 2010, Winkler et al. 2020). Offspring from
53 nests initiated comparatively late within a season may have lower first-year return rates or
54 apparent survival (Verhulst et al. 1995, Brown and Brown 1999, Dolan et al. 2009) and/or these
55 offspring may themselves have reduced reproductive success (Visser and Verboven 1999).

56 The initiation of breeding may be influenced by several environmental factors (reviewed
57 by Chmura et al. 2019b). For example, increasing daylength is a key predictive cue in birds in
58 temperate regions (Dawson 2008), but ambient temperature in spring is also important
59 (Wingfield 2008, Visser et al. 2009, Drake and Martin 2018). Advances in laying date observed
60 in long-term studies (Crick et al. 1997, Winkler et al. 2002, Dunn 2004, Dunn and Winkler 2010)
61 have corresponded with an earlier onset of warm temperatures in spring and milder winters
62 (Cayan et al. 2001, Schwartz et al. 2006). There is substantial evidence that temperature can have
63 a direct influence on breeding initiation independent of its influence on the phenology of plants
64 and insects, and, hence, food availability (Wingfield et al. 2003, Charmantier et al. 2008, Visser
65 et al. 2009, Pereyra 2011, Ockendon et al. 2013, Drake and Martin 2018). This pattern of

66 variation in lay initiation date among years as a function of spring temperature is evidence of a
67 phenological reaction norm, a relationship between the timing of the expression of a trait and
68 some environmental variable (Stearns and Hoekstra 2005, Chmura et al. 2019a, Inouye et al.
69 2019). Presumably, this plasticity reflects some underlying gene-by-environment interaction
70 that has been naturally selected to optimize reproductive success over some range of
71 environmental conditions that an organism regularly experiences. The slope of a regression of
72 lay date on temperature is indicative of the sensitivity of the former to the latter (Inouye et al.
73 2019).

74 In mountainous landscapes, air temperature typically decreases with increasing elevation
75 as a result of adiabatic cooling (Whiteman 2000). Although topographical aspect, vegetation
76 (e.g., degree of shading), and snow cover can influence small-scale temperature variation, other
77 factors being equal, on a given calendar day the air temperature at a higher elevation will tend to
78 be cooler than at a lower elevation (Whiteman 2000, Körner 2007). Not surprisingly, then, in
79 bird species that occupy mountainous landscapes, populations at higher elevations typically
80 initiate breeding later in the season than populations at lower elevations (Bears et al. 2009,
81 Camfield et al. 2010, Lu et al. 2010a, b; Koslovsky et al. 2018, Saracco et al. 2019, Bründl et al.
82 2020). Furthermore, additional environmental conditions that differ with elevation may also
83 constrain the timing of breeding for birds at higher elevations compared to those that breed at
84 lower ones. At higher elevations in mid- and northern latitudes, snow may persist later into
85 spring in cooler years (Koslovsky et al. 2018, Saracco et al. 2019), and conditions in early spring
86 can be relatively harsh due to variable weather, including fluctuating temperatures that tend to be
87 cold (Martin 2001). Importantly, at higher elevations, the length of time over which conditions
88 are suitable to rear a brood is shorter (e.g., a reduction in the length of the growing season, a

89 decline in plant productivity, colder temperatures during the post-fledging period as summer
90 transitions to autumn). Thus, these differences in environmental conditions that exist across a
91 gradient of elevation may lead to different constraints on the timing of breeding for birds at
92 higher elevations compared to those that breed at lower elevations.

93 Decisions about the optimal time at which to breed would thus appear to carry greater
94 consequences at high elevations than at lower ones. On the one hand, the risk of failure by
95 initiating breeding too early may increase with increasing elevation, because although
96 temperature generally rises as the spring progresses, the occurrence of spring storms can result in
97 sudden and marked temperature declines that can be more severe as elevation increases. For
98 example, a weather frontal passage that brings rain, or no precipitation at all, to lower elevations
99 may bring snow and freezing temperatures to higher ones. Such a sudden change in conditions
100 poses a greater threat to nesting success for individuals at higher elevations (Hendricks and
101 Norment 1992, Martin and Wiebe 2004, Decker and Conway 2009). However, this likely entails
102 a benefit/cost tradeoff, because while delaying the initiation of breeding at higher elevation may
103 reduce the risk of experiencing the negative consequences of spring storms, delaying can also
104 lead to an increased probability that environmental conditions deteriorate or resources become
105 insufficient to complete a reproductive cycle successfully (Wilson and Martin 2008, Bears et al.
106 2009). Under such contrasting constraints, birds breeding at different elevations may differ in
107 their responses to local conditions with respect to onset of reproduction, leading to differences in
108 phenological reaction norms (Martin et al. 2017, Koslovsky et al. 2018, Saracco et al. 2019,
109 Bründl et al. 2020).

110 We identified three alternative strategies for how reaction norms describing laying
111 initiation date and temperature might vary among populations breeding at different elevations.

112 These strategies differ in how a higher-elevation population responds to a “critical temperature”
113 (one that triggers breeding at a lower elevation) depending on when in the spring that
114 temperature occurs (i.e., there is an interaction between the triggering temperature and
115 photoperiod in initiating breeding). We initially emphasize temperature as a potential driver of
116 differences in reproductive onset across elevations because it differs among elevations whereas
117 photoperiod does not. Additionally, we assume that temperature serves as a proxy for a variety
118 of other ecological and climatic factors that are usually highly correlated with temperature, such
119 as snow depth, that may influence breeding date (Koslovsky et al. 2018, Sarraco et al. 2019). We
120 also assumed that members of a population initiate the reproductive cycle (e.g., begin egg laying)
121 after the ambient temperature they experience in spring reaches some critical value or threshold
122 (e.g., temperature minimum, maximum, range, cumulative degree-days, sliding window
123 averaged over some preceding period; Charmentier et al. 2008, Visser et al. 2009, Schaper et al.
124 2012, van de Pol et al. 2016).

125 The first strategy, “simple offset,” is essentially a null model of no difference in behavior
126 among populations at different elevations, and is what would be expected if, within each
127 elevation category, birds initiate breeding in response to the same critical temperature regardless
128 of whether that temperature appears relatively early or relatively late in springtime (i.e., there is
129 no within-season interaction between critical temperature and date). Within a given year, a
130 higher-elevation population would experience the critical temperature later in spring than a
131 lower-elevation population, and egg laying would commence later in birds at the higher
132 elevation. Expanded across multiple years, regression lines (reaction norms) relating breeding
133 onset to a common reference spring temperature for populations at these two different elevation
134 categories would be parallel with equal slopes and different intercepts (Fig. 1A).

135 The second and third strategies describe relationships if birds breeding at a higher
136 elevation respond to weather-related risk differently from a low-elevation population, in either
137 one of two ways: birds might either (1) avoid breeding too early when risk of exposure to
138 inclement spring weather may be high, yielding a “delay” strategy, or (2) avoid breeding too late
139 under increasing risk of having insufficient time to successfully complete a reproductive cycle
140 due to environmental deterioration, either resource- or weather-related, leading to an “advance”
141 strategy. For both of these alternatives, we assume that for the lower-elevation population the
142 critical temperature is more or less constant, as in the simple offset strategy (Fig. 1A), but that in
143 the higher-elevation population the temperature that cues breeding varies with date within a
144 season; that is, there is an interaction between critical temperature and day length (i.e., day of the
145 year) (e.g., Visser et al. 2010, Chmielewski et al. 2013, Phillimore et al. 2016, Simmonds et al.
146 2019, Bründl et al. 2020).

147 Considering the delay strategy (1 above), compared to a population at a lower elevation,
148 initiating breeding following the occurrence of the same critical temperature may expose high-
149 elevation birds to a greater likelihood of subsequent adverse weather. We might expect the
150 pressure to avoid inclement weather to be greater in cooler years, since it is colder weather that
151 poses a greater risk (Martin and Wiebe 2004, Martin et al. 2017, Pereyra and Sedgwick 2020). If
152 so, cooler springtime temperatures might result in higher-elevation birds requiring a higher
153 critical temperature to initiate egg laying, and thus laying dates between higher- and lower-
154 elevation birds diverging the cooler the spring. When examined over multiple years, this delay
155 strategy produces diverging non-parallel regression lines with unequal slopes and y-intercepts
156 (Fig. 1B).

157 Whereas delaying breeding to avoid early-season risks may be a suitable strategy under
158 some conditions, the advance strategy (2 above) considers sensitivity to the alternative risk,
159 namely, of not breeding early enough to complete the reproductive cycle. In early spring the
160 critical temperature for both higher-elevation birds and lower-elevation birds is similar, as in the
161 simple offset model. However, if the temperature is still comparatively cooler at high elevations
162 later into the season (as in a relatively cool year), higher-elevation birds may be triggered to
163 breed at a lower critical temperature than lower-elevation populations as the season progresses to
164 avoid breeding too late. In this advance strategy, regressions of annual laying initiation dates on
165 springtime temperatures for higher- and lower-elevation populations would yield converging
166 lines with non-parallel slopes and unequal intercepts (Fig. 1C). As supporting material we
167 provide a mathematical model consistent with the graphical framework in Figure 1 that explicitly
168 incorporates our assumptions about annual and elevational variation in weather (Supplemental
169 Material: Mathematical Modeling of Alternative Strategies).

170 As a case study, we analyzed these strategies for two species nesting over a relatively
171 steep elevation gradient in the Sierra Nevada of California, which allowed us to exploit
172 temperature variation without the confounding effects of variable day length and, hence,
173 photoperiod, that vary with latitude. We examined two species with different life history and
174 ecological traits. One species, the Dusky Flycatcher (*Empidonax oberholseri*), builds an open-
175 cup nest and is a long-distance (i.e., latitudinal) migrant. The other species, the Mountain
176 Chickadee (*Poecile gambeli*), nests in cavities, and individuals are either year-round residents or
177 make short-distance (elevational) movements. We expected that the two species might show
178 different strategies due to variation in exposure to cold temperatures and precipitation because of
179 differences in nest types and in foraging and migratory behavior. To the extent that cavity-

180 nesting chickadees might be “buffered” to exposure to adverse conditions, we expected
181 populations at higher elevations to be no more sensitive to variation in annual temperature than
182 populations at lower elevations. In this case, reaction norms at different elevations should be
183 parallel and simply offset. Open-cup nesting flycatchers, on the other hand, may be more
184 sensitive to weather variation with increasing elevation (Pereyra and Sedgwick 2020). Although
185 it is not clear a priori whether sensitivity would be manifest in response to the risks from early
186 season bad weather vs. running out of time at the end of the season, we might expect the slope of
187 the reaction norm of a higher-elevation population to differ from that of a lower one.

188

189 **METHODS**

190 **Study Site and Species**

191 We quantified laying initiation dates for chickadees and flycatchers breeding on 14 study plots in
192 the Sierra Nevada of California (Sierra National Forest; see Supplemental Material: Study Plot
193 Locations) in three elevational groups characterized by different vegetation types. “Lowest” plots
194 ($n = 6$) ranged in elevation from 1669-2023 m and consisted of mixed conifer forest, “middle”
195 plots ($n = 4$) ranged in elevation from 2160-2384 m and consisted of true fir forest, and “highest”
196 plots ($n = 4$) ranged in elevation from 2465-2750 m and consisted of lodgepole pine forest. Plots
197 were sampled each year from 1995 through 2001 except in the lowest group, where four of the
198 six were sampled each year on a rotating basis such that each of the six was sampled an equal
199 number of years during the study. Mixed conifer stands consisted primarily of white fir (*Abies*
200 *concolor*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), ponderosa
201 pine (*P. ponderosa*), and California black oak (*Quercus kelloggii*). True fir stands were
202 dominated by white fir and red fir (*A. magnifica*). Lodgepole stands were comprised primarily of

203 lodgepole pine (*P. contorta*). Nest searching in each study plot was focused on an interior 40-ha
204 gridded plot embedded within a 60-ha plot of similar habitat. We selected plots to be
205 representative of mature forest with relatively high canopy cover, although naturally-occurring
206 heterogeneity existed in the form of open, rocky, or brushy areas, and small meadows or streams
207 on all plots.

208 The Dusky Flycatcher is an insectivorous migrant that winters in the southwestern U.S.,
209 Mexico, and Guatemala (Pereyra and Sedgwick 2020), and breeds in western North America in a
210 variety of plant communities. Its open-cup nests are placed in shrubs or trees (Sedgwick 1993,
211 Pereyra and Sedgwick 2020). The Mountain Chickadee is an abundant breeder in coniferous
212 forests in western North America, nesting in cavities excavated by other species and in natural
213 crevices, and is mostly insectivorous during the breeding season (McCallum et al. 2020). Dusky
214 Flycatchers are typically single-brooded, but may renest following a failed first attempt. The
215 same applies to Mountain Chickadees in our study area (personal observations), although they
216 may rear a second brood in other regions (Dahlsten and Copper 1979). We located Dusky
217 Flycatcher and Mountain Chickadee nests from 1995 through 2001 and monitored them twice a
218 week until they failed or fledged young. When flycatcher nest contents could not be observed
219 directly, we used a compass mirror or a mirror on a pole for viewing. We checked chickadee
220 nests with a fiberscope (Purcell 1997) or a light and automotive inspection mirror. The date that
221 the first egg was laid (hereafter, laying initiation date) was determined based on all observations
222 collected at a nest. Observations prior to completion of the clutch were backdated, assuming one
223 eggs laid per day. For other nests, clutch size and a date to anchor the timing of the nesting cycle,
224 such as initiation of incubation or hatching, were necessary for backdating. Included in the
225 analysis were those nests for which we were confident that our estimate was within two days of

226 the true laying initiation date. We included a few nests whose laying initiation was 15-19 days
227 after the first laying initiation date when the earliest laying initiation date was notably earlier
228 than subsequent nests. To reduce the risk of including nests that were renesting attempts after a
229 failed first nesting attempt, we excluded most nests with laying dates that were greater than 14
230 days after the earliest laying initiation date in each year, with a few exceptions. This criterion
231 was based on the range of initiation days in a study of Dusky Flycatchers in Montana (Sedgwick
232 1993) and observed for Mountain Chickadees in a separate study that took place on a subset of
233 the plots in the current study (Coe 2009). For many nests (including most flycatcher nests) we
234 were able to ascertain the number of eggs laid and whether the nest was successful (i.e., fledged
235 one or more young). We were unable to access the lowest elevation plots in 1997 before
236 chickadees began breeding, and thus lack observations for those plots in that year.

237 **Temperature Recording**

238 Comparing patterns of breeding initiation among birds at different elevations and across
239 different years in response to weather variation requires a consistent approach to measuring the
240 weather (Inouye et al. 2019). We implemented this by recording temperature during a specific
241 fixed period each year at a specific fixed elevation. The effectiveness of this “reference
242 temperature” in capturing annual and elevational variation in environmental conditions was
243 based on observations of seasonal and elevational patterns of temperature variation, and because
244 temperatures display significant autocorrelation over relevant spatial and temporal scales (e.g.,
245 Vinnikov et al. 2011). Within broad limits the specific reference site and dates we chose are not
246 critical to our analysis, i.e., it was not necessary that we choose the precise time the decision to
247 breed was made, as the purpose of the reference temperature was to quantify whether the season
248 was early/warm or late/cool relative to long-term weather at the site. Our criteria were that the

249 location and period be both geographically and phenologically relevant to our study site and
250 species. We empirically validated our assumptions concerning patterns of spatial and temporal
251 correlations in temperatures by analysis of temperature patterns taken over a quarter-century
252 period in the region from which our bird data were taken (see Supplemental Material: Validating
253 Model Assumptions). Collectively these correlations indicate that reference temperatures
254 measured during a fixed specific period at a fixed specific location represent the relative coolness
255 or warmth of a breeding season in relation to other years, and that this annual relation is
256 consistent across different elevations throughout a study area. Although additional factors (e.g.,
257 depth of snowpack, timing of snow melt, bud burst) may play proximate roles in when birds
258 initiate egg laying, we expected those additional factors to be strongly correlated with
259 temperature.

260 We based our reference temperature on data that we collected at a forested location in the
261 Sierra National Forest at 1140m elevation, Peterson Mill, slightly lower than but close to our
262 lowest-elevation study plot. Temperature data were recorded at one-hour intervals using a
263 Hobotemp temperature logger (Onset Computer, Bourne, Massachusetts, USA) placed inside a
264 vented white wooden box (“weather box”) inside a waterproof case with a temperature probe
265 threaded out the end of the case. The weather box was attached to a fencepost approximately one
266 meter above the ground.

267 We calculated reference temperature as the average hourly temperature over a seven-day
268 period in spring in each year as measured at our reference site in 1995 and 1997-2001. Due to
269 logger failure in 1996, temperature data were missing and therefore we excluded nest data for
270 that year from analysis. Averaging over multiple days provided a better summary of pre-breeding
271 conditions than temperature measured on a single day (e.g., a storm passing through the region

272 causing a brief drop in temperature would provide an anomalous measure). We chose a period
273 that was earlier than, but relatively close to, the earliest initiation of breeding for each species at
274 our study site. Since the mean earliest average laying date for chickadees and flycatchers at the
275 lowest elevation plots (13 and 27 May, respectively) differed by two weeks, we averaged
276 temperatures over the seven-day period that ended six days prior to these dates; thus, we
277 averaged temperature over first week of May (May 1-7) for Mountain Chickadees and the third
278 week of May (May 14-21st) for Dusky Flycatchers. To confirm a correlation between
279 temperature and snow depth, we obtained snow depths nominally measured on 1 April (± 5 days)
280 at a National Resources Conservation Service snow course/aerial marker site (Beard Meadow,
281 2990 m, 37.11 N, -118.84 E; <https://www.nrcs.usda.gov/wps/portal/wcc/home/>) ~ 15 km from
282 our highest elevation plots (Supplemental Material: Validating Weather Assumptions).

283 **Statistical Analysis**

284 We conducted a mixed model analysis for each species using PROC GLIMMIX in SAS
285 9.4 (SAS Institute 2016) to evaluate differences in laying initiation date between elevations as a
286 function of annual variation in spring temperature (i.e., the slopes of elevation-specific reaction
287 norms). Nest was the unit of observation and temperature and elevation category were treated as
288 fixed effects. Study plot was included as a random effect to account for potential correlation
289 among nests occurring on the same plot. We included an additional random effect to account for
290 between-elevation variance heterogeneity. The models also included a repeated-measures
291 component for each plot across years to account for potential auto-correlated responses that
292 could bias estimated standard errors. We verified assumptions for each model by examination of
293 studentized residuals for both normality and variance heterogeneity. We used a test of
294 differences of least square means with a Tukey-Kramer adjustment for p -values to test for

295 differences in mean laying initiation date by elevation at a set of representative temperatures (8°
296 C, 10° C, 12° C, 14° C, and 16° C) for pairs of regressions. We report *p*-values of statistical tests
297 to indicate the strength of evidence against the null hypothesis (Murtaugh 2014). We compared
298 Akaike Information Criterion corrected for small sample size (AICc) to assess whether reference
299 temperature or snow depth provided a better fit to lay-date data using the same mixed model
300 (smaller is better; Burnham and Anderson 2002). Throughout, we report means \pm one standard
301 error unless otherwise noted.

302 To assess whether clutch size varied with the timing of reproduction, we performed an
303 analysis similar to the preceding for lay date using PROC GLIMMIX, only with a log link and
304 Poisson error distribution, and including lay date as an additional main effect along with
305 temperature and elevation. We tested a total of 12 models, including each main effect separately,
306 in two- and three-variable combinations, and all possible interactions. However, due to an
307 unbalanced distribution of nests across lay dates when modeling clutch size with the main effects
308 and interactions of elevation and temperature, the regressions failed to converge unless we
309 removed individual study plots as a random effect.

310 To assess whether nest success varied with lay date, we used the logistic exposure
311 method (Shaffer 2004), testing the same 12 models used in the analyses of clutch size and
312 number fledged. We first calculated daily survival rates for nests in each elevation group and
313 tested for differences among them, using a Tukey's Studentized Range test to control for Type I
314 experimentwise error rates. We used AICc to rank the candidate models. Analyses were
315 conducted using PROC NLMIXED (SAS Institute, Inc. 2016). We examined the same 12 models
316 used in the analyses for clutch size.

317 Data are available from the Dryad Digital Repository (Coe et al. 2021).

318

319 **RESULTS**

320 **Weather**

321 Average temperature at the reference site during the third week in May varied from 7.2° C in
322 1998 to 16.9° C in 2001 (Supplemental Material: Validating Model Assumptions). Annual
323 variation paralleled that of the high and low elevation regional weather stations we used to
324 validate our weather assumptions. Based on 25 years of snowfall data from Beard Meadow that
325 overlapped with temperature data from the high elevation validation station, snow depth on April
326 1 was highly correlated with temperature averaged over the preceding 7 days ($r = -0.708$). For
327 both species average temperature provided a better fit to lay-date data than did snow depth. For
328 flycatchers, the temperature mixed model yielded $AIC = 1422.85$ (vs. a null model AIC of
329 1685.91), whereas for snow depth $AIC = 1548.42$. For chickadees, $AIC_{\text{temperature}} = 1312.17$,
330 $AIC_{\text{snow}} = 1441.30$, and $AIC_{\text{null}} = 1543.23$. Akaike weights for both temperature models closely
331 approached 1, and thus snow depth was not a useful predictor and all analyses were performed
332 and interpreted using temperature.

333 **Mountain Chickadees**

334 Mean laying initiation dates in Mountain Chickadees were earliest in the lowest-elevation plots
335 and latest in the highest-elevation plots in each year, with a difference of as much as 14 days in
336 two of the years (Fig. 2A; see figure for sample sizes). Lay dates varied significantly with
337 respect to temperature and elevation, but there was little support for an interaction between
338 temperature and elevation, and slopes of the three regression lines were not strongly
339 differentiated from each other (Table 1; Fig. 3A). Thus, the results for this species were
340 consistent with a simple-offset strategy (Fig. 1A). Laying initiation date was estimated to be 8.6

341 (± 1.48) days later in middle compared to lowest elevations (test of differences in least square
342 means $t = -5.81$, $p_{adj} < 0.001$) and $12.0 (\pm 1.46)$ days later at highest elevations compared to
343 lowest ($t = 8.19$, $p_{adj} = < 0.001$). The difference between highest and middle (3.4 ± 1.28 days
344 later in highest) was relatively slight ($t = 2.65$, $p_{adj} = 0.081$). Because slopes of initiation date
345 versus temperature were essentially parallel for the three elevations, least square mean
346 differences were the same at all temperatures tested.

347 Although the sample size was relatively small ($n = 49$), clutch sizes of Mountain
348 Chickadees varied with lay date ($F = 4.93$, $df = 1, 47$; $p = 0.031$), declining through time
349 (Supplemental Material: Clutch Size and Daily Survival Rates). However, clutch sizes did not
350 vary among elevation categories ($F = 0.36$, $df = 2, 46$; $p = 0.701$) or with reference temperature
351 ($F = 0.05$, $df = 1, 47$; $p = 0.829$). When considered simultaneously (i.e., a model with three main
352 effects), lay date remained well-supported (Type III main effect $p = 0.015$; elevation $p = 0.231$,
353 temperature $p = 0.069$). No main effects in two-way interactions nor the one three-way
354 interaction received any support (all $p > 0.90$).

355 We had larger sample sizes for nest outcomes for chickadees ($n = 205$). Results for daily
356 nest survival for chickadees were dominated by differences among elevation categories, with
357 nest success at the lowest elevation considerably less than either of the two higher ones ($p_{adj} <$
358 0.002 for highest, 0.006 for middle), but middle elevation was similar to the highest elevation
359 ($p_{adj} = 0.097$) (Supplemental Material: Clutch Size and Daily Survival Rates). The most
360 supported model for daily survival rate of chickadee nests included only elevation, with an
361 Akaike weight of 0.40. Two other models were competitive and, in addition to elevation,
362 included either lay date or temperature; however the 95% confidence intervals for these variables
363 included zero, suggesting these variables were not informative.

364 **Dusky Flycatchers**

365 Mean laying initiation dates in Dusky Flycatchers were also earliest in the lowest-elevation plots
366 and latest in the highest-elevation plots in each year, with the exception of two years (1998 and
367 2001; Fig. 2B; see figure for sample sizes); in both cases the differences were slight (about a
368 day). Otherwise, lowest- and highest-elevation mean breeding onset date for flycatchers differed
369 by as many as 27 days (in 1995). Dusky Flycatchers initiated laying later than Mountain
370 Chickadees within the same elevation category (Fig. 2). In both species, laying initiation date
371 and the annual reference temperature were negatively associated within all elevation categories
372 (Fig. 3).

373 Phenological patterns in the Dusky Flycatcher were more complex than for chickdees.
374 As with chickadees, the main effects of temperature and elevation were both substantial, but
375 there was more statistical support for their interaction (Table 1). This support was amplified
376 when examining pairwise comparisons. Comparing middle and lowest elevations, regression
377 slope of the former was steeper and diverged from the latter (Table 1, Fig. 3B), and laying
378 initiation dates were different at cooler temperatures, but not at warmer temperatures.
379 Specifically, laying initiation dates differed at 8° C, 10° C, 12° C, and 14° C (e.g., test of
380 differences in least square means at 14° C, $t_{19,3} = -2.68$, $p_{\text{adj}} = 0.04$;) but were not different at 16° C
381 ($t_{22,7} = -1.71$, $p_{\text{adj}} = 0.22$). At 8° C, laying initiation date was estimated to be 12.6 ± 3.1 days later
382 at middle than at lowest elevations whereas at 16° C, the estimate was 5.1 ± 2.9 days later.
383 Overall, these results are consistent with birds in the middle elevation demonstrating a delay
384 strategy relative to the lowest-elevation birds (Fig. 1C).

385 Slopes of the regression lines for the highest-elevation population and the middle-
386 elevation population also differed (Table 1, Fig. 3B). However, in contrast to the low-middle

387 comparison, laying initiation dates were different between the two elevations when the yearly
388 reference temperature was higher, but not when it was lower. Specifically, there was little
389 support for differences in dates at 8° C, 10° C or 12° C (e.g., test of differences in least square
390 means at 12° C, $t_{14,6} = 2.13$, $p_{adj} = 0.12$;) but more so at 14° C and 16° C (e.g., at 14° C, $t_{19,3} = 2.81$,
391 $p_{adj} = 0.03$). At 16° C, laying initiation date was estimated to be 11.3 ± 3.7 days later at highest
392 than at middle elevations, whereas at 8° C it was only 1.1 ± 3.6 days. Overall, the results for
393 Dusky Flycatcher are consistent with individuals in the highest elevation demonstrating an
394 advance strategy relative to birds in the middle elevation (Fig. 1B). Slopes did not differ between
395 the highest and lowest plots (Table 1), suggesting a simple-offset strategy when omitting the
396 middle elevation plots (Fig. 1A).

397 Dusky Flycatcher clutch sizes ($n = 161$) also varied with lay date ($F = 6.45$, $df = 1$, 159; p
398 $= 0.012$), declining through time as well (Supplemental Material: Clutch Size and Daily Survival
399 Rates). Although there was a tendency for clutch sizes at the highest elevation to be less than
400 those at lower ones (p_{adj} for middle = 0.080, for lowest = 0.067), the overall effect of elevation
401 was marginal ($F = 2.78$, $df = 2$, 158; $p = 0.065$). The reference site temperature appeared to have
402 little effect on clutch size ($F = 0.86$, $df = 1$, 159; $p = 0.355$). When considering all pairs of
403 variables, clutch size remained associated with lay date as a main effect (Type III main effect $p =$
404 0.012), somewhat less so with elevation ($p = 0.65$), but with little support for temperature ($p =$
405 0.355); when considered simultaneously, lay date again remained important (Type III main
406 effects lay date $p = 0.012$; elevation $p = 0.130$, temperature $p = 0.164$). Only two- and three-way
407 interactions that included lay date had much support ($p < 0.10$).

408 In flycatchers, as with chickadees, variation in daily survival rate of nests ($n = 208$) was
409 dominated by differences among elevational categories, with the lowest elevation having a lower

410 survival rate than the highest elevation ($p_{adj} < 0.001$). Differences in rates between the lowest and
411 the middle elevations ($p_{adj} = 0.157$) and between the middle and the highest ($p_{adj} = 0.111$) were
412 slight. The most-supported model for daily survival rates of flycatchers again included only
413 elevation, with an Akaike weight of 0.999. No other models were competitive, with the second-
414 ranked model having ΔAIC_c of 14.62.

415

416 **DISCUSSION**

417 Phenological reaction norms in the Mountain Chickadee conformed to a simple offset
418 strategy consistent with populations that breed at different elevations having a constant, or
419 relatively consistent, response to seasonal temperature among years, regardless of elevation.

420 Patterns were more complex in the Dusky Flycatcher, where birds breeding at our mid-elevation
421 plots in cooler years conformed to a delay strategy compared to those at lower elevations,
422 whereas flycatchers breeding at our highest elevation plots started breeding earlier in cooler
423 years relative to those at the mid-elevation plots, consistent with an advance strategy for the
424 higher elevation populations. Clearly, Dusky Flycatchers exhibited a breeding phenology
425 consistent with an interaction between photoperiod and temperature (Visser et al. 2010,
426 Phillimore et al. 2016, Bründl et al. 2020), leading to different apparent reaction norms at
427 different elevations.

428 Comparing mid-elevation flycatchers to those at the low elevation suggests that at mid-
429 elevations there is still a sufficiently long period, on average, when conditions are suitable for
430 rearing offspring such that a delay carries little additional cost. In contrast, the advance pattern of
431 the highest-elevation flycatchers suggests that, compared to those in mid-elevations, these
432 individuals are sensitive to a season that is shorter than at lower elevations. For Dusky

433 Flycatchers breeding at the highest elevation, the costs associated with initiating breeding early,
434 when there is a greater risk of being exposed to cold temperatures and other harsh conditions,
435 appear to be lower than the costs associated with delaying breeding, which could include failing
436 to produce any surviving young. In a cool spring, the mid-elevation birds that form the basis for
437 comparison with high elevation ones are already delaying breeding initiation compared to those
438 at lower elevations; it appears that high-elevation birds cannot afford to delay still longer. The
439 consequences of Dusky Flycatchers breeding late have been confirmed at another high-elevation
440 area in the Sierra Nevada, where delayed laying resulted in small but significant reductions in the
441 number of young fledged per female and the total number of fledglings produced on the study
442 area (Pereyra 2011). In the same study the likelihood of re-nesting after a failed nesting attempt
443 declined steeply after the first week of July.

444 The difference in observed patterns between Mountain Chickadees and Dusky
445 Flycatchers may result from a variety of ecological differences between the two. Dusky
446 Flycatchers, an open-cup nesting species, may be at greater risk from exposure to cold
447 temperatures, precipitation, and wind during nesting compared to cavity-nesting Mountain
448 Chickadees. The cavity nests of Mountain Chickadees buffer individuals against adverse weather
449 conditions, and the energy savings from reduced exposure to wind by occupying cavities as
450 compared to roosting outside a cavity can be considerable (Cooper 1999). Dusky Flycatchers
451 nests have been observed to fail due to the effects of late season storms at high elevations while
452 incubating eggs or brooding young (K. Purcell, pers. obs.; Pereyra and Sedgwick 2020).
453 Mountain Chickadees are also buffered from the effects of colder temperatures by their year-
454 round ability to use nocturnal hypothermia, which can lead to nighttime energy savings of up to
455 50% (Cooper and Gessaman 2005). If chickadees are less at risk from cold temperatures than

456 flycatchers, a delay strategy may not offer significant gains in reproductive success. Ecological
457 differences in food and foraging behavior may also contribute to different sensitivities of the two
458 species. Whereas chickadees are primarily gleaners that include both a variety of arthropods and
459 seeds in their diets (McCallum et al. 2020), flycatchers are primarily aerial foragers that sally
460 after flying insects (Pereyra and Sedgwick 2020), a food source less available when temperatures
461 are low. Importantly, at the other end of the season, flycatchers need sufficient time to
462 accumulate substantial energetic resources to undertake migration, and to satisfy the high
463 nutrient demand for molting, some of which takes place before departure for the wintering
464 grounds beginning in late July (Biebach 1996, Murphy 1996, Pereyra 2011, Pereyra and
465 Sedgwick 2020). We also note that whereas open-cup nesters generally have a shorter nesting
466 cycle (egg laying to fledging) than cavity nesters (Martin and Li 1992), Dusky Flycatchers have a
467 relatively long nesting cycle for an open-cup nesting species (Pereyra 2011), ~35 days on these
468 study plots (K. Purcell, pers. obs.). Thus, not employing an advance strategy at high elevations
469 would reduce an already comparatively shorter window for Dusky Flycatchers breeding there.

470 In both species, clutch size was the only fitness metric that appeared associated with
471 phenology, declining with lay date across all years. This decline implies some apparent cost to
472 breeding later, suggesting the potential for directional selection for breeding earlier. However,
473 this result is also consistent with an “environmental constraints” hypothesis (Visser et al. 2015),
474 that potentially challenging environmental conditions that may occur early in the spring weaken
475 the strength of selection for breeding earlier, an effect that may be enhanced at higher elevations
476 (Bründl et al. 2020). Furthermore, although we found little variation in fitness components with
477 temperature as a phenological cue, we should not conclude that temperature is not important. If
478 natural selection has already shaped an adaptive response to phenological variation (i.e., a

479 reaction norm) then we might not expect to see much variation in reproductive success unless
480 environmental conditions exceed the normal range of variation in temperature. With a reaction
481 norm the response phenotype (lay date) varies depending on conditions, presumably to generate
482 reproductive success optimal under those conditions; we may not see a strong signal of fitness
483 differences until the environment moves to extremes. Alternatively, if the main source of natural
484 selection were due to stochastic, catastrophic fitness-depressing events, then there would be little
485 selection for a reaction norm; phenotypic plasticity should not evolve in environments that
486 fluctuate less predictably, because that would lead to plastic responses to cues that do not match
487 the subsequent selective environment (Gavrilets and Scheiner 1993, Leung et al. 2020).

488 Our study has implications for predicting how populations may respond to the effects of
489 temperature variation should spring temperatures increase as predicted by global climate
490 projections (IPCC 2014). In the short term (i.e., prior to potential changes in plant and prey
491 species phenology and/or community composition), we would predict that increasing spring
492 temperatures would likely result in both species initiating breeding earlier, consistent with more
493 general observations of the advancement of breeding in birds with increasing temperatures
494 (Dunn 2004). We have more confidence in this being the case for the Mountain Chickadee,
495 which does not undergo long-distance migration. Thus, in the short-term, based on the simple-
496 offset model, for chickadees we expect the relationship between laying date and spring
497 temperature among elevations to remain more or less the same but be uniformly advanced
498 overall as climate warms.

499 For Dusky Flycatchers, even short-term changes are more difficult to predict than for the
500 Mountain Chickadee not only because of the difference in strategies across elevations observed
501 in this species, but also because the species undergoes long-distance migration, and thus any

502 response in laying date to seasonal temperature may be constrained by arrival date and the time
503 required to subsequently establish territories and attract mates (Both and Visser 2001, Lany et al.
504 2016). Pereyra (1998, cited in Pereyra 2011) observed that arrival dates of flycatchers at Tioga
505 Pass, California (elevation 2,900–3,500 m) were comparable from year to year, suggesting that
506 any advances in spring temperature on the breeding grounds may not be matched by earlier
507 arrival by flycatchers; conditions on the breeding grounds at arrival may be largely independent
508 of those triggering departure from the wintering grounds a thousand kilometers away (e.g.,
509 Fontaine et al. 2009, Jones and Cresswell 2010, Rubolini et al. 2010, Usui et al. 2017).
510 Furthermore, because Dusky Flycatchers have a relatively broad diet of insect prey (Pereyra and
511 Sedgwick 2020) and as peak prey abundance during the breeding season appears less strongly
512 correlated with temperature (Pereyra 2011; see also Dunn et al. 2011, Franks et al. 2018, Lany et
513 al. 2016), the likelihood of a trophic mismatch (a decoupling of the relationship between
514 environmental temperature as a cue for initiating breeding in birds and the phenology of insect
515 species that are prey for insectivorous birds; e.g., Visser et al. 1998) seems small. However, if
516 warming is accompanied by favorable conditions expanding into later summer, then advancing
517 to avoid environmental deterioration may be less a consideration for highest-elevation birds,
518 bringing their norm of reaction more parallel to middle-elevation birds.

519 Although we were able to connect differences in phenological reaction norms to
520 differences in ecological traits between two species, additional analyses of a variety of species
521 will be required to develop reliable generalizations. Although we would predict that cavity
522 nesting species are more likely to follow a simple offset strategy than open nesters, different
523 species of cavity nesters exploit different food resources and forage in different ways. Likewise,
524 nests of open-cup nesting species are placed in different locations, varying from ground level to

525 upper canopy with different levels of exposure, and collectively these species span a wide range
526 of foraging behaviors and food types. Differences in migration strategies and tradeoffs with
527 arrival dates are likely important, and the degree of urgency to set up and defend territories
528 quickly at the beginning of the breeding season will certainly influence the initiation of nesting.
529 We also note that if we had compared only the highest- and the lowest-elevation populations of
530 flycatchers this would have yielded a pattern consistent with simple offset, yet such a comparison
531 would mask the complexity shown by the significant interaction observed when three elevation
532 categories were examined. A key component of our analysis is the ability to use a reference
533 temperature consistently measured at a particular time and place as representative of the nature
534 of the season (early/late, warm/cool) across elevations; any future applications of this approach
535 to analyze species at a different place or scale requires a similar approach.

536 In conclusion, we developed a framework for evaluating relationships between ambient
537 temperature in the spring and the timing of breeding initiation across an elevational gradient, and
538 for distinguishing among possible patterns of risk sensitivity for breeders at higher elevations.
539 This framework explicitly recognizes that there can be an interaction between the temperatures
540 that trigger breeding and the date within the season on which they occur. In application of this
541 framework to two species breeding at multiple elevations, we demonstrated how responses in
542 timing of breeding in relation to variation in seasonal temperature can vary across elevations. We
543 combined these results with other species attributes, such as nest site selection, foraging
544 behavior, and migratory status, to understand how species may balance competing risks in
545 deciding when to breed, and to predict how species that occupy mountainous regions may cope
546 with a changing global climate. By focusing on emergent phenological patterns within
547 populations as a function of thermal variation, the scale of our framework falls between studies

548 focused mainly on the proximate effect of thermal microclimate in and around the nest on the
549 initiation of egg-laying, and those concerned with large scale geographical models of latitudinal
550 temperature variation and the resulting patterns observed within and across species (e.g.,
551 Gienapp et al. 2010). This scale is relevant in terms of both conservation and evolutionary
552 biology.

553

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568 The authors declare no conflict of interest.

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572 **Author Contributions**

573 All authors contributed to the design of the project. KLP collected the data, which were
574 analyzed by SJC and JTR. All authors contributed to the writing and editing of the manuscript.

575 **Data Availability**

576 Analyses reported in this article can be reproduced using the data provided by Coe et al. (2021).

577

578 **LITERATURE CITED**

579 Bears, H., K. Martin, and G. C. White (2009). Breeding in high-elevation habitat results in shift

580 to slower life-history strategy within a single species. *Journal of Animal Ecology*

581 78:365-375.

582 Biebach H. (1996) Energetics of winter and migratory fattening. Pp. 280-323 In *Avian*

583 *Energetics and Nutritional Ecology* (C. Carey, editor). Springer, Boston, MA.

584 Both, C., and M. E. Visser (2001). Adjustment to climate change is constrained by arrival date

585 in a long-distance migrant bird. *Nature* 411:296–298.

586 Brown, C. R., and M. B. Brown (1999). Fitness components associated with laying date in the

587 Cliff Swallow. *The Condor* 101:230-245.

588 Bründl, A. C., L. Sallé, I. A. Lejeune, E. Sorato, A. C. Thiney, A. S. Chainie, and A. F. Russell

589 (2020). Elevational gradients as a model for understanding associations among

590 temperature, breeding phenology and success. *Frontiers in Ecology and Evolution*

591 8:563377. Doi: 10.3378/fevo.2020.563377.

592 Burnham, K. P., and D. R. Anderson (2002). Model selection and multimodel inference: a
593 practical information-theoretic approach (2nd ed.). Springer-Verlag, Berlin.

594 Camfield, A.F., S. F. Pearson, and K. Martin (2010). Life history variation between high and
595 low elevation subspecies of horned larks *Eremophila* spp. *Journal of Avian Biology*
596 41:273-281.

597 Cayan, D. R., S. A. Kammerdiener, M. D. Dettinger, J. M. Caprio, and D. H. Peterson (2001).
598 Changes in the onset of spring in the western United States. *Bulletin of the American*
599 *Meteorological Society* 82:399-415.

600 Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon
601 (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird
602 population. *Science* 320:800-803.

603 Chmielewski, F. M., K. Blümel, C. Scherbaum-Heberer, B. Koppmann-Rumpf, and K. H.
604 Schmidt (2013). A model approach to project the start of egg laying of Great Tit (*Parus*
605 *major* L.) in response to climate change. *International Journal of Biometeorology* 57:287-
606 297.

607 Chmura, H. E., H. M. Kharouba, J. Ashander, S. M. Ehlman, E. B. Rivest, and L. H. Yang
608 (2019a). The mechanisms of phenology: the patterns and processes of phenological
609 shifts. *Ecological Monographs* 89:e01337.

610 Chmura, H. E., J. C. Wingfield, and T. P. Hahn (2019b). Non-photoc environmental cues and
611 avian reproduction in an era of global change. *Journal of Avian Biology*
612 doi:10.1111/jav.02243.

613 Coe, S. J. (2009). The influence of ambient temperature on avian reproduction. Ph.D.
614 dissertation, University of California, Riverside, CA, USA.

615 Coe, S. J., K. L. Purcell, and J. T. Rotenberry (2021). Data from: Modeling phenological
616 reaction norms over an elevational gradient reveals contrasting strategies of Dusky
617 Flycatchers and Mountain Chickadees in response to early season temperatures.
618 Ornithology. doi:10.6086/D1S689.

619 Cooper, S. J. (1999). The thermal and energetic significance of cavity roosting in Mountain
620 Chickadees and Juniper Titmice. *The Condor* 101:863-866.

621 Cooper, S. J., and J. A. Gessaman (2005). Nocturnal hypothermia in seasonally acclimatized
622 Mountain Chickadees and Juniper Titmice. *The Condor* 107:151-155.

623 Crick, H. Q. P., C. Dudley, D. E. Glue, and D. L. Thomson (1997). UK birds are laying eggs
624 earlier. *Nature* 388:526.

625 Dahlsten, D. L. and W. A. Copper (1979). The use of nesting boxes to study the biology of the
626 Mountain Chickadee (*Parus gambeli*) and its impact on selected forest insects. Pp. 217-
627 260 In *The Role of Insectivorous Birds in Forest Ecosystems* (D. G. Dickson, R. N.
628 Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson (editors). Academic Press, New York,
629 NY.

630 Dawson, A. (2008). Control of the annual cycle in birds: endocrine constraints and plasticity in
631 response to ecological variability. *Philosophical Transactions of the Royal Society B*
632 363:1621–1633.

633 Decker, K. L., and C. J. Conway (2009). Effects of an unseasonable snowstorm on Red-faced
634 Warbler nesting success. *The Condor* 111:392-395.

635 Dolan, A. C., M. T. Murphy, L. J. Redmond, and D. Duffield (2009). Maternal characteristics
636 and the production and recruitment of sons in the Eastern Kingbird (*Tyrannus tyrannus*).
637 *Behavioral Ecology and Sociobiology* 63:1527–1537.

638 Drake, A., and K. Martin (2018). Local temperatures predict breeding phenology but do not
639 result in breeding synchrony among a community of resident cavity nesting birds.
640 Scientific Reports 8:2756. Doi: 10.1038/s41598-018-20977-y

641 Dunn, P. O. (2004). Breeding dates and reproductive performance. In Birds and Climate
642 Change (A.P. Møller and W. Fiedler, Editors). Advances in Ecological Research 35:69-
643 87.

644 Dunn, P. O., and D. W. Winkler (2010). Effects of climate change on timing of breeding and
645 reproductive success in birds. In Effects of Climate Change on Birds (A. P. Møller, W.
646 Fiedler, and P. Berthold, Editors). Pages 113-128. Oxford University Press, Oxford, UK.

647 Dunn, P.O., D. W. Winkler, L. A. Whittingham, S. J. Hannon, and R. J. Robertson (2011). A
648 test of the mismatch hypothesis: How is timing of reproduction related to food abundance
649 in an aerial insectivore? Ecology 92:450-461.

650 Fontaine, J. J., K. L. Decker, S. K. Skagen, and C. van Riper III (2009). Spatial and temporal
651 variation in climate change: a bird's eye view. Climatic Change 97:305-311.

652 Franks, S. E., J. W. Pearce-Higgins, S. Atkinson, J. R. Bell, M. S. Botham, T. M. Brereton, R.
653 Harrington, and D. I. Leech (2018). The sensitivity of breeding songbirds to changes in
654 seasonal timing is linked to population change but cannot be directly attributed to the
655 effects of trophic asynchrony on productivity. Global Change Biology 24:957-971.

656 Gavrilets, S., and S. M. Scheiner (1993). The genetics of phenotypic plasticity: V. Evolution of
657 reaction norm shape. Journal of Evolutionary Biology 6:31-48.

658 Gienapp, P., R. A. Väisänen, and J. E. Brommer (2010). Latitudinal variation in breeding time
659 reaction norms in a passerine bird. Journal of Animal Ecology 79:836-842.

660 Hendricks, P., and C. J. Norment (1992). Effects of a severe snowstorm on subalpine and alpine
661 populations of nesting American Pipits. *Journal of Field Ornithology* 63:331-338.

662 Inouye, B. D., J. Ehrlén, and N. Underwood (2019). Phenology as a process rather than an event:
663 from individual reaction norms to community metrics. *Ecological Monographs*
664 89:e01352.

665 IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II,*
666 *and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*
667 *(Core Writing Team, R.K. Pachauri and L.A. Meyer, Editors). IPCC, Geneva,*
668 *Switzerland, 151 pp.*

669 Jones, T., and W. Cresswell (2010). The phenology mismatch hypothesis: Are declines of
670 migrant birds linked to uneven global climate change? *Journal of Animal Ecology*
671 79:98–108.

672 Koslovsky, D. Y., C. L. Branch, A. M. Pitera, and V. V. Pravosudov (2018). Fluctuations in
673 annual climatic extremes are associated with reproductive variation in resident mountain
674 chickadees. *Royal Society Open Science* 5:1711604.
675 <http://dx.doi.org/10.1098/rsos.171604>

676 Körner, C. (2007). The use of ‘altitude’ in ecological research. *Trends in Ecology and*
677 *Evolution* 22:569-574.

678 Lany, N. K., M. P. Ayres, E. E. Stange, T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes
679 (2016). Breeding timed to maximize reproductive success for a migratory songbird: the
680 importance of phenological asynchrony. *Oikos* 125:656-666.

681 Leung, C., M. Rescan, D. Grulois, and L.-M. Chevin (2020). Reduced phenotypic plasticity
682 evolves in less predictable environments. *Ecology Letters* 23:1664-1672.

683 Lu, X., C. Wang, and T. Yu (2010a). Nesting ecology of the Grey-backed Shrike (*Lanius*
684 *tephronotus*) in South Tibet. *Wilson Journal of Ornithology* 122:395-398.

685 Lu, X., T. Yu, W. Liang, and C. Yang (2010b). Comparative breeding ecology of two White-
686 bellied Redstart populations at different altitudes. *Journal of Field Ornithology* 81:167-
687 175.

688 Martin, K. and K. L. Wiebe (2004). Coping mechanisms of alpine and arctic breeding birds:
689 extreme weather and limitations to reproductive resilience. *Integrative and Comparative*
690 *Biology* 44:177-185.

691 Martin, K., S. Wilson, E. C. MacDonald, A. F. Camfield, M. Martin, and S. A. Trefry (2017).
692 Effects of severe weather on reproduction for sympatric songbirds in an alpine
693 environment: Interactions of climate extremes influence nesting success. *The Auk:*
694 *Ornithological Advances* 134:696-709.

695 Martin, T. E. (2001). Abiotic vs. biotic influences on habitat selection of coexisting species:
696 Climate change impacts? *Ecology* 82:175–188.

697 Martin, T. E., and P. J. Li (1992). Life-history traits of open- vs. cavity-nesting birds. *Ecology*
698 73:579-592.

699 McCallum, D. A., R. Grundel, and D. L. Dahlsten (2020). Mountain Chickadee (*Poecile*
700 *gambeli*), version 1.0. In *Birds of the World* (A. F. Poole and F. B. Gill, Editors). Cornell
701 Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.mouchi.01>

702 Murphy, M. E. (1996). Energetics and nutrition of molt. Pp. 158–198 In *Avian Energetics and*
703 *Nutritional Ecology* (C. Carey, editor). Springer, Boston, MA.

704 Murtaugh, P. A. (2014). In defense of *P* values. *Ecology* 95:611-617.

705 Ockendon, N., D. Leech, and J. W. Pearce-Higgins (2013). Climatic effects on breeding grounds
706 are more important drivers of breeding phenology in migrant birds than carry-over effects
707 from wintering grounds. *Biology Letters* 9:20130669. Doi: 10.1098/rsbl.2013.0669

708 Pereyra, M. E. (1998). Effects of environment and endocrine function on control of reproduction
709 in a high elevation tyrannid. Ph.D. dissertation, Northern Arizona University, Flagstaff,
710 AZ.

711 Pereyra, M. E. (2011). Effects of snow-related environmental variation on breeding schedules
712 and productivity of a high-altitude population of Dusky Flycatchers (*Empidonax*
713 *oberholseri*). *The Auk* 128:746-758.

714 Pereyra, M. E. and J. A. Sedgwick (2020). Dusky Flycatcher (*Empidonax oberholseri*), version
715 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY,
716 USA. <https://doi.org/10.2173/bow.dusfly.01>

717 Perrins, C. M., and R. H. McCleery (1989). Laying dates and clutch size in the Great Tit.
718 *Wilson Bulletin* 101:236-253.

719 Phillimore, A. B., D. I. Leech, J. W. Pearce-Higgins, and J. D. Hadfield (2016). Passerines may
720 be sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Global*
721 *Change Biology* 22:3259–3272.

722 Purcell, K. L. (1997). Use of a fiberscope for examining cavity nests. *Journal of Field*
723 *Ornithology* 68:283-286.

724 Rubolini, D., N. Saino, and A. P. Møller (2010). Migratory behaviour constrains the
725 phenological response of birds to climate change. *Climate Research* 42:45–55.

726 Saracco, J. F., R. B. Siegal, L. Helton, S. L. Stock, and D. F. DeSante (2019). Phenology and
727 productivity in a montane bird assemblage: trends and responses to elevation and climate
728 variation. *Global Change Biology* 25:985-996.

729 SAS Institute. (2016). SAS Version 9.4. SAS Institute, Cary, NC.

730 Schaper, S. V., A. Dawson, P. J. Sharp, P. Gienapp, S. P. Caro, and M. E. Visser (2012).
731 Increasing temperature, not mean temperature, is a cue for avian timing of reproduction.
732 *American Naturalist* 179:E55-E69.

733 Schwartz, M. D., R. Ahas, and A. Aasa (2006). Onset of spring starting earlier across the
734 Northern Hemisphere. *Global Change Biology* 12:343-351.

735 Sedgwick, J. A. (1993). Reproductive ecology of Dusky Flycatchers in western Montana.
736 *Wilson Bulletin* 105:84-92.

737 Shaffer, T. L. (2004). A unified approach to analyzing nest success. *The Auk* 121:526-540.

738 Simmonds, E. G., E. F. Cole, and B. C. Sheldon (2019). Cue identification in phenology: a case
739 study of the predictive performance of current statistical tools. *Journal of Animal*
740 *Ecology* 88:1428-1440.

741 Stearns, S., and H. Hoekstra (2005). *Evolution*, 2nd Edition. Oxford University Press, Oxford,
742 UK.

743 Usui, T., S. H. M. Butchart, and A. B. Phillimore (2017). Temporal shifts and temperature
744 sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. *Journal*
745 *of Animal Ecology* 86:250-261.

746 van de Pol, M., L. D. Bailey, N. McLean, L. Rijdsdijk, C. R. Lawson, and L. Brouwer (2016).
747 Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology*
748 *and Evolution* 7:1246-1257.

749 Verhulst, S., J. H. van Balen, and J. M. Tinbergen (1995). Seasonal decline in reproductive
750 success of the Great Tit: variation in time or quality? *Ecology* 76:2392-2403.

751 Verhulst, S., and J-Å. Nilsson (2008). The timing of birds' breeding seasons: a review of
752 experiments that manipulated timing of breeding. *Philosophical Transactions of the*
753 *Royal Society B* 363:399-410.

754 Vinnikov, K. Y., Y. Yu, M. D. Goldberg, M. Chen, and D. Tarpley (2011). Scales of temporal
755 and spatial variability of midlatitude land surface temperature. *Journal of Geophysical*
756 *Research* 116, D02105. Doi: 10.1029/2010JD014868.

757 Visser, M. E., S. P. Caro, K. van Oers, S.V. Schaper, and B. Helm (2010). Phenology, seasonal
758 timing and circannual rhythms: towards a unified framework. *Philosophical Transactions*
759 *of the Royal Society B* 365:3113–3127.

760 Visser, M. E., Gienapp, P., Husby, A., Morrissey, M., de la Hera, I., Pulido, F., et al. (2015).
761 Effects of spring temperatures on the strength of selection on timing of reproduction in a
762 long-distance migratory bird. *PLoS Biol.* 13:e1002120.
763 doi:10.1371/journal.pbio.1002120

764 Visser, M. E., L. J. M. Holleman, and S. P. Caro (2009). Temperature has a causal effect on
765 avian timing of reproduction. *Philosophical Transactions of the Royal Society B*
766 276:2323-2331.

767 Visser, M.E., and N. Verboven (1999). Long-term fitness effects of fledging date in Great Tits.
768 *Oikos* 85:445-450.

769 Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells (1998). Warmer springs
770 lead to mistimed reproduction in great tits (*Parus major*). *Philosophical Transactions of*
771 *the Royal Society B* 265:1867-1870.

772 Whiteman, C. D. (2000). Mountain meteorology: fundamentals and applications. Oxford
773 University Press, New York, New York. USA.

774 Wiebe, K. L., and H. Gerstmar (2010). Influence of spring temperatures and individual traits on
775 reproductive timing and success in a migratory woodpecker. *The Auk* 127:917-925.

776 Wilson, S., and K. Martin (2008). Breeding habitat selection of sympatric White-tailed, Rock
777 and Willow ptarmigan in the southern Yukon Territory, Canada. *Journal of Ornithology*
778 149:629–637.

779 Wingfield, J. C. (2008). Comparative endocrinology, environment, and global change. *General*
780 *and Comparative Endocrinology* 157:207-216.

781 Wingfield, J. C., T. P. Hahn, D. L. Maney, S. J. Schoech, M. Wada, and M. L. Morton (2003).
782 Effects of temperature on photoperiodically induced reproductive development,
783 circulating plasma luteinizing hormone and thyroid hormones, body mass, fat deposition,
784 and molt in Mountain White-crowned Sparrows, *Zonotrichia leucophrys oriantha*.
785 *General and Comparative Endocrinology* 131:143-158.

786 Winkler, D. W., and P. E. Allen (1996). The seasonal decline in Tree Swallow clutch size:
787 Physiological constraint or strategic adjustment. *Ecology* 77:922-932.

788 Winkler, D. W., P. O. Dunn, and C. E. McCulloch (2002). Predicting the effects of climate
789 change on avian life-history traits. *Proceedings of the National Academy of Science*
790 USA 99:13595-13599.

791 Winkler, D. W., K. K. Hallinger, T. M. Pegan, C. C. Taff, M. A. Verhoeven, D. C van Oordt, M.
792 Stager, J. J. Uehling, M. N. Vitousek, M. J. Andersen, D. R. Ardia, A. Belmaker, V.
793 Ferretti, A. M. Forsman, J. R. Gaul, P. E., Llambias, S. C. Orzechowski, J. R. Shipley, M.

794 Wilson, and H. S. Yoon (2020). Full lifetime perspectives on the costs and benefits of
795 lay-date variation in tree swallows. *Ecology* 101:e03109.
796

797 Table 1. Results of Type III tests of main and interaction effects of temperature and elevation on
 798 lay initiation date in Mountain Chickadees and Dusky Flycatchers based on generalized linear
 799 mixed models, and significance of difference of pair-wise comparison of regression slopes across
 800 elevations.

	Effect	<i>F</i>	<i>P</i>			
Mountain Chickadee	temperature	251.07 _{1, 108.5}	<0.001			
	elevation	5.3 _{2, 100.9}	0.007			
	interaction	1.75 _{2, 104.8}	0.179			
		Model Estimates	Standard Error			
	intercept	183.60	2.852			
	temperature	-3.29	0.247			
	elevation - high	-2.66	4.053			
	elevation - middle	0	--			
	elevation - low	-16.13	5.047			
	temperature*high	0.57	0.349			
	temperature*middle	0	--			
	temperature*low	0.71	0.483			
		Slope Comparisons	Difference	Standard Error	<i>t</i>	<i>P</i>
		high vs. low	-0.138	0.483	-0.29 _{71.9}	0.776
		high vs. middle	0.568	0.349	1.63 _{159.8}	0.106
	low vs. middle	0.706	0.483	1.46 _{73.3}	0.148	
Dusky Flycatcher	temperature	198.35 _{1, 83.4}	<0.001			
	elevation	7.09 _{2, 64.1}	0.002			
	interaction	3.02 _{2, 61.0}	0.056			
		Model Estimates	Standard Error			
	intercept	209.12	5.340			
	temperature	-3.44	0.399			
	elevation - high	-9.13	7.229			
	elevation - middle	0	--			
	elevation - low	-20.16	5.805			

temperature*high	1.28	0.553
temperature*middle	0	--
temperature*low	0.94	0.428

Slope Comparisons	Difference	Standard Error	<i>t</i>	<i>p</i>
high vs. low	0.331	0.414	0.80 _{53.4}	0.427
high vs. middle	1.275	0.553	2.31 _{71.7}	0.024
low vs. middle	0.944	0.428	2.2 _{44.0}	0.032

801 **FIGURE LEGENDS**

802 Figure 1. Alternative strategies resulting from relationships between spring temperatures and the
803 date that egg laying is initiated at different elevations. Each regression line is a phenological
804 reaction norm of a population of a single species breeding at a “low” or “high” elevation sampled
805 over multiple years. A. “Simple Offset” – laying initiation at the high elevation relative to low
806 elevation is constant across years. (B. “Delay” –populations at the high elevation breed
807 comparatively later in years when spring is colder; the left portion of the “high” line is elevated
808 compared to “simple offset.” .C. “Advance” – birds at the high elevation breed comparatively
809 earlier in years when spring is colder (“advance”); the left portion of the “high” line is depressed
810 compared to “simple offset.”

811

812 Figure 2. Mean egg laying initiation date (± 1 SE) in 1995 and 1997-2001 at three elevation
813 categories for (A) Mountain Chickadee and (B) Dusky Flycatcher. Temperature data were
814 missing for 1996, as are chickadee data for low elevation in 1997. Sample sizes across the study
815 years within each elevation for Mountain Chickadee were: (1) highest: 4, 9, 5, 19, 17, 19; (2)
816 middle: 11, 12, 11, 14, 26, 20; (3) lowest: 7, 0, 8, 15, 9, 6. Sample sizes for Dusky Flycatcher
817 categories were (1) highest: 5, 7, 8, 9, 9, 4; (2) middle: 6, 6, 5, 6, 7, 7; (3) lowest: 10, 13, 23, 28,
818 27, 32.

819

820 Figure 3. Laying initiation dates at three elevation categories relative to seasonal reference
821 temperature for (A) Mountain Chickadee and (B) Dusky Flycatcher. For each of the 6 years of
822 the study (1995, 1997-2001), seasonal temperature was averaged over the first week of May for
823 Mountain Chickadee and over the third week of May for Dusky Flycatcher. Error bars represent

824 ± 2 standard errors. Highest elevation points are shifted -0.1°C and lowest elevation points
825 shifted $+0.1^{\circ}\text{C}$ to improve legibility of error bars. Regression lines fitted to elevation means to
826 illustrate trends.