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1   **The effect of latitude on photoperiodic control of gonadal maturation, regression and**

2   **molt in birds**

3   Running title: Latitude and photoperiodic responses

4   Submitted as an invited mini-review for the ISAE Special issue

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8

9   Abstract

10   Photoperiod is the major cue used by birds to time breeding seasons and molt. However, the

11   annual cycle in photoperiod changes with latitude. Within species, for temperate and high

12   latitude species, gonadal maturation and breeding start earlier at lower latitudes but

13   regression and molt both occur at similar times at different latitudes. Earlier gonadal

14   maturation can be explained simply by the fact that considerable maturation occurs before the

15   equinox when photoperiod is longer at lower latitudes – genetic differences between

16   populations are not necessary to explain earlier breeding at lower latitudes. Gonadal

17   regression is caused either by absolute photorefractoriness or, in some species with long

18   breeding seasons, relative photorefractoriness. In either case, the timing of regression and

19   molt cannot be explained by absolute prevailing photoperiod or rate of change in photoperiod

20   – birds appear to be using more subtle cues from the pattern of change in photoperiod.

21   However, there may be no difference between absolute and relative photorefractory species

22   in how they utilise the annual cycle in photoperiod to time regression.

23

24

25 Keywords

26 Photoperiodism; birds; latitude; breeding season; gonadal maturation; photorefractoriness;

27 molt

1. Introduction

29 It has been known for many decades that the annual cycle in photoperiod is the major

30 proximate cue used by birds to time vernal gonadal maturation (Rowan 1926) and subsequent

31 gonadal regression (Burger 1952) and molt; see Wingfield (1992) and Dawson et al. (2001)

32 for reviews. However, the annual cycle in photoperiod differs at different latitudes: absolute

33 photoperiod (apart from at the equinoxes), rate of change in photoperiod (apart from at the

34 solstices) and the annual amplitude, all differ. These differences increase per degree of

35 latitude further from the equator. This paper reviews how the timing of gonadal maturation

36 and regression, and molt, differs within species at different latitudes and speculates on how

37 this may be controlled given the differences in photoperiod.

38 Data used in the review are restricted to temperate and high latitude species. Although

39 breeding seasons (i.e, the period during which eggs are laid) are largely determined by the

40 duration of ovarian maturity, the experimental data reviewed are mainly restricted to males

41 because females require cues in addition to photoperiod to attain full gonadal maturity

42 (Farner et al. 1966) but see Visser et al. (2011).

2. How do breeding seasons and molt vary with latitude?

44   The beginning of the breeding season can be defined as the date on which first eggs are laid.

45   Data on first egg dates are comparatively easy to collect and are abundant. In general, for

46   temperate and high latitude species, egg-laying within a species starts later at latitudes further

47   from the equator (hereafter higher latitudes). Baker (1938) estimated that laying started 20-30

48   days later per 10° latitude. Obviously eggs can only be laid after gonadal maturation is

49   complete and presumably first eggs are normally laid soon after maturation. The end of the

50   breeding season is more difficult to define and therefore to quantify. For the purpose of this

51   review it is the timing of gonadal regression that is important. No eggs can be laid after this

52   time. Although the end of the breeding season is difficult to define accurately, in many

53   species the onset of molt is delayed until the end of breeding, and so data on the start of molt

54   can be used as a surrogate for the end of breeding.

55   For blackbirds *Turdus merula*, first egg dates are 1-2 weeks earlier in the southern half of

56   England compared to the north (5° latitude range) (Myers 1955). A recent analysis of British

57   Trust for Ornithology molt records for 8000 blackbirds showed that molt starts just 2 days

58   earlier for males in the southern half of England and 3 days earlier for females (Dawson,

59   unpublished data). So although breeding starts earlier at lower latitudes, it ends at much the

60   same time at different latitudes.

61   Data on the timing of gonadal maturation and regression in free-living birds are scarce, and

62   such data from birds of the same species at different latitudes are even fewer. Miller (1960)

63   showed that the period of active spermatogenesis within species and subspecies of the genus

64   *Zonotrichia* started earlier in those whose breeding range was at lower latitudes, but ended at

65   the same time at all latitudes (Fig.1).

66   Two independent studies investigated changes in reproductive behavior and physiology in

67   California quail *Lophortyx californicus*: Genelly (1955) studied free-living quail on San

3

68   Pablo Ridge, California (38°N) and Anthony (1970) studied them along the Snake River,

69   southeastern Washington (47°N). The timing of testicular maturation and regression was

70   similar at both latitudes (Fig.2). However laying started 2-3 weeks earlier at the lower

71   latitude. In both studies, molt started at the same time, in mid June for males and mid July for

72   females. So for these two populations of quail, differing by 9° latitude, breeding started

73   earlier at the lower latitude but ended at the same time in both.

74   A study of common starlings *Sturnus vulgaris* in England at 52°N (Dawson and Goldsmith

75   1982) showed that maximum testis mass was attained in April, which coincided with first egg

76   dates (third week of April). More recently, George Bentley, University of California,

77   Berkeley, has collected starlings in California (37°N). The testis volumes that he recorded are

78   superimposed on the 52°N data in Fig. 2. Testis volumes were larger at 37°N during the

79   earlier part of the year, and maximum volume was attained in March, corresponding to first

80   egg dates in California. However, the timing of testicular regression was similar at both

81   latitudes. The mean date for the start of molt in starlings at 52°N is 7 June (Rothery et al.

82   2001). Birds collected at 37°N also started to molt in early June.

83   So the general pattern appears to be that, within species, gonadal maturation starts earlier at

84   lower latitudes, but gonadal regression and the start of molt occur at the same time at

85   different latitudes. The question then is: how is this controlled by the annual cycle in

86   photoperiod at different latitudes? Since many species start breeding after the spring equinox,

87   when photoperiod is longer at higher latitudes, an earlier start to breeding at lower latitudes

88   can seem paradoxical. Do there need to be genetic differences in photoperiodic responses at

89   different latitudes, or can this pattern be accounted for by the same photoperiodic responses?

90   **3. Photoperiodic control of gonadal maturation**

4

3.1 Constant artificial photoperiods

92 In an effort to understand the physiology underlying photoperiodic control, many studies

93 have used the paradigm of transferring birds from a short to different constant longer

94 photoperiods. The initial rate of gonadal maturation is a function of that longer photoperiod.

95 Specifically, the logarithmic rate of testicular growth (k) has a nearly linear relationship with

96 photoperiod (p) (Farner and Wilson 1957). This k/p relationship has been calculated for a

97 number of species (Farner and Lewis 1971) and has a linear relationship over a wide range of

98 photoperiods (typically 8L to 18L). Although this clearly demonstrates that the rate of

99 maturation is greater on longer photoperiods, it must be borne in mind when estimating

100 growth rates at different times of year at different latitudes that this is an entirely unnatural

101 scenario. Firstly, free-living birds will rarely experience an acute change in photoperiod.

102 [One possible exception to this is that birds migrating long distances could change latitude

103 rapidly, but such migrations tend to be in spring or autumn, i.e. near the equinoxes, when

104 latitudinal differences in photoperiod are not great.] Secondly, by the time birds naturally

105 experience fairly long photoperiods, they already will have undergone a degree of gonadal

106 maturation and gonadal steroid feedback will tend to inhibit gonadotrophin secretion. The k/p

107 p relationship is therefore likely to exaggerate growth rate at longer photoperiods.

108 Nevertheless, this relationship does explain that the natural increase in photoperiod during

109 spring stimulates gonadal maturation. More importantly, in the context of this review, k/p

110 curves show that gonadal maturation starts under photoperiods less than 12L.

3.2 Simulated natural increases in photoperiod

112 Experiments involving artificial photoperiods that simulate natural changes in photoperiod

113 are likely to generate more realistic data. In starlings exposed to simulated photoperiods at

114 52°N, testicular maturation starts immediately after termination of photorefractoriness in

115 November, before the winter solstice and under a photoperiod of less than 8L (Dawson

116 2005). Similarly, starlings held in outdoor aviaries also start testicular maturation in

117 November (Dawson 2003). Great tits *Parus major* (Visser et al. 2011) and greenfinches

118 *Carduelis chloris* (Dawson unpublished data) held under simulated natural photoperiods both

119 show testicular maturation starting in December. For great tits, ovarian maturation starts at

120 the same time. Moreover, maturation in the sense of histological changes can occur even

121 earlier, in advance of an increase in gonadal size (Mundinge 1972).

122 *3.3 Gonadal maturation at different latitudes*

123 From the above it is clear that in many, and possibly most, species gonadal maturation starts

124 early in the year when photoperiod is considerably less than 12L, in other words well before

125 the spring equinox. Maturation is exponential before the equinox. It is also clear that the rate

126 of maturation is greater under longer photoperiods. Before the equinox, birds at lower

127 latitudes will experience longer photoperiods than birds at higher latitudes and therefore

128 gonadal maturation will be advanced over birds at higher latitudes by the time of the equinox.

129 This could explain why breeding tends to start earlier at lower latitudes, particularly in birds

130 with early breeding seasons. For example, in starlings maturation starts in November and full

131 maturity is attained shortly after the spring equinox at 52°N, and in fact before the equinox at

132 38°N (Fig. 2). So all, or nearly all, of the maturation process occurs before the equinox, when

133 birds at lower latitudes will experience longer photoperiods. At the other extreme, in

134 Japanese quail *Coturnix japonica*, gonadal maturation under increasing photoperiods does not

135 start until photoperiod reaches approximately 11L (Follett and Maung 1978) and so under

136 natural photoperiods does not start until the beginning of March, just before the equinox

137 (Robinson and Follett 1982). This may account for the comparative lack of advance in

138 testicular maturation in California quail from lower latitudes (Fig. 2).

139 Because breeding seasons often start after the equinox, when photoperiods are longer at

140 higher latitudes, it has been suggested that genetic differences in photoperiodic responses

141 may account for earlier breeding at lower latitudes. That is, birds at lower latitudes have a

142 lower photoperiodic threshold requirement to induce maturation. Silverin et al. (1993) kept

143 groups of great tits collected from three different latitudes (45, 57, and 70°N) on gradually

144 increasing photoperiods. The birds from 45°N showed earlier maturation apparently

145 supporting the hypothesis. However, birds from the higher latitudes showed similar responses

146 suggesting that there was no genetic difference.

147 In a study on starlings, in which birds were held on photoperiods simulating natural changes

148 at 52°N or 9°N, birds at the lower latitude showed significantly earlier testicular maturation

149 in each of three years (Dawson 2007).

150 In conclusion, earlier gonadal maturation and breeding at lower latitudes can be accounted for

151 by photoperiodic responses alone, since maturation starts before the equinox when

152 photoperiods are longer at lower latitudes. However, that does not exclude the possibility that

153 there may be genetic or non-photoperiodic differences between different populations; two

154 populations of blue tits *Cyanistes caeruleus* (Caro et al. 2005) and song sparrows *Melospiza*

155 *melodia morphna* (Perfito et al. 2004, Perfito et al. 2005) breeding at the same latitude breed

156 at different times. But it does not mean that genetic differences are required to explain

157 differences in breeding dates at different latitudes.

158 Presumably, in partial and short distance migrants, gonadal maturation will be advanced in

159 birds migrating north to breeding grounds over individuals that remained resident over-

160 winter. For long distance trans-equatorial migrants the situation is more complicated because

161 the timing of the end of photorefractoriness during the autumn of the previous year needs to

162 be considered, and how this operates remains unknown.

4. Gonadal regression and molt

164 *4.1 Absolute photorefractoriness*

165 Although the start of the breeding season differs at different latitudes, the end appears to be

166 similar at all latitudes. In species with short breeding seasons, breeding ends before the

167 summer solstice while photoperiod is still increasing, e.g. starlings in Fig. 2. In others, with

168 longer breeding seasons, breeding ends after the solstice as photoperiod is decreasing e.g.

169 quail in Fig. 2. Under experimental situations, if birds are transferred to a constant long

170 photoperiod in excess of 12L, some species show spontaneous gonadal regression. Such

171 species are said to become absolutely photorefractory. In such cases, the time to

172 photorefractoriness is inversely proportional to the fixed long photoperiod – the longer the

173 photoperiod the sooner birds become photorefractory (Burger 1952, Dawson and Goldsmith

174 1983). This would appear to be incompatible with the situation in the wild, where birds at

175 higher latitudes will experience longer photoperiods but end breeding at the same time as

176 birds at lower latitudes. I suspect that this is an artefact of the experimental design –

177 regression occurring at some time after a single acute change in photoperiod. In reality, birds

178 will be exposed to, and responding to, continuously changing photoperiod.

179 In experimental designs in which birds are exposed to changes in photoperiod that simulate

180 natural changes in photoperiod at different latitudes, gonadal regression and molt occur at the

181 same time, as they do in free-living birds. In starlings on photoperiods simulating 52°N or

182 9°N, although testicular maturation occurred earlier at the lower photoperiod, regression and

183 molt occurred at the same time (Dawson 2007). 9°N is outside the natural range of starlings

184 and has an annual amplitude in photoperiod of just 1 hour, ranging from 11.5L to 12.5L.

185 Nevertheless, this was sufficient to entrain a repeated annual cycle of gonadal maturation,

186 regression and molt. In siskins *Carduelis spinus* exposed to natural photoperiods simulating

187   40, 55 and 70°N, which encompass the natural breeding range of this species, cloacal gland

188   regression and molt occurred at the same time in all three groups (Newton and Dawson

189   2011). Similarly, greenfinches held on photoperiods simulating natural cycles at 20° and

190   60°N showed testicular regression and molt at the same time (Dawson unpublished results).

191   These data suggest that birds are not using absolute photoperiod, or rate of change in

192   photoperiod, to time regression. They suggest that birds are using photoperiod in some more

193   subtle way. They also suggest that the differing times for regression and molt in birds held on

194   different constant long photoperiods is an artefact of the experimental design.

195   *4.2 Relative photorefractoriness*

196   Species that become absolutely photorefractory show spontaneous testicular regression at

197   some time after being transferred to a constant long photoperiod. Other species, those that

198   have a long breeding season such as quail, do not show spontaneous regression. Testes

199   remain mature apparently indefinitely. This would appear to be a fundamental difference

200   from absolutely photorefractory species. But perhaps this too is an artefact of the

201   experimental design – a single large acute change in photoperiod. Species that do not show

202   spontaneous regression do show regression following a decrease in photoperiod (Fig. 3 A.).

203   The decreased photoperiod required to induce regression is longer than that required earlier to

204   induce maturation. Such species are said to be relatively photorefractory. Are there

205   homologies between absolute and relative photorefractoriness? California quail showed

206   testicular regression and molt at the same time at different latitudes (Fig. 2). There have been

207   no studies simulating different latitudes as there have been for absolutely photorefractory

208   species. Assuming that regression does occur at the same time of year at different latitudes,

209   then birds at higher latitudes will have experienced a greater decrease in photoperiod between

210   the summer solstice and the time of regression (see Fig. 3 B). There are no data to support

211   this. However, in quail kept on different constant long photoperiods, birds on longer

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212   photoperiods do need to experience a greater decrease in photoperiod to induce regression

213   (see Fig. 3 A). This implies that relatively photorefractory species do not use absolute

214   photoperiod or rate of change in photoperiod to time regression – they must use more subtle

215   information in the same way as do absolutely photorefractory species. Thus the apparently

216   fundamental difference between the two mechanisms may be an artefact of experimental

217   design. In absolutely photorefractory species such as starlings, regression is associated with a

218   decrease in GnRH-1. In relatively photorefractory quail, it is not (Foster et al. 1988). There

219   are examples of species that fall between the two extremes; captive white-winged crossbills

220   *Loxia leucoptera*, an opportunistic breeder, showed initiation of gonadal regression but no

221   change in GnRH-1 when held on a constant long photoperiod (Hahn et al. 2004, Pereyra et al.

222   2005), whereas birds held on photoperiods that simulated natural changes showed both

223   regression and modest changes in GnRH-1 (MacDougall-Shackleton et al. 2001). The

224   changes in GnRH-1 may be a consequence of regression rather than its cause. A comparative

225   analysis of photorefractoriness amongst songbirds also led Hahn and MacDoudall-Shackleton

226   (2008) to the conclusion that that evolved differences between species ("adaptive

227   specializations") are not required to explain latitudinal variation in annual schedules and that

228   "conditional plasticity" may explain the variation in many cases.

5. Conclusion

230   In general, within species of temperate and high latitude species of birds, breeding starts

231   earlier at lower latitudes. Earlier gonadal maturation can be explained by the fact that

232   considerable gonadal maturation occurs before the equinox when photoperiod is longer at

233   lower latitudes. This means that genetic differences between populations at different latitudes

234   are not necessary to explain earlier breeding at lower latitudes. Breeding ends and molt starts

235   at the same time at different latitudes. Gonadal regression is caused by absolute or relative

236   photorefractoriness. The timing of this cannot be explained by absolute prevailing

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237   photoperiod or rate of change in photoperiod – birds appear to be using more subtle cues

238   from the pattern of change in photoperiod. However, there may not be a fundamental

239   difference between absolute and relative photorefractory species in how they utilise the

240   annual cycle in photoperiod to time regression and molt.

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328

329   Figure legends

330   Fig. 1. The duration of the period during which males of various *Zonotrichia* species are

331   normally in active spermatogenesis. Data from Miller (1960). Breeding starts earlier at lower

332   latitudes but ends at the same time at different latitudes.

333

334   Fig. 2. Changes in testis size in free-living California quail and common starlings at different

335   latitudes during the year. Data for quail are taken from birds caught at 38°N (Genelly 1955)

336   or 47°N (Anthony 1970). Data for starlings are monthly means ± S.E. from birds caught at

337   52°N (Dawson and Goldsmith 1982) and individuals caught at 37°N by George Bentley

338   (unpublished data). Solid circles and lines represent means of testicular mass (right axis) and

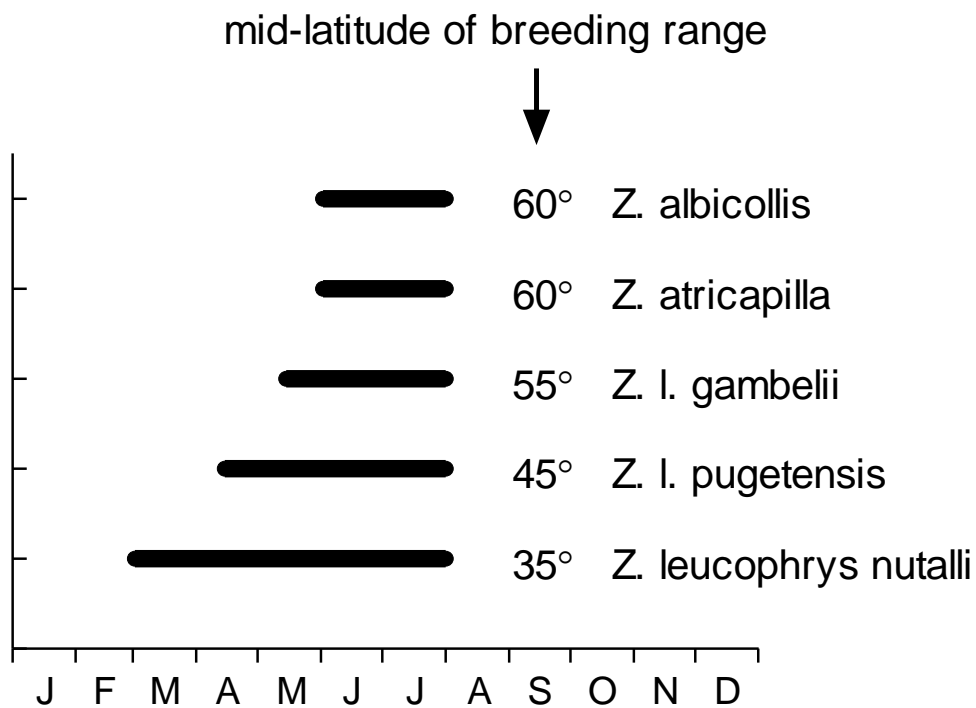339   open circles are individual values for testicular volume (left axis).

340

341   Fig. 3. Relative photorefractoriness and latitude.

342   A. Japanese quail held on long photoperiods need to experience a decrease in photoperiod to

343   induced testicular regression. The longer the initial long photoperiod (left axis) the greater the

344   decrease in photoperiod required to induce regression (right axis). For example, birds held

345   initially on 20L need to experience a decrease of 5 hours to 15L to induce regression,

346   whereas birds held on 16L only need a decrease in photoperiod of 3 hours, to 13L, to induce

347   regression. Note that the photoperiods that induce regression would all have been stimulatory

348   earlier in the year. Data from (Follett and Nicholls 1984).

349   B. The two solid curves represent change in photoperiod at 60°N and 40°N. Japanese quail

350   held in outdoor aviaries at 50°N showed testicular regression and molt starting in mid-

351   August, indicated by the solid vertical line (Robinson and Follett 1982). Assuming that quail
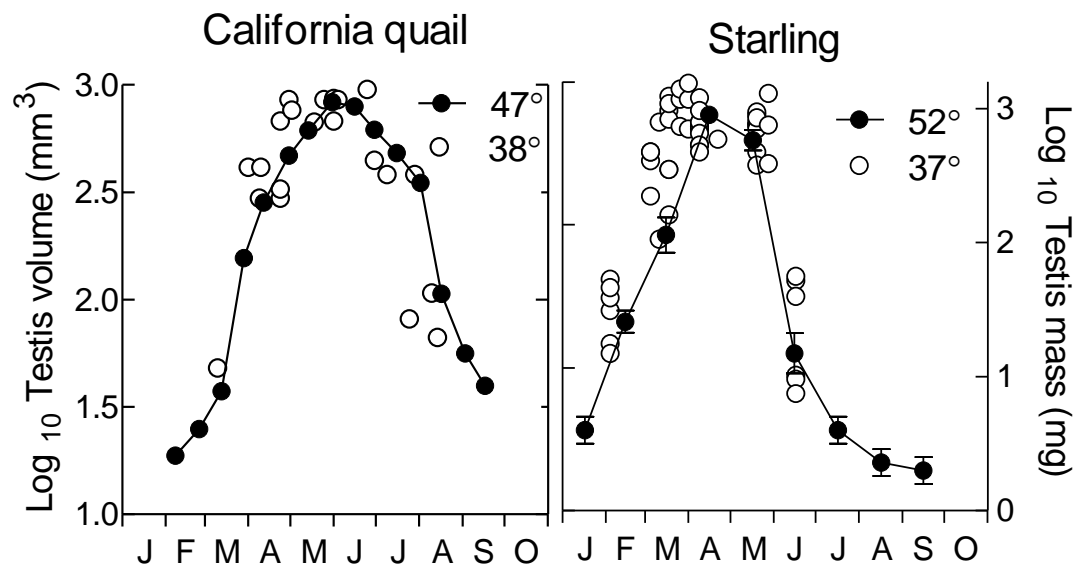
352   held at different latitudes show testicular regression at the same time, then birds at 60°N

353   would have experienced a decrease in photoperiod of 3 hours from the solstice (19L) to the

354   time of regression (16L), whereas birds at 40°N would have experienced a decrease in

355   photoperiod of only 1.5 hours (15L to 13.5L). This is consistent with experimental data from

356   A.

357

358   Fig. 1

mid-latitude of breeding range

60°	Z. albicollis
60°	Z. atricapilla
55°	Z. l. gambelii
45°	Z. l. pugetensis
35°	Z. leucophrys nutalli

J F M A M J J A S O N D
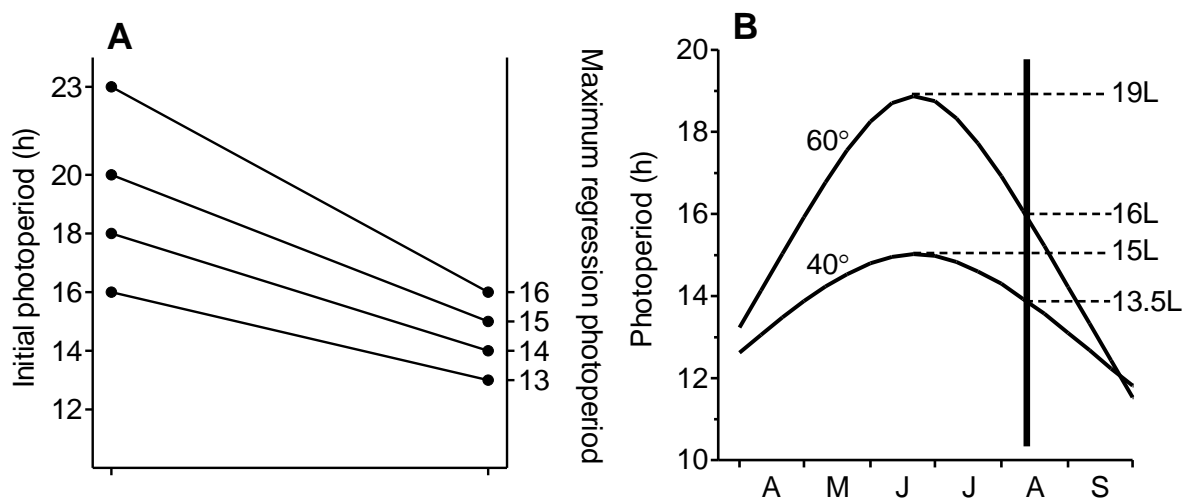
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360

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362   Fig. 2

363

California quail

Starling

364

365   Fig. 3

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