1 **"Estimating abundance and phenology from transect count data with GLMs"**

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7 **Abstract**

8 Estimating population abundance is central to population ecology. With increasing concern over

9 declining insect populations, estimating trends in abundance has become even more urgent. At

10 the same time, there is an emerging in interest in quantifying phenological patterns, in part

11 because phenological shifts are one of the most conspicuous signs of climate change. Existing

12 techniques to fit activity curves (and thus both abundance and phenology) to repeated transect

13 counts of insects (a common form of data for these taxa) frequently fail for sparse data, and often

14 require advanced knowledge of statistical computing. These limitations prevent us from

15 understanding both population trends and phenological shifts, especially in the at-risk species for

16 which this understanding is most vital. Here we present a method to fit repeated transect count

17 data with Gaussian curves using linear models, and show how robust abundance and

18 phenological metrics can be obtained using standard regression tools. We then apply this method

19 to eight years of Baltimore checkerspot data using generalized linear models (GLMs). This case

20 study illustrates the ability of our method to fit even years with only a few non-zero survey

21 counts, and identifies a significant negative relationship between population size and annual

22 variation in thermal environment (in growing degree days). We believe our new method provides

23 a key tool to unlock previously-unusable sparse data sets, and may provide a useful middle

24 ground between ad hoc metrics of abundance and phenology and custom-coded mechanistic

25 models.

26 **Key words**: *population dynamics, phenology; climate change; peak abundance; activity period;*

27 *first emergence; Gaussian curve; Euphydryas phaeton, growing degree days, general linear*

28 *model*

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30

31   **Introduction**

32   Ecologists are observing massively elevated extinction rates (Turvey and Crees 2019),

33   driven in part by direct anthropogenic activities, climate change, and the spread of invasive

34   species (Pievani 2014). We are also seeing frequent changes in the phenology of populations, a

35   "globally coherent fingerprint of climate change" (Parmesan and Yohe 2003). Both of these

36   patterns are particularly pronounced in insects, for which there are alarming signs of declining

37   populations for many well-studied taxa (e.g. Thomas et al. 2005, Forister et al. 2010, Potts et al.

38   2010) and more broadly (e.g. Hallman et al. 2017, van Klink et al. 2020). However, evidence for

39   global trends is mixed, with other studies showing no overall trends and in some cases

40   contradicting previous papers that found declines (Wagner et al. 2021). This conflicting literature

41   highlights the limitations of current tools and data sets (Thomas et al. 2019, Didham et al. 2020).

42   One key limitation is often the lack of data to estimate trends for individual species or

43   populations as opposed to broad taxonomic groups or guilds (Wagner et al. 2021), which is

44   especially problematic for rare or at-risk species.

45   One of the common forms of sampling for insect populations are systematic repeated

46   surveys throughout an activity period, such as "Pollard" transect walks (Pollard 1977), bee bowls

47   (e.g. Stemkovski et al. 2020), or trap nests (Forrest and Thomson 2011). Historically, the main

48   goal of these surveys was simply to estimate yearly abundance (e.g. Zonneveld 1991, Pollard and

49   Yates 1993, Schultz and Hammond 2003). More recently, there has been growing interest in also

50   estimating phenology from this type of data, starting at least with Sparks and Yates (1997), but

51   with considerable recent interest (e.g. Stewart et al. 2020, Fric et al. 2020). Estimating

52   abundance and phenology from repeated count data seems like it should be easy, yet often

53   remains a challenge. Initial approaches for estimating abundance involved averaging the counts

54   of surveys across the activity period (Pollard et al. 1975, Pollard 1977, Thomas 1983, Pollard

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55 and Yates 1993), which has clear limitations (e.g. requires appropriate estimation of activity

56 period, appropriate sampling within activity period, and if the same population spreads its

57 activity across a longer period, the average count will shrink). Initial approaches for estimating

58 phenology often looked at the first day individuals were observed (e.g. Sparks and Yates 1997),

59 but this metric can covary with population abundance and sampling effort, so can confound

60 phenological shifts with other changes (Van Strien et al. 2008, Miller-Rushing et al. 2008,

61 Inouye et al. 2019).

62   To improve on these basic approaches, numerous studies have proposed realistic or

63 highly flexible models (for a list of examples, see Table 1). However, with few exceptions, these

64 methods were developed or proposed in the context of repeated measures of flowering plants,

65 where there are often dozens of time points in a year (e.g. Malo 2002, Clark and Thompson

66 2011, Malo 2002, Clark and Thompson 2011, Proia et al. 2015, Austen et al. 2014). Perhaps as a

67 consequence of being developed with such rich data, current methods generally require

68 considerable data to work. This limitation holds both for the suite of models developed for

69 flowering plants, the "Zonneveld model" – a mechanistic phenology curve commonly used to

70 analyze insect counts (Zonneveld 1991, INCA 2002, Haddad et al. 2008) --, and more generic

71 approaches like generalized additive models (GAMs) (Rothery and Roy 2001, Hodgson et al.

72 2011, Newson et al. 2016, Stemkovski et al. 2020).

73   Ecologists sometimes address the limitations of current analytical techniques by working

74 only with abundant species, or years for which there are many non-zero survey counts. For

75 example, in a recent analysis of Ohio butterfly populations using GAMs, Wepprich et al. (2019)

76 limited their analysis to cases where they had 10 or more surveys in a year. When fitting

77 Spanish butterfly populations with Gaussian curves using a Bayesian model, Stewart et al.

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78   (2020) use only species that were present in at least half of their surveys, with at least 35

79   individuals observed per year. In their analysis of UK butterfly populations using GAMs,

80   Hodgson et al. (2011) generally excluded sites where the species was observed in less than half

81   the surveys. In simulations of data for the rare St. Francis' satyr butterfly, Haddad et al. (2008)

82   found that when survey frequency dropped to three times per week, the Zonneveld model

83   (implemented using INCA (2002)) failed more than 30% of the time.

84   While ecologists can gain a lot of information by fitting elegant models to rich data sets,

85   having only tools that require rich data may prevent the analysis of rare species or years of low

86   abundance, both of which are likely to lead to infrequent non-zero survey counts. Ignoring rare

87   species in turn can bias our understanding of global trends (Didham et al. 2020), and ignoring

88   years of low abundance limits our ability to infer population dynamics or carry out population

89   viability analysis (e.g. Gerber and Demaster 1999, Morris et al. 2002). To make matters worse,

90   even with considerable data, there is no guarantee that existing methods can be solved

91   numerically. For example, the Zonneveld model, which has become something of a standard for

92   Pollard-walk style time series, can run into issues of confounded parameters; it is difficult to tell

93   if you have a few long-lived butterflies or many short-lived ones, leading the Zonneveld model

94   to fail (Gross et al. 2007, Table S1). Similarly, Malo (2002) presented an elegant phenological

95   model based on the exponential sine function, but found that their numerical solvers failed to

96   find reasonable solutions. They thus had to modify the 5-parameter model to include two

97   additional parameters per year – defining the beginning and ending of the activity peaks for each

98   year – which have to be determined ad-hoc by users for each year of data. In some other cases,

99   Bayesian methods are recommended when data are sparse compared to model complexity.

100   However, custom-coded Bayesian analyses can fail in ways that are not obvious to non-experts

101   (Lele and Dennis 2009, Seaman et al. 2012).

102   A final challenge with current analytical methods is that many require substantial

103   knowledge of computational statistics to implement successfully. There are certainly statistical

104   ecologists with the skill and experience to write custom-coded hierarchical Bayesian models and

105   ensure that the resulting estimates are sensible (e.g. Lindén and Mäntyniemi 2011, Chapman et

106   al. 2015), but they are the minority of ecologists. Of the statistical methods we encountered in

107   writing this paper, only two (the Zonneveld model and GAMs) have seen much use. Not

108   coincidentally, these are the two methods with easy-to-use program implementations (INCA

109   (INCA 2002) and the **mgcv** package in R (Wood 2017), respectively). In contrast, another seven

110   methods published in the last 20 years have only been used in subsequent publications a

111   combined total of six times[1] (Table 1), and only one of those was applied to insect data (Belitz et

112   al. (2020), itself proposing a new method). To date, the majority of the apparent surplus of

113   analytical tools for repeated count data are not actually being used to study insect abundance or

114   phenology.

115   Taken together, it is clear that ecologists lack an accessible, robust statistical tool for

116   quantifying population abundance and phenology for species, years, or sites with sparse data. In

117   this paper, we propose an approach to fit such data with Guassian curves using generalized linear

118   models (GLMs). To illustrate this method, we first outline the algebra behind the procedure, then

119   demonstrate its application to a 9-year time series of monitoring from a population of Baltimore

120   checkerspot butterflies (*Euphydryas phaeton*) in Massachusetts. In the supplements we offer a

121   detailed explanation of how to implement this approach in the programming language R (R Core

122   Team 2020), and provide simple code to act as a template. The simplicity of Gaussian curves

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[1] In ecology. The Gaussian mixture model (Proia et al. 2016) has been used several times in publications on highway maintenance and once on diagnostics of ventricular septal defects.

123   (defined by only 3 parameters) means that our proposed method can be applied to almost all data

124   – we find that even three non-zero days of count is sufficient to fit an activity curve (admittedly

125   one with wide confidence intervals). The familiarity of linear regression and Gaussian curves

126   (and our example code) make this approach accessible to any ecologist who can run a linear

127   regression in R.

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130   **Gaussian curve as a linear model**

131   The basis of our method is that a Gaussian curve has the form

$$f(x) = a e^{\frac{-(x-\mu)^2}{2\sigma^2}}$$
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132   When a is chosen to make Equation 1 integrate to 1, this is the normal or Gaussian distribution.

133   Since everything in Equation 1 is a constant except for x, if we multiply it out and define β_0, β_1,

134   β_2 appropriately in terms of the other constants (see Appendix S1 for the algebra), we can rewrite

135   the Gaussian curve as

$$f(x) = e^{\beta_0 + \beta_1 x + \beta_2 x^2}$$
2

136   Here we can see that the terms in the exponent are a quadratic equation. This means that if we

137   take the natural log of both sides, we are left with a familiar linear model with both a linear and a

138   quadratic term:

$$\ln(y) = \beta_0 + \beta_1 x + \beta_2 x^2$$
3

139   (Note that to produce an appropriate Guassian curve, β_1 must be positive and β_2 must be

140   negative; otherwise this equation produces a monotonic or convex curve). Despite our special

141   use for it, Equation 3 is an ordinary linear model of a quadratic equation, and can be fit with

142   standard tools for linear models. In the context of phenology, the most straightforward analysis

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143   would use empirical estimates of abundance or activity (e.g. transect counts of butterflies or

144   flowers) for dependent variable y, which is distributed following a Gaussian curve in relation to

145   some measure of time (e.g. day of year) for the independent variable x (Fig. 1A-I).

146   Fitting a linear model of $ln(y)$ vs. x provides estimates and confidence intervals for β_0, β_1,

147   and β_2. By reversing the algebra between Equations 1 and 2, we can recover the parameters of

148   the Gaussian curve (mean μ, variance σ^2), as well as metrics determined by the gaussian curve

149   (e.g. area under the curve) that may be useful in interpreting the fitted activity curves (Appendix

150   S1: Fig. S1). First, μ, the estimated **day of peak activity** and **mean day of activity** (these are the

151   same since the Gaussian curve is symmetrical) can be calculated from the slopes of the linear and

152   quadratic terms:

$$\mu = -\frac{\beta_1}{2\beta_2} \qquad\qquad 4$$

153   The standard deviation of the Gaussian curve, σ, is a function of the slope of the quadratic term:

$$\sigma = \sqrt{-\frac{1}{2\beta_2}} \qquad\qquad 5$$

154   In the case study below, we refer to $2*1.285*\sigma$ as the **activity period**. This corresponds to the

155   range of dates between the 0.1 and the 0.9 quantiles, and so this measures the duration of time

156   when the middle 80% of observations are estimated to occur (e.g. Jonzén et al. 2006, Michielini

157   et al. 2020).

158   The area under the gaussian curve, N, is a **population abundance index:**

$$N = \left(\sqrt{-\frac{2\pi}{2\beta_2}}\right)\exp\left(\beta_0 - \frac{\beta_1^2}{4\beta_2}\right) \qquad\qquad 6$$

159   We use the term "abundance index" because, for constant sampling effort, survival, and

160   detection probability, N will be proportional to the number of active individuals (e.g. Gross et al.

161   2007). However, it is actually a measure of estimated observed activity-days (Dennis et al. 2015,

162   Wepprich et al. 2019).

163   We note that here we have focused on a few phenological metrics, including the days of

164   0.1, 0.5 (e.g. day of peak) and 0.9 quantile. However, because our proposed approach fits a

165   Guassian curve, from estimated μ and σ it is trivial to calculate any characteristics of a Gaussian

166   curve, including (a) any arbitrary quantiles (e.g. the 0.05 and 0.95 quantiles used in Stemkovski

167   et al. 2020), (b) the height of the curve (e.g. maximum number of flowers, Miller-Rushing and

168   Inouye (2009)), or (c) the "observable flight season" (days when the curve exceeds 1, a metric

169   reflecting the period of likely human detection that parallels first and last observation dates)

170   (Bonoan et al., *in review*).

171   Standard errors of derived parameters such as μ, σ^2, or N can be estimated using the delta

172   method (Williams et al. 2002), or by parametric bootstrapping (Dennis 1996). Code for these

173   analyses is given in Appendices S2 (tutorial as html), S3 (analysis as html) and S4 (data and

174   Rmarkdown sources for Appendices S2 and S3). All code was written and run in R version 4.0.0

175   (R Core Team, 2020).

176

177   **Case study**

178   *Data set*

179   From 2012-2020, we conducted a capture-recapture study of Baltimore checkerspot

180   (*Euphydryas phaeton*) butterflies at a natural area (Williams Conservation Land) in the town of

181   Harvard MA, USA (Brown and Crone 2016, Brown et al. 2017, Crone 2018). Baltimore

182   checkerspot is a univoltine species, with one clear flight period of adults per year. Surveys were

183   conducted by visiting the site 2-3 times a week from mid-June until the population was clearly

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184   finished for the year; the onset of checkerspot flight at this site is usually in late June or early

185   July. To illustrate the use of a Gaussian curve to estimate phenological metrics, we converted

186   capture-recapture data to counts of individual animals handled on each visit to the site. This

187   monitoring protocol creates a data structure that is similar to traditional "Pollard walk" style

188   monitoring (Pollard 1977, Pollard and Yates 1993, Wepprich et al. 2019) but differs from Pollard

189   walks in that the site was searched freely, rather than by walking a fixed route. For comparison

190   with the Gaussian analyses below, we estimated population size each year using standard open

191   population capture-recapture models (see supplemental methods). For comparison to existing

192   methods, we fit our data to the Zonneveld model using INCA (INCA 2002). We chose to

193   compare with the Zonneveld model because it is also easy to use, and as a 4-parameter model, it

194   is one of the simplest (and thus most likely to fit our sparse data).

195

196   *Methods:*

197   *Estimation of phenology metrics:* We fit Gaussian curves to these data using generalized

198   linear models (GLM) with a negative binomial family and log link function, with the number of

199   butterflies seen on each day as the dependent variable, day of year and day of year squared as

200   independent variables; we used a single model with interaction terms to allow curves to fit each

201   year separately, but with shared estimation of the model variance term. After fitting the linear

202   model, we used equations 4-7 to calculate the estimated mean day of activity, standard deviation

203   of flight period, population abundance, and peak abundance for each year, and use mean day of

204   activity and standard deviation of activity to calculate onset (day of 0.1 quantile) and end (day of

205   0.9 quantile) of activity. For heuristic purposes, we calculated confidence intervals for these

206   metrics using both the delta method and parametric bootstrapping. To test for asymmetry in

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207   activity curves (a feature common in some systems and models), we regressed residuals by day

208   of year using a linear model and then again with a cubic regression spline (using the **mgcv**

209   package) (Wood 2017).

210   *Comparison to INCA fits:* We used the INCA program to fit each year of our data (INCA

211   2002). We carried out this analysis with INCA twice: first we fit INCA using default settings,

212   putting INCA on a level playing field with the Gaussian method; second, we fit INCA again,

213   providing an informative prior on mortality rate, defined by the mean and standard error of daily

214   mortality for the Baltimore Checkerspot (Brown and Crone 2016, their Table 1). Both INCA and

215   the Gaussian curve produce indices of population abundance rather than complete population

216   estimates, and these indices are on different scales. As such, we focus on the correlation between

217   INCA and Gaussian metrics.

218   *Evaluating an environmental driver:* After estimating abundance and phenology, a

219   common next question is to ask whether changes in these population characteristics are

220   associated with changes in environmental conditions (see, e.g., Roy and Sparks 2000, Forister

221   and Shapiro 2003, Marra et al. 2005, Jonzén et al. 2006, Miller-Rushing et al. 2008, van Buskirk

222   et al. 2009, Hodgson et al. 2011, Gordo et al. 2013, Bertin 2015, Cayton et al. 2015, Barton and

223   Sandercock 2018, Heberling et al. 2019, Oke et al. 2019, Park et al. 2019, Fric et al. 2020,

224   Horton et al. 2020, Stewart et al. 2020, Stemkovski et al. 2020). It is possible in principle to

225   simultaneously fit drivers of population or phenological change and parameters themselves (e.g.

226   Mizel et al. 2019). However, the algebra of converting a Gaussian curve to a linear model does

227   not enable easy inclusion of covariates of the ecologically meaningful derived metrics such as

228   onset of activity or peak dates (XXX, unpubl. calculations). One accessible alternative to

229   custom-coding complex models is a two-step process of first estimating derived parameters (e.g.

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230   population abundance index) with linear models, then using these derived parameters in

231   subsequent models (e.g. the approach used in Wepprich et al. (2019), but using GLMs instead of

232   GAMs for the first step). To account for uncertainty in derived parameters, it is straightforward

233   to use parameteric bootstrapping.

234   To illustrate this approach, we compared yearly estimates of the day of mean activity,

235   flight period, and population abundance to temperature. Determining the most appropriate

236   metrics to capture environmental drivers of population dynamics or phenology is an open

237   question in ecology, and beyond the scope of this study. We instead chose to demonstrate the

238   principles with growing degree days (GDD), a common measure of thermal environment that has

239   been found to predict plant and insect phenology (e.g. Hodgson et al. 2011, Cayton et al. 2015).

240   We used a developmental threshold of 10 degrees as in Cayton et al. (2015), and calculated GDD

241   over the period from January 1 through July 1 of each year to represent the time before most

242   butterflies eclosed (for details, see Appendix S1). For each population metric (abundance, mean

243   day of activity, flight period), we fit a simple linear regression with GDD as the predictor. We

244   also calculated 95% confidence intervals for the slope using parametric bootstrapping, and the

245   proportion of p values that were less than 0.05 among these bootstrapped model fits.

246

247   *Results:*

248   *Estimation of phenology metrics:* For this univoltine butterfly population, the Gaussian

249   curve provides a visually satisfying fit, with the model reasonably fitting years with many

250   surveys (Fig. 1 A-F) and those with few (2018-2020, Fig. 1G-I). We found no overall indication

251   of asymmetry in activity when fitting our residuals with a linear model (slope = 0.085, p=0.57),

252   and our fitted cubic spline showed no notable deviations from a linear model (estimated degrees

253   of freedom for the smoothing term was 1, suggesting a straight line is the best fit). Estimates of

254   our three metrics (Abundance index, flight period, and day of peak activity) were generally very

255   precise, with notable exceptions for 2019 and 2020, years with only a few non-zero survey

256   counts (Figs. 2A-C). We also see a strong correspondence between our abundance index and

257   population estimates from the capture-recapture study ($R^2 = 0.94$) (Fig. 3A). These data also

258   demonstrate the bias of first and last dates of observations in relation to population size (Fig. 3C-

259   D); compared to 0.1 and 0.9 quantiles estimated from annual Gaussian curves, years with smaller

260   populations had later first observations and earlier last observations.

261   *Comparison to INCA fits:* Without independent estimates of mortality, INCA fit only 3

262   of the 9 years of data (Table S1). Using published mortality estimates (Brown and Crone 2016)

263   as an informative prior probability distribution, INCA was able to fit more years of data (7 of the

264   9), but still failed to fit 2019 and 2020. For the years in which the informed INCA model fit,

265   there was a very strong correspondence between the informed INCA fit and the Gaussian fit,

266   with an R-squared of 0.996 (population abundance indices) and 0.883 (day of peak activity) (Fig.

267   3B).

268   *Evaluating an environmental driver:* Temperature had a strong association with

269   population abundance index, with warmer years associated with smaller population indices

270   (estimate slope: -2.12; bootstrapped 95% CI of slope of N vs GDD: [-2.3087, -2.0598]; across

271   our bootstraps, this was almost always significant ($p<0.05$ in 99.6% of bootstraps) (Fig. 3D)).

272   Mean day of activity was consistently earlier in warmer years (estimated slope: -0.004;

273   bootstrapped 95% CI of slope of μ vs. GDD: [-0.0065, -0.0024]), but it was rarely statistically

274   significant ($p<0.05$ only 6 out of 10,000 times) (Fig. 3E). Temperature was not associated with

275   differences in flight period (estimated slope: -0.002; bootstrapped 95% CI of σ vs. GDD: [-

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276   0.0023, 0.0007], p<0.05 0 of 10,000 times) (Fig 3F).

277

Discussion

279   In this paper, we show how a Gaussian curve can be fit to insect count data using familiar

280   methods for linear models, and that it allows us to estimate abundance and phenology even for

281   years of sparse data where other methods can fail. We hope this approach provides a much-

282   needed tool for ecologists trying to study insect decline or the phenology and dynamics for at-

283   risk species (or species that have sparse count data for other reasons). There is a particular need

284   for tools like this given the growing interest in documenting and understanding insect decline;

285   our ability to do so is in large part limited by available data and methods (Didham et al. 2020).

286   We are not the first to use Gaussian curves to fit count data (e.g. Lindén and Mäntyniemi 2011,

287   Dennis et al. 2015, Oke et al. 2019, Stewart et al. 2020), but past implementations have required

288   custom coding and more advanced knowledge of statistical computing.

289   The combination of a simple mathematical form (3 parameters) and the robust fitting

290   algorithms associated with linear models allows Gaussian models to estimate phenology and

291   abundance even in years with relatively few observations (see, e.g., Fig 1H). Recent studies of

292   butterfly (Hodgson et al. 2011, Wepprich et al. 2019, Stewart et al. 2020) and bee (Stemkovski et

293   al. 2020) populations have generally been restricted to relatively abundant species by the needs

294   of their more data-hungry methods. These more flexible analytical tools like GAMs provide

295   more detailed information about activity curves, but at the cost of requiring sufficient data to

296   differentiate between the many possible shapes those more flexible curves can take. In contrast,

297   while the Guassian curve is constrained in shape and cannot capture complex activity curves, we

298   are consistently able to fit curves with only 3 non-zero surveys (XXX unpubl. simulations). Our

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299   goal is not to replace existing tools, which often provide more detailed information than a

300   Guassian curve can, like capturing multimodality (e.g. GAMs) or measuring asymmetry and

301   linking it to biological processes (e.g. the Zonneveld model). Rather, we want to "unlock" data

302   sets which were previously unusable either because the observations were too sparse for other

303   methods, or interested parties did not have the computational statistics background needed to fit

304   more complex models. We explain and demonstrate this method assuming a simple data

305   structure (e.g. multiple years, but one species and one site). With hierarchical data (e.g. multiple

306   sites, multiple species), this method can be expanded upon to fit separate curves for statistical

307   unit (e.g. each year of each site) (Bonoan et al., *in review).*

308   Comparing fits and estimates of the Baltimore checkerspot butterfly using our Gaussian

309   method, the INCA implementation of the Zonneveld model, and capture-recapture tools

310   demonstrate the value of our approach. Without outside information, the INCA model fit only

311   one third of our 9 years of data, and even with the inclusion of an independent estimate of

312   mortality rates, INCA failed to fit the two years with the lowest estimated abundance (Table S1).

313   However, for years when we could fit the data using the Zonneveld/INCA model informed by

314   independent estimates of mortality, we see a very strong correspondence between INCA and

315   Gaussian estimates of population abundance indices ($R^2 = 0.99$) (Fig. 3B), suggesting that our

316   proposed method is a useful and comparable alternative to INCA when data are sparse. We also

317   see a tight correlation between the abundance index of the Gaussian model, and capture-

318   recapture estimates of population size calculated separately from the same data (Fig. 3A), which

319   suggests that abundance estimates are unbiased. This correlation compares favorably with other

320   methods of fitting transect data; Haddad et al. (2008) found no correlation between mark-

321   recapture estimates of population size and population size estimated using the Zonneveld model.

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322   However, the fact that we find a 1:1 match of N (an index that reflects longevity as well as

323   abundance) and capture-recapture estimates is likely coincidental. By chance, our capture

324   probability during surveys was $\approx$ 0.15 (XXX and YYY unpubl.), and the apparent survival of

325   Baltimore checkerspot butterflies at our site is 0.844/day (Brown and Crone 2016); these values

326   mean that in our example, the capture probability - by chance - exactly cancelled out the fact that

327   N is actually in units of "butterfly days".

328   While it is becoming increasingly rare, objectively problematic metrics for phenological

329   patterns such as first or last observations are still used by at least some ecologists (e.g. Fric et al.

330   2020, Colom et al. 2020). For many types of data sets, observations of first and last events are

331   known to be biased, as the day of first or last observation depends in part on population size and

332   detectability (Van Strien et al. 2008, Miller-Rushing et al. 2008, Inouye et al. 2019). Of course,

333   sometimes data limitations constrain analysis to only use first or last metrics, especially when

334   comparing with historic data sets (e.g. Heberling et al. 2019). However, in many cases ecologists

335   have much more complete data, and should not be limited to using problematic phenological

336   metrics. This point has been made thoroughly in other studies; as expected, for the Baltimore

337   Checkerspot we see consistent biases in first and last date observed based on population size

338   (Fig. 3C-D). As an alternative to problematic metrics, fitting Gaussian curves may be a

339   reasonable first step for many ecologists interested in describing phenology. Early and late

340   quantiles (e.g. 0.1 and 0.9, as in Jonzén et al. (2006) and Michielini et al. (2020), or 0.05 and

341   0.95 as in Stemkovski et al. 2020) can easily be calculated from estimated μ and σ, and are

342   unbiased analogs to represent the early and late parts of the activity season (cf. Bonoan et al., *in*

343   *review*).

344   We demonstrated how our approach can be used to link population-level patterns with

345 environmental (or other) drivers. In doing so, we found a significant negative relationship

346 between growing degree day (GDD) and abundance indices, and a non-significant pattern of

347 earlier activity in warmer years that was consistent across bootstraps. These results are largely

348 consistent with the patterns found in other studies. Warmer temperatures have led to earlier

349 activity for butterfly species in the UK (MacGregor et al. 2019), Spain (Stefanescu et al. 2003,

350 Stewart et al. 2020), and Ohio (Cayton et al. 2015), and studies have found that in recent decades

351 butterflies have advanced their phenology in the UK (MacGregor et al. 2019) and across the

352 northern hemisphere (Parmesan 2007). The relationship between temperature and abundance

353 across studies is more complicated. Studies have found warmer temperatures leading to higher

354 population abundance in most butterfly species in the UK (Roy et al. 2001) and a mixture of

355 butterfly abundance responses to temperature in Spain (Stewart et al. 2020). In contrast, Isaac et

356 al. (2011) found butterfly density in England was generally lower in regions with higher

357 temperatures, and Colom et al. (2020) found warmer summers were associated with smaller

358 butterfly populations on the Spanish island of Menorca. In Massachusetts USA, butterfly

359 populations near their species' northern range limits are generally increasing, and populations

360 near their species southern range limits are generally decreasing (Breed et al. 2012, Michielini et

361 al. 2020).

362　　　　Gaussian curves are only well-suited to represent data that is unimodal and approximately

363 symmetric. For many phenological events, the assumption of symmetry may be a reasonable

364 approximation (see Fig 1, and Stewart et al. 2020), although this is of course a hypothesis that

365 could be explored depending on the goals of an analysis (in our analysis of Baltimore

366 checkerspot, residuals did not indicate skew). Multimodal distributions may be more

367 problematic. For multivoltine insects, Generalized Additive Models (GAMs) (e.g. Knudsen et al.

368   2007, Moussus et al. 2009, Hodgson et al. 2011, Newson et al. 2016, Stemkovski et al. 2020)

369   have been used to capture changes in phenology over time. Although they are not described by a

370   parametric equation, features like the onset (0.1 quantile) or end (0.9 quantile) can be extracted

371   from GAMs numerically (cf. Stemkovski et al. 2020). Another approach to evaluating

372   phenological events without assuming a particular distribution is quantile regression (Cade and

373   Noon 2003, Koenker 2019), which has been used in several studies of bird migration (e.g. Gordo

374   et al. 2013, Barton and Sandercock 2018), and occasionally for Lepidoptera (Gimesi et al. 2012,

375   Michielini et al. 2020). Like GAMs and GLMs, quantile regression shares the property of

376   drawing on well-established and well-validated statistical approaches, rather than developing

377   new ones.

378   Understanding trends in abundance has long been a goal of both population ecology and

379   conservation management, and this has become all the more urgent with observed and suspected

380   population declines in a wide range of species, particularly insects. Similarly, because

381   phenological shifts are one of the most conspicuous signs of climate change, there is growing

382   interest in their causes and consequences. We expect that the widespread interest in abundance

383   and phenology will continue to lead to a growing number of new methods for interpreting

384   patterns in count data. At the same time, not every new method is guaranteed to work for all (or

385   even most) data, and custom-coding for every question can be error-prone, time consuming, and

386   intimidating to many ecologists. We encourage ecologists to be aware of well-established

387   existing methods, and provide the linearized Gaussian model as a simple tool for unlocking

388   previously-inaccessible sparse data sets.

389

390   **Declarations:** This work was conducted with support from NSF DEB 19-20834 and the DOD

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629 **Figure 1:** Gaussian model fitted to Baltimore checkerspot butterfly data. Points show raw data,

630 blue lines show best-fitting Gaussian curve, dashed gray lines show +/- 1 standard error. For

631 comparability, day of month for axis labels in this and other figures is based on a 365 day year

632 (excludes leap days). Note the different scales on the y-axes.

633 **Figure 2:** Fitted population metrics: (A-C) abundance index (A), mean day of activity (B), flight

634 period (C) across years (sequentially). Bars show +/- 1 standard error, calculated using the delta

635 method (black) or parametric bootstrapping (blue). (D-F) Comparison of same population

636 metrics with the Growing Degree Days (GDD) on July 10 for each year. Solid and dashed black

637 lines show best-fitting model for significant (solid) and non-significant (dashed) linear

638 regression. In all panels, parametric bootstrap standard errors are based on 0.16 and 0.84

639 quantiles of bootstrap samples (quantiles corresponding to +/- 1 standard error).

640 **Figure 3:** Comparing derived estimates from GLM approach to other commonly used

641 approaches (A) Comparison of GLM estimated abundance index to mark-recapture estimates.

642 Black lines show +/- 1 standard error of each metric, dashed line shows best-fitting curve (R^2 =

643 0.94). (B) Comparing CLM estimated abundance index with INCA estimated abundance index

644 (INCA is an implementation of the Zonneveld model) (R^2 = 0.99). (C-D) Comparison of

645 quantile-based estimates of onset (C) and end (D) of activity to day of first (C) and last (D)

646 observation for each year, with point size scaled by GLM estimated population index (square-

647 root scale). Black lines show a 1:1 line going through the mean of observed values. As expected,

648 years with smaller population sizes show less extreme observations (i.e., points above (C) and

649 below (D) the 1:1 line).

650 **Table 1:** Summary of ad-hoc literature review on statistical methods for fitting activity curves to

651 repeated count data, looking to see how often the proposed methods have actually been used.

31

652 Note that there were a few non-English publications citing these methods papers which we were

653 unable to evaluate. In addition to these methods, Generalized Additive Models (GAMs) have

654 been widely used in a variety of phenological studies and one older method (Zonneveld et al.

655 1991) is widely used by some insect ecologists (see discussion in main text). We also did not

656 include custom-coded (typically Bayesian) approaches that would need substantial recoding of

657 the method to be applied to a new data set.

658 **Table S1:** Comparing ability of GLM and INCA models to fit the Baltimore checkerspot data.

659 "Non-zero counts" represents the number of survey days in that year with at least one butterfly

660 observed; "Gaussian fits?" shows whether or not our GLM approach fit the data"; "INCA fits?"

661 shows whether or not the Zonneveld method implemented in the INCA program fit the data

662 (using default settings); "INCA+ fits?" shows the same results, but when INCA is given

663 mortality information independently determined from Brown and Crone 2016. We see that INCA

664 struggles to fit much of our data, INCA+ fits most of our data, and the GLM approach fits all of

665 our data.

666
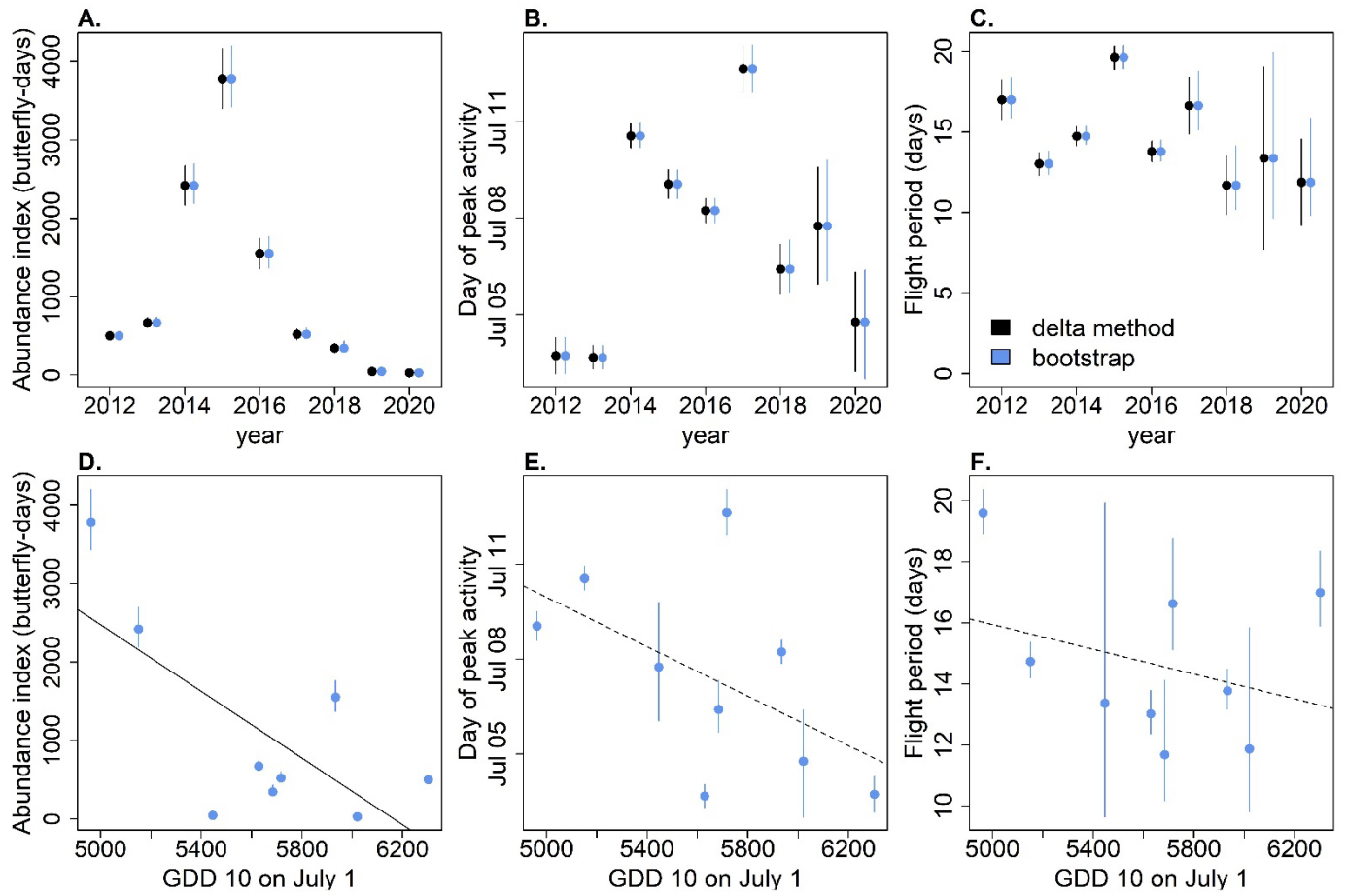
667

668   **Figure 1.**

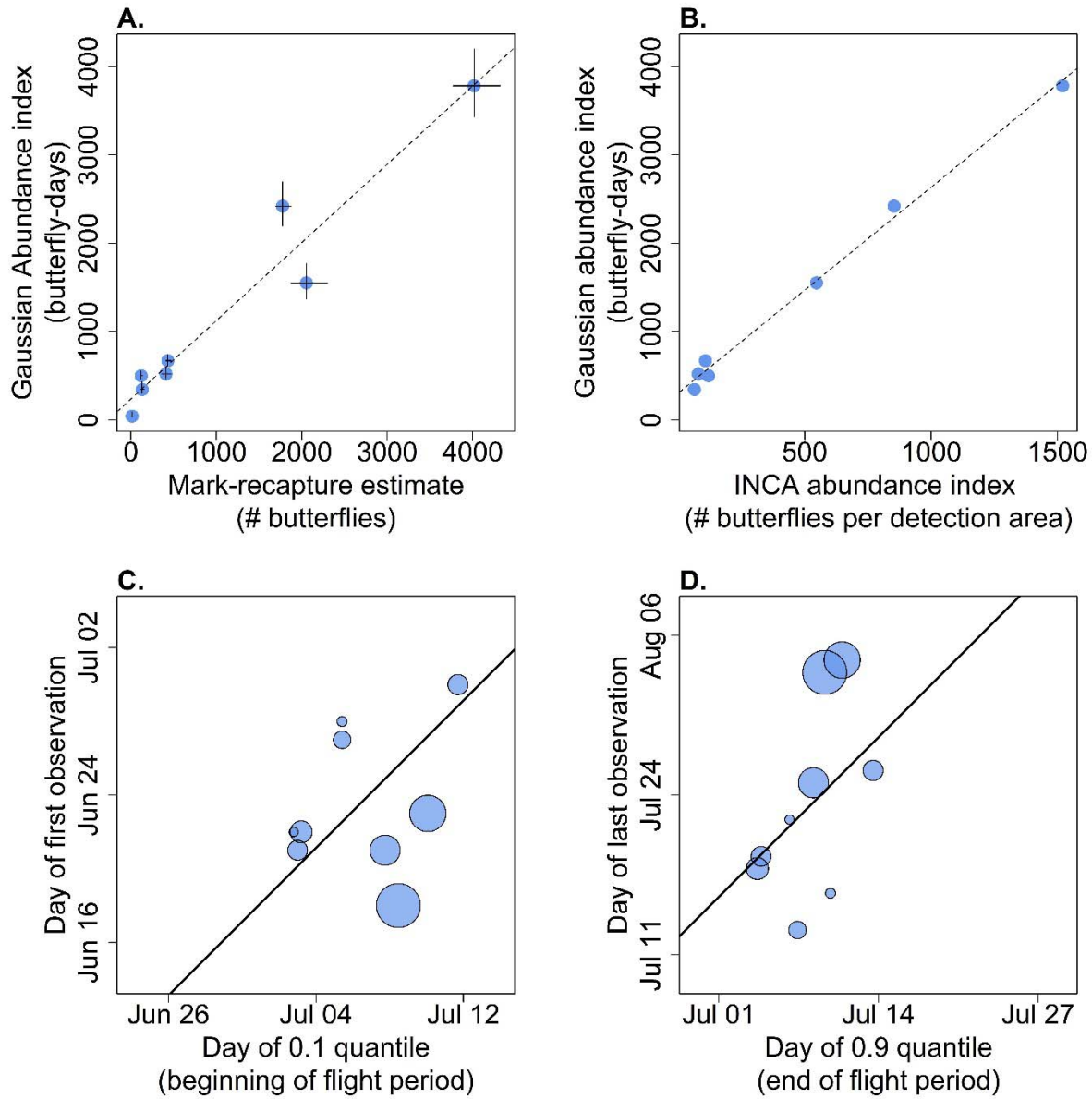669
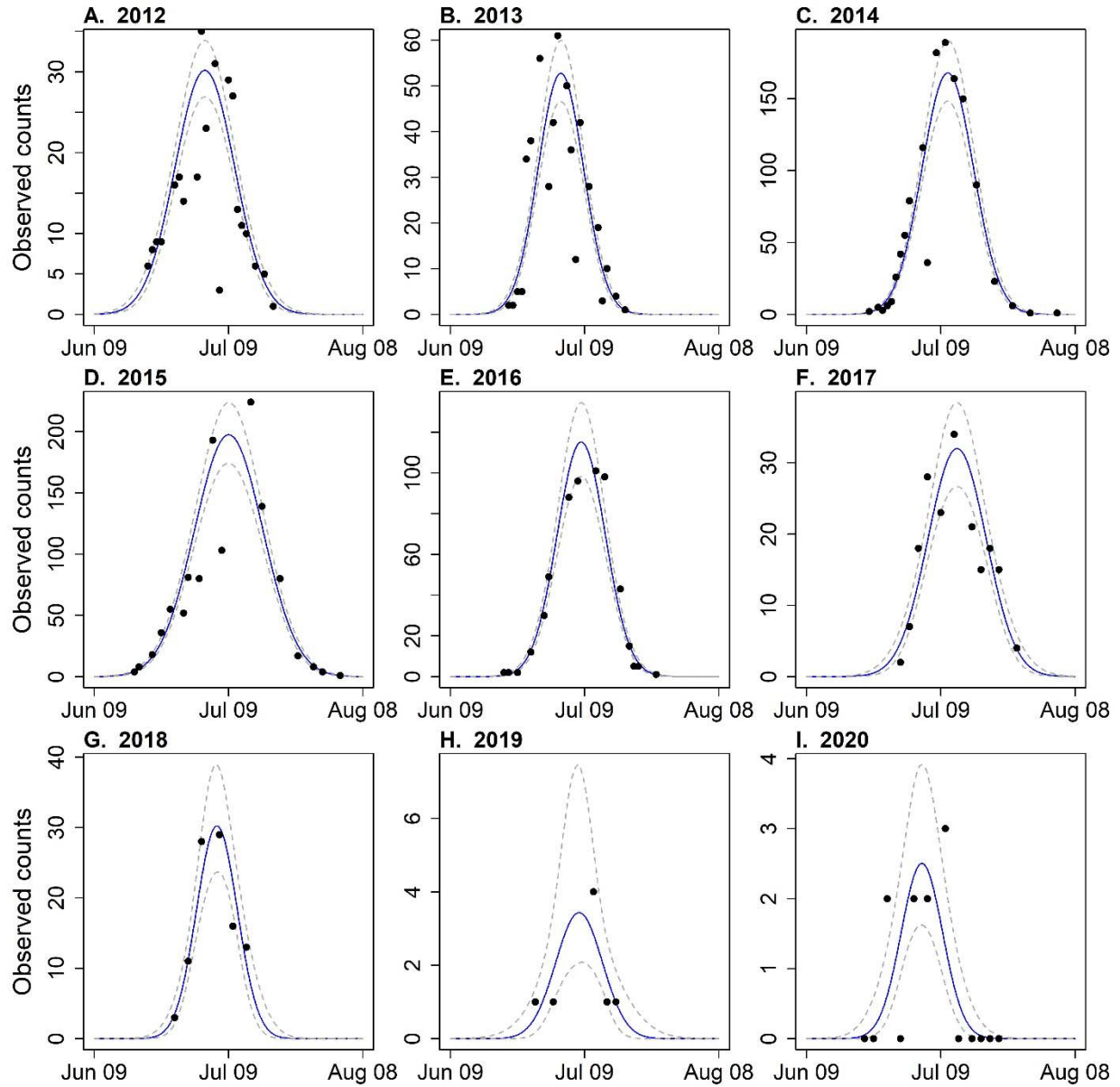
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671   **Figure 2**

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675 **Figure 3**

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678   **Table 1**

Method	Publication	System	Description	Used in
Generalized epsilon-skew-Gaussian	Clark and Thompson 2011	plants	5-parameter function - imagine a Gaussian flexible enough to have skew.	Yule and Bronstein 2018 (plants), Weis et al. 2014 (plants).
Gaussian mixture models	Proia et al. 2015	plants	Gaussian mixture models	0
Principle coordinate analysis	Austen et al. 2014	plants	Take matrix of open flowers on date (col) per plant (row). Calculate difference between entries as a new coordinate system. Now summarize that with a PCoA, kind of like we would with a PCA. From this, calculate Chord distance and Komogorov-Smirnov distances.	0
Weibull	Pearse et al. 2017	plants (presence/absence)	Note: implemented in the phest package	Taylor 2019 (methods-testing paper), Belitz et al. 2020 (although not really - builds on weibull distribution, but distinct method) (plants, monarch butterflies)
survival modeling	Elmendorf et al. 2019	plants (presence/absence)	hierarchical survival models. Seems good for presence/absence of phenological state	0
Weibull-based percentile metric	Belitz et al. 2020	flowers, monarchs	Using weibull distribution for any quantile. R package phenesse.	0, but not a fair comparison – very recently published.
Exponential Sine	Malo 2002	Flowers	Exponential Sine.	Forrest and Thomson 2011 (only used to estimate flower data on missing dates for two plant species); Herrer`ias-Diego 2006 (using a simplified version that is symmetrical) (plants)

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682 **Table S1**

Year	Non-zero counts	INCA fit?	INCA+ fit?	Gaussian fit?
2012	23	**<u>No</u>**	Yes	Yes
2013	20	Yes	Yes	Yes
2014	20	**<u>No</u>**	Yes	Yes
2015	18	**<u>No</u>**	Yes	Yes
2016	15	**<u>No</u>**	Yes	Yes
2017	11	Yes	Yes	Yes
2018	6	Yes	Yes	Yes
2019	5	**<u>No</u>**	**<u>No</u>**	Yes
2020	4	**<u>No</u>**	**<u>No</u>**	Yes

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