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1 **The influence of data type and functional traits on native bee phenology** 2 **metrics: Opportunistic versus inventory records**

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ABSTRACT

18 Efforts to understand activity patterns of bees, our most important pollinators, often rely
19 on opportunistically collected museum records to model temporal shifts or declines. This type of
20 data, however, may not be suitable for this purpose given high spatiotemporal variability of
21 native bee activity. By comparing phenological metrics calculated from intensive systematic
22 inventory data with those from opportunistic museum records for bee species spanning a range of
23 functional traits, we explored biases and limitations of data types to determine best practices for
24 bee monitoring and assessment. We compiled half a million records of wild bee occurrence from
25 opportunistic museum collections and six systematic inventory efforts, focusing analyses on 45
26 well-represented species that spanned five functional traits: sociality, nesting habits, floral
27 specialization, voltinism, and body size. We then used permutation tests to evaluate differences
28 between data types in estimating three phenology metrics: flight duration, number of annual
29 abundance peaks, and date of the highest peak. We used GLMs to test for patterns of data type
30 significance across traits. All 45 species differed significantly in the value of at least one
31 phenology metric depending on the data type used. The date of the highest abundance peak
32 differed for 40 species, flight duration for 34 species, and the number of peaks for 15 species.
33 The number of peaks was more likely to differ between data types for larger bees, and flight
34 duration was more likely to differ for larger bees and specialist bees. Our results reveal a strong
35 influence of data type on phenology metrics that necessitates consideration of data source when
36 evaluating changes in phenological activity, possibly applicable to many taxa. Accurately
37 assessing phenological change may require expanding wild bee monitoring and data sharing.

38 KEYWORDS

39 native bees; phenology; data type; opportunistic data; inventory data; functional traits

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INTRODUCTION

41 Accurately estimating species phenology is central to understanding ecological systems
42 (J. Forrest & Miller-Rushing, 2010; Inouye, 2008; Nakazawa & Doi, 2012). When species are
43 active determines the abiotic conditions they face; the identity, quality, and quantity of resources
44 available to them; and the specific competitors and predators they encounter. Yet the relative
45 timing of ecosystem components can be difficult and costly to assess. The activity pattern of any
46 given species may vary both temporally (across years) and spatially, in response to a cacophony
47 of abiotic and biotic conditions, which themselves fluctuate at various scales (de Keyzer et al.,
48 2017). The more environmentally-sensitive and species-rich the taxon of interest, the more
49 complicated it can be to determine the magnitude, or even the direction, of any generalized
50 phenological trends (de Keyzer et al., 2017; Primack et al., 2009). On top of these biological
51 considerations, the amount and type of data necessary to evaluate phenological patterns or
52 navigate known biases remains unclear (de Keyzer et al., 2017; Isaac & Pocock, 2015; Miller-
53 Rushing et al., 2010; Strien et al., 2008). A better understanding of these consequential
54 uncertainties is necessary to reliably determine the effects of environmental change on both
55 natural and managed systems.

56 Native bees include highly variable and diverse taxa that are of particular interest for
57 phenological studies due to their value as pollinators and their vulnerability to ecosystem change
58 (Fabina et al., 2010; Ogilvie & Forrest, 2017; Rafferty & Ives, 2011). Many native bees are
59 solitary, and respond to a host of environmental cues to time emergence from overwintering
60 nests, including changes in soil moisture from snowmelt or precipitation, and temperature, which
61 can influence the rate at which larvae exhaust food supplies and undergo metamorphosis
62 (Danforth, 1999; Helm et al., 2017; Michener, 2007). The interplay of species-specific

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63 demography and responses to abiotic emergence cues is poorly understood for the majority of
64 native bee species, and may or may not align with factors determining local seed germination
65 and bloom time (Aldridge et al., 2011; Danforth, 1999; Miller-Rushing et al., 2010). The
66 potential for temporal mismatches between pollinators and their host plants, which could result
67 in inadequate pollination for plant reproduction and nutritional deficits for bees, has inspired
68 many recent studies of phenological shifts. Studies of this phenomenon have returned mixed
69 results, with evidence both of problematic disruptions of historical pollinator-plant relationships
70 (Aldridge et al., 2011; Burkle et al., 2013; Robbirt et al., 2014; Schenk et al., 2018) and of
71 inconclusive or parallel shifts in emergence and bloom time (Bartomeus et al., 2011; J. R. K.
72 Forrest, 2015; J. R. K. Forrest & Thomson, 2011; Ogilvie & Forrest, 2017). Little attention,
73 however, has been paid to how the type, quantity, or quality of data used to measure phenology
74 in bees – or other species – may produce conflicting conclusions.

75 To assess the vulnerability of plant-pollinator relationships to climate change, we first
76 need to examine whether data used to assess bee phenology accurately reflects real changes in
77 bee activity, as opposed to noise from unevenly-sampled biological variability, biased collecting
78 protocols, or sample-size limitations of the data. Sampling diverse organisms at large spatial and
79 temporal scales can be an incredibly laborious and expensive process. As a result, our knowledge
80 of bee trends necessarily draws from patchy and inconsistently-collected data (Meiners et al.,
81 2019). Understanding what available data can and cannot tell us about phenological trends over
82 time is an oft-overlooked prerequisite for accurately modeling the status, trends, and impacts of
83 wild bee abundance, as well as forecasting declines, range shifts, risks to network stability, and
84 vulnerability of particular species to climate change (Biesmeijer et al., 2006; Forrest, 2015;
85 Meiners et al., 2017; Potts et al., 2016). This oversight is apparent in pollinator studies but may

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86 impact phenological analyses of other taxa as well. Furthermore, testing and communicating all
87 sources of error and uncertainty is an important step in advancing scientific understanding and
88 maintaining public trust and investment in the ability of science to measure and mitigate changes
89 in our natural world.

90 Data available to researchers interested in large-scale animal activity trends can generally
91 be divided into two types: “opportunistic” and “inventory”. “Opportunistic” data usually consist
92 of records compiled from museum specimens belonging to specific groups of interest that are the
93 result of various disparate project collections, often of unknown and unspecified purposes. With
94 millions of records served from curated, digitized museums to public, online hubs, opportunistic
95 data are a rich resource of natural history information uniquely voluminous and useful for a
96 range of research questions (Lister & Climate Change Research Group, 2011). They are also
97 known, however, to contain biases and limitations derived from their unstandardized and
98 composite origins (Isaac & Pocock, 2015), and to lack metadata that would allow for easy
99 exclusion of biased records from small projects with specific objectives, such as sampling only
100 the bees visiting a particular plant. “Inventory” data, on the other hand, are collected in a
101 systematic manner, often for the explicit purpose of answering broad questions about place-
102 specific biodiversity patterns and community processes. A standardized protocol for conducting
103 inventories of native bee communities was established in 2003 by a group of melittologists
104 (LeBuhn et al., 2003), and has been used in many inventories of bees in natural areas (Griswold
105 et al., 1999; Kuhlman & Burrows, 2017; Meiners, 2016; Messinger, 2006). The expense and
106 effort required to follow a systematic inventory protocol is higher, but the assumption is that
107 inventory records have fewer biases, resulting in superior estimates of bee activity, floral
108 reliability (Wright et al., 2015), and baseline community patterns against which evaluations of

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109 future change can be measured (Meiners et al., 2019). Despite these core data type differences,
110 however, both opportunistic and inventory data have been used interchangeably in studies of
111 native bee phenology without an assessment of their relative suitability for the task. Drawing
112 mistaken conclusions from data that is flawed, incomplete, or was collected for another purpose
113 may result in mismanagement of natural resources, misdirected sampling efforts, and missed
114 opportunities to harness the full power of both opportunistic and inventory datasets.

115 We use data from six systematic bee inventories and approximately a quarter million
116 opportunistic museum records collected over twenty years to compare estimates per data type of
117 three phenology metrics for forty-five abundant native bee species. To assess the possibility of
118 extrapolating conclusions to additional species, we also examine trends related to five functional
119 life history traits, which recent research has shown to be predictive of native bee rates of decline
120 (Bartomeus et al., 2013), vulnerability to insecticides (Brittain & Potts, 2011), response to
121 anthropogenic disturbance (Williams et al., 2010), and pollinating behavior (Pisanty &
122 Mandelik, 2015). With this approach, we seek to answer two central questions: 1) can
123 opportunistic data produce parameter estimates of native bee species phenology that are
124 statistically equivalent to more expensive inventory data?, and 2) if phenology metrics differ
125 between data types, are there patterns associated with functional traits that could be useful
126 indicators of which species are more susceptible to erroneous phenology estimates? In answering
127 these questions, we seek to improve the utility of natural history collection data, the
128 determination of native bee trends and conservation practices, and the broad reliability of
129 phenology results.

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METHODS

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Data, species, and trait selection

133 Opportunistic and inventory data were sourced from the USDA-ARS National Pollinating

134 Insects Collection (NPIC) (USDA-ARS, 2016). We defined opportunistic data as specimen

135 records which were collected irrespective of each other or standard protocols, instead typically

136 irregularly targeting regions, specific floral resources, or bee taxa of special interest. We defined

137 inventory data as records arising from standardized efforts to systematically document bee

138 species richness in specific geographic areas across the local season(s) of bee activity. Six

139 studies with collections housed at the NPIC fit this definition of inventory data. These were

140 systematic inventory studies located at: Carlsbad Caverns National Park (*Griswold & Ikerd*

141 *unpublished data*); Clark County, Nevada (Griswold et al., 1999); Grand Staircase-Escalante

142 National Monument (Carril et al., 2018; Messinger, 2006); Pinnacles National Park (Meiners,

143 2016; Meiners et al., 2019); and Yosemite National Park (*Griswold & Ikerd unpublished data*).

144 All six inventory studies were conducted between 1996 and 2012 following protocols similar to

145 that outlined in LeBuhn et al. (2003), and shared at dx.doi.org/10.17504/protocols.io.wfhfbj6

146 from Meiners et al. (2019).

147 We restricted the temporal and spatial range of our study within reason, while keeping

148 our dataset large to limit the phenological variability introduced solely by spatiotemporal factors.

149 For both inventory and opportunistic data, we only used specimen records that met all of the

150 following criteria: 1) identified to a valid species, 2) collected between 1990 and 2015 in the

151 USA or Canada, and 3) contained complete and reliable georeferencing. Data cleaning to meet

152 these criteria was conducted in R (R Core Team, 2015). To ensure sufficient sample sizes for

153 species-level comparisons between data types, we excluded any species with fewer than 180

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154 occurrences for each data type, retaining only the fifty most abundant species shared between the
155 two data sets.

156 Once we finalized our list of fifty species, we conducted literature searches and expert
157 surveys to assign them into categories of five pre-selected life history traits that literature
158 searches and expert consensus suggested have relevance to phenological trends: *body size*,
159 *sociality*, *floral specialization*, *nest location*, and *voltinism* (Araújo et al., 2004; Heithaus, 1979;
160 Osorio-Canadas et al., 2016; Rodriguez-Girones & Bosch, 2012; Williams et al., 2010). We used
161 a Keyence digital microscope to measure *body size* as the average inter-tegular distance (between
162 wing bases) for five female specimens of each species, following the method specified by Cane
163 (1987). Based on species-specific literature searches, we categorized the *sociality* of a bee
164 species as either 1) solitary, or 2) social, which included bee species that can be described as
165 eusocial, communal, and primitively social, or 3) unknown (our list of fifty did not include any
166 cleptoparasitic species). We noted whether a species was considered a *floral specialist* in the
167 literature by a simple 1) yes, 2) no, or 3) unknown. We noted *nest location* as a binary trait, with
168 species categorized as nesting primarily 1) above ground or 2) below ground. Due to a lack of
169 published information, we classified *voltinism* based on a survey of expert opinion into the
170 following classes: 1) univoltine (one generation), 2) multivoltine (>1 generation), 3) social (since
171 these species replace members throughout the season but not in the same way as multiple
172 generations of solitary bees in a single season), and 4) unknown.

173

174 *Final Dataset Specimen, Species, and Trait Composition*

175 The final dataset contained 104,101 bee occurrence records, of which 71,152 were from
176 inventory collections and 32,949 were opportunistically collected. From the original fifty

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177 species, we removed five from the dataset because they are either: 1) commonly managed (*Apis*
178 *mellifera*); 2) have an unusual, socially-parasitic life history (*Bombus insularis*); or 3) could not
179 reliably be distinguished in females (*Agapostemon angelicus*, *Agapostemon texanus*,
180 *Agapostemon angelicus/texanus*), resulting in a final set of 45 species (Table 1).

181 The final 45 species selected for phenology metric analyses showed a relatively even
182 spread of traits. Some trait category assignments for certain species were impossible to assign
183 based on current knowledge and remain labeled as “unknown” in our trait dataset (Table 1). All
184 assigned trait categories were represented by at least 12 out of 45 total species.

185

186 *Calculation of phenology metrics*

187 We identified three measurable metrics of bee phenology that would be useful and
188 reliable for quantitatively estimating changes in patterns of bee species activity over time: 1)
189 flight duration, or the number of days in a year the bee species was active; 2) clusters, or the
190 number of distinct peaks in abundance in a year; and 3) the date of a bee species’ highest annual
191 peak in abundance (Fig. 1). We defined flight duration as the middle 90% of occurrences,
192 removing the upper and lower 5% of values to eliminate outliers that may represent unusual
193 activity in any given year. We determined the number of clusters in a set of occurrences, with a
194 maximum possible of three clusters, using a gap statistic. We then used kmeans clustering to find
195 the location along the day-of-year axis of all clusters. The cluster with the highest value on the
196 density plot was chosen as the date for the greatest abundance of occurrences. We calculated
197 these three metrics twice for each species, once each for all occurrences from the inventory data
198 type and once for all the opportunistic data type occurrences. In order to have a single number
199 for each metric that showed how different they were for the two data types, we calculated a test

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200 statistic for each of the three metrics. We chose the test statistic as the absolute difference
201 between the opportunistic and inventory metric, so that each species had three test statistics, one
202 each for flight duration, number of clusters, and location of greatest abundance.

203 In order to determine if these test statistics indicated that there was a substantial
204 difference between phenology patterns for data types, we compared these observed test statistics
205 to a set of simulated test statistics that came from shuffling the data. We randomly shuffled the
206 data type labels for all occurrences of each species, retaining the same relative number of
207 opportunistic and inventory labels for each species. We then recalculated the three phenology
208 metrics for the two data types and the test statistic, so that each species had three simulated test
209 statistics. Finally, we repeated this process 1000 times, so that each species had a distribution of
210 simulated test statistics.

211 To determine if the observed test statistics were statistically significantly different than
212 the distribution of simulated test statistics, which would indicate that data type mattered for that
213 phenological pattern, we calculated a p-value based on the number of simulated test statistics that
214 were greater than the observed one. We used an alpha cut-off of 0.05, and each species had one
215 p-value for each of the three phenology metrics. Given the multitude of pairwise comparisons,
216 we also include a more stringent alpha cut-off of 0.001, which is the lowest value that can be
217 achieved given the number of permutations.

218

219 *Modeling influence of functional traits*

220 After assigning a category value to each bee species for each of the five selected
221 functional traits, as described above, we used generalized linear models to assess the influence of
222 functional traits on significant differences between data types from permutation tests for each of

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223 the three identified bee phenology metrics (Fig. 1). This evaluation of the influence of functional
224 traits on data type significance was only conducted for species with complete trait category
225 information (Table 1). Species with “unknowns” were removed, and voltinism levels “social”
226 and “multi” were ultimately combined so that all categorical traits were binary variables. All data
227 manipulation, plotting, and statistical tests were conducted in the R statistical package (R Core
228 Team, 2015).

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RESULTS

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Phenology Metrics by Data Type

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With three phenology metrics for each of 45 species, we compared a total of 135 pairs of phenology variable calculations based on data type. We found significantly different values depending on which data type was used (inventory or opportunistic) in 87 out of 135 cases, which represents 64% of the possible total, much higher than the 5% expected under a null hypothesis and assuming a 5% alpha. The date of highest peak in abundance was the metric with the greatest number of value discrepancies due to data type: the date of the seasonal peak was significantly different depending on which dataset was used for 40 out of 45 species (89%, Fig. 3). Flight duration, or the number of days a species was active, differed based on data type for 34 out of 45 species (76%, Fig. 3). And the number of clusters, or distinct peaks in abundance, was different between data types for 15 out of 45 species (33%, Fig. 3). It should be noted, however, that the number of clusters was the least reliable of the three phenology metrics, due to limitations of the gap statistic used to calculate it, sensitivity to variable collection efforts over time in the opportunistic data, and the narrow range of options between just one and three for

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245 number of clusters detected. We considered other options for calculating number of clusters but
246 found the gap statistic to be the most defensible, if still flawed.

247 All 45 species had at least one metric that was significantly different depending on data
248 type (Table 2). Ten out of 45 species had significantly different results for all three phenology
249 metrics depending on the type of data used to evaluate them. Occurrence curves for each species
250 and data type illustrate the comparison between inventory and opportunistic data types of the
251 three phenology metrics (Fig. 4). The species *Ceratina nanula*, for example, differed in flight
252 duration between data types, seen as the width of the x-axis between dotted lines, but had
253 statistically similar results for the date of the highest peak and the number of clusters in
254 abundance (Fig. 4, top left). *Lasioglossum sisymbrii* had the same number of clusters in both
255 inventory and opportunistic datasets, but different values for both flight duration and date of the
256 highest peak, shown by the solid vertical line on the plot (Fig. 4, top right). Two species of
257 *Osmia* had different results for the number of clusters reported by the gap statistic (Fig. 4, middle
258 row), as well as either a different flight duration or different date of highest peak depending on
259 data type. As mentioned above, ten species differed in all three metrics between data types, as
260 illustrated by *Lasioglossum hudsoniellum* and *Anthophora urbana* (Fig. 4, bottom row). Because
261 significance of the difference between data type was based on 1000 different permutations of the
262 occurrence records, not all figures showing species-level results match the reported conclusions.

263

264 *Relationship of Functional Traits to Data Type Significance*

265 For the group of forty species without any unknown trait values, body size was a
266 significant ($p = 0.047$) predictor of whether flight duration would differ between data types, with
267 larger bees being more likely to have different results for seasonal activity length depending on

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268 which dataset was used (Table 3). Generalized linear model results also found body size to be a
269 marginally significant ($p = 0.055$) predictor of whether the number of clusters would differ
270 between data types, with larger bees more likely to return different number of clusters depending
271 on whether opportunistic or inventory records were used to calculate them. Floral specialization
272 was also a marginally significant ($p = 0.051$) predictor of difference between data type in flight
273 duration, with species designated as floral specialists more likely to return different values for
274 number of days they were active over a season depending on data type (Table 3). The likelihood
275 for date of the highest peak to differ between opportunistic and inventory data was not
276 significantly related to any of the five functional traits.

277

278

DISCUSSION

279 We found widespread and significant differences in estimates of phenology metrics
280 depending on the type of data used to calculate them. Out of 45 tested native bee species
281 spanning a range of life history traits, one hundred percent had a significantly different value for
282 at least one key phenology metric depending only on the type of data used to calculate it. This
283 result should raise concerns about the influence of data source on our understanding of patterns
284 and changes in phenology, not only for pollinators but potentially for other taxa studied using
285 compiled museum records. With the high natural variability of many small organisms already
286 obscuring measurable signals of behavior, adding noise to phenology models by using messy or
287 inappropriate data may confound phenological estimations to the point that they become
288 uninformative. If biases are consistent and directional, phenology studies that do not take into
289 account the influence of data may even report patterns opposite the truth.

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290 Our study reveals an urgent need to ensure that the data used for evaluating changes in
291 phenology, not only of native bees but likely of many other organisms as well, are of sufficient
292 quality to produce reliable results. Comparing metrics over time that are not compatible – for
293 example, checking for changes in the date of peak species activity by comparing recent inventory
294 records to older opportunistic records from historical study sites – may add noise instead of
295 clarity to collective efforts to detect real changes in phenology, or may create false impressions
296 of a pattern. Critical interaction mismatches between any organisms reliant on each other could
297 be obscured. Such misleading results may also hinder scientific progress and conservation
298 efforts, erode public trust in science, and dilute the gravity of warnings about pollinator declines
299 and other environmental changes.

300 The implications of our study may be relevant in many systems but are certainly of
301 consequence as applied to native bees. Since plant reproductive success depends on the timing of
302 local pollinator activity, recently found to be shifting with climate change (Aldridge et al., 2011;
303 Burkle et al., 2013; Robbirt et al., 2014; Schenk et al., 2018), phenology research on biodiverse
304 networks of coexisting native bee species and their hosts is highly complex but vitally important.
305 Even with the best data, results from one study may provide limited insight for patterns in
306 another area, species, or time. Primack et al. (2009), for example, conducted phenology studies
307 for twelve taxa using long-term, spatially-expansive, and systematically-collected data, and still
308 found results to be highly variable and hard to interpret due to species-level variability. With the
309 explosion of technology, museum data-basing efforts, and the open science movement, the
310 availability of data to ask important questions about bee species phenology is entering a new
311 frontier. It is, therefore, necessary to also update our understanding of data and methodological
312 limitations before extrapolating findings across regions or species, potentially muddying

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313 conclusions about the high-profile issues of bee decline and worldwide loss of pollination
314 services (Biesmeijer et al., 2006; Burkle et al., 2013; Goulson et al., 2015).

315 Despite the overall increased availability of data, records are still very limited for many
316 taxa, and that is where common parameters like functional traits can be useful. Until further
317 technological advances in bee species identification and specimen processing make it feasible to
318 obtain sufficient data to evaluate phenological trends for a majority of cryptic or rare native bee
319 species, efforts to identify unifying variables that correspond to data type reliability or
320 phenological variability will be relevant. Our result that the importance of having high-quality
321 data increases with increasing body size and increasing floral specialization for native bees, for
322 instance, can help guide studies of smaller groups of species when deciding how to allocate data
323 collection resources. Larger bees can emerge earlier in the season than smaller-bodied bees, due
324 to their greater ability to generate and maintain elevated body temperatures under cold conditions
325 (Osorio-Canadas et al., 2016). Being active earlier in spring may make spring-flying larger bees
326 more variable in the interannual timing of their activity as the date of snowmelt and first bloom
327 also vary. Likewise, being tied to a particular floral group as a foraging specialist bee species
328 may require greater flexibility in emergence time and a stronger reliance on specific
329 environmental cues to time emergence that may make specialist phenology more difficult to
330 evaluate. Opportunistic data yielded inconsistent values for flight duration for larger-bodied and
331 specialist bees in our study. Knowing, as a result, that inventory data is more appropriate for
332 these species allows for cleaner interpretation of their behavior. Likewise, it is useful to know
333 from this result that opportunistic data may be more appropriate for estimating phenology
334 metrics for smaller species and floral generalists, at least where many records are available. In

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335 these ways, our functional trait model illustrates how exploring limitations of data types can have
336 both biological and statistical value.

337 Our study does not seek to undermine the great importance or value of natural history or
338 museum collections, but rather to explore and illuminate best practices for data use in the study
339 of phenology. The appropriate source of data may depend entirely on the nature or scale of the
340 question being asked, or the level of specificity desired. Systematic inventories of native bee
341 fauna provide ideal data for understanding bee ecology, but are hugely expensive and time-
342 consuming, and should not take the place of opportunistic data for every research endeavor. In
343 some cases, such as when gauging phenological changes across decades, it may not be possible
344 to rely on inventory data, but the limitations of the data available must still be understood,
345 because the best available data may fail to provide the correct answers, regardless of the methods
346 employed. There is much to be gained from appropriate use of opportunistic data to estimate
347 metrics of species phenology, and much to be lost from ignoring it. The influence of data type on
348 phenology estimation is likely important for many other taxa with spotty records and high
349 inherent variability. Incorporating measures of data bias and associated relevance of functional
350 traits to guide interpretation of results may benefit the study of phenology and ecology in a
351 myriad of ways.

352 While we improve our use of data, we must also continue expanding our knowledge base.
353 Natural history collections across the world are struggling to attain the financial, institutional,
354 and cultural support required to develop, curate, document, and digitize museum collections.
355 Improving the flow of high-quality data records from diverse areas and time periods is an
356 important step in alleviating data bias and improving our understanding of phenology.
357 Expanding and further standardizing inventory efforts will also be important. The majority of

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358 broad-scale bee phenology studies have taken place in montane or agricultural landscapes, or on
359 social, cavity-nesting bees, leaving other environments and guilds poorly understood (Bosch &
360 Kemp, 2002; CaraDonna et al., 2014; Hanley et al., 2015; Klein et al., 2007; Ogilvie &
361 Thomson, 2015; Winfree et al., 2011). Since we know that the extrapolation of conclusions about
362 phenology patterns across space, species, and data type is flawed (Davis et al., 2010; Primack et
363 al., 2009), we should not continue to use studies from limited habitats and species to represent
364 trends across much broader areas or groups. In conclusion, more data is always better, inventory
365 data is often (but not always) better, and functional traits can help guide assessments of data
366 needs. Only when we acknowledge the limitations of the data in hand can we begin to fill in the
367 gaps.

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LITERATURE CITED

382

Aldridge, G., Inouye, D. W., Forrest, J. R. K., Barr, W. A., & Miller-Rushing, A. J. (2011).

383

Emergence of a mid-season period of low floral resources in a montane meadow

384

ecosystem associated with climate change. *Journal of Ecology*, 99(4), 905–913.

385

<https://doi.org/10.1111/j.1365-2745.2011.01826.x>

386

Araújo, E. D., Costa, M., Chaud-Netto, J., & Fowler, H. G. (2004). Body size and flight distance in

387

stingless bees (Hymenoptera: Meliponini): inference of flight range and possible

388

ecological implications. *Brazilian Journal of Biology*, 64(3B), 563–568.

389

<https://doi.org/10.1590/S1519-69842004000400003>

390

Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D. L., Hedtke, S. M., & Winfree, R.

391

(2013). Historical changes in northeastern US bee pollinators related to shared

392

ecological traits. *Proceedings of the National Academy of Sciences*, 110(12), 4656–4660.

393

<https://doi.org/10.1073/pnas.1218503110>

394

Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S., & Winfree, R.

395

(2011). Climate-associated phenological advances in bee pollinators and bee-pollinated

396

plants. *Proceedings of the National Academy of Sciences*, 108(51), 20645–20649.

397

<https://doi.org/10.1073/pnas.1115559108>

398

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemueller, R., Edwards, M., Peeters, T.,

399

Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E. (2006).

400

Parallel declines in pollinators and insect-pollinated plants in Britain and the

401

Netherlands. *Science*, 313(5785), 351–354. <https://doi.org/10.1126/science.1127863>

Submitted Article

- 402 Bosch, J., & Kemp, W. P. (2002). Developing and establishing bee species as crop pollinators:
403 The example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of*
404 *Entomological Research*, 92(1), 3–16. <https://doi.org/10.1079/BER2001139>
- 405 Brittain, C., & Potts, S. G. (2011). The potential impacts of insecticides on the life-history traits
406 of bees and the consequences for pollination. *Basic and Applied Ecology*, 12(4), 321–
407 331. <https://doi.org/10.1016/j.baae.2010.12.004>
- 408 Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-Pollinator Interactions over 120 Years:
409 Loss of Species, Co-Occurrence, and Function. *Science*, 339(6127), 1611–1615.
410 <https://doi.org/10.1126/science.1232728>
- 411 Cane, J. H. (1987). Estimation of Bee Size Using Intertegular Span (Apoidea). *Journal of the*
412 *Kansas Entomological Society*, 60(1), 145–147. <https://doi.org/10.2307/25084877>
- 413 CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a
414 subalpine plant community. *Proceedings of the National Academy of Sciences*, 111(13),
415 4916–4921. <https://doi.org/10.1073/pnas.1323073111>
- 416 Carril, O. M., Griswold, T., Haefner, J., & Wilson, J. S. (2018). Wild bees of Grand Staircase-
417 Escalante National Monument: Richness, abundance, and spatio-temporal beta-
418 diversity. *PeerJ*, 6, e5867. <https://doi.org/10.7717/peerj.5867>
- 419 Danforth, B. (1999). Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*.
420 *PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES*, 266(1432), 1985–1994.
421 <https://doi.org/10.1098/rspb.1999.0876>
- 422 Davis, C. C., Willis, C. G., Primack, R. B., & Miller-Rushing, A. J. (2010). The importance of
423 phylogeny to the study of phenological response to global climate change. *Philosophical*

Submitted Article

- 424 *Transactions of the Royal Society of London B: Biological Sciences*, 365(1555), 3201–
425 3213. <https://doi.org/10.1098/rstb.2010.0130>
- 426 de Keyzer, C. W., Rafferty, N. E., Inouye, D. W., & Thomson, J. D. (2017). Confounding effects of
427 spatial variation on shifts in phenology. *Global Change Biology*, 23(5), 1783–1791.
428 <https://doi.org/10.1111/gcb.13472>
- 429 Fabina, N. S., Abbott, K. C., & Gilman, R. T. (2010). Sensitivity of plant-pollinator-herbivore
430 communities to changes in phenology. *ECOLOGICAL MODELLING*, 221(3), 453–458.
431 <https://doi.org/10.1016/j.ecolmodel.2009.10.020>
- 432 Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of
433 phenology in ecology and evolution. *Philosophical Transactions of the Royal Society of*
434 *London B: Biological Sciences*, 365(1555), 3101–3112.
435 <https://doi.org/10.1098/rstb.2010.0145>
- 436 Forrest, J. R. K. (2015). Plant–pollinator interactions and phenological change: What can we
437 learn about climate impacts from experiments and observations? *Oikos*, 124(1), 4–13.
438 <https://doi.org/10.1111/oik.01386>
- 439 Forrest, J. R. K., & Thomson, J. D. (2011). An examination of synchrony between insect
440 emergence and flowering in Rocky Mountain meadows. *Ecological Monographs*, 81(3),
441 469–491. <https://doi.org/10.1890/10-1885.1>
- 442 Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined
443 stress from parasites, pesticides, and lack of flowers. *Science*, 347(6229), 1255957.
444 <https://doi.org/10.1126/science.1255957>

Submitted Article

- 445 Griswold, T. L., Andres, M., Andrus, R., Garvin, G., Keen, K., Kervin, L., Messinger, O., Messinger,
446 S., Miller, W., Receveur, K., Shultz, C., & Tepedino, V. J. (1999). A survey of the rare bees
447 of Clark County, Nevada. *Final Report, The Nature Conservancy, Las Vegas, NV.*
448 http://works.bepress.com/terry_griswold/63
- 449 Hanley, N., Breeze, T. D., Ellis, C., & Goulson, D. (2015). Measuring the economic value of
450 pollination services: Principles, evidence and knowledge gaps. *Ecosystem Services, 14*,
451 124–132. <https://doi.org/10.1016/j.ecoser.2014.09.013>
- 452 Heithaus, E. R. (1979). Community Structure of Neotropical Flower Visiting Bees and Wasps:
453 Diversity and Phenology. *Ecology, 60*(1), 190–202. <https://doi.org/10.2307/1936480>
- 454 Helm, B. R., Rinehart, J. P., Yocum, G. D., Greenlee, K. J., & Bowsher, J. H. (2017).
455 Metamorphosis is induced by food absence rather than a critical weight in the solitary
456 bee, *Osmia lignaria*. *Proceedings of the National Academy of Sciences*, 201703008.
457 <https://doi.org/10.1073/pnas.1703008114>
- 458 Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral
459 abundance of montane wildflowers. *Ecology, 89*(2), 353–362.
460 <https://doi.org/10.1890/06-2128.1>
- 461 Isaac, N. J. B., & Pocock, M. J. O. (2015). Bias and information in biological records. *Biological*
462 *Journal of the Linnean Society, 115*(3), 522–531. <https://doi.org/10.1111/bij.12532>
- 463 Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., &
464 Tschardtke, T. (2007). Importance of pollinators in changing landscapes for world crops.
465 *Proceedings of the Royal Society of London B: Biological Sciences, 274*(1608), 303–313.
466 <https://doi.org/10.1098/rspb.2006.3721>

Submitted Article

- 467 Kuhlman, M., & Burrows, S. (2017). Checklist of bees (Apoidea) from a private conservation
468 property in west-central Montana. *Biodiversity Data Journal*, 5, e11506.
469 <https://doi.org/10.3897/BDJ.5.e11506>
- 470 LeBuhn, G., Griswold, T., Minckley, R., Droege, S., Roulston, T., Cane, J., Parker, F., Buchmann,
471 S., Tepedino, V., Williams, N., & others. (2003). *A standardized method for monitoring*
472 *bee populations—the bee inventory (BI) plot.*
473 [http://cybercemetery.unt.edu/archive/nbii/20120111121317/http://online.sfsu.edu/~b](http://cybercemetery.unt.edu/archive/nbii/20120111121317/http://online.sfsu.edu/~beeplot/pdfs/Bee%20Plot%202003.pdf)
474 [eeplot/pdfs/Bee%20Plot%202003.pdf](http://cybercemetery.unt.edu/archive/nbii/20120111121317/http://online.sfsu.edu/~beeplot/pdfs/Bee%20Plot%202003.pdf)
- 475 Lister, A. M., & Climate Change Research Group. (2011). Natural history collections as sources
476 of long-term datasets. *Trends in Ecology & Evolution*, 26(4), 153–154.
477 <https://doi.org/10.1016/j.tree.2010.12.009>
- 478 Meiners, J. M. (2016). *Biodiversity, Community Dynamics, and Novel Foraging Behaviors of a*
479 *Rich Native Bee Fauna across Habitats at Pinnacles National Park, California* [Masters of
480 Science]. Utah State University.
- 481 Meiners, J. M., Griswold, T. L., & Carril, O. M. (2019). Decades of native bee biodiversity surveys
482 at Pinnacles National Park highlight the importance of monitoring natural areas over
483 time. *PLOS ONE*, 14(1), e0207566. <https://doi.org/10.1371/journal.pone.0207566>
- 484 Meiners, J. M., Griswold, T. L., Harris, D. J., & Ernest, S. K. M. (2017). Bees without Flowers:
485 Before Peak Bloom, Diverse Native Bees Find Insect-Produced Honeydew Sugars. *The*
486 *American Naturalist*, 190(2), 281–291. <https://doi.org/10.1086/692437>

Submitted Article

- 487 Messinger, O. (2006). *A survey of the bees of Grand Staircase-Escalante National Monument,*
488 *Southern Utah: Incidence, Abundance, and Community dynamics* [Masters of Science].
489 Utah State University.
- 490 Michener, C. D. (2007). *The Bees of the World*. Johns Hopkins University Press.
- 491 Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological
492 mismatches on demography. *Philosophical Transactions of the Royal Society of London*
493 *B: Biological Sciences*, 365(1555), 3177–3186. <https://doi.org/10.1098/rstb.2010.0148>
- 494 Nakazawa, T., & Doi, H. (2012). A perspective on match/mismatch of phenology in community
495 contexts. *OIKOS*, 121(4), 489–495. <https://doi.org/10.1111/j.1600-0706.2011.20171.x>
- 496 Ogilvie, J. E., & Forrest, J. R. (2017). Interactions between bee foraging and floral resource
497 phenology shape bee populations and communities. *Current Opinion in Insect Science*,
498 21, 75–82. <https://doi.org/10.1016/j.cois.2017.05.015>
- 499 Ogilvie, J. E., & Thomson, J. D. (2015). Male bumble bees are important pollinators of a late-
500 blooming plant. *Arthropod-Plant Interactions*, 9(2), 205–213.
501 <https://doi.org/10.1007/s11829-015-9368-x>
- 502 Osorio-Canadas, S., Arnan, X., Rodrigo, A., Torné-Noguera, A., Molowny, R., & Bosch, J. (2016).
503 Body size phenology in a regional bee fauna: A temporal extension of Bergmann's rule.
504 *Ecology Letters*, 19(12), 1395–1402. <https://doi.org/10.1111/ele.12687>
- 505 Pisanty, G., & Mandelik, Y. (2015). Profiling crop pollinators: Life history traits predict habitat
506 use and crop visitation by Mediterranean wild bees. *Ecological Applications*, 25(3), 742–
507 752. <https://doi.org/10.1890/14-0910.1>

Submitted Article

- 508 Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks,
509 L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding
510 pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229.
511 <https://doi.org/10.1038/nature20588>
- 512 Primack, R. B., Ibáñez, I., Higuchi, H., Lee, S. D., Miller-Rushing, A. J., Wilson, A. M., & Silander, J.
513 A. (2009). Spatial and interspecific variability in phenological responses to warming
514 temperatures. *Biological Conservation*, *142*(11), 2569–2577.
515 <https://doi.org/10.1016/j.biocon.2009.06.003>
- 516 R Core Team. (2015). *R: A language and environment for statistical computing*. [https://www.R-](https://www.R-project.org)
517 [project.org](https://www.R-project.org) (Version Version 3.2.3) [Computer software].
- 518 Rafferty, N. E., & Ives, A. R. (2011). Effects of experimental shifts in flowering phenology on
519 plant-pollinator interactions. *Ecology Letters*, *14*(1), 69–74.
520 <https://doi.org/10.1111/j.1461-0248.2010.01557.x>
- 521 Robbirt, K. M., Roberts, D. L., Hutchings, M. J., & Davy, A. J. (2014). Potential Disruption of
522 Pollination in a Sexually Deceptive Orchid by Climatic Change. *Current Biology*, *24*(23),
523 2845–2849. <https://doi.org/10.1016/j.cub.2014.10.033>
- 524 Rodriguez-Girones, M. A., & Bosch, J. (2012). Effects of body size and sociality on the anti-
525 predator behaviour of foraging bees. *Oikos*, *121*(9), 1473–1482.
526 <https://doi.org/10.1111/j.1600-0706.2011.19473.x>
- 527 Schenk, M., Krauss, J., & Holzschuh, A. (2018). Desynchronizations in bee-plant interactions
528 cause severe fitness losses in solitary bees. *The Journal of Animal Ecology*, *87*(1), 139–
529 149. <https://doi.org/10.1111/1365-2656.12694>

Submitted Article

- 530 Strien, A. J. van, Plantenga, W. F., Soldaat, L. L., Swaay, C. A. M. van, & WallisDeVries, M. F.
531 (2008). Bias in phenology assessments based on first appearance data of butterflies.
532 *Oecologia*, 156(1), 227–235. <https://doi.org/10.1007/s00442-008-0959-4>
- 533 USDA-ARS. (2016). *U.S. National Pollinating Insects Collection: USDA ARS*.
534 [https://www.ars.usda.gov/pacific-west-area/logan-ut/pollinating-insect-biology-](https://www.ars.usda.gov/pacific-west-area/logan-ut/pollinating-insect-biology-management-systematics-research/docs/us-national-pollinating-insects-collection/)
535 [management-systematics-research/docs/us-national-pollinating-insects-collection/](https://www.ars.usda.gov/pacific-west-area/logan-ut/pollinating-insect-biology-management-systematics-research/docs/us-national-pollinating-insects-collection/)
- 536 Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., & Potts, S. G. (2010).
537 Ecological and life-history traits predict bee species responses to environmental
538 disturbances. *Biological Conservation*, 143(10), 2280–2291.
539 <https://doi.org/10.1016/j.biocon.2010.03.024>
- 540 Winfree, R., Bartomeus, I., & Cariveau, D. P. (2011). Native Pollinators in Anthropogenic
541 Habitats. *Annual Review of Ecology, Evolution, and Systematics*, 42(1), 1–22.
542 <https://doi.org/10.1146/annurev-ecolsys-102710-145042>
- 543 Wright, K. W., Vanderbilt, K. L., Inouye, D. W., Bertelsen, C. D., & Crimmins, T. M. (2015).
544 Turnover and reliability of flower communities in extreme environments: Insights from
545 long-term phenology data sets. *Journal of Arid Environments*, 115, 27–34.
546 <https://doi.org/10.1016/j.jaridenv.2014.12.010>
- 547

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TABLES

549 Table 1. Species (N=45) selected for analysis based on number of records (N >180 for each data
550 type) and spread of representative traits (N = 5). Sources of trait information are included in SI.

ID	Bee Genus and species	Sociality category	Body Size (mm)	Floral specialist	Voltinism category	Nesting category
1	<i>Agapostemon melliventris</i>	unknown	1.61	N	unknown	below
2	<i>Andrena prunorum</i>	solitary	2.30	N	multi	below
3	<i>Anthidium utahense</i>	solitary	2.14	N	uni	below
4	<i>Anthophora petrophila</i>	solitary	2.03	N	multi	below
5	<i>Anthophora urbana</i>	solitary	2.88	N	multi	below
6	<i>Ashmeadiella gillettei</i>	solitary	1.19	N	multi	above
7	<i>Bombus bifarius</i>	social	4.24	N	social	below
8	<i>Bombus huntii</i>	social	4.79	N	social	below
9	<i>Bombus melanopygus</i>	social	3.60	N	social	below
10	<i>Bombus sylvicola</i>	social	3.39	N	social	below
11	<i>Bombus vosnesenskii</i>	social	4.22	N	social	below
12	<i>Calliopsis fracta</i>	solitary	1.40	Y	uni	below
13	<i>Calliopsis puellae</i>	solitary	1.81	Y	uni	below
14	<i>Calliopsis subalpina</i>	solitary	1.78	Y	uni	below
15	<i>Ceratina nanula</i>	unknown	1.16	N	uni	above
16	<i>Colletes louisae</i>	solitary	2.20	N	multi	below
17	<i>Dianthidium pudicum</i>	solitary	2.06	Y	uni	above
18	<i>Dianthidium ulkei</i>	solitary	2.17	Y	uni	above
19	<i>Halictus farinosus</i>	social	2.33	N	social	below
20	<i>Halictus ligatus</i>	social	1.73	N	social	below
21	<i>Halictus rubicundus</i>	social	2.20	N	social	below
22	<i>Halictus tripartitus</i>	social	1.21	N	social	below
23	<i>Hoplitis albifrons</i>	solitary	2.38	N	uni	above
24	<i>Hoplitis fulgida</i>	solitary	1.81	N	uni	above
25	<i>Lasioglossum hudsoniellum</i>	social	0.84	N	social	below
26	<i>Lasioglossum hyalinum</i>	social	1.15	N	social	below
27	<i>Lasioglossum incompletum</i>	social	0.90	N	social	below
28	<i>Lasioglossum sisymbrii</i>	solitary	1.84	N	multi	below
29	<i>Melissodes paroselae</i>	solitary	2.40	N	multi	below
30	<i>Melissodes tristis</i>	solitary	2.62	N	multi	below
31	<i>Osmia atrocyanea</i>	solitary	2.60	unknown	uni	above
32	<i>Osmia brevis</i>	solitary	2.28	Y	uni	below
33	<i>Osmia coloradensis</i>	solitary	2.23	Y	uni	above
34	<i>Osmia cyanella</i>	solitary	2.24	unknown	uni	above
35	<i>Osmia lignaria</i>	solitary	2.72	N	uni	above
36	<i>Osmia montana</i>	solitary	2.60	Y	uni	above
37	<i>Osmia nemoris</i>	solitary	2.08	N	uni	above
38	<i>Osmia paradisiaca</i>	solitary	2.33	unknown	uni	below
39	<i>Osmia trevoris</i>	solitary	1.98	N	uni	below
40	<i>Perdita albonotata</i>	solitary	1.14	Y	multi	below
41	<i>Perdita aridella</i>	solitary	0.85	Y	unknown	below
42	<i>Perdita callicerata</i>	solitary	1.02	Y	multi	below
43	<i>Perdita calloleuca</i>	solitary	0.76	Y	uni	below
44	<i>Perdita larreae</i>	solitary	0.67	Y	multi	below
45	<i>Perdita punctosignata</i>	solitary	0.84	Y	uni	below

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551 Table 2. Incidences where each metric returned significantly different results between two data
 552 types for each of 45 species (* indicates $p < 0.05$ and ** indicates $p < 0.001$).

ID	Bee Genus and species	Number of clusters	Flight duration	Date highest peak	# metrics differing
1	<i>Agapostemon melliventris</i>		**	*	2
2	<i>Andrena prunorum</i>		**	**	2 555
3	<i>Anthidium utahense</i>		**	**	1 556
4	<i>Anthophora petrophila</i>			*	1
5	<i>Anthophora urbana</i>	**	**	**	3 557
6	<i>Ashmeadiella gillettei</i>		**	**	2 558
7	<i>Bombus bifarius</i>		**	**	2
8	<i>Bombus huntii</i>			*	1
9	<i>Bombus melanopygus</i>			**	1
10	<i>Bombus sylvicola</i>	**		**	2
11	<i>Bombus vosnesenskii</i>		**	**	2
12	<i>Calliopsis fracta</i>	**	**		2
13	<i>Calliopsis puellae</i>			*	1
14	<i>Calliopsis subalpina</i>		**	*	2
15	<i>Ceratina nanula</i>		**		1
16	<i>Colletes louisae</i>		**	**	2
17	<i>Dianthidium pudicum</i>	*	**	*	3
18	<i>Dianthidium ulkei</i>		**	**	2
19	<i>Halictus farinosus</i>		**	**	2
20	<i>Halictus ligatus</i>		**	**	2
21	<i>Halictus rubicundus</i>			*	1
22	<i>Halictus tripartitus</i>	**	**	**	3
23	<i>Hoplitis albifrons</i>		**	**	2
24	<i>Hoplitis fulgida</i>		*	**	2
25	<i>Lasioglossum hudsoniellum</i>	**	**	**	3
26	<i>Lasioglossum hyalinum</i>	*	**	**	3
27	<i>Lasioglossum incompletum</i>	**	*	**	3
28	<i>Lasioglossum sisymbrii</i>		**	*	2
29	<i>Melissodes paroselae</i>		**	**	2
30	<i>Melissodes tristis</i>		*		1
31	<i>Osmia atrocyanea</i>	**	**	**	3
32	<i>Osmia brevis</i>			**	1
33	<i>Osmia coloradensis</i>		**	**	2
34	<i>Osmia cyanella</i>			**	1
35	<i>Osmia lignaria</i>		*	**	2
36	<i>Osmia montana</i>			**	1
37	<i>Osmia nemoris</i>		**	**	2
38	<i>Osmia paradisica</i>	**		**	2
39	<i>Osmia trevoris</i>	*	**		2
40	<i>Perdita albonotata</i>	*	*	*	3
41	<i>Perdita aridella</i>	**	**	**	3
42	<i>Perdita callicerata</i>			**	1
43	<i>Perdita calloleuca</i>		*	**	2
44	<i>Perdita larreae</i>		**		1
45	<i>Perdita punctosignata</i>	*	**	**	3
Totals		15	34	40	87
Percent of possible		33	76	89	64

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559 Table 3. Results of generalized linear models evaluating significance of species (N=40, those
 560 without any unknown traits) functional traits on the difference between data types in calculating
 561 values of three phenology metrics.

562

A. NUMBER OF CLUSTERS				
Trait (ref. level)	Estimate	Std. Error	z value	Pr (> z)
(Intercept)	-0.99	1.92	-0.52	0.60
Sociality(solitary)	1.72	1.19	1.44	0.15
Body Size	1.00	0.52	1.92	0.055*
Specialist(yes)	0.01	1.14	0.01	0.99
Voltinism(uni)	-0.87	1.13	-0.77	0.44
Nesting(below)	-1.03	1.29	-0.80	0.43
B. FLIGHT DURATION				
Trait (ref. level)	Estimate	Std. Error	z value	Pr (> z)
(Intercept)	-5.27	2.71	-1.95	0.05*
Sociality(solitary)	-0.71	1.42	-0.50	0.62
Body Size	1.15	0.58	1.99	0.047**
Specialist(yes)	3.10	1.59	1.95	0.051*
Voltinism(uni)	-0.92	1.40	-0.65	0.51
Nesting(below)	1.29	1.48	0.88	0.38
C. DATE OF HIGHEST PEAK				
Trait (ref. level)	Estimate	Std. Error	z value	Pr (> z)
(Intercept)	-38.05	7482.10	-0.005	0.99
Sociality(solitary)	19.43	4790.19	0.004	0.99
Body Size	-0.96	1.47	-0.66	0.51
Specialist(yes)	-1.15	1.98	-0.58	0.56
Voltinism(uni)	0.48	1.25	0.39	0.70
Nesting(below)	19.38	5747.70	0.003	0.99

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FIGURE LEGENDS

565 Fig. 1. Visualization of three phenology metrics calculated for each of 45 species and two data
566 types. Number of occurrences each day of the year are plotted as orange points, which are also
567 represented as a density plot by the orange smoothed histogram. Vertical black dotted lines
568 indicate the beginning and end of flight duration, the number shows the number of clusters in
569 occurrences, and the location of the maximum peak in occurrences is represented by a vertical
570 solid black line. In subsequent graphs, a gray line indicates secondary peaks in abundance.

571

572 Fig. 2. Distribution of 45 species across categories and values of five functional traits.

573

574 Fig. 3. Number of species, out of 45, for which values of each of three phenology metrics
575 differed significantly ($\alpha = 0.05$) based on the data type used to calculate them.

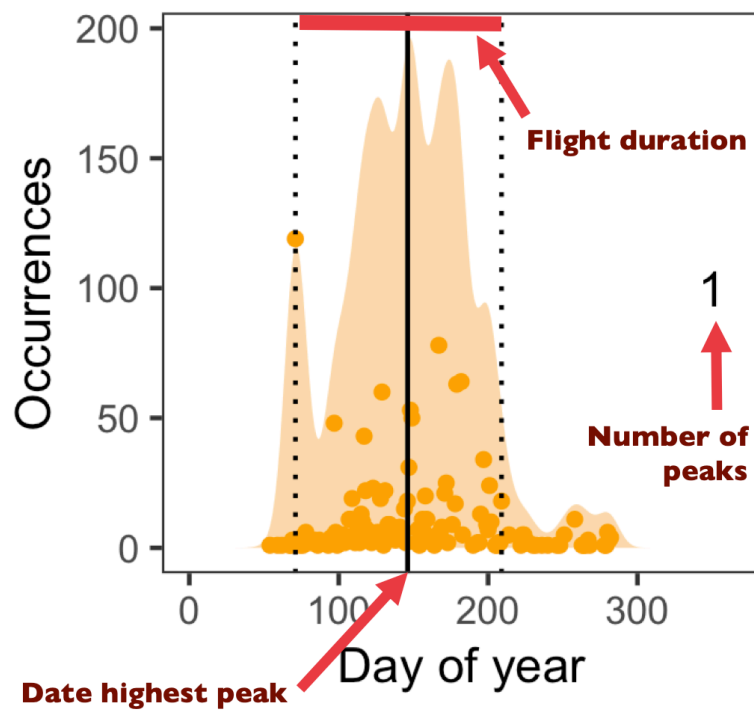
576

577 Fig. 4. Examples of permutation tests results comparing phenology metrics of bee species
578 (N=45) occurrence distributions between two data types. In each cell panel, inventory data is
579 plotted on the left and opportunistic for the same species is plotted data on the right. Column and
580 row names indicate phenology metrics that were found to be significantly different between data
581 types for the species plotted in those cells. In the top left, only flight duration was different
582 between data types, while in the top right both flight duration and date of the highest peak were
583 different, and all three metrics were different for both species in the bottom row. Occurrence
584 curves showing results for all 45 species are in Supporting Information.

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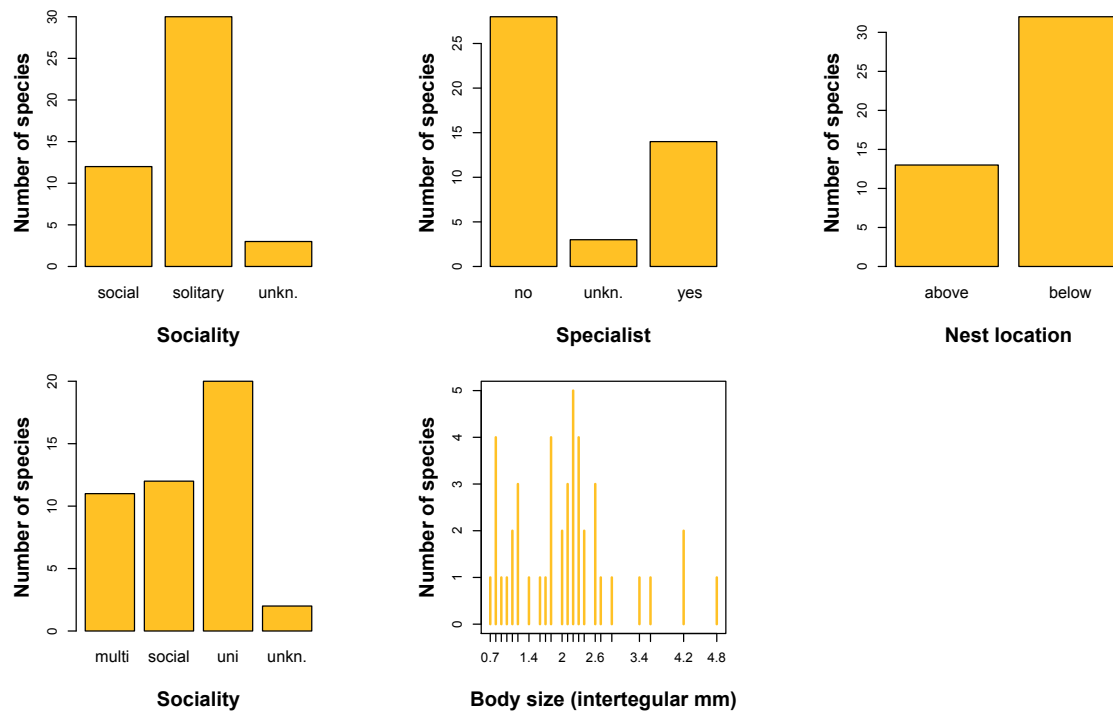
FIGURES



586

587 Figure 1

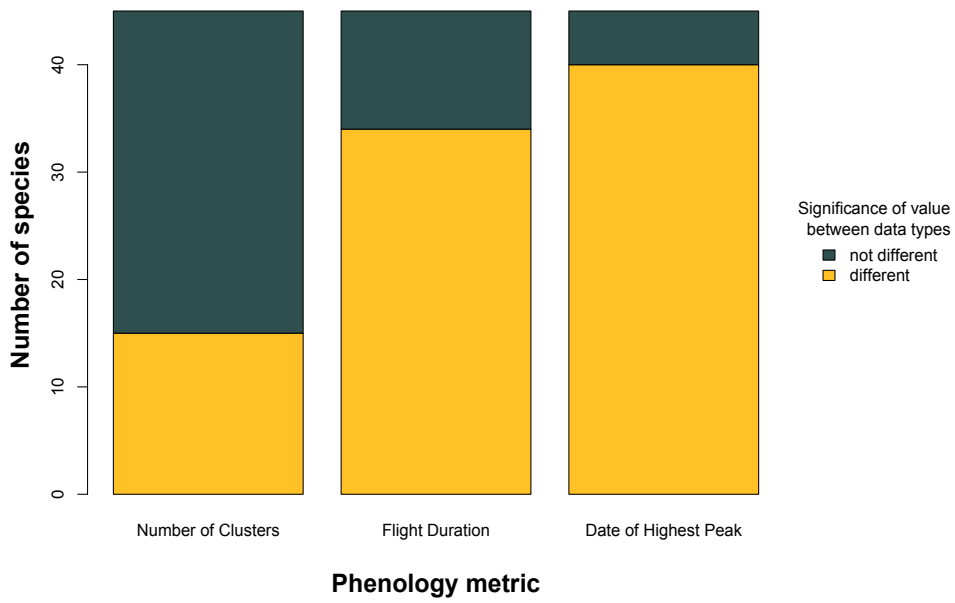
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589 Figure 2

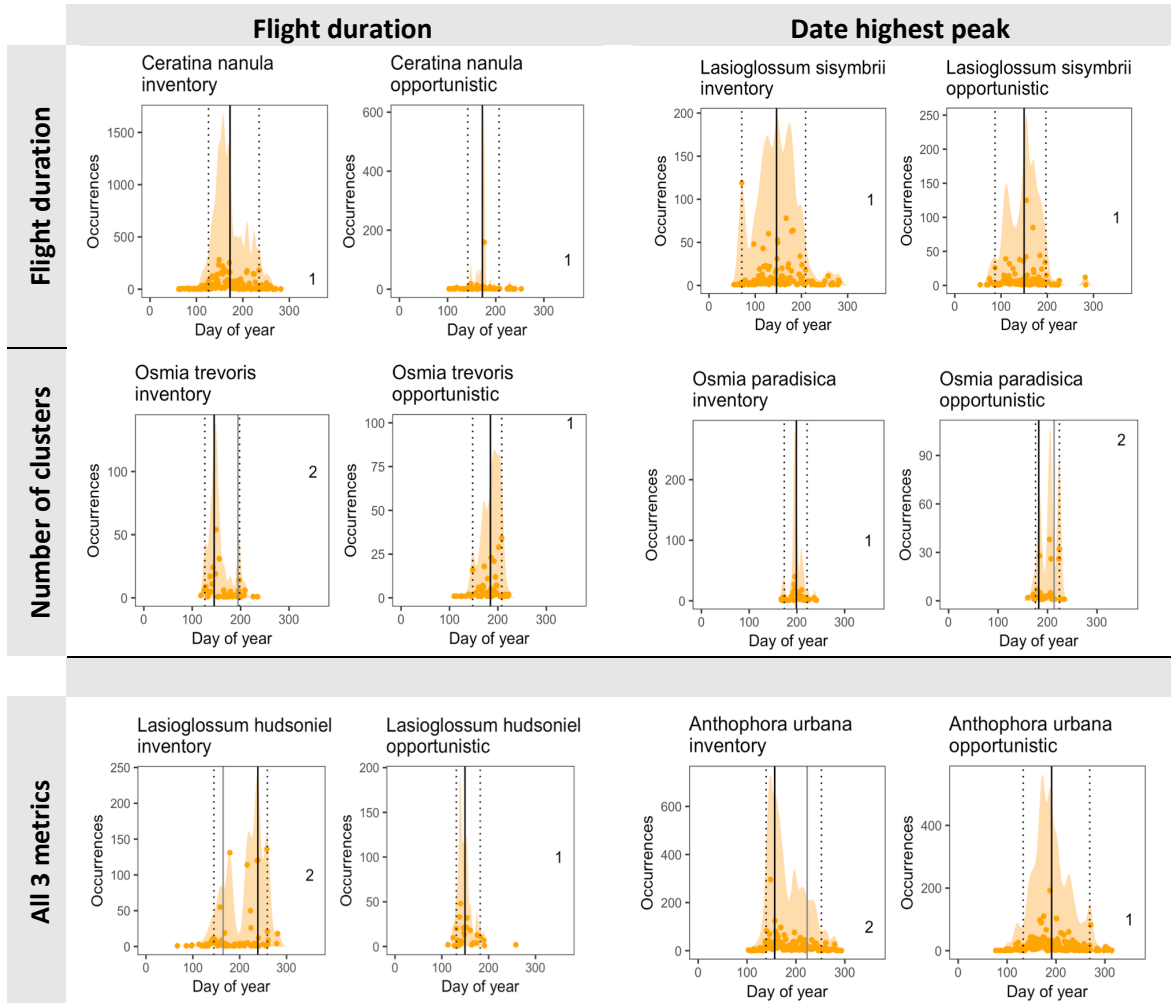
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591 Figure 3

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592 Figure 4