

1 **Larger workers outperform smaller workers across resource**
2 **environments: an evaluation of demographic data using functional**
3 **linear models**
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5 Running headline: Worker size composition effects in bumblebee colonies
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39 AUTHOR CONTRIBUTIONS

40 NZK, EEC and NMW conceived the ideas and designed methodology; NZK, RLM, and
41 NMW collected the data; NZK and EEC analyzed the data; and NZK, EEC, RLM, and NMW
42 wrote the manuscript. All authors contributed critically to the drafts and gave final approval for
43 publication.

44

45 DATA ACCESSIBILITY

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48 ABSTRACT

49 1. Behavior and organization of social groups is thought to be vital to the functioning of
50 societies, yet the contributions of various roles within social groups [towards population growth](#)
51 [and dynamics](#) have been difficult to quantify. A common approach to quantifying these role-
52 based contributions is evaluating the [number](#) of individuals conducting certain roles, [which](#)
53 ignores how [behavior](#) might scale up to effects at the population-level. Manipulative experiments
54 are another common approach to determine population-level effects, but they often ignore
55 potential feedbacks associated with these various roles.

56 2. Here, we evaluate the effects of worker size distribution in bumblebee colonies on worker
57 production [in 24 observational colonies across three environments](#), using functional linear
58 models. Functional linear models are [an underused](#) correlative technique that has been used to
59 assess lag effects of environmental drivers on plant performance. We demonstrate potential
60 applications of this technique [for exploring high-dimensional ecological systems, such as the](#)
61 contributions of [individuals with different traits](#) to [colony dynamics](#).

62 3. We found that more larger workers had mostly positive effects and more smaller workers
63 had negative effects on worker production. Most of these effects were only detected under low or
64 fluctuating resource environments suggesting that the advantage of colonies with larger-bodied
65 workers becomes more apparent under stressful conditions.

66 4. We [also](#) demonstrate the wider ecological application of functional linear models. We
67 highlight the advantages and limitations when considering these models, and how they are a
68 valuable complement to many of these performance-based and manipulative experiments.

69

70 Keywords: *Bombus vosnesenskii*, functional linear models, colony age, egg production, larval
71 survival, development, callow size

72 INTRODUCTION

73 In animal societies, individuals are often observed performing different tasks, such as
74 guarding nests and burrows (Clutton-Brock *et al.* 2001a), nursing and caring for young
75 (Wilkinson 1992; Kerth 2008; Sparkman *et al.* 2011), or reproducing (Jarvis 1981; Faulkes &
76 Bennett 2001). The roles within these social groups are commonly assigned based on the age
77 (Jarvis 1981; Seeley & Kolmes 1991; Brent *et al.* 2015; Zöttl *et al.* 2016), size (Porter &
78 Tschinkel 1985; Wenzel 1992; Schwander, Rosset & Chapuisat 2005; Goulson 2009), and/or
79 status (Frank 1986; Sparkman *et al.* 2011) of individuals. For example, in Meerkats, which are
80 cooperative breeders, younger non-breeding individuals often stand on ‘sentinel duty’ during
81 group foraging bouts and care for offspring of the dominant breeding pair (Clutton-Brock *et al.*
82 2001b; Clutton-Brock *et al.* 2002; Clutton-Brock, Russell & Sharpe 2004). Without the co-
83 operation of these non-breeders, the survival of individuals within the colonies is likely to
84 decrease, particularly for the young (Doolan & Macdonald 1999; Russell *et al.* 2007). This social
85 behavior and organization is often assumed to be vital to the functioning and survival of these
86 societies.

87 The most common approach to understanding the contribution of roles within social
88 groups is to observe the behavior and performance of individuals. However, [observing certain](#)
89 [individuals performing a task does not mean they are better than other individuals at performing](#)
90 [that task](#). To attempt to tackle the challenges associated with quantifying trait-based
91 contributions, a few studies have manipulated colonies in the laboratory to evaluate the effects of
92 the social organization of age- and size- polymorphic species, such as mole rats (Jarvis 1981;
93 Zöttl *et al.* 2016), ants (Porter & Tschinkel 1985; Billick & Carter 2007), and bumblebees
94 (Cnaani & Hefetz 1994; Jandt & Dornhaus 2009; Couvillon *et al.* 2010; Jandt & Dornhaus 2011;

95 Jandt & Dornhaus 2014). In laboratory colonies of a eusocial ant *Pheidole dentata*, larvae gained
96 more mass when reared by older workers, suggesting that older workers contribute more towards
97 worker production in these ant colonies than their younger sisters (Muscedere, Willey &
98 Traniello 2009). However, colonies within these laboratory experiments were not faced with the
99 same external environmental stressors as those in the wild. In the case of bumblebees, larger
100 workers are more susceptible to predators and parasites (Cartar & Dill 1991; Muller, Blackburn
101 & Schmid-Hempel 1996; Malfi & Roulston 2014), despite being better foragers. Therefore, the
102 behaviors of social organism under artificial conditions might not capture all the feedbacks
103 associated with size or age-based roles.

104 Functional linear models (FLMs) provide an [additional](#) method of inference [about high-](#)
105 [dimensional ecological systems using observational data](#). For example, FLMs can evaluate the
106 contributions of age- or size-based roles within societies [to population dynamics](#). These models
107 assume that the effect of a predictor variable (e.g. number of workers) on a response variable
108 (e.g. egg production) is a smooth function of some feature of the predictor variable (e.g. size of
109 workers). Past applications of FLMs in ecology have investigated environmental drivers of plant
110 population dynamics (Teller *et al.* 2016; Tenhumberg *et al.* 2018). These studies evaluated the
111 effects of environmental conditions (e.g. precipitation) on plant performance (e.g. growth)
112 assuming the slope of the effect of environmental conditions and plant performance varies as a
113 smooth function of the time lag between conditions and performance (e.g. precipitation in the
114 past 1, 2, 3... months). For example, the slope of precipitation versus plant growth could go from
115 positive in recent months to zero at longer time lags. This method has potential for wider
116 ecological application to investigate life history phenomena. Here, we explore application of

117 FLMS to quantifying the relationship between aspects of new worker production as a function of
118 the body size of existing workers in bumblebee colonies.

119 Bumblebees (*Bombus* spp.) are primitively eusocial insects that form relatively small
120 colonies and have a discrete life cycle lasting only for a single season, which makes them a
121 tractable system for studying trait-based roles within societies. Bumblebees also exhibit worker
122 size polymorphism, where workers within colonies vary up to 10-fold in mass (Goulson 2009).
123 In bumblebee colonies, larger workers are often found foraging and guarding, while smaller
124 workers spend more time in the colony conducting in-nest tasks such as fanning and incubating
125 (Richards 1946; Cumber 1949; Goulson *et al.* 2002; Jandt & Dornhaus 2009; Inoue *et al.* 2010).
126 Many studies have measured the importance of body size in determining how well workers
127 perform various tasks, ranging from foraging and flight dynamics to thermoregulating and
128 undertaking. Most of these have found that larger workers are better at multiple tasks, such as
129 foraging and nursing (Cnaani & Hefetz 1994; Goulson *et al.* 2002; Spaethe & Weidenmüller
130 2002; Peat & Goulson 2005; Ings 2007; Spaethe *et al.* 2007; Kerr, Crone & Williams 2019), with
131 a few studies concluding either that intermediate-size is better (Jandt & Dornhaus 2014), or that
132 there is no size-based difference in performance (Jandt & Dornhaus 2014). Although these
133 studies demonstrate that body size affects worker performance at certain tasks, they do not
134 demonstrate how their size-based performance at tasks may, in turn, affect colony growth and
135 development.

136 No studies have found smaller bumblebee workers to be better at performing tasks
137 essential to colony function. However, smaller workers are more resilient to starvation
138 (Couvillon & Dornhaus 2010). Therefore, their value may become more apparent when food
139 resources are limiting. In addition, smaller workers have lower production costs, so they may be

140 more cost-effective (Kerr, Crone & Williams 2019). Here, we used FLMs to evaluate the
141 contribution of workers of different sizes to worker production in bumblebee colonies under
142 three different environments: a low resource environment; an environment with an early season
143 pulse followed by low resources ('high-low'); and a high resource environment. We looked at
144 five vital rates relating to worker production: (1) number of new eggs laid, (2) development time,
145 (3) larval survival, and (4) mean and (5) variance in worker emergence size, i.e. the size of
146 callow workers. By evaluating the contribution of different-sized workers under different
147 resources environments to worker production, we can assess whether larger workers are more
148 beneficial when resource conditions are more favorable and whether the benefit of small workers
149 to colonies is only seen when resources are low, making both production cost and resistance to
150 starvation a premium.

151

152 MATERIALS AND METHODS

153 *Study species and sites*

154 We hand reared *Bombus vosnesenskii* colonies from wild-caught queens collected at the
155 University of California McLaughlin Reserve (N38 52 25.74, W122 25 56.25) in early spring
156 2015 and 2016 while they searched for nest sites. These colonies were the basis for two separate
157 studies, both of which are previously published (Kerr, Crone & Williams 2019; Malfi, Crone &
158 Williams 2019). Here, we use previously unpublished data (*Brood mapping, below*) from these
159 studies to investigate effects of worker size on colony growth, so we briefly describe the rearing
160 process.

161 In 2015 and 2016, we hand-reared colonies in the laboratory in a dark room at 26-28°C for
162 6 to 9 weeks until their second or first cohort of worker bees eclosed. In 2015, we relocated

163 seven colonies outside (N38 32 12.21, W121 47 16.95) at the Harry H. Laidlaw Jr. Honey Bee
164 Research Facility (Davis, CA), where the surrounding landscape consisted of agricultural crops,
165 floral research plots, and a 0.2 ha pollinator garden (Fig. S3a). In 2016, we relocated 14 colonies
166 outside in agricultural fields at UC Davis Experimental Farm property (N38 31 32.3, W121 46
167 56.54). Half of the colonies (n = 7) had access to flight cages that provided a pulse of native
168 California wildflower species for ~4 weeks early in the season (“pulse” treatment) and the other
169 half had no supplemental forage (“control” treatment) (Malfi, Crone & Williams 2019). The
170 surrounding landscapes were croplands consisting of mainly non-flowering cereals, corn, and a
171 strip of riparian habitat (Fig. S3b).

172 In this study, we broadly categorized the resource environments experienced by our
173 experimental colonies in each of these years based on observational differences in the quality and
174 abundance of forage. The 2015 colonies, located next to a pollinator garden at the Honey Bee
175 Research Facility, had the highest resource availability and quality (“high”), colonies in the 2016
176 pulse treatment had the second highest resource availability and quality (“high-low”), and
177 colonies in the 2016 control treatment had the lowest availability and quality (“low”). These
178 three environments will now be referred to as high, high-low, and low. Note that comparisons
179 between the 2015 colonies and 2016 should be interpreted with the caveat that differences could
180 be due to factors other than nutrition. Based on our observations, the most noticeable differences
181 among treatments were the quality and abundance of floral resources (discussed further in the
182 *Discussion*).

183

184 *Brood mapping*

185 Each week, we photographed the brood from multiple angles (above, side, diagonal) to fully
186 capture all brood cells. We individually numbered each brood cell in the photographs as it
187 differentiated and tracked the fate of all marked cells throughout colony development (Fig. 1).
188 We classified each living brood cell into five categories: (1) clump stage, which represents the
189 egg stage where individual cells have not yet differentiated; (2) pre-differentiated stage, which
190 represents early larval instars where individual cells have begun differentiating; (3) differentiated
191 stage, which represents later larval instars where individual brood cells are clearly differentiated;
192 (4) cocoon stage, where cells had darkened indicating that pupa have spun their cocoons; and (5)
193 eclosed stage, where the cell has opened and an adult worker emerged (Fig. 2 for stages). We
194 also had two other categories: (6) dead, where we had observed a dead cell, and (7) unseen,
195 where the cell could no longer be seen in the brood photos.

196 Some brood clumps did not develop into distinct cells before the end of brood mapping,
197 while other clumps died before cell partitioning. Rather than exclude these indistinct, dead, or
198 undeveloped brood clumps in our analyses ($N_{\text{low}} = 24/115$; $N_{\text{high-low}} = 36/150$; $N_{\text{high}} = 36/163$),
199 which could result in underestimating egg production and overestimating larval survival, we
200 estimated the number of cells for these clumps. We did this by classifying these indistinct brood
201 clumps into five size categories (tiny, small, medium, large, extra-large) based on comparisons
202 with similarly-sized brood clumps that did divide into individual cells and assigning the mean
203 value of cells for these size categories to indistinct clumps. From the 322 distinct clumps with a
204 total of 3917 cells with known fates, we estimated 432 cells from 96 indistinct clumps appeared
205 to have died before differentiating, which comprises of less than 10% of total cells in our larval
206 survival analyses.

207 From the brood mapping, we estimated three vital rates: egg production, larval development
208 time, and larval survival. We considered weekly egg production to be the number of newly
209 visible cells in either clump or pre-differentiated stages. We assumed that the number of distinct
210 cells formed by a brood clump represented the total number of eggs laid, i.e. no eggs died before
211 larval cells differentiated. We calculated development time for each cell as the number of days
212 from when it was first seen as an egg (defined as the ‘clump’ stage) to when it was first seen as
213 an eclosed cell. Cells that were not detected in the clump stage or that disappeared from view
214 before visibly eclosing were excluded from our analyses of larval development time. Finally, we
215 classified larval survival as the success of each cell [at surviving to](#) eclosion. We excluded 43
216 unseen brood cells from our larval analyses because more than 8 days (50% the normal
217 bumblebee development time) passed between photos of them so their fates could not be
218 unambiguously mapped. These represent 10% of 437 unseen cells or 1% of all 4,640 cells
219 mapped across the 21 colonies and three resource environments.

220

221 *Worker surveys*

222 We conducted weekly night-time surveys to estimate the mean and coefficient of variation
223 (CV) in the size of newly emerged workers (hereafter referred to as “callow size”). We assigned
224 each bee a unique tag using a combination enamel paint and numbered, color-tags or
225 Microsensys radio-frequency identification (RFID) tags (Kerr, Crone & Williams 2019; Malfi,
226 Crone & Williams 2019). For each newly emerged (“callow”) worker, we estimated body size by
227 measuring intertegular (IT) span to the nearest 0.01 mm using digital calipers (Cane 1987; Hagen
228 & Dupont 2013) and wet weight to the nearest 0.01 mg using [an](#) analytical microbalance (Mettler
229 Toledo XS205DU). The size of each worker at initial capture was used to estimate the mean and

230 CV of callow size. We used these size measurements in combination with presence/absence data
231 to determine the number of workers of each size (now referred to as “worker size composition”)
232 present in each colony for each week of the survey in order to evaluate the effects of worker size
233 composition on aspects of worker production.

234

235 *Functional linear models*

236 We used functional linear models (FLMs) to estimate how five vital rates varied with
237 worker size composition. FLMs are a type of regression spline that allows a covariate to vary
238 smoothly over a continuous domain (Ramsay & Silverman 2005; Ramsay, Hooker & Graves
239 2009). Therefore, instead of restricting our predictors (X) to unidimensional space (i.e. simple
240 linear models, such as total worker number predicts number of eggs), we can evaluate the effect
241 of the number of workers on some response variable (e.g. number of eggs) as a continuous
242 function of worker size (i.e. a separate attribute of the predictor variable), such that the smooth
243 function of size-specific slopes versus worker size can be described as:

$$244 \quad E(Y) = \beta_0 + \sum_{x=1}^{\max(x)} (s_x) W(n_x) \quad (1)$$

245 where $E(Y)$ is the expected value of the response variable Y (e.g. number of eggs); β_0 is the
246 intercept; $W(n_x)$ is the number of workers n of size x ; and (s_x) is the slope of Y versus the number
247 of workers of each size category x (c.f. methods in Teller *et al.* 2016). Here, the continuous
248 attribute (i.e. worker size) of the predictor variable (i.e. number of workers) is discretized into
249 many size categories (14 size categories for both low and high-low, and 17 for high resource
250 colonies) to approximate a continuous distribution of sizes (i.e., the worker size composition).
251 The expected value of the response variable is the sum of the product of the size-specific slopes
252 (s_x) multiplied by the number of workers of size x (Fig. 3). If the slope of Y versus the number of

253 workers of size x is positive, then more workers of size x increase values of Y and vice versa
254 when the slope is negative (Fig. 3).

255 We parameterized the smooth functions of the size-specific slopes using general additive
256 models (GAMs). We fit our GAMs using the cubic spline basis for all smooth covariates, so that
257 the coefficients will be set to 0 if our covariates have no effects on the response (see Zuur 2012,
258 for an excellent textbook introduction to GAMs). We used worker size composition in the
259 previous week to predict both the number of eggs laid and larval survival in the present time step
260 for our size composition FLMs. For the other three vital rates relating to worker production, we
261 quantified worker size composition as the average number of workers in each size category
262 across their larval development period.

263 Models were fit separately to data from each study (i.e. low, high-low, and high resource
264 environments), and we included colony ID as a fixed effect (i.e. a different intercept term for
265 each colony) for each model to account for between-colony effects. We used negative binomial
266 GAMs to account for overdispersion for estimating new eggs laid and development time. We
267 offset the number of new eggs laid by the number of days between brood photos. We used
268 binomial and Gaussian-distributed GAMs for larval survival and callow size, respectively. We
269 parameterized the binomial GAMs for estimating larval survival using successes and failures,
270 where the total number of trials was defined as the number of days between brood photos, and
271 the number of successes was defined as the total number of days if the cell survived (i.e., zero
272 failures) and the total number of days minus 1 if the cell died (i.e., one failure). We restricted the
273 number of knots for our smooth terms of the number of workers of size j to a maximum of five.
274 We also rejected any model structure that did not produce unimodal functions for our smooth
275 term of worker size composition, since GAMs are prone to overfitting, and multimodal functions

276 generally did not appear to be biologically meaningful. We used likelihood ratio tests to assess
277 the fit of the parametric intercept term and the number of knots for each smooth term in our
278 models given our data. We used cutoff of $P < 0.05$ for parametric terms and a cutoff of $P < 0.01$
279 for smooth terms, since P values for smooth terms are only approximate and are likely too low
280 (Wood 2017). We ran these general additive models (using `mgcv::gam`; Wood 2004; Wood
281 2011) in program R (R Core Team 2017); see Appendix S1 for example code for our functional
282 linear models.

283 To evaluate whether size-specific slopes of worker size differed among treatments, we
284 ran a model with all data combined and evaluated the AIC of the combined model with an AIC
285 of models separated by treatment δ and by year (Table 1). We repeated all analyses with slopes
286 scaled to size-based worker production costs (see Appendix S2 for methods; Kerr, Crone &
287 Williams 2019 for production costs), rather than numbers of individuals. Because these results
288 were largely parallel (Appendix S2), we do not discuss them further.

289 Colony size (i.e. number of observed workers) increased with colony age across three
290 resource environments (Fig. S2-4). To avoid potentially confounding effects due to collinearity
291 between colony age and worker number, we ran models separately with colony age and worker
292 size composition as predictors of various measures of worker production success. Results for
293 colony age are described in Appendix S3. Relationships between worker size composition and
294 larval survival and mean callow size were somewhat confounded with colony age effects, and
295 should be interpreted with caution (Table 2, Appendix S4). We found no evidence for potentially
296 confounding relationships of colony age and worker number on mean worker size or CV in
297 worker size across the three resource environments.

298

299 RESULTS

300 Average worker size increased with available ambient resources (likelihood ratio (LR)
301 test for models with and without treatment; $\chi^2 = 14701$, $d.f. = 3$, $P \ll 0.001$). Worker size was
302 smallest in the low (mean and SE in IT span: 3.16 ± 0.049) and largest in the high resource
303 environment (IT span: 3.68 ± 0.048) (multiple comparison of means between high and low;
304 estimated difference, $E = 0.52$, $Z = 7.5$, $P \ll 0.001$), with the high-low resource environment
305 being intermediate (IT span: 3.31 ± 0.049) (multiple comparison of means between high-low and
306 low: $E = 0.14$, $Z = 2.1$, $P = 0.09$; high and high-low: $E = 0.37$, $Z = 5.4$, $P \ll 0.001$). These
307 results broadly recapitulate results of previous analyses of the separate experiments as reported
308 by Kerr et al. (2019) and Malfi et al. (2019) for the 2015 and 2016 data, respectively.

309

310 *Daily egg production*

311 Worker size composition did not affect egg production in the low resource environment
312 (Fig. 4a; $\chi^2 = 6.3E-6$, $e.d.f. = 4.2E-5$, $P = 0.75$). More larger workers increased egg production in
313 both the high-low and high resource environments (Fig. 4b-c; $\chi^2 = 83.3$, $e.d.f. = 2.8$, $P < 0.001$,
314 and $\chi^2 = 6.4$, $e.d.f. = 1.3$, $P = 0.01$ for high-low and high (respectively)), but more larger workers
315 had greater impact on egg production in the high-low resource environment than in the
316 constantly high resource environment (Table 1). To illustrate these differences for each vital rate,
317 we plotted the lines predicted by FLMs for workers of different sizes (see egg production
318 relationships in Fig 5a-c).

319

320 *Larval development time*

321 Larval development time increased with more smaller workers in all three resource
322 environments (Fig. 4d-f; LR test of smooth term vs constant: $\chi^2 = 124.6$, *e.d.f.* = 2.7, $P < 0.001$;
323 $\chi^2 = 422.8$, *e.d.f.* = 2.4, $P < 0.001$; $\chi^2 = 21.4$, *e.d.f.* = 1.9, $P < 0.001$ for low, high-low and high
324 (respectively)). Worker size composition affected larval development time differently in each
325 environment (Table 1). More larger workers decreased development time in both the high-low
326 and high resource environment (Fig. 4e-f) but not in the low resource environment (Fig. 4d).
327 However, these effects were negligible in the high resource environment compared to the low
328 and high-low resource environments (Fig. 5).

329

330 *Larval survival*

331 Larval survival decreased with more smaller workers in the low and high-low resource
332 environments (Fig. 4g-h; $\chi^2 = 18.9$, *e.d.f.* = 2.6, $P < 0.001$; $\chi^2 = 103.9$, *e.d.f.* = 2.6, $P < 0.001$ for
333 low and high-low (respectively)). The difference between the low and high-low environments
334 was not statistically significant (Table 1). Larval survival slightly decreased with more workers
335 of all sizes in the high resource environment (Fig. 4i; $\chi^2 = 29.1$, *e.d.f.* = 1.7, $P < 0.001$). This
336 effect was negligible (Fig. 5i), and this relationship for high resource colonies (i.e., colonies in
337 2015) differed significantly from both lower resource environments (i.e., treatments in 2016)
338 (Table 1).

339

340 *Callow size*

341 In the low resource environment, mean callow size decreased with more smaller workers
342 (Fig. 4j & 5j; $F = 3.3$, *e.d.f.* = 1.9, $P = 0.007$), but worker size composition was unrelated to CV
343 in callow size (Fig. 4m & 5m; $F = 2.5E-6$, *e.d.f.* = 1.7E-5, $P = 0.52$). In the high-low resource

344 environment, mean callow size decreased with more smaller workers and increased with more
345 larger workers (Fig. 4k & 5k; $F = 6.4$, $e.d.f. = 2$, $P < 0.001$), whereas more larger workers
346 slightly decreased the CV in callow size (Fig. 4n & 5n; high-low - $F = 3.8$, $e.d.f. = 3$, $P < 0.001$).
347 In the high resource environment, more workers of any size decreased the mean callow size (Fig.
348 4l & 5l; $F = 16.5$, $e.d.f. = 1.7$, $P < 0.001$), but worker size composition was unrelated to the CV
349 in callow size (Fig. 4o & 5o; high - $F = 5.2E-6$, $e.d.f. = 4.6E-5$, $P = 0.59$). The effect of worker
350 size on mean callow size of new workers did not differ between the lower resource environments
351 (i.e., 2016 treatments), but both differed from the high-resource treatment (i.e., 2015 colonies)
352 (Table 1). The effects of worker size on the CV in callow size differed among all three
353 treatments (Table 1).

354

355 DISCUSSION

356 Size-based contributions of bumble bee workers to worker production differed among
357 vital rates and resource environments. Despite these differences, we never detected cases where
358 smaller workers outperformed larger workers for vital rates relating to in-nest tasks. Therefore,
359 the fact that smaller workers remain in the nest is likely not due to their superior skill at those in-
360 colony tasks (Jandt & Dornhaus 2014). Instead, colonies with more larger workers often had
361 greater worker production compared to colonies with smaller workers. This pattern is similar to
362 many performance-based (Goulson *et al.* 2002; Spaethe & Weidenmüller 2002; Peat & Goulson
363 2005; Ings 2007; Kapustjanskij *et al.* 2007; Spaethe *et al.* 2007) and manipulative experiments
364 (Cnaani & Hefetz 1994). However, we found the opposite effect in two cases: more workers of
365 any size slightly decreased both larval survival and mean callow size in the high resource

366 environment. We discuss each result in turn below, as well as some advantages and limitations of
367 functional linear models.

368 For two vital rates, larval survival and mean callow size, both treatments applied in 2016
369 differed from 2015, and not from each other. Therefore, these differences could be due to other
370 features that differed among the sites where the two experiments were conducted or conditions in
371 the two years. For example, the site of the 2016 experiment was an agricultural field in an
372 agricultural landscape. The field of the experiment was used only for growing flowers to create
373 the “high” resource pulse in the “high-low” treatment. Nevertheless, pesticides and other factors
374 (such as nest temperatures) may have differed between the two landscape contexts. In general,
375 conditions for bumble bees in the 2016 experiment appeared to be more stressful than conditions
376 in the 2015 experiment. Although the results are not uniquely attributable to floral resources, our
377 analyses provide a reasonable test of size-based differences under relatively low to high stress
378 levels.

379

380 *Functional implications of worker size distribution*

381 Across social organisms, the number of offspring produced often increases with the
382 number of helpers (Brown *et al.* 1982; Malcolm & Marten 1982; Biedermann & Taborsky 2011;
383 Young *et al.* 2015), particularly when resources are high (Harrington, Mech & Fritts 1983;
384 Doolan & Macdonald 1997). We found a similar per capita effect on colony egg production in
385 both our high-low and high resource treatments, yet FLMs also revealed that in these
386 environments more larger workers increased colony egg production relative to more smaller
387 workers. Laboratory studies of bumblebees have shown that colonies consisting of only larger
388 workers produce more eggs than colonies consisting of only smaller workers (Cnaani & Hefetz

389 1994). Larger workers are known to return more resources to the colony (Goulson *et al.* 2002;
390 Kerr, Crone & Williams 2019), but they are less resilient against starvation (Couvillon &
391 Dornhaus 2010). This tradeoff might explain why larger workers increased colony egg
392 production only in the high-low and high resource environment **but not in the low resource**
393 **environment**. The opposite effect has been found in a fire ant, *Solenopsis invicta*, where
394 monomorphic colonies of large workers produced almost no brood compared to monomorphic
395 colonies of small workers (Porter & Tschinkel 1985). However, the size-based roles of workers
396 in these two eusocial insects differs. Larger bumblebees are foragers (Cumber 1949; Goulson *et*
397 *al.* 2002; Goulson 2009), but smaller fire ant workers do most of the foraging and feeding
398 (Wilson 1978; Cassill & Tschinkel 1999). Larger fire ant workers live longer than smaller
399 workers (Porter & Tschinkel 1985; Calabi & Porter 1989), which is the opposite of bumblebee
400 workers (da Silva-Matos & Garofalo 2000; Kerr, Crone & Williams 2019). Therefore, the
401 general mechanism may be similar, despite contrasting patterns.

402 **The** smallest observed workers **had** negative effects on both development time and larval
403 survival in the low and high-low resource environments; note that this worker size was not
404 present in the high resource colonies. In bumblebees, there seems to be a resource-driven trade-
405 off between provisioning for developing larvae and production of new eggs when resources are
406 low. **For example, in the low resource environment, egg-laying did not depend on the number of**
407 **large workers. In contrast, in higher resource environments, the number of eggs laid increased**
408 **with more larger workers. This contrast suggests that workers in the low resource environment**
409 **are allocating more resources to maintaining larval survival and development time, rather than**
410 **supporting more workers.** Results for small workers in the lower resource environments are
411 similar to those for cooperative breeding species, in which the presence of more helpers often

412 reduces offspring survival when resources are low (Harrington, Mech & Fritts 1983; Woodroffe
413 & Macdonald 2000). These negative impacts of helpers in cooperative breeding species may be
414 due to them shifting efforts towards increasing their own survival (Bruitjies, Hekman &
415 Taborsky 2010), which seems less likely in bumblebees because workers are non-reproductive.
416 Indeed, bumblebee workers are reported to switch from nursing to foraging tasks when resources
417 are low (Cartar 1992), indicating that workers overall increase (not decrease) cooperative efforts.
418 Additionally, bumblebee workers predominantly feed on nectar and larvae predominantly feed
419 on pollen (Plowright & Pendrel 1977; Goulson 2009), which may reduce competition among
420 siblings and enhance cooperative behaviors. It would be interesting to monitor foraging behavior
421 of bumblebee workers during resource dearths, i.e. changes in nectar vs. pollen collection rates,
422 to better understand their cooperative efforts.

423 Across our three environments, observed average size of all workers decreased in
424 colonies with less available resources. In the high resource environment, more workers of any
425 size decreased the size of callow workers. Worker size is known to decrease with colony age
426 (Couvillon *et al.* 2010), which correlated with colony size. In the low and high-low resource
427 environments, more smaller workers resulted in callow workers of smaller sizes and more larger
428 workers resulted in callow workers of larger sizes. Bumblebee workers have been recorded to be
429 smaller on average in simple, intensively managed landscapes (Persson & Smith 2011).
430 Laboratory experiments also show that colonies produce smaller workers during food shortages
431 (Schmid-Hempel & Schmid-Hempel 1998). The correlation between worker size distribution and
432 callow worker size [in the low and high-low resource environment](#) suggests that stressful resource
433 conditions may produce a negative feedback loop, where colonies of smaller workers cannot
434 properly feed and care for brood (Cartar & Dill 1991) causing the emergence of smaller callow

435 workers. Therefore, the cost and benefits of helpers within social groups may often regulate the
436 traits of individuals (e.g. sex ratios, worker sizes) that are expressed (Griffin, Sheldon & West
437 2005). Functional linear models are only a correlative technique, so an alternative shared driver
438 could be shifting the size distribution towards smaller workers. For example, lower resources
439 could cause differential mortality of larger workers due to starvation (Couvillon & Dornhaus
440 2010) and cause larvae to develop into smaller callow workers because of fewer resources
441 brought back by the remaining workers. Laboratory monomorphic colonies consisting of only
442 small or large workers had no difference in the mean and variance in callow size when supplied
443 with abundant resources (Cnaani & Hefetz 1994). If these laboratory colonies had to forage for
444 resources and still produced workers of similar sizes, then we might be able to determine
445 whether a shared driver is most likely causing these effects in our study.

446

447 *Functional linear models as a statistical approach in ecology*

448 Previously, FLMs have been used to evaluate the lagged effects of environmental drivers
449 on plant population dynamics (Teller *et al.* 2016; Tenhumberg *et al.* 2018). Here, we extend the
450 use of FLMs to evaluate the size-based contribution of workers in bumblebee colonies. FLMs
451 could be applied to understanding many high-dimensional social systems. For example, they
452 could be used to explore [the contributions of trait-based sociality, such as the contributions of](#)
453 [age polyethism](#) within social groups of different taxa and levels of sociality, [including](#) eusocial
454 honey bees (Seeley & Kolmes 1991), semi-social mole rates (Jarvis 1981; Zöttl *et al.* 2016), and
455 cooperative breeding meerkats (Clutton-Brock *et al.* 2001a) or cichlid fish (Bruitjies &
456 Taborsky 2011). In the African mole rat, larger groups had higher rates of offspring recruitment
457 (Young *et al.* 2015) and cooperative behaviors were found to increase with age (Zöttl *et al.*

458 2016). Therefore, FLMs might be able to determine how vital rates (e.g. offspring recruitment)
459 differ with the number of helpers of different ages for the African mole rate. FLMs provide an
460 alternative way to study these high-dimensional ecological systems using field observational
461 data, particularly where manipulative experiments may not be possible.

462 Correlative techniques, such FLMs, provide a valuable complement to many
463 manipulative experiments that aim to test similar hypotheses. However, these separate
464 approaches have their own set of advantages and limitations that need to be considered when
465 making conclusions [from these models](#). For example, FLMs can be data-heavy (e.g., 20-25
466 independent observations of the signal and response; Teller *et al.* 2016); only inform us about
467 correlations and not causations; and may have collinear predictors that obscure the true driver of
468 these responses. Collinearity is not specific to FLMs but is equally problematic for many simple
469 (e.g. multiple regression) and complex statistical techniques (e.g. structural equation models). To
470 date, only two studies have reported applying functional smoothing approaches to high-
471 dimensional ecological systems by exploring how lagged environmental drivers influence plant
472 performance (Teller *et al.* 2016; Tenhumberg *et al.* 2018). Teller *et al.* (2016) predicted how
473 lagged effects of past precipitation and local competition influenced plant growth and survival;
474 however, they would not be able to parse out the true driver of plant performance if density and
475 precipitation covaried across some gradient. When exploring the trends and collinearity for these
476 several vital rates (Appendix S4), two of four vital rates (Table 2) had confounding effects of
477 colony age and size composition suggesting that either or both might be driving these trends
478 (Table 2). When using simple or complex correlative methods, it is important to explicitly
479 evaluate the collinearity of predictor variables as we have demonstrated here.

480

481 *Summary*

482 Overall, we found that the advantages and disadvantages of workers of different sizes on
483 worker production only became apparent when exploring these effects across these three
484 different resource environments. We also found that bumblebee colonies shifted their worker
485 size distribution across these resource environments. Among eusocial insects, caste size
486 polymorphism is hypothesized to be an adaption to expand accessibility of resources, such as
487 seed size in ants (Davidson 1978; Traniello & Beshers 1991; Retana & Cerdá 1994) and flower
488 size in bumblebees (Peat, Tucker & Goulson 2005). However, the shift in worker size
489 distribution across these resource environments could have emerged from the lower tolerance of
490 larger workers to starvation (Couvillon & Dornhaus 2010). Prior to this study, quantifying the
491 contribution of individuals in social groups has been challenging. Here, we demonstrate that
492 functional linear models have the potential to evaluate observational data for complex, trait-
493 based life histories of social organisms. As such, they provide a valuable complement to the
494 constraints of experimental work, and a mechanism to focus hypotheses for further experimental
495 studies.

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662 FIGURE LEGENDS

663

664 **Figure 1.** Example of brood mapping photos used to track the fate of individual cells. These
665 mapping photos are aerial photographs for colony 6 in (a) week 5 and (b) week 6 since the first
666 brood photo. Aerial, side, and diagonal photos were taken to capture all cells. Each cell has been
667 individually numbered to track each cell. [The larger stand-alone open wax structures are honey](#)
668 [pots.](#)

669

670 **Figure 2.** Brood mapping photos showing each of the six categories of living or dead stages of
671 cell development. The six stages are: (a) clump stage, which are egg stages; (b) pre-popcorn
672 stages, which represents early larval instars; (c) popcorn stage, which are late instar larvae; (d)
673 cocoon stage; (e) eclosed stage, and (f) a dead cell (dashed circle). These categories assisted with
674 estimating three vital rates [relating to worker production](#): eggs laid, development time, and larval
675 survival.

676

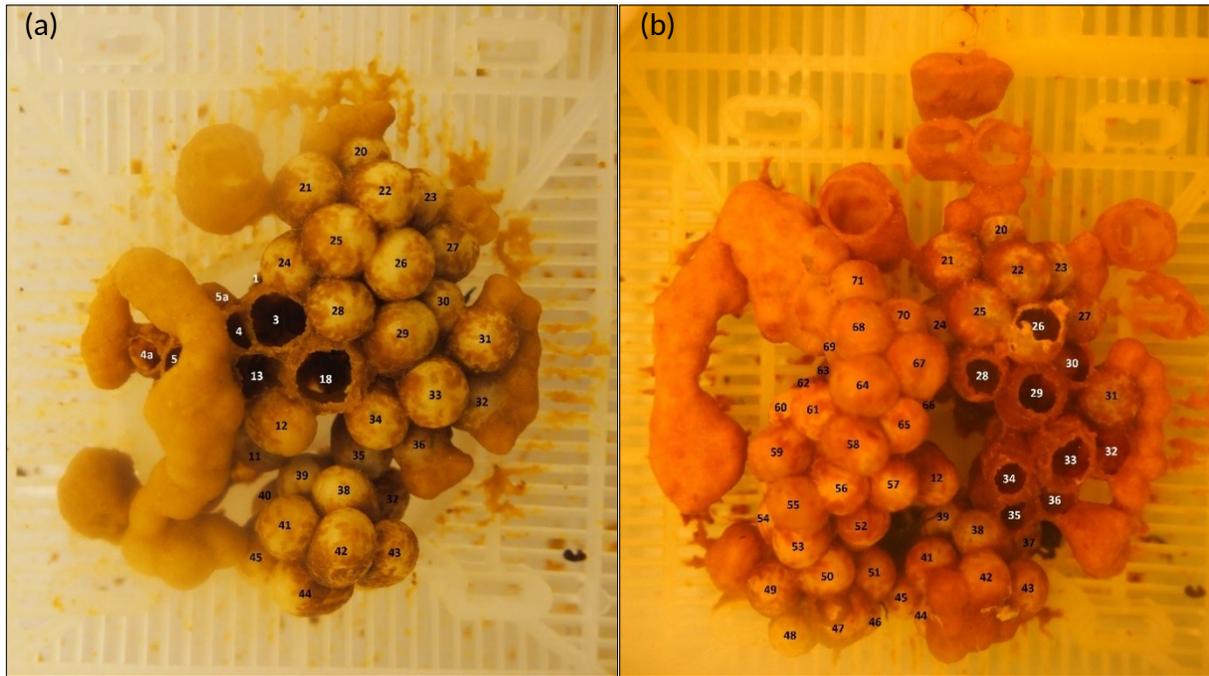
677 **Figure 3.** Example of functional linear model results showing the smooth function of the slopes
678 of Y versus the number of workers as a function of worker size, x . Y covariate could be one of the
679 five metrics of worker production: egg production, larval development time, larval survival, and
680 mean and variance in callow size. We illustrate the following examples: (a) [no size-based per](#)
681 [capita effect, but more workers of any size increases \(\$\beta_0 > 0\$ \) or decreases \(\$\beta_0 < 0\$ \) \$Y\$](#) ; (b) [positive](#)
682 [size-based per capita effects on \$Y\$](#) ; (c) [negative size-based per capita effects on \$Y\$](#) ; and (d) [mixed](#)
683 [size-based per capita effects, i.e., more workers of one size have negative effects and more](#)
684 [workers of another size have positive effects. The dotted line on each panel represents no per](#)
685 [capita effects of workers.](#)

686 **Figure 4.** Generalized additive model results depicting the smooth function of the size-specific
687 slopes for all five vital rates relating to worker production versus the number of workers of size x
688 for the low (left), high-low (middle), and high (right) resource environments. Dashed horizontal
689 line at zero represent deviations from mean slope values, i.e. slopes above the line means more
690 workers of size x have positive impact on Y . Grey dashed vertical line represents the mean
691 worker size for colonies in each of the resource environments. Plots with a significant smooth
692 term of WSC are labeled with $P < 0.01$. Note different scales on the Y-axes in each row.
693

694 **Figure 5.** The relationship between number of workers of three observed worker sizes and the
695 five vital rates relating to worker production across the three treatments. Three workers sizes
696 range from the smallest size of 2.5 mm (light grey), intermediate size of 3.5 mm (dark grey), and
697 largest size of 4.5 mm (black line) that are observed in colonies across all three treatments. Each
698 of these lines represents the function defined by $x = 2.5, 3.5$ and 4.5 on the x-axis of figure 4.
699 Parametric intercepts were used from the GAMs, and intercepts were averaged on the link
700 function scale if the model had a significant fixed effect of colony.
701

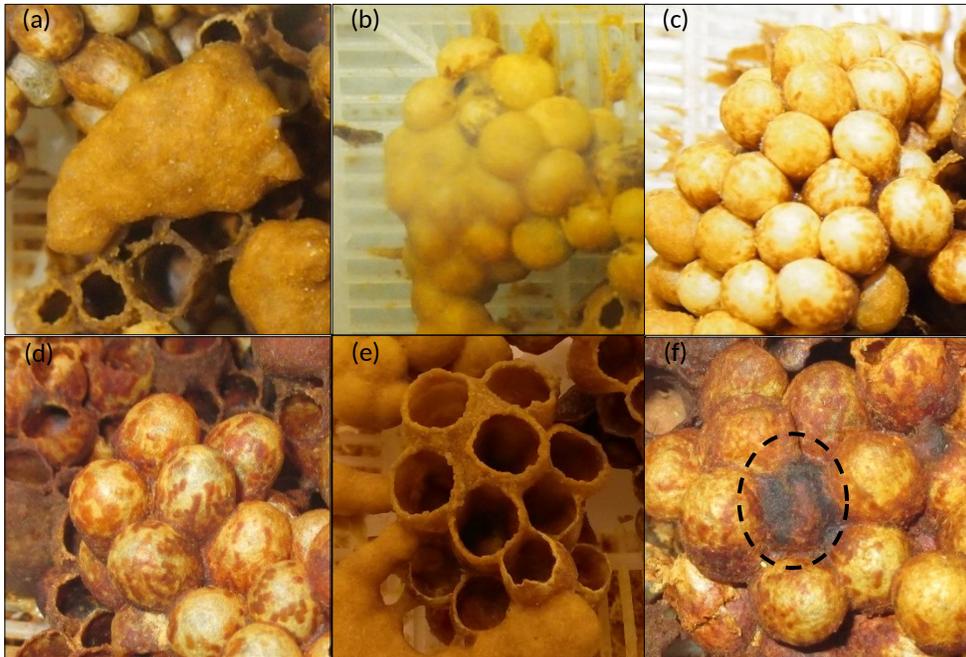
702 FIGURES

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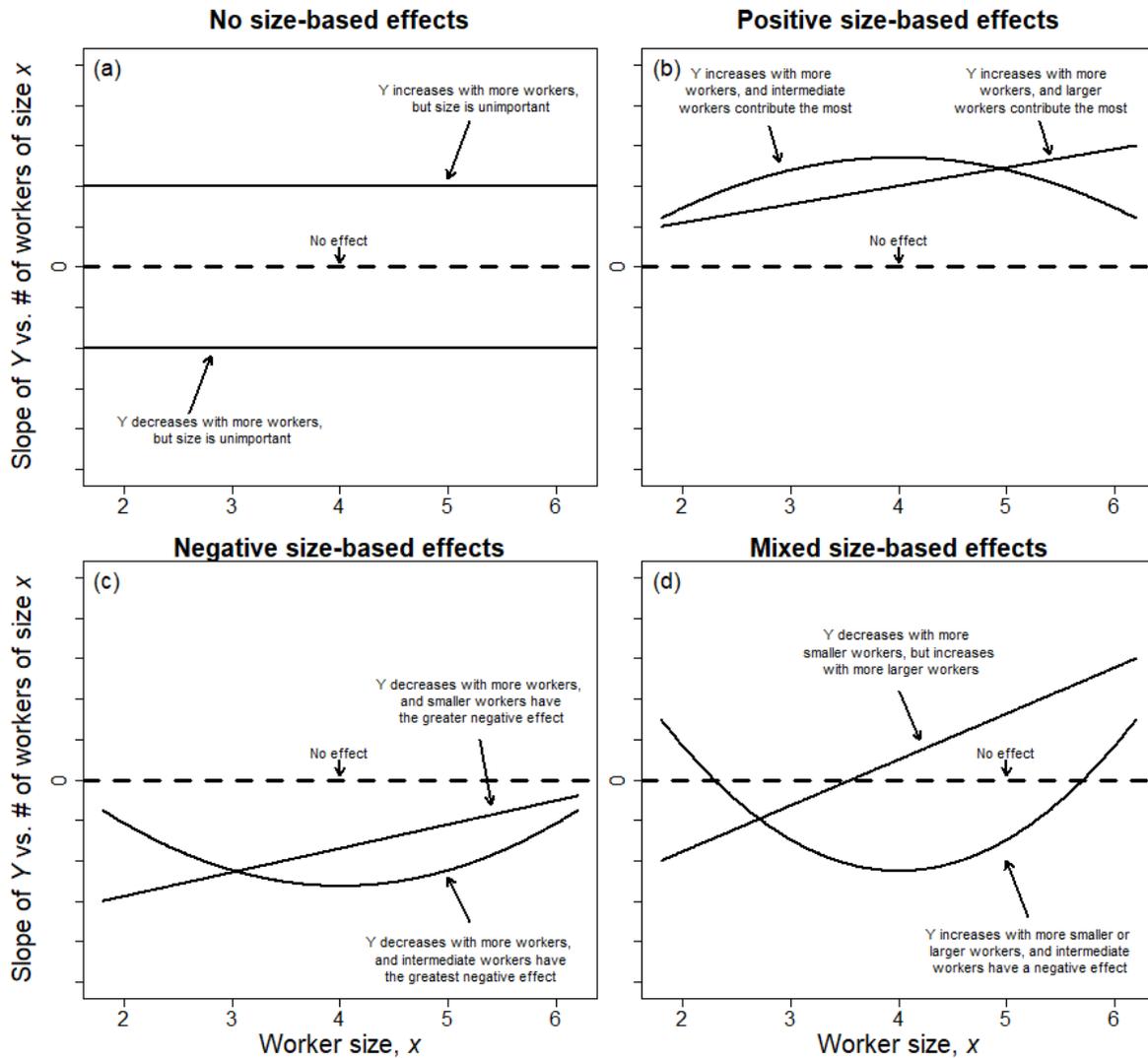
704

705 **Figure 1.** Example of brood mapping photos used to track the fate of individual cells. These
706 mapping photos are aerial photographs for colony 6 in (a) week 5 and (b) week 6 since the first
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708 individually numbered to track each cell. [The larger stand-alone open wax structures are honey](#)
709 [pots.](#)



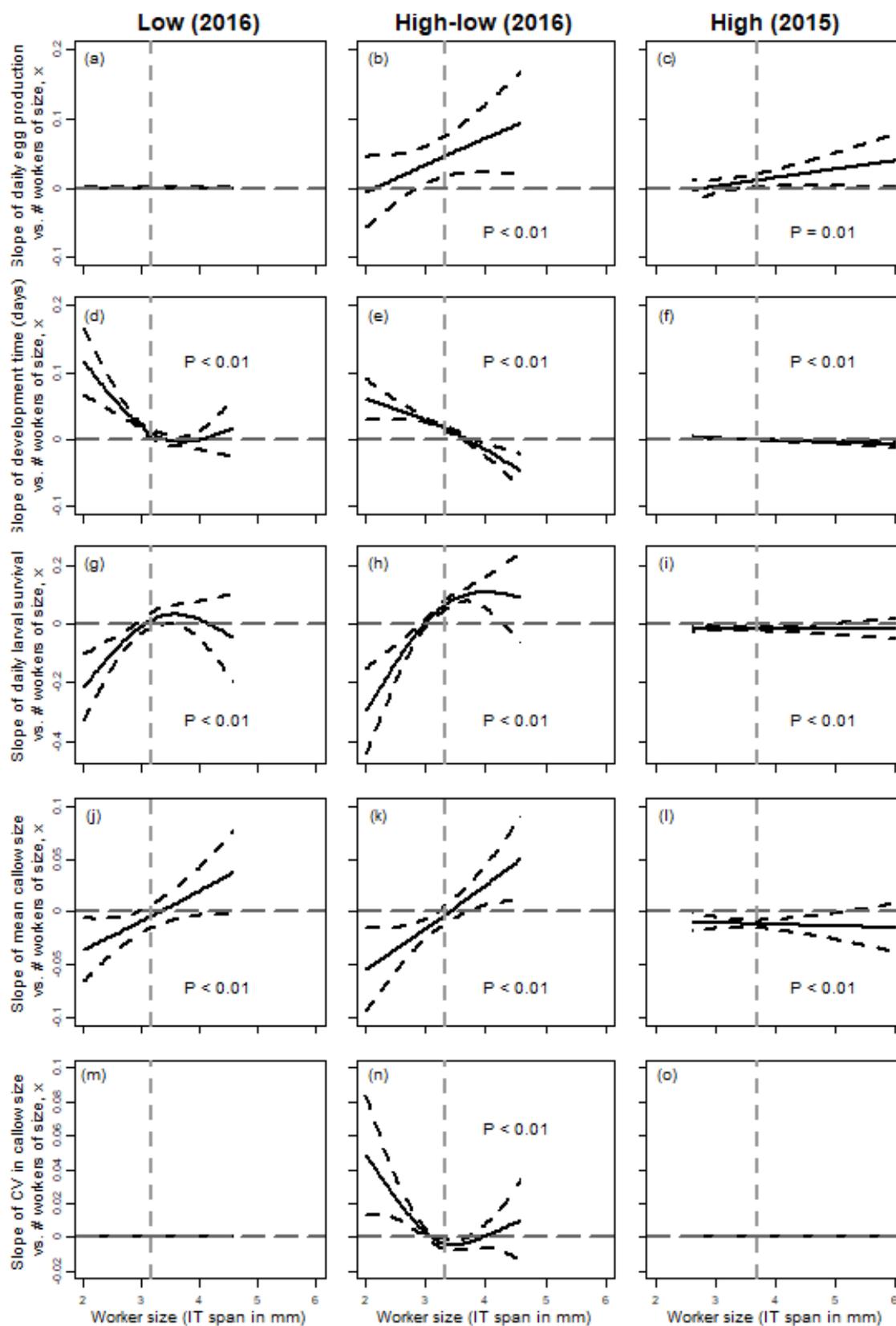
710

711 **Figure 2.** Brood mapping photos showing each of the six categories of living or dead stages of
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715 estimating three vital rates [relating to worker production](#): eggs laid, development time, and larval
716 survival.

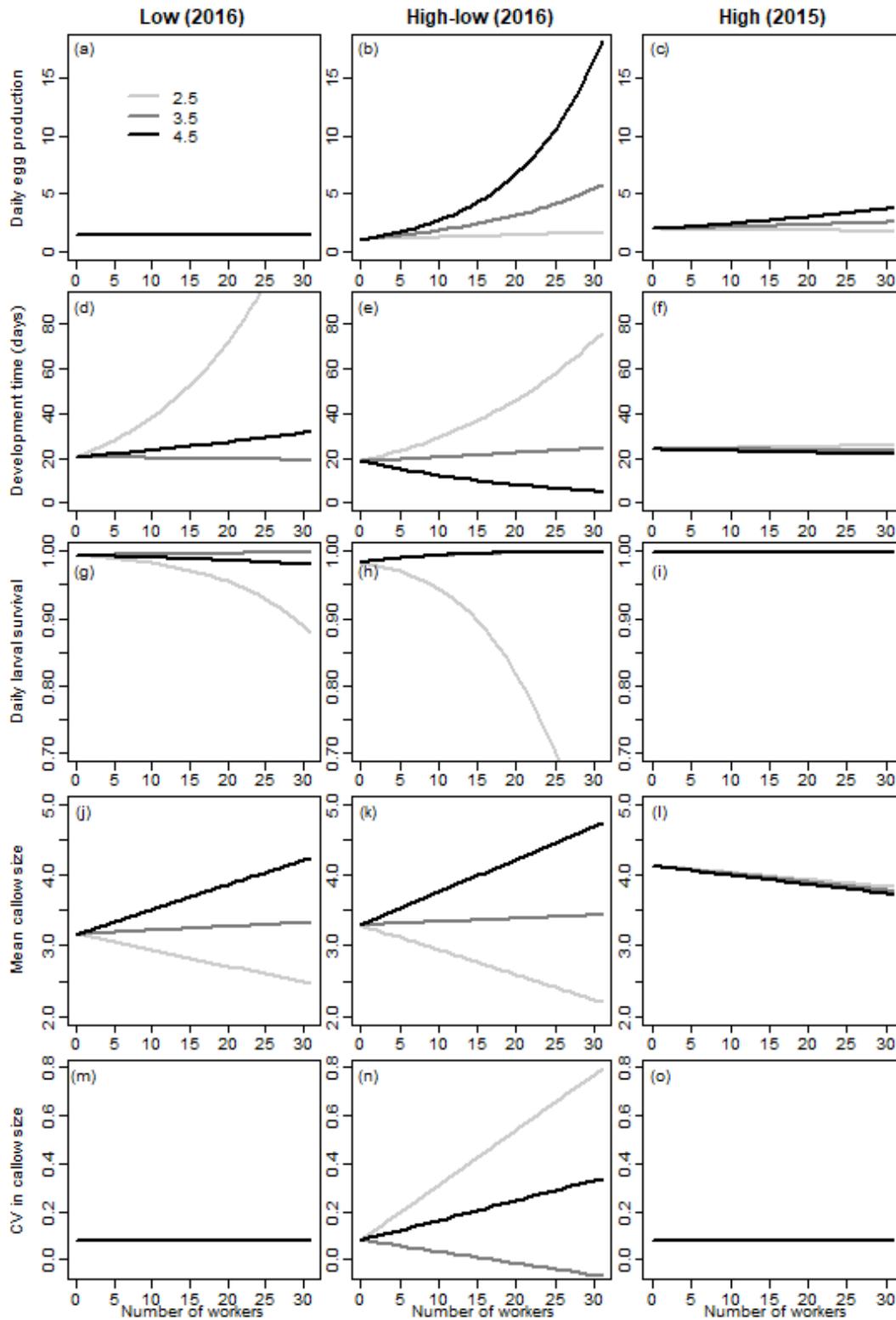


717

718 **Figure 3.** Example of functional linear model results showing the smooth function of the slopes
 719 of Y versus the number of workers as a function of worker size, x . Y covariate could be one of the
 720 five metrics of worker production: egg production, larval development time, larval survival, and
 721 mean and variance in callow size. We illustrate the following examples: (a) no size-based per
 722 capita effect, but more workers of any size increases ($\beta_0 > 0$) or decreases ($\beta_0 < 0$) Y ; (b) positive
 723 size-based per capita effects on Y ; (c) negative size-based per capita effects on Y ; and (d) mixed
 724 size-based per capita effects, i.e., more workers of one size have negative effects and more
 725 workers of another size have positive effects. The dotted line on each panel represents no per
 726 capita effects of workers.



728 **Figure 4.** Generalized additive model results depicting the smooth function of the [size-specific](#)
729 slopes for all five vital rates [relating to worker production](#) versus the number of workers of size x
730 for the low (left), high-low (middle), and high (right) resource environments. Dashed horizontal
731 line at zero represent deviations from mean slope values, i.e. slopes above the line means more
732 workers of size x have positive impact on Y . [Grey dashed vertical line represents the mean](#)
733 [worker size for colonies in each of the resource environments](#). Plots with a significant smooth
734 term of WSC are labeled with $P < 0.01$. Note different scales on the Y-axes in each row.



735

736 **Figure 5.** The relationship between number of workers of three observed worker sizes and the

737 five vital rates relating to worker production across the three treatments. Three workers sizes

738 range from the smallest size of 2.5 mm (light grey), intermediate size of 3.5 mm (dark grey), and
739 largest size of 4.5 mm (black line) that are observed in colonies across all three treatments. Each
740 of these lines represents the function defined by $x = 2.5, 3.5$ and 4.5 on the x-axis of figure 4.
741 Parametric intercepts were used from the GAMs, and intercepts were averaged on the link
742 function scale if the model had a significant fixed effect of colony.

743 TABLES

744 **Table 1.** dAIC values for functional linear models using data combined (i.e., no effect of
745 treatment or year) for each daily vital rate.

Vital rates	dAIC (models fit to all data)			dAIC (Pairwise comparisons) ¹		
	<i>Combined</i>	<i>By treatment</i>	<i>By year</i>	<i>Low vs High-low</i>	<i>Low vs High</i>	<i>High-low vs High</i>
Daily egg production	23.1	0	6.4	6.4	15.6	7.9
Development time (days)	352.7	0	48.2	5.2	96.8	272.3
Daily larval survival	24004.1	23.2	0	-23.1	12568.6	17488.6
Mean callow size	10.8	3.1	0	-3.1	7.7	1.25
CV in callow size	41.4	0	11.5	11.5	34.2	40.8

¹ AIC of models fit to data from both groups together, minus AIC of models fit to data from each treatment group separately. Positive values indicate significant differences between groups.

747 **Table 2.** Size-specific relationships of the smooth terms of colony age, the number of workers of
748 each size (i.e. worker size composition, WSC), and standardized (“std”) WSC for each of the
749 five vital rates relating to worker production. Relationship descriptions provided are restricted
750 over the observed range of worker body sizes and colony ages including days spent in the
751 laboratory. Since colony age and population size are correlated, we were unable to determined
752 which smooth term was driving these effects if both smooth terms have similar effects. Shaded
753 cells had a significant fixed effect of colony ID on the parametric intercept in the GAM.

Response variable	Resource environment	Sample size	Smooth terms			Confounding effects ²
			Colony age	WSC ¹	Std WSC ¹	
Egg production	<i>Low</i>	72	Concave	×, ×	×, ×	
	<i>High-low</i>	74	Concave	±, ↑	±, ↑	Possibly
	<i>High</i>	65	Concave	±, ↑	±, ↑	No
Development time	<i>Low</i>	541	Multimodal	±, ↓	±, ↓	Possibly
	<i>High-low</i>	974	Concave	±, ↓	±, ↓	Possibly
	<i>High</i>	1108	Convex	±, ↓	±, ↓	Possibly
Larval survival	<i>Low</i>	3521	Multimodal	±, ↓	±, ↓	Yes
	<i>High-low</i>	6045	Decreases	±, ↑	±, ↓	Yes
	<i>High</i>	5364	Convex	-, ×	-, ↑	Yes
Mean callow size	<i>Low</i>	65	Decreases	±, ↑	±, ↑	Yes
	<i>High-low</i>	59	Multimodal	±, ↑	±, ↑	Yes
	<i>High</i>	57	Multimodal	-, ×	-, ↑	Yes
CV in callow size	<i>Low</i>	65	Concave	×, ×	×, ×	
	<i>High-low</i>	59	Multimodal	±, ↓	±, ↓	No
	<i>High</i>	57	Constant	×, ×	×, ×	

¹For WSC and std WSC, the first symbol refers to whether the relationship has a positive (+), negative (-), mixed (±), or no (×) per capita effect, and the second symbol refers to whether the relationship increases (↑), decreases (↓), both (↓), or has no effect (×) with worker size. Sample sizes are also provided for each of the five vital rates.

²The column “confounding effects” describes whether both colony age and WSC had similar effects on the response variable when both smooth terms are significant.