

Bumblebee worker body size affects new worker production in different resource environments

Running headline: Size polymorphism effects on worker production

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1 ABSTRACT

2 1. Behavior and organization of social groups is thought to be vital to the functioning of
3 societies, yet the contributions of various roles within social groups have been difficult to
4 quantify. A common approach to quantifying these role-based contributions is evaluating the
5 performance of individuals at conducting certain roles, these studies ignore how these
6 performances might scale up to effects at the population-level. Manipulative experiments are
7 another common approach to determine population-level effects, but they often ignore potential
8 feedbacks associated with these various roles.

9 2. Here, we evaluate the effects of worker size distribution in bumblebee colonies on worker
10 production, using functional linear models. Functional linear models are a recent correlative
11 technique that has been used to assess lag effects of environmental drivers on plant performance.
12 We demonstrate potential applications of this technique to explore contributions of social
13 animals to ecological phenomenon.

14 3. We found that the worker size distribution differentially affected new worker production
15 across three resource environments. Specifically, more larger workers had mostly positive effects
16 and more smaller workers had negative effects on worker production. Most of these effects were
17 only detected under low or fluctuating resource environments suggesting that the advantage of
18 colonies with larger-bodied workers becomes more apparent under stressful conditions.

19 4. We demonstrate the wider ecological application of functional linear models. We
20 highlight the advantages and limitations when considering these models, and how they are a
21 valuable complement to many of these performance-based and manipulative experiments.

22

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

25 INTRODUCTION

26 In animal societies, individuals are often observed performing different tasks, such as
27 guarding nests and burrows (Clutton-Brock *et al.* 2001a), nursing and caring for young
28 (Wilkinson 1992; Kerth 2008; Sparkman *et al.* 2011), or reproducing (Jarvis 1981; Faulkes &
29 Bennett 2001). The roles within these social groups are commonly assigned based on the age
30 (Jarvis 1981; Seeley & Kolmes 1991; Brent *et al.* 2015; Zöttl *et al.* 2016), size (Porter &
31 Tschinkel 1985; Wenzel 1992; Schwander, Rosset & Chapuisat 2005; Goulson 2009), and/or
32 status (Frank 1986; Sparkman *et al.* 2011) of individuals. For example, in Meerkats, which are
33 cooperative breeders, younger non-breeding individuals often stand on ‘sentinel duty’ during
34 group foraging bouts and care for offspring of the dominant breeding pair (Clutton-Brock *et al.*
35 2001b; Clutton-Brock *et al.* 2002; Clutton-Brock, Russell & Sharpe 2004). Without the co-
36 operation of these non-breeders, the survival of individuals within the colonies is likely to
37 decrease, particularly for the young (Doolan & Macdonald 1999; Russell *et al.* 2007). This social
38 behavior and organization is often assumed to be vital to the functioning and survival of these
39 societies.

40 The most common approach to understanding the contribution of roles within social
41 groups is to observe the behavior and performance of individuals. However, most observational
42 performance-based investigations do not quantify the contribution of individuals that perform
43 certain roles to the functioning of the society. To attempt to tackle the challenges associated with
44 quantifying trait-based contributions, a few studies have manipulated colonies in the laboratory
45 to evaluate the effects of the social organization of age- and size- polymorphic species, such as
46 mole rats (Jarvis 1981; Zöttl *et al.* 2016), ants (Porter & Tschinkel 1985; Billick & Carter 2007),
47 and bumblebees (Cnaani & Hefetz 1994; Jandt & Dornhaus 2009; Couvillon *et al.* 2010; Jandt &

48 Dornhaus 2011; Jandt & Dornhaus 2014). In laboratory colonies of a eusocial ant *Pheidole*
49 *dentata*, larvae gained more mass when reared by older workers, suggesting that older workers
50 contribute more towards worker production in these ant colonies than their younger sisters
51 (Muscedere, Willey & Traniello 2009). However, colonies within these laboratory experiments
52 were not faced with the same external environmental stressors as those in the wild. In the case of
53 bumblebees, larger workers are more susceptible to predators and parasites (Cartar & Dill 1991;
54 Muller, Blackburn & Schmid-Hempel 1996; Malfi & Roulston 2014), despite being better
55 foragers. Therefore, the behaviors of social organism under artificial conditions might not
56 capture all the feedbacks associated with size or age-based roles.

57 A recent statistical approach called functional linear models (FLMs) provides an
58 alternative method of inference to manipulative laboratory experiments. FLMs can evaluate the
59 contributions of age- or size-based roles within societies using observational data. FLMs assume
60 that the effect of a predictor variable (e.g. number of workers) on a response variable (e.g. egg
61 production) is a smooth function of some feature of the predictor variable (e.g. size of workers).
62 Past applications of FLMs in ecology have investigated environmental drivers of plant
63 population dynamics (Teller *et al.* 2016; Tenhumberg *et al.* 2018). These studies evaluated the
64 effects of environmental conditions (e.g. precipitation) on plant performance (e.g. growth)
65 assuming the slope of the effect of environmental conditions and plant performance varies as a
66 smooth function of the time lag between conditions and performance (e.g. precipitation in the
67 past 1, 2, 3... months). For example, the slope of precipitation versus plant growth could go from
68 positive in recent months to zero at longer time lags. This method has potential for wider
69 ecological application to investigate life history phenomena. Here, we explore application of

70 FLMs to quantifying the relationship between aspects of new worker production as a function of
71 the body size of existing workers in bumblebee colonies.

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

88 No studies have found smaller bumblebee workers to be better at performing tasks
89 essential to colony function. However, smaller workers are more resilient to starvation
90 (Couvillon & Dornhaus 2010). Therefore, their value may become more apparent when food
91 resources are limiting. In addition, smaller workers have lower production costs, so may be more
92 cost-effective (Kerr, Crone & Williams 2019). Here, we used FLMs to evaluate the contribution

93 of worker size polymorphism to worker production in bumblebee colonies under three different
94 resource environments: a low resource environment; an environment with an early season pulse
95 followed by low resources ('high-low'); and a high resource environment. We looked at five
96 vital rates relating to worker production: (1) number of new eggs laid, (2) development time, (3)
97 larval survival, and (4) mean and (5) variance in worker emergence size, i.e. the size of callow
98 workers. By evaluating the contribution of different-sized workers under different resources
99 environments to worker production, we can assess whether larger workers are more beneficial
100 when resource conditions are more favorable and whether the benefit of small workers to
101 colonies is only seen when resources are low, making both production cost and resistance to
102 starvation a premium.

103

104 MATERIALS AND METHODS

105 *Study species and sites*

106 We hand reared *Bombus vosnesenskii* colonies from wild-caught queens collected at the
107 University of California McLaughlin Reserve (N38 52 25.74, W122 25 56.25) in early spring
108 2015 and 2016 while they searched for nest sites. These colonies are the same as used for other
109 studies (Kerr, Crone & Williams 2019; Malfi, Crone & Williams 2019), so we only briefly
110 describe the rearing process here.

111 In 2015 and 2016, we hand-reared colonies in the laboratory in a dark room at 26-28°C for
112 6 to 9 weeks until their second or first cohort of worker bees eclosed. In 2015, we relocated
113 seven colonies outside (N38 32 12.21, W121 47 16.95) at the Harry H. Laidlaw Jr. Honey Bee
114 Research Facility (Davis, CA), where the surrounding landscape consisted of agricultural crops,
115 floral research plots, and a 0.2 ha pollinator garden (Fig. S1a). In 2016, we relocated 14 colonies

116 outside in agricultural fields at UC Davis Experimental Farm property (N38 31 32.3, W121 46
117 56.54). Half of the colonies ($n = 7$) had access to flight cages that provided a pulse of native
118 California wildflower species for ~4 weeks early in the season (“pulse” treatment) and the other
119 half had no supplemental forage (“control” treatment) (Malfi, Crone & Williams 2019). The
120 surrounding landscapes were croplands consisting of mainly non-flowering cereals, corn, and a
121 strip of riparian habitat (Fig. S1b).

122 In this study, we broadly categorized the resource environments experienced by our
123 experimental colonies in each of these years according to the amount of available forage. The
124 2015 colonies, located next to a pollinator garden at the Honey Bee Research Facility, had the
125 highest resource availability (“high”), colonies in the 2016 pulse treatment had the second
126 highest resource availability (“high-low”), and colonies in the 2016 control treatment had the
127 lowest availability (“low”). These three environments will now be referred to as high, high-low,
128 and low.

129

130 *Brood mapping*

131 Each week, we photographed the brood from multiple angles (aerial, side, diagonal) to fully
132 capture all brood cells. We individually numbered each brood cell as it differentiated and tracked
133 the fate of all marked cells throughout colony development (Fig. 1). We classified each living
134 brood cell into five categories: (1) clump stage, which represents the egg stage where individual
135 cells have not yet differentiated; (2) pre-differentiated stage, which represents early larval instars
136 where individual cells have begun differentiating; (3) differentiated stage, which represents later
137 larval instars where individual brood cells are clearly differentiated; (4) cocoon stage, where
138 cells have darkened indicating that pupa have spun their cocoons; and (5) eclosed stage, where

139 cell has opened and an adult worker emerged (Fig. 2 for stages). We also had two other
140 categories: (6) dead, where we have observed a dead cell, and (7) unseen, where the cell can no
141 longer be seen in the brood photos.

142 Some brood clumps did not develop into distinct cells before the end of brood mapping,
143 while other clumps died before cell partitioning. Rather than exclude these indistinct, dead, or
144 undeveloped brood clumps in our analyses, which could result in underestimating egg production
145 and overestimating larval survival, we estimated the number of cells for these clumps. We did
146 this by classifying these indistinct brood clumps into five size categories (tiny, small, medium,
147 large, extra-large) based on comparisons with similarly-sized brood clumps that did divide into
148 individual cells and assigning the mean value of cells for these size categories to indistinct
149 clumps.

150 From the brood mapping, we estimated three vital rates: egg production, larval development
151 time, and larval survival. We considered weekly egg production to be the number of newly
152 visible cells in either clump or pre-differentiated stages. We assumed that the number of distinct
153 cells formed by a brood clump represented the total number of eggs laid, i.e. no eggs died before
154 larval cells differentiated. We calculated development time for each cell as the number of days
155 from when it was first seen as an egg (defined as the ‘clump’ stage) to when it was first seen as
156 an eclosed cell. Cells that were not detected in the clump stage or that disappeared from view
157 before visibly eclosing were excluded from our analyses of larval development time. Finally, we
158 classified larval survival as the success of each cell reaching eclosion. We excluded 43 unseen
159 brood cells from our larval analyses because more than 8 days (50% the normal bumblebee
160 development time) passed between photos of them so their fates could not be unambiguously

161 mapped. These represent 10% of 437 unseen cells or 1% of all 4,640 cells mapped across the 21
162 colonies and three resource environments.

163

164 *Worker surveys*

165 We conducted weekly night-time surveys to estimate the mean and standard deviation in
166 the size of newly emerged workers (hereafter referred to as “callow size”). We assigned each bee
167 a unique tag using a combination enamel paint and numbered, color-tags or Microsensus radio-
168 frequency identification (RFID) tags (Kerr, Crone & Williams 2019; Malfi, Crone & Williams
169 2019). For each newly emerged (“callow”) worker, we estimated body size by measuring
170 intertegular (IT) span to the nearest 0.01 mm using digital calipers (Cane 1987; Hagen & Dupont
171 2013) and wet weight to the nearest 0.01 mg using analytical microbalance (Mettler Toledo
172 XS205DU). The size of each worker at initial capture was used to estimate the mean and
173 standard deviation in callow size. We used these size measurements in combination with
174 presence/absence data to determine the number of workers of each size (now referred to as
175 “worker size composition”) present in each colony for each week of the survey in order to
176 evaluate the effects of worker size composition on aspects of worker production.

177

178 *Functional linear models*

179 We used functional linear models (FLMs) to estimate how five vital rates varied with
180 worker size composition. FLMs are a type of regression spline that allows a covariate to vary
181 smoothly over a continuous domain (Ramsay & Silverman 2005; Ramsay, Hooker & Graves
182 2009). Therefore, instead of restricting our predictors (X) to unidimensional space (i.e. simple
183 linear models, such as total worker number predicts number of eggs), we can evaluate the effect

184 of the number of workers on some response variable (e.g. number of eggs) as a continuous
185 function of worker size (i.e. a separate attribute of the predictor variable), such that the smooth
186 function of size-specific slopes versus worker size can be described as:

$$187 \quad E(Y) = \beta_0 + \sum_{x=1}^{\max(x)} \beta(s_x)W(n_x) \quad (1)$$

188 where $E(Y)$ is the expected value of the response variable Y (e.g. number of eggs); β_0 is the
189 intercept; $W(n_x)$ is the number of workers n of size x ; and $\beta(s)$ is the slope of Y versus the
190 number of workers of each size category x (c.f. methods in Teller *et al.* 2016). Here, the
191 continuous attribute (i.e. worker size) of the predictor variable (i.e. number of workers) is
192 discretized into many size categories (14 size categories for both low and high-low, and 17 for
193 high resource colonies) to approximate a continuous distribution of sizes (i.e., the worker size
194 composition). The expected value of the response variable is the sum of the product of the size-
195 specific slopes $\beta(s_x)$ multiplied by the number of workers of size x (Fig. 3). If the slope of Y
196 versus the number of workers of size x is positive, then more workers of size x increase values of
197 Y and vice versa when the slope is negative (Fig. 3).

198 We parameterized the smooth functions of the size-specific slopes using general additive
199 models (GAMs). We fit our GAMs using the cubic spline basis for all smooth covariates, so that
200 the coefficients will be set to 0 if our covariates have no effects on the response (see Zuur 2012,
201 for an excellent textbook introduction to GAMs). For new eggs laid, we used worker size
202 composition in the previous week to predict the number of eggs laid in the present time step for
203 our size composition FLMs. For the other three vital rates, we quantified worker size
204 composition as the average number of workers in each size category across their larval
205 development period.

206 Models were fit separately to data from each study (i.e. low, high-low, and high resource
207 environments), and we included colony ID as a fixed effect (i.e. a different intercept term for
208 each colony) for each model. We used negative binomial GAMs to account for overdispersion
209 for estimating new eggs laid and development time. We offset the number of new eggs laid by
210 the number of days between brood photos. We used binomial and Gaussian-distributed GAMs
211 for larval survival and callow size, respectively. We parameterized the binomial GAMs for
212 estimating larval survival using successes and failures, where the total number of trials was
213 defined as the number of days between brood photos, and the number of failures was defined as
214 “1” if the cell died and “0” if it survived. We restricted the number of knots for our smooth terms
215 of the number of workers of size j to a maximum of five. We also rejected any model structure
216 that did not produce unimodal functions for our smooth term of worker size composition, since
217 GAMs are prone to overfitting, and multimodal functions generally did not appear to be
218 biologically meaningful. We used likelihood ratio tests to assess the fit of the parametric
219 intercept term and the number of knots for each smooth term in our models given our data. We
220 ran these general additive models (using `mgcv::gam`; Wood 2004; Wood 2011) in program R (R
221 Core Team 2017). We repeated all analyses with slopes scaled to worker production costs, rather
222 than numbers of individuals. Because these results were largely parallel (Appendix S2), we do
223 not discuss them further.

224 Colony size (i.e. number of observed workers) increased with colony age across three
225 resource environments (Fig. S2-4). To avoid potentially confounding effects due to collinearity
226 between colony age and worker number, we ran models separately with colony age and worker
227 size composition as predictors of various measures of worker production success. Results for
228 colony age are described in Appendix S1. Relationships between worker survival and larval

229 survival and mean callow size in the low resource environment were somewhat confounded with
230 colony age effects, and should be interpreted with caution (Table 1, Appendix S4). We found no
231 evidence for other pairwise relationships for colony age, worker number, mean worker size, and
232 standard deviation in worker size across the three resource environments.

233

234 RESULTS

235 Average worker size increased with available ambient resources. Malfi et al (2019) report
236 smaller worker size in the low (mean and SE in IT span: 3.19 ± 0.03) than the high-low (IT span:
237 3.32 ± 0.06) resource environment. Consistent with this pattern, workers were largest in the high
238 resource environments (IT span: 3.68 ± 0.04).

239

240 *Daily egg production*

241 Worker size composition did not affect egg production in the low resource environment
242 (Fig. 4a; low $-\chi^2 = 1E-4$, d.f = $5.1E-5$, $P = 0.15$). More larger workers increased egg production
243 in both the high-low and high resource environments (Fig. 4b-c; high-low $-\chi^2 = 11.5$, d.f. = 1.1,
244 $P < 0.001$; high $-\chi^2 = 5.6$, d.f. = 1.1, $P = 0.01$), but more larger workers had greater impact on
245 egg production in the high-low resource environment than in the constantly high resource
246 environment.

247

248 *Larval development time*

249 Larval development time decreased with more larger workers in the low and high-low
250 resource environments (Fig. 4d-e; LR test of smooth term vs constant: low $-\chi^2 = 108.8$, d.f. =
251 2.15, $P < 0.001$; high-low $-\chi^2 = 200.7$, d.f. = 2.71, $P < 0.001$). In the high resource environment,

252 more workers of any size seemed to marginally increase development time (Fig. 4f; high - $\chi^2 =$
253 14.4, d.f. = 1.45, $P < 0.001$); however, these effects are negligible compared to the effects of
254 worker size composition in the low and high-low resource environments (Fig. 4d-f).

255

256 *Larval survival*

257 Larval survival decreased with more smaller workers in the low and high-low resource
258 environments (Fig. 4g-h; low - $\chi^2 = 78$, d.f. = 2.2, $P < 0.001$; high-low - $\chi^2 = 21.6$, d.f. = 1.8, $P <$
259 0.001), but more of the largest observed workers had no effect on larval survival. Larval survival
260 slightly decreased with more workers in the high resource environment, particularly with more
261 larger workers (Fig. 4i; high - $\chi^2 = 22.3$, d.f. = 1.5, $P < 0.001$).

262

263 *Callow size*

264 In the low resource environment, mean callow size increased with more larger workers
265 and decreased with more smaller workers (Fig. 4j; $F = 2.5$, d.f. = 1.78, $P = 0.018$), but worker
266 size composition was unrelated to standard deviation of callow size (Fig. 4m; low - $F = 2.3E-7$,
267 d.f. = 3.9E-6, $P = 0.74$). In the high-low resource environment, worker size composition had
268 little to no effect on mean callow size (Fig. 4k; $F = 0.7$, d.f. = 0.61, $P = 0.068$), whereas more
269 larger workers slightly decreased the standard deviation in callow size (Fig. 4n; high-low - $F =$
270 2.6, d.f. = 1.75, $P = 0.016$). In the high resource environment, more workers of any size
271 decreased the mean callow size (Fig. 4l; $F = 17.3$, d.f. = 1.7, $P < 0.001$), whereas worker size
272 composition did not affect standard deviation in callow size (Fig. 4o; high - $F = 0.7$, d.f. = 0.66,
273 $P = 0.06$).

274

275 DISCUSSION

276 Size polymorphism in bumblebee colonies had different effects on worker production
277 vital rates under different resource environments. Overall, colonies with more larger workers
278 often had greater worker production compared to colonies with smaller workers. This pattern is
279 similar to many performance-based (Goulson *et al.* 2002; Spaethe & Weidenmüller 2002; Peat &
280 Goulson 2005; Ings 2007; Kapustjanskij *et al.* 2007; Spaethe *et al.* 2007) and manipulative
281 experiments (Cnaani & Hefetz 1994). We found the opposite effect in two cases: more larger
282 workers slightly decreased larval survival and more workers of any size decreased mean callow
283 size in the high resource environment. We also never detected stronger per capita benefits of
284 smaller workers relative to larger workers. We discuss each result in turn below, as well as some
285 advantages and limitations of functional linear models.

286

287 *Functional implications of worker size distribution*

288 Across social organisms, offspring number often increases with the number of helpers
289 (Brown *et al.* 1982; Malcolm & Marten 1982; Biedermann & Taborsky 2011; Young *et al.*
290 2015), particularly when resources are high (Harrington, Mech & Fritts 1983; Doolan &
291 Macdonald 1997). We found a similar impact on colony egg production in our high-low and high
292 resource treatments, yet FLMs also revealed that in these environments more larger workers
293 increased colony egg production relative to more smaller workers. Laboratory studies of
294 bumblebees have shown that colonies consisting of only larger workers produce more eggs than
295 colonies consisting of only smaller workers (Cnaani & Hefetz 1994). Larger workers are known
296 to return more resources to the colony (Goulson *et al.* 2002; Kerr, Crone & Williams 2019), but
297 they are less resilient against starvation (Couvillon & Dornhaus 2010). This tradeoff might

298 explain why larger workers increased colony egg production only in the high-low and high
299 resource environment. The opposite effect has been found in a fire ant, *Solenopsis invicta*, where
300 monomorphic colonies of large workers produced almost no brood compared to monomorphic
301 colonies of small workers (Porter & Tschinkel 1985). However, the size-based roles of workers
302 in these two eusocial insects differs. Larger bumblebees are foragers (Cumber 1949; Goulson *et*
303 *al.* 2002; Goulson 2009), but smaller fire ant workers do most of the foraging and feeding
304 (Wilson 1978; Cassill & Tschinkel 1999). Larger fire ant workers live longer than smaller
305 workers (Porter & Tschinkel 1985; Calabi & Porter 1989), which is the opposite of bumblebee
306 workers (da Silva-Matos & Garofalo 2000; Kerr, Crone & Williams 2019). Therefore, the
307 general mechanism may be similar, in spite of contrasting patterns.

308 In contrast to conclusions for egg production, more larger workers had either beneficial
309 or neutral effects on development time and larval survival only in low and high-low
310 environments, whereas more smaller workers had negative impacts on these vital rates. In
311 bumblebees, there seems to be a resource-driven trade-off between provisioning for developing
312 larvae and production of new eggs when resources are low; i.e., more larger workers under low
313 resources maintain similar larval development time that is comparable to colonies under high
314 resources at the cost of no apparent increase in egg production. Results for small workers in
315 these colonies are similar to those for cooperative breeding species, in which the presence of
316 more helpers often reduces offspring survival when resources are low (Harrington, Mech & Fritts
317 1983; Woodroffe & Macdonald 2000). These negative impacts of helpers in cooperative
318 breeding species may be due to them shifting efforts towards increasing their own survival
319 (Bruintjes, Hekman & Taborsky 2010), which seems less likely in bumblebees because workers
320 are non-reproductive. Indeed, bumblebee workers are reported to switch from nursing to foraging

321 tasks when resources are low (Cartar 1992), indicating that workers overall increase (not
322 decrease) cooperative efforts. Additionally, bumblebee workers predominantly feed on nectar
323 and larvae predominantly feed on pollen (Plowright & Pendrel 1977; Goulson 2009), which may
324 reduce competition among siblings and enhance cooperative behaviors. It would be interesting to
325 monitor foraging behavior of bumblebee workers during resource dearths, i.e. changes in nectar
326 vs. pollen collection rates, to better understand their cooperative efforts. Life history and level of
327 sociality might play a role in determining the cooperative efforts of individuals, where long lived
328 species can afford to either reduce offspring number or cooperative behaviors towards offspring
329 when resource are low.

330 Across our three environments, observed average size of all workers decreased in
331 colonies with less available resources. In the low resource environment, more smaller workers
332 resulted in callow workers of smaller sizes. Bumblebee workers have been recorded to be
333 smaller on average in simple, intensively managed landscapes (Persson & Smith 2011).
334 Laboratory experiments also show that colonies produce smaller workers during food shortages
335 (Schmid-Hempel & Schmid-Hempel 1998). The correlation between worker size distribution and
336 callow worker size suggests that stressful resource conditions may produce a negative feedback
337 loop, where colonies of smaller workers cannot properly feed and care for brood (Cartar & Dill
338 1991) causing the emergence of smaller callow workers. Therefore, the cost and benefits of
339 helpers within social groups may often regulate the traits of individuals (e.g. sex ratios, worker
340 sizes) that are expressed (Griffin, Sheldon & West 2005). Functional linear models are only a
341 correlative technique, so an alternative shared driver could be shifting the size distribution
342 towards smaller workers. For example, lower resources could cause differential mortality of
343 larger workers due to starvation (Couvillon & Dornhaus 2010) and cause larvae to develop into

344 smaller callow workers because of fewer resources brought back by the remaining workers.
345 Laboratory monomorphic colonies consisting of only small or large workers had no difference in
346 the mean and variance in callow size when supplied with abundant resources (Cnaani & Hefetz
347 1994). If these laboratory colonies had to forage for resources and still produced workers of
348 similar sizes, then we might be able to determine whether a shared driver is most likely causing
349 these effects in our study.

350

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

352 Previously, FLMs have been used to evaluate the lagged effects of environmental drivers
353 on plant population dynamics (Teller *et al.* 2016; Tenhumberg *et al.* 2018). Here, we extend the
354 use of FLMs to evaluate the size-based contribution of workers in bumblebee colonies. FLMs
355 could be applied to understanding individual contributions in many high-dimensional social
356 systems. For example, they could be used to explore the effects of age within social groups of
357 different taxa and levels of sociality, such as eusocial honey bees (Seeley & Kolmes 1991), semi-
358 social mole rates (Jarvis 1981; Zöttl *et al.* 2016), and cooperative breeding meerkats (Clutton-
359 Brock *et al.* 2001a) or cichlid fish (Bruitjes & Taborsky 2011). In the African mole rat, larger
360 groups had higher rates of offspring recruitment (Young *et al.* 2015) and cooperative behaviors
361 were found to increase with age (Zöttl *et al.* 2016). Therefore, FLMs might be able to determine
362 how vital rates (e.g. offspring recruitment) differ with the number of helpers of different ages for
363 the African mole rate. FLMs provide an alternative way to study these high-dimensional
364 ecological systems using field observational data, particularly where manipulative experiments
365 may not be possible.

366 Correlative techniques, such FLMs, provide a valuable complement to many
367 manipulative experiments that aim to test similar hypotheses. However, these separate
368 approaches have their own set of advantages and limitations that need to be considered when
369 making conclusions about these high-dimensional systems such as lagged effects or size
370 polymorphism. For example, FLMs can be data-heavy (e.g., 20-25 independent observations of
371 the signal and response; Teller *et al.* 2016); only inform us about correlations and not causations;
372 and may have collinear predictors that obscure the true driver of these responses.

373 Collinearity is not specific to FLMs but is equally problematic for many simple (e.g.
374 multiple regression) and complex statistical techniques (e.g. structural equation models). To date,
375 only two studies have reported applying functional smoothing approaches to high-dimensional
376 ecological systems by exploring how lagged environmental drivers influence plant performance
377 (Teller *et al.* 2016; Tenhumberg *et al.* 2018). Teller *et al.* (2016) predicted how lagged effects of
378 past precipitation and local competition influenced plant growth and survival; however, they
379 would not be able to parse out the true driver of plant performance if density and precipitation
380 covaried across some gradient. In our study, colony age and worker size composition had similar
381 effects for half of our vital rates ($n = 8$ of 15) across the three resource environments. When
382 exploring the trends and collinearity for these several vital rates (Appendix S4), two of four vital
383 rates (Table 1) had confounding effects of colony age and size composition suggesting that either
384 or both might be driving these trends (Table 1). When using simple or complex correlative
385 methods, it is important to explicitly evaluate the collinearity of predictor variables as we have
386 demonstrated here.

387

388 *Summary*

389 Overall, we found that the advantages and disadvantages of workers of different sizes on
390 worker production only became apparent when exploring these effects across these three
391 different resource environments. We also found that bumblebee colonies shifted their worker
392 size distribution across these resource environments. Among eusocial insects, caste size
393 polymorphism is hypothesized to be an adaption to expand accessibility of resources, such as
394 seed size in ants (Davidson 1978; Traniello & Beshers 1991; Retana & Cerdá 1994) and flower
395 size in bumblebees (Peat, Tucker & Goulson 2005). However, the shift in worker size
396 distribution across these resource environments could have emerged from the lower tolerance of
397 larger workers to starvation (Couvillon & Dornhaus 2010). Prior to this study, quantifying the
398 contribution of individuals in social groups has been challenging. Here, we demonstrate that
399 functional linear models are not constrained to evaluating lagged effects on individual
400 performance, but these models are a valuable complement to manipulative experiments and have
401 the potential to explain many complex, trait-based life histories of social organisms.

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407

408 AUTHOR CONTRIBUTIONS

409 NZK, EEC and NMW conceived the ideas and designed methodology; NZK, RLM, and
410 NMW collected the data; NZK and EEC analyzed the data; and NZK, EEC, RLM, and NMW
411 wrote the manuscript.

412

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578 **FIGURE LEGENDS**

579

580 **Figure 1.** Example of brood mapping photos used to track the fate of individual cells. These
581 mapping photos are aerial photographs for colony 6 in (a) week 5 and (b) week 6 since the first
582 brood photo. Aerial, side, and diagonal photos were taken to capture all cells. Each cell has been
583 individually numbered to track each cell.

584

585 **Figure 2.** Brood mapping photos showing each of the six categories of living or dead stages of
586 cell development. The six stages are: (a) clump stage, which are egg stages; (b) pre-popcorn
587 stages, which represents early larval instars; (c) popcorn stage, which are late instar larvae; (d)
588 cocoon stage; (e) eclosed stage, and (f) a dead cell (dashed circle). These categories assisted with
589 estimating three vital rates: eggs laid, development time, and larval survival.

590

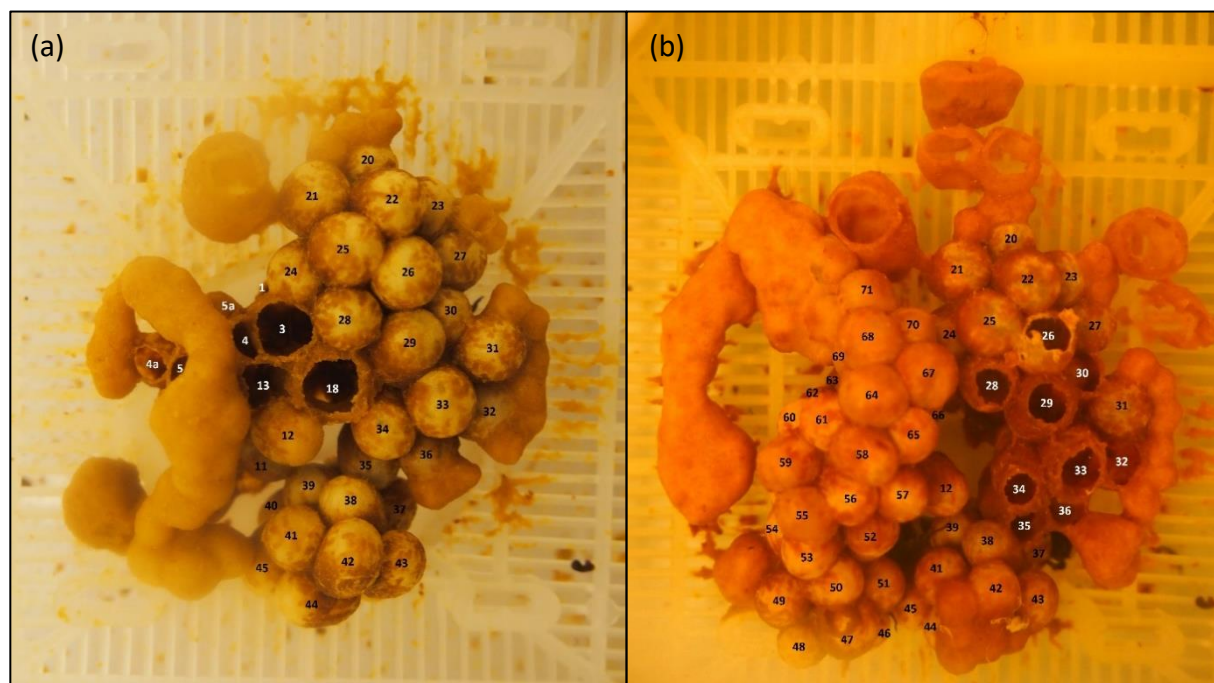
591 **Figure 3.** Example of functional linear model results showing the smooth function of the slopes
592 of Y versus the number of workers of size x as a function of worker size, x . Y covariate could be
593 one of the five metrics of worker production: egg production, larval development time, larval
594 survival, and mean and variance in callow size. We illustrate the following examples, where #
595 number of workers or their size has no effect on Y (solid line); either more workers increases (β_0
596 > 0) or decreases ($\beta_0 < 0$) Y , but size is unimportant (dotted lines); more workers increase Y and
597 larger workers contribute the most (dashed line); and more increase Y and intermediate workers
598 contribute the most (dotted and dashed line).

599

600 **Figure 4.** Generalized additive model results depicting the smooth function of the slopes for all
601 five vital rates versus the number of workers of size x as a function of worker size x for the low
602 (left), high-low (middle), and high (right) resource environments. Worker size was measured as
603 the distance between the tegulae, i.e. intertegular (IT) span in mm. Grey dotted horizontal line at
604 zero represent deviations from mean slope values, i.e. slopes above the line means more workers
605 of size x have positive impact on Y . Plots with a significant smooth term of WSC are labeled
606 with $P < 0.01$. Note different scales on the Y -axes in each row.

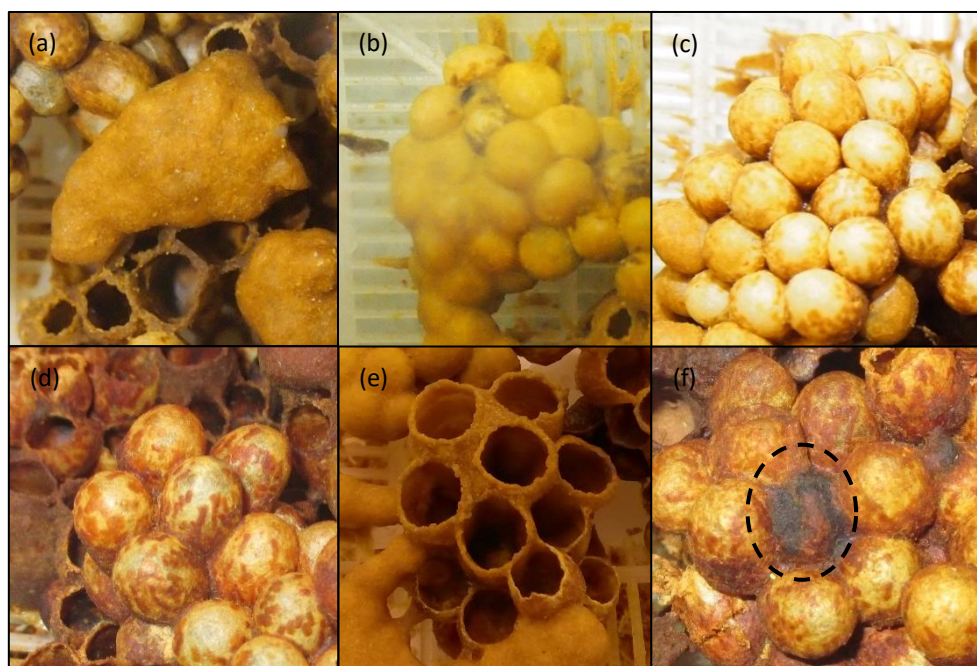
607 FIGURES

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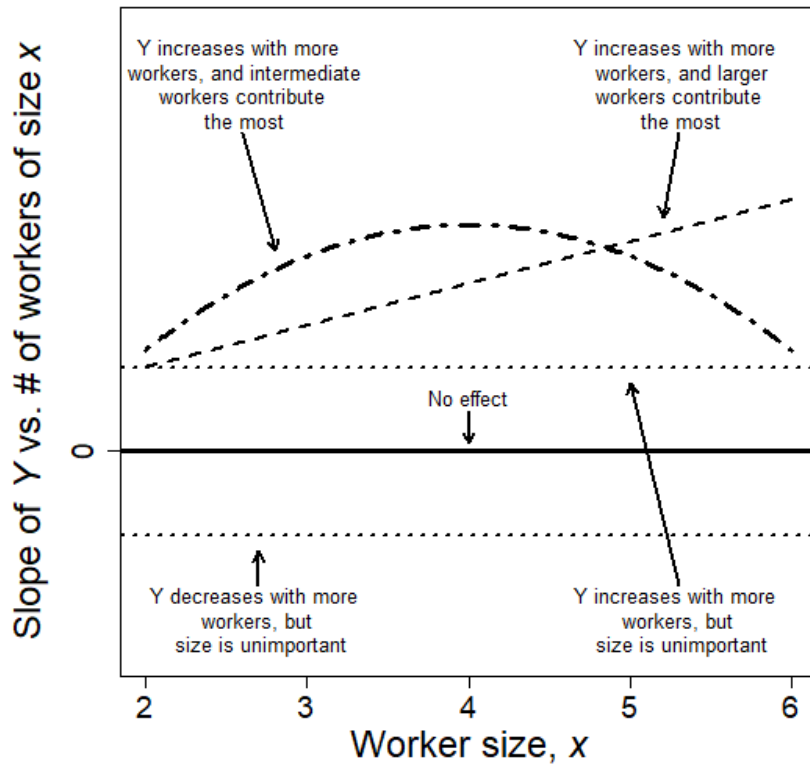
609

610 **Figure 1.** Example of brood mapping photos used to track the fate of individual cells. These
611 mapping photos are aerial photographs for colony 6 in (a) week 5 and (b) week 6 since the first
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613 individually numbered to track each cell.



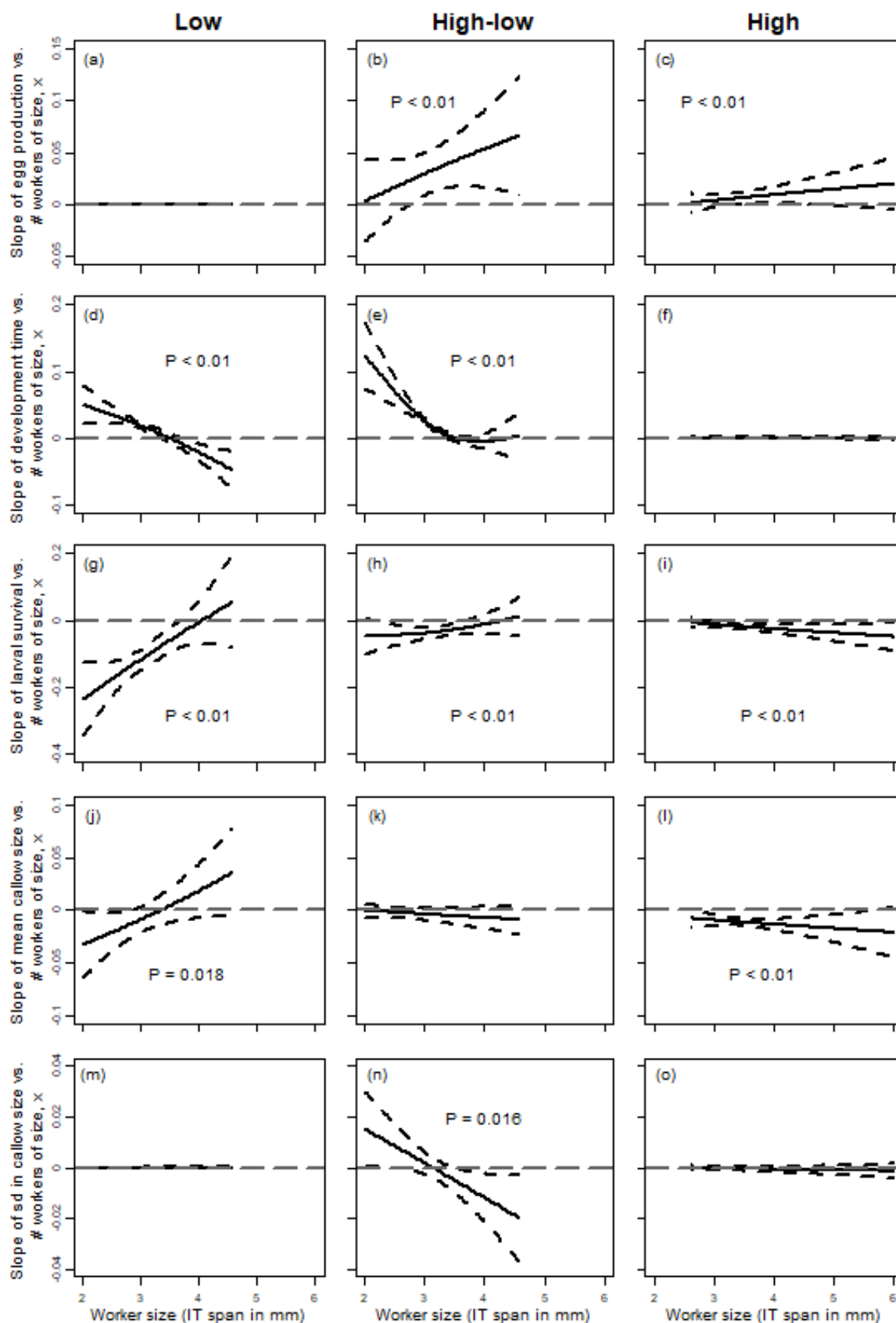
614

615 **Figure 2.** Brood mapping photos showing each of the six categories of living or dead stages of
616 cell development. The six stages are: (a) clump stage, which are egg stages; (b) pre-popcorn
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620

621 **Figure 3.** Example of functional linear model results showing the smooth function of the slopes
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624 survival, and mean and variance in callow size. We illustrate the following examples, where #
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626 > 0) or decreases ($\beta_0 < 0$) Y , but size is unimportant (dotted lines); more workers increase Y and
627 larger workers contribute the most (dashed line); and more increase Y and intermediate workers
628 contribute the most (dotted and dashed line).



630 **Figure 4.** Generalized additive model results depicting the smooth function of the slopes for all
631 five vital rates versus the number of workers of size x as a function of worker size for the low
632 (left), high-low (middle), and high (right) resource environments. Worker size was measured as
633 the distance between the tegulae, i.e. intertegular (IT) span in mm. Grey dotted horizontal line at
634 zero represent deviations from mean slope values, i.e. slopes above the line means more workers
635 of size x have positive impact on Y . Plots with a significant smooth term of WSC are labeled
636 with $P < 0.01$. Note different scales on the Y-axes in each row.

637 TABLES

638 **Table 1.** Relationship of the five vital rates relating to worker production and the smooth terms
 639 of colony age, the number of workers of each size (i.e. worker size composition, WSC), and
 640 standardized (“std”) WSC meaning that we accounted for production costs associated with each
 641 worker size. Relationship descriptions provided are restricted over the observed range of worker
 642 body sizes and colony ages including days spent in the laboratory. The column “confounding
 643 effects” describes whether both colony age and WSC had similar effects on the response variable
 644 when both smooth terms are significant. Since colony age and population size are correlated, we
 645 were unable to determined which smooth term was driving these effects if both smooth terms
 646 have similar effects. Asterisks (*) represents a significant effect of a main effect of colony ID on
 647 the parametric intercept in the GAMs.

Response variable	Resource environment	Smooth terms			Confounding effects
		<i>Colony age</i>	<i>WSC</i>	<i>Std WSC</i>	
Egg production	<i>Low</i>	Concave*	– *	–	–
	<i>High-low</i>	Concave*	Increases*	Increases	Possibly
	<i>High</i>	– *	Increases	Increases	–
Development time	<i>Low</i>	Multimodal*	Decreases*	Decreases	Possibly
	<i>High-low</i>	Concave*	Decreases*	Decreases	Possibly
	<i>High</i>	– *	– *	Decreases	–
Larval survival	<i>Low</i>	Decreases*	Increases*	Increases	Yes
	<i>High-low</i>	Decreases*	Increases*	Increases	Yes
	<i>High</i>	Decreases*	Decreases*	Decreases	No
Mean callow size	<i>Low</i>	Decrease	Increases	Increases	Yes
	<i>High-low</i>	Multimodal*	– *	Decreases	–
	<i>High</i>	Decreases*	Decreases*	–	No
Standard deviation in callow size	<i>Low</i>	–	–	–	–
	<i>High-low</i>	–	Decreases	Decreases	–
	<i>High</i>	–	–	Decreases	–