

The sensitivity of a honeybee colony to worker mortality depends on season and resource availability

Natalie J Lemanski (✉ natalie.lemanski@gmail.com)

University of California Los Angeles <https://orcid.org/0000-0002-4685-5093>

Siddhant Bansal

Rutgers The State University of New Jersey

Nina H Fefferman

University of Tennessee Knoxville

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1 **Title:** The sensitivity of a honeybee colony to worker mortality depends on season and resource
2 availability

3 **Authors:** Natalie J. Lemanski^{1,3*}, Siddhant Bansal¹, and Nina H. Fefferman²

4 ¹Department of Ecology, Evolution, and Natural Resources, Rutgers University, New
5 Brunswick, New Jersey, United States of America

6 ²Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville,
7 Tennessee, United States of America

8 ³Department of Ecology and Evolutionary Biology, University of California, Los Angeles,
9 California, United States of America

10 *Corresponding author. Email: natalie.lemanski@gmail.com. Current address: 4114 Life
11 Sciences Building, University of California, Los Angeles, CA 90024.

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Abstract

28 **Background:** Honeybees have extraordinary phenotypic plasticity in their senescence rate,
29 making them a fascinating model system for the evolution of aging. Seasonal variation in
30 senescence and extrinsic mortality results in a tenfold increase in worker life expectancy in
31 winter as compared to summer. To understand the evolution of this remarkable pattern of aging,
32 we must understand how individual longevity scales up to effects on the entire colony. In
33 addition, threats to the health of honey bees and other social insects are typically measured at the
34 individual level. To predict the effects of environmental change on social insect populations, we
35 must understand how individual effects impact colony performance. We develop a matrix model
36 of colony demographics to ask how worker age-dependent and age-independent mortality affect
37 colony fitness and how these effects differ by seasonal conditions.

38 **Results:** We find that there are seasonal differences in honeybee colony elasticity to both
39 senescent and extrinsic worker mortality. Colonies are most elastic to extrinsic (age-independent)
40 nurse and forager mortality during periods of higher extrinsic mortality and resource availability
41 but most elastic to age-dependent mortality during periods of lower extrinsic mortality and lower
42 resource availability.

43 **Conclusions:** These results suggest that seasonal changes in the strength of selection on worker
44 senescence partly explain the observed pattern of seasonal differences in worker aging in honey
45 bees. More broadly, these results extend our understanding of the role of extrinsic mortality in
46 the evolution of senescence to social animals and improve our ability to model the effects of
47 environmental change on social insect populations of economic or conservation concern.

48

49 **Key words**

50 *Apis Mellifera*, demography, disposable soma theory, evolution of aging, honeybee, life history
51 theory, phenotypic plasticity, resource allocation, senescence, social animals

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56 **Background**

57 A major challenge of life history theory is explaining the great diversity of lifespans and
58 patterns of senescence in the natural world. Senescence, defined as a decline in physiological
59 functioning usually accompanied by an increase in the rate of mortality with age, seems puzzling
60 since natural selection should eliminate traits that reduce survival or fecundity.

61 The main evolutionary explanation of senescence is that a decline in the force of selection
62 with age due to random mortality allows the accumulation of late-acting deleterious mutations
63 [1, 2] or positive selection for genes that are beneficial early in life but detrimental later [3]. One
64 physiological mechanism for this antagonistic pleiotropy is an energetic cost to somatic
65 maintenance [4]. If there is a tradeoff between investment in reproduction and maintenance,
66 selection may favor an optimal level of investment in maintenance that allows some
67 accumulation of damage, resulting in senescence [4–6].

68 Early proponents of the above theories predicted that higher extrinsic mortality should
69 accelerate the decline in selection with age, resulting in increased senescence [1–3]. However,
70 further refinement has led to debate over how the force of selection changes with age and how
71 extrinsic mortality affects the force of selection against senescence. For instance, the effect of
72 extrinsic mortality on senescence depends on the type of density dependence [7]. In addition, the
73 force of selection may not inevitably decline with age and can even increase [8] resulting in
74 negligible or negative senescence [9]. These more nuanced theoretical findings may explain why
75 there has been mixed empirical support for the prediction that higher extrinsic mortality causes
76 faster senescence [10–16].

77 The honeybee (*Apis mellifera*) is a useful model system for empirically testing
78 predictions about how changes in the force of selection influence the evolution of senescence.

79 Honeybees have a remarkable degree of phenotypic plasticity in the rate of aging within the
80 worker caste, with workers having up to a tenfold difference in life expectancy based on season,
81 social environment, and task performance [17–21]. Because of their division of labor and
82 seasonally changing environment, we would expect a large degree of variation in the selective
83 pressure on the senescence of honeybee workers.

84 Although it is recognized that sociality strongly influences the evolution of senescence
85 [22], there is a relative dearth of theory on factors affecting the force of selection against
86 senescence in eusocial organisms. One challenge of understanding senescence in social
87 organisms is that it can be difficult to know how changes in the longevity of individuals will
88 scale up to effects on the whole colony, the relevant unit of selection [23]. Understanding how
89 to estimate the selective pressure against worker senescence in honeybees can thus give us
90 broader insights into the evolution of aging in social systems.

91 The question we therefore seek to address is how seasonal changes in extrinsic mortality
92 and resource availability influence the selective pressure on worker senescence in honeybees.
93 Using a demographic model, we ask a) how sensitive is colony growth to changes in age-
94 dependent and age-independent worker mortality, b) how does this sensitivity differ by season,
95 and c) do seasonal changes in the force of selection predict the observed pattern of worker
96 senescence?

97 Honeybee colonies have an age-based division of labor in which young workers work
98 inside the hive as nurses and older workers forage outside [24]. Nurses have a lower senescence
99 rate than foragers [18] and a lower risk of accidental mortality because of the protected
100 environment of the hive [17]. Worker lifespan also has a distinct seasonal pattern. Summer bees
101 have the shortest lifespans of 2–6 weeks, spring and fall bees have intermediate lifespans, and

102 winter bees have the longest lifespans of up to 20 weeks [24]. Honeybees rely on a seasonal food
103 resource and colonies must survive the winter when they are unable to forage or rear brood.
104 Because of seasonal changes in both extrinsic mortality and food availability, we would expect
105 the fitness effects to the colony of changes in worker senescence to vary strongly by season. In
106 addition, pathogens and parasites, such as *Varroa destructor*, are a significant source of
107 overwinter mortality in honey bee colonies [25, 26]. A reduction in brood survival resulting from
108 high parasite loads may influence the colony's sensitivity to adult worker mortality as well.

109 To answer our research question, we adapt a method commonly used in demographic
110 modeling: the Leslie matrix model. This framework is typically used to estimate the growth rate
111 of an age-structured population and to examine how different life stages contribute to the growth
112 of a population [27]. The relative contribution of a matrix element (i.e. age-specific survival or
113 fecundity) to the population growth rate is called elasticity [28]. In evolutionary ecology,
114 elasticity can be used to estimate the relative impacts of different vital rates on fitness [28]. In
115 conservation, it can be used to determine which life stage to target to have the biggest impact on
116 a population's growth [27].

117 We adapt this method to model the growth of a social insect colony instead of a
118 population. Since honeybee workers have little or no direct reproduction, their fitness is
119 determined by the reproductive success of their colony [23]. We assume that the selective
120 pressure on worker traits is proportional to the effect of the trait value on colony growth and/or
121 survival. We therefore estimate the selective pressure on worker senescence by calculating the
122 elasticity of colony growth to changes in worker mortality. To examine whether increased
123 parasite loads in winter influence the selective pressures on adult worker senescence, we also
124 repeat the elasticity analyses with a range of values for brood survival.

125

126 This method gives us a computationally simple way to estimate how different worker life
127 stages differ in their contribution to colony growth and how changes in the vital rates of
128 individual workers affect the fitness of the colony.

129 **Results**

130 We find that the elasticity of the colony growth rate, λ , to the age-independent (extrinsic)
131 component of nurse mortality, γ_n , is highest under summer conditions (high productivity and
132 high extrinsic mortality) and lowest under winter conditions (low productivity and low extrinsic
133 mortality). The elasticity to γ_n under spring/fall conditions (intermediate productivity and
134 extrinsic mortality) is similar to that of summer conditions (Fig. 1).

135 In contrast, we find that the elasticities of the colony growth rate to the age-dependent
136 increase in nurse mortality, β_n , and to the initial age-dependent nurse mortality, α_n , are both
137 highest under winter conditions and lowest under summer and spring/fall conditions (Fig. 1).
138 Taken together, these results suggest that a honeybee colony is most sensitive to changes in nurse
139 senescence during the winter but most sensitive to changes in nurse extrinsic mortality during the
140 summer.

141 We further find that the elasticity of the colony growth rate to γ_f , the age-independent
142 (extrinsic) component of forager mortality, is highest under summer conditions (high
143 productivity and high extrinsic mortality) and lowest under winter conditions (low productivity
144 and low extrinsic mortality). Unlike for nurse mortality, the elasticity of the growth rate to γ_f
145 under fall/spring conditions is intermediate between that of summer and winter (Fig. 2). This
146 suggests that the selective pressures against extrinsic forager mortality, like extrinsic nurse
147 mortality, are strongest in summer and weakest in winter.

148 In contrast, we find that the elasticity of λ to α_f , the initial age-dependent forager
149 mortality, is highest under winter conditions, intermediate under spring/fall conditions, and
150 lowest under summer conditions (Fig. 2). Similarly, we find that the elasticity of λ to β_f , the age-
151 dependent increase in forager mortality, is highest under winter conditions and similarly low
152 under summer and fall/spring conditions, although it is lowest in summer conditions (Fig. 2).
153 Together this suggests that the selective pressures against forager senescence are strongest in
154 winter and weakest in summer.

155 When we repeat the winter elasticity analyses with varying brood survival, we find that
156 reduced brood survival increases the elasticity to β_f , the age-dependent increase in forager
157 mortality (Fig. 3). On the other hand, varying brood survival has little impact on the elasticity to
158 forager age-independent mortality (γ_f) or initial mortality (α_f). Similarly, varying brood survival
159 has very little effect on the elasticity of λ to any of the nurse mortality parameters.

160 Discussion

161 Much of our evolutionary understanding of senescence is based on the principle that
162 organisms experience a decline in the force of selection with age [1, 2] resulting in positive
163 selection for traits that increase early-life survival or fecundity at the expense of late-life survival
164 [3]. Theory further predicts that investing in somatic maintenance to postpone senescence is
165 energetically costly [4]; when selection declines more rapidly with age, organisms should invest
166 less in somatic maintenance and experience more rapid senescence. Differences in mean
167 longevity and senescence rate among organisms should therefore be explained at least in part by
168 differences in the pattern and degree to which selection changes with age.

169 Social insects, such as honeybees, are excellent model systems for exploring the
170 evolution of senescence because of their large degree of phenotypic plasticity in senescence rate

171 and lifespan among genetically similar individuals [10, 17, 29]. Different workers experience
172 different levels of extrinsic hazards depending on their behavioral role in the colony [30]. In
173 addition, extrinsic mortality, resource availability, and worker behavior vary seasonally, allowing
174 us to examine how senescence in workers is influenced by ecological context.

175 There has been much theoretical work refining predictions about how extrinsic mortality
176 [31], density-dependence [7], and other ecological factors [32] affect the selection against
177 senescence in individuals. However, it is less straightforward how these ecological factors
178 influence the strength of selection against senescence in social organisms, where individuals
179 have little or no direct reproduction and fitness depends on their contribution to the colony as a
180 whole. Using a simple stage-structured demographic model, we seek to bridge this theoretical
181 gap to explore how ecological context influences selection against worker senescence in
182 honeybees and other eusocial animals.

183 We find that there are seasonal differences in the strength of selection against senescence
184 in honeybee workers, as measured by the sensitivity of the colony growth rate to age-dependent
185 worker mortality. We find that the colony is more sensitive to changes in both nurse and forager
186 senescence in winter conditions, when resources are scarce and extrinsic mortality is lower, than
187 in summer conditions, when resources are plentiful and extrinsic mortality is high (Figs 1 and 2).
188 The colony sensitivity to forager senescence is even higher when winter also reduces brood
189 survival (Fig. 3). Since colonies cannot easily produce new workers in winter, small increases in
190 the senescence of existing workers have larger effects on the colony. This difference in
191 sensitivity may largely explain why winter honeybee workers have a much lower senescence rate
192 than spring or summer workers [33]. In contrast, colonies are most sensitive to changes in
193 extrinsic mortality (Figs 1 and 2) in summer when resources are plentiful; this may be because

194 summer workers spend more of their lives in the riskier forager state rather than the more
195 protected nurse state [24].

196 We also find the seasonal pattern of selection changes with worker life stage. There is
197 much stronger selection against nurse senescence in winter, when most workers remain in the
198 nurse stage, than in summer and spring/fall, both periods when they are likely to transition into
199 foragers sooner (Fig. 1). Since nurses have much lower age-dependent and -independent
200 mortality than foragers, selection against nurse senescence in summer is driven partly by how
201 quickly they transition to the riskier forager state. The selection against forager senescence, on
202 the other hand, is strongest in winter, but intermediate in spring/fall and lowest in summer (Fig.
203 2), suggesting that selection on forager senescence decreases as extrinsic mortality increases.
204 This aspect of our results highlights how behavioral role can interact with ecological context to
205 influence how the selection against senescence changes with age.

206 Overall, our model predicts that the selection against worker senescence should be
207 strongest in winter and weakest in summer. This should lead to the evolution of seasonal
208 differences in worker senescence rate, with the slowest senescence in winter and the fastest in
209 summer. This prediction about the seasonal pattern of senescence rate matches what we observe
210 empirically in temperate honeybee colonies [17, 33, 34]. This model therefore suggests that
211 seasonal changes in the force of selection are important in shaping the phenotypically plastic
212 pattern of senescence in honeybees.

213 Although the main objective of this model is to estimate how seasonally varying selective
214 pressures affect the evolution of aging in honeybee workers, this method could also be used to
215 predict how anthropogenic sources of mortality will affect the health and survival of honeybee
216 colonies. The European honeybee is an economically important pollinator, whose crop

217 pollination services are worth an estimated at \$11.68 billion annually in the United States [35].
218 Managed honeybees face numerous stressors including parasites, nutrition stress, and pesticide
219 exposure [36]. In addition, the severity of these stressors often varies by season, with the
220 majority of colony losses usually occurring in the winter [26, 37, 38], when our model predicts
221 that colonies are most sensitive to worker senescence. Because of logistical constraints, the
222 impact of potential threats to honeybee health are usually evaluated at the individual rather than
223 colony level [39]. This model can therefore help predict how changes in individual worker
224 mortality will scale up to colony-level effects in different parts of the year, which is important to
225 evaluating threats to honeybee health and also can give clues to the causes of colony declines
226 [40, 41]. For instance, our model demonstrates that reduced brood survival also makes the
227 colony more sensitive to changes in forager senescence (Fig 3). This suggests that stressors that
228 reduce brood survival (e.g. American Foulbrood [42], pesticide residues [43], *Varroa destructor*
229 [26]) may act synergistically with stressors that reduce adult worker lifespan [43–45] to
230 accelerate colony failure.

231 In addition, many other social insect species are of great ecological importance as
232 pollinators [46, 47], seed dispersers [48], and ecosystem engineers [49–51]; many of these
233 species' populations are also threatened or declining [47, 52]. Incorporating an evolutionary
234 perspective on how ecological context shapes resource allocation within colonies can help to
235 better inform management practices for social species of conservation concern.

236 **Conclusions**

237 The principle that selection changes with age has been a cornerstone of much of
238 evolutionary senescence theory [1–3, 6–8]. There has been much interest in refining our
239 understanding of how ecological factors, such as extrinsic hazards, influence the age-specific

240 patterns of selection and in turn the evolution of lifespan. Previous work has shown that the force
241 of selection doesn't simply decline linearly with age, but can have more complex patterns [7–9,
242 53]. We here demonstrate how seasonal changes in the strength of selection can explain
243 phenotypically plastic differences in lifespan among individuals in a social species. This simple
244 approach to quantifying the effect of worker mortality on colony fitness can lead to better
245 empirical predictions about how ecological factors should influence the evolution of senescence
246 in social organisms.

247 **Methods**

248 We construct an age-structured Leslie matrix model of a honeybee colony. We divide the
249 worker population into brood, nurse, and forager stages, with each stage further divided into age
250 classes. We define $B_{i,t}$ as the number of i day old brood in the colony on day t , $N_{i,t}$ as the number
251 of i day old nurse bees in the colony on day t , and $F_{i,t}$ as the number of i day old foragers in the
252 colony on day t .

253 Rather than fecundity, as in a traditional Leslie matrix, the top row of the Leslie matrix
254 represents the contribution of each forager to the production of new worker brood. We assume
255 that brood development is limited only by the ability of the colony to feed them (i.e., assuming
256 the colony is not near the queen's egg laying capacity). We assume that workers remain in the
257 brood stage for 21 days [24] and brood survive to the next age class with probability s_b . We
258 define r as the number of new brood that can be provisioned by a forager per day, with $r = \frac{p}{c}$,
259 where c is the amount of food required by a brood per day and p is the amount of food
260 provisioned by a forager per day. Thus, the number of i day old brood on day t is defined by:

261

$$B_{i,t} = \begin{cases} \sum_{j=1}^{19} r F_{j,t-1} & i = 1 \\ s_b B_{i-1,t-1} & i = 2:21 \end{cases}$$

262 We assume all adult workers start as nurse bees and become foragers after a variable
 263 number of days [54]. We define g as the probability a nurse becomes a forager the next day (note
 264 that this is different from a deterministic progression to forager after a fixed number of days).
 265 We assume nurse bees have a low rate of senescence and a low probability of extrinsic mortality
 266 because of the protected environment of the hive [30, 55]. We assume nurse survival is
 267 influenced by both senescence (age-dependent mortality) and extrinsic hazards (age-independent
 268 mortality) [30]. We define $s_{n,i}$ as the daily survival probability of an i day old nurse and $m_{n,i}$ as
 269 the daily mortality probability of an i day old nurse. We represent nurse mortality as a Gompertz-
 270 Makeham function where:

$$271 \quad s_{n,i} = 1 - m_{n,i}$$

$$272 \quad m_{n,i} = \alpha_n e^{\beta_n i} + \gamma_n$$

273 We refer to the intercept γ_n as the nurse extrinsic mortality parameter since it represents
 274 the age-independent component of nurse mortality. We refer to α_n as the initial age-dependent
 275 nurse mortality parameter and to β_n as the age-dependent increase in nurse mortality parameter.
 276 We assume that changes in α_n and β_n reflect changes in senescence. The number of i day old
 277 nurses on day t is given by:

$$278 \quad N_{i,t} = \begin{cases} s_b B_{21,t-1} & i = 1 \\ s_{n,i-1}(1-g)N_{i-1,t-1} & i = 2:120 \end{cases}$$

279 We assume, like nurses, forager survival is influenced by both age-dependent mortality
 280 and age-independent mortality [30]. We define $s_{f,i}$ as the daily survival probability of an i day old
 281 forager and $m_{f,i}$ as the daily mortality probability of an i day old forager. We represent forager
 282 mortality as a Gompertz-Makeham function where:

$$283 \quad s_{f,i} = 1 - m_{f,i}$$

$$284 \quad m_{f,i} = \alpha_f e^{\beta_f i} + \gamma_f$$

285 We refer to the intercept γ_f as the forager extrinsic mortality parameter. We refer to α_f as
286 the initial age-dependent forager mortality parameter and to β_f as the age-dependent increase in
287 forager mortality parameter. As with nurses, we assume α_f and β_f represent forager senescence.
288 We assume all workers go through a nurse stage before becoming foragers. We assume the
289 number of workers living more than 19 days as foragers is negligible [30]. The number of i day
290 old foragers on day t is given by:

$$291 F_{i,t} = \begin{cases} \sum_{j=1}^{120} s_{n,j} g N_{j,t-1} & i = 1 \\ s_{f,i-1} F_{i-1,t-1} & i = 2: 19 \end{cases}$$

292 To examine how the selective pressures shaping worker aging differ across annual
293 environmental fluctuations, we modeled a colony under three different seasonal conditions:
294 spring/fall, summer, and winter. We represented each season by different parameter values for
295 forager extrinsic mortality (γ_f), food availability (p), and nurse-to-forager transition rate (g). (For
296 the full list of parameter values used in the model, see Supplementary Information, Table S1.)
297 We represented summer as a season with high food availability, high extrinsic mortality, and a
298 high nurse-to-forager transition rate. We represented fall and spring as intermediate food
299 availability, intermediate extrinsic mortality, and a high nurse-to-forager transition rate. We
300 represented winter as near zero food availability, low extrinsic mortality, and low nurse-to-
301 forager transition rate since winter bees do not leave the hive to forage.

302 To examine the effects of forager and nurse extrinsic mortality and senescence on the
303 growth of the colony, we performed a numeric elasticity analysis by perturbation [56]. Elasticity
304 is a measure of sensitivity that is scaled to be unitless [27]. We calculated the elasticity of the
305 colony growth rate (the dominant eigenvalue of the Leslie matrix) to perturbations in parameters
306 γ_n , α_n , and β_n (the nurse mortality parameters) and γ_f , α_f , and β_f (the forager mortality

307 parameters). If we define λ as the colony growth rate, the elasticity of the growth rate to
308 parameter x is defined as:

309
$$\frac{\Delta\lambda}{\Delta x} \frac{x}{\lambda}$$

310 We repeated this elasticity analysis for each set of seasonal parameter conditions (Table
311 S1) to examine how the selective pressure on worker age-dependent and age-independent
312 mortality differs by season. We assumed that brood survival did not differ seasonally. However,
313 to examine whether reduced brood survival in winter would influence the colony's sensitivity to
314 adult worker mortality, we re-calculated the elasticities for various values of brood survival (s_b)
315 with all other parameters set to winter levels.

316

317 **Declarations**

318 *Ethics approval and consent to participate*

319 Not applicable.

320 *Consent for publication*

321 Not applicable.

322 *Availability of data and materials*

323 The datasets used and/or analysed during the current study are available from the corresponding
324 author on reasonable request.

325 *Competing interests*

326 The authors declare that they have no competing interests.

327 *Funding*

328 Not applicable.

329 *Authors' contributions*

330 NJL and NHF conceived of the study question. NJL and SB developed and implemented the
331 model and interpreted the results. NJL wrote the first draft of the manuscript. All authors read
332 and approved the final manuscript.

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337 5-10, 2018 conference in Guarujá, Brazil [57].

338

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467

468 **Figure Legends**

469 Figure 1. Elasticity of colony growth rate to nurse mortality. Nurse mortality is represented as a
470 Gompertz-Makeham function, with γ_n as the age-independent component of nurse mortality, α_n
471 as the initial age-dependent component of nurse mortality, and β_n as the age-dependent increase
472 in nurse mortality. Colonies are less elastic to age-independent mortality in winter (low extrinsic
473 mortality, low forager productivity, low forager transition rate) than in summer (high extrinsic
474 mortality, high forager productivity, high forager transition rate) or spring (intermediate extrinsic
475 mortality, intermediate forager productivity, high forager transition rate). In contrast, colonies
476 are more elastic to initial age-dependent mortality and age-dependent increase in mortality in
477 winter than in summer or spring. For full parameter values, see Supplementary Information,
478 Table S1.

479

480 Figure 2. Elasticity of colony growth rate to forager mortality. Forager mortality is represented as
481 a Gompertz-Makeham function, with γ_f as the age-independent component of forager mortality,
482 α_f as the initial age-dependent component of forager mortality, and β_f , the age-dependent
483 increase in forager mortality. Colonies are least elastic to forager age-independent mortality in
484 winter (low extrinsic mortality, low forager productivity, low forager transition rate) and most
485 elastic in summer (high extrinsic mortality, high forager productivity, high forager transition
486 rate), with spring/fall (intermediate extrinsic mortality, intermediate forager productivity, high
487 forager transition rate) elasticity being intermediate between that of summer and winter. In
488 contrast, colonies are most elastic to forager age-dependent mortality in winter and least elastic
489 in summer, with spring/fall elasticity again being intermediate. Colonies are also most elastic to
490 the age-dependent increase in forager mortality in winter and least elastic in summer, with

491 spring/fall elasticity being intermediate but closer to that of summer. Note that to make seasonal
492 differences more visible, the y-axis scale is larger in this figure than that in Figure 1. For full
493 parameter values, see Supplementary Information, Table S1.

494

495 Figure 3. Elasticity of colony growth rate to worker mortality as a function of brood survival. To
496 estimate how colony growth responds to changes in adult worker mortality, we calculated the
497 elasticity for six parameters: age-independent forager mortality (γ_f), age-dependent forager
498 mortality (α_f), age-dependent increase in forager mortality (β_f), age-independent nurse mortality
499 (γ_n), age-dependent nurse mortality (α_n), age-dependent increase in nurse mortality (β_n). To
500 examine whether reduced reduced brood survival in winter influences the colony's sensitivity to
501 adult worker mortality, we re-calculated the elasticities for various values of brood survival (s_b)
502 with all other parameters set to winter levels (Table S1). Open markers show results for forager
503 mortality parameters, while solid markers show results for nurse mortality parameters. Note that
504 bottom panel has a smaller scale than top panel to make lines more visible.

505

506 **Supplementary Information**

507 Table S1. Full list of model parameters and their values.

Parameter	Definition	Summer	Fall/Spring	Winter
p	Food production per forager per day	0.098	.058	0.0001
c	Total food consumption per brood	0.151	0.151	0.151
r	Number of brood provisioned per forager per day	p/c	p/c	p/c
s_b	Daily brood survival probability	0.993	0.993	0.993
α_n	Nurse initial age-dependent mortality rate	0.001	0.001	0.001
β_n	Nurse age-dependent increase in mortality rate	0.1	0.1	0.1
γ_n	Nurse age-independent mortality rate	0.04	0.04	0.0134
α_f	Forager initial age-dependent mortality rate	0.001	0.001	0.001
β_f	Forager age-dependent increase in mortality rate	0.369	0.369	0.369
γ_f	Forager age-independent mortality rate	0.134	0.067	0.0134
g	Nurse probability of becoming forager per day	0.05	0.05	0.01
T	Number of days considered	90	90	90

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Figures

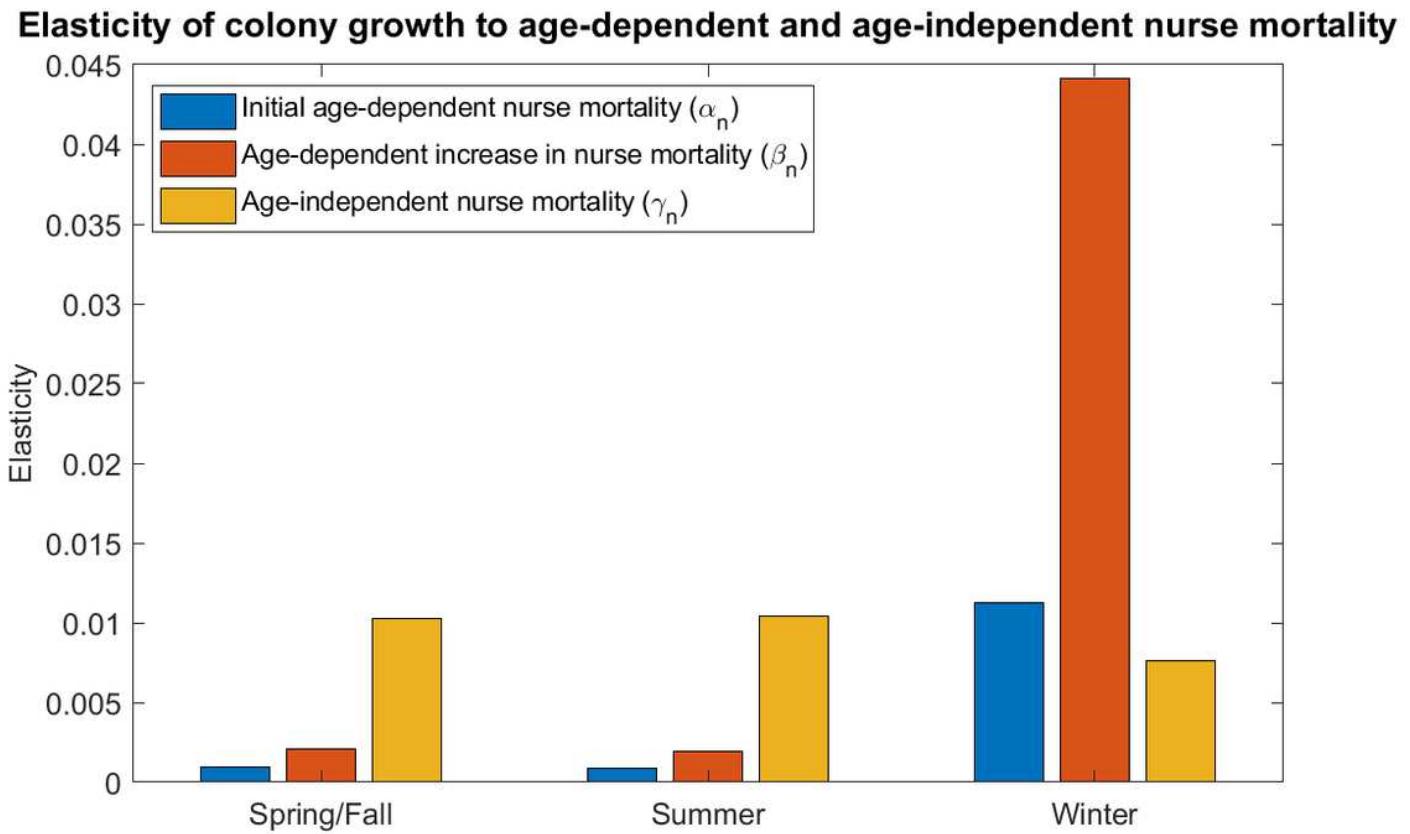


Figure 1

Elasticity of colony growth rate to nurse mortality. Nurse mortality is represented as a Gompertz-Makeham function, with γ_n as the age-independent component of nurse mortality, α_n as the initial age-dependent component of nurse mortality, and β_n as the age-dependent increase in nurse mortality. Colonies are less elastic to age-independent mortality in winter (low extrinsic mortality, low forager productivity, low forager transition rate) than in summer (high extrinsic mortality, high forager productivity, high forager transition rate) or spring (intermediate extrinsic mortality, intermediate forager productivity, high forager transition rate). In contrast, colonies are more elastic to initial age-dependent mortality and age-dependent increase in mortality in winter than in summer or spring. For full parameter values, see Supplementary Information, Table S1.

Elasticity of colony growth to age-dependent and age-independent forager mortality

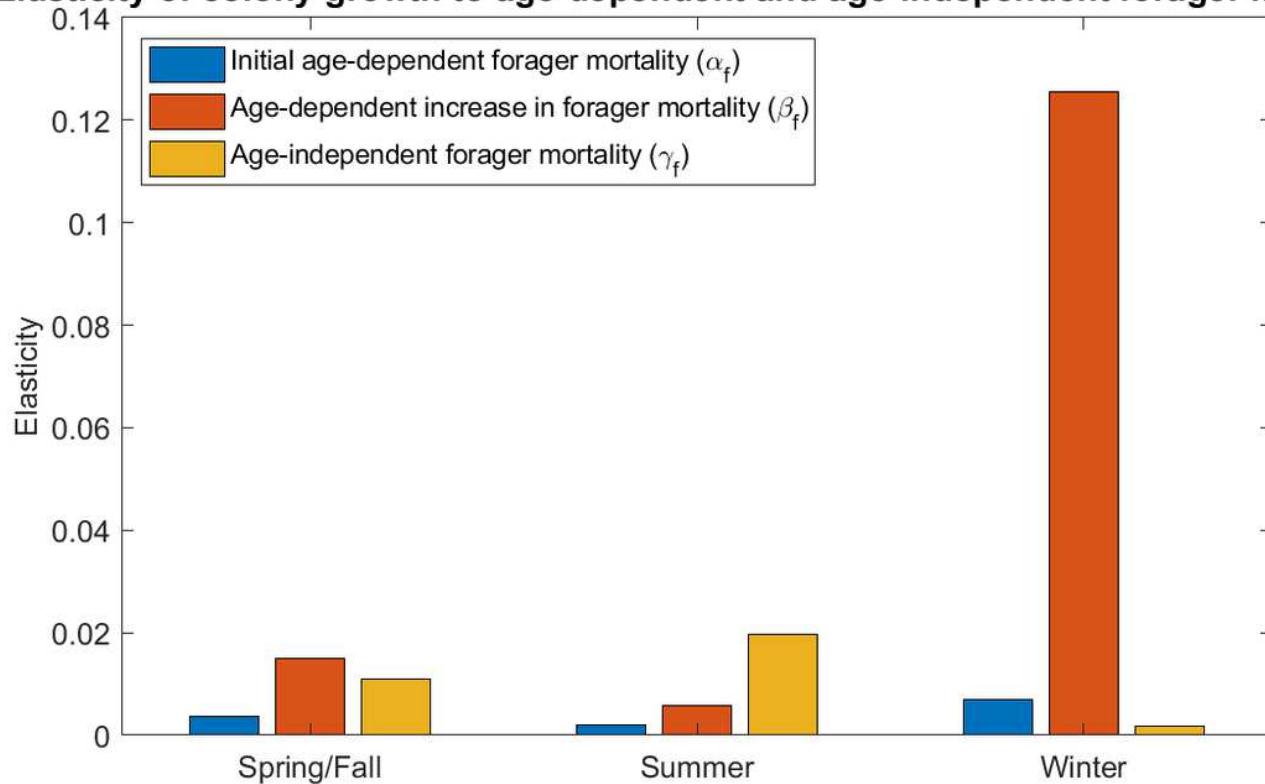


Figure 2

Elasticity of colony growth rate to forager mortality. Forager mortality is represented as a Gompertz-Makeham function, with γ_f as the age-independent component of forager mortality, α_f as the initial age-dependent component of forager mortality, and β_f , the age-dependent increase in forager mortality. Colonies are least elastic to forager age-independent mortality in winter (low extrinsic mortality, low forager productivity, low forager transition rate) and most elastic in summer (high extrinsic mortality, high forager productivity, high forager transition rate), with spring/fall (intermediate extrinsic mortality, intermediate forager productivity, high forager transition rate) elasticity being intermediate between that of summer and winter. In contrast, colonies are most elastic to forager age-dependent mortality in winter and least elastic in summer, with spring/fall elasticity again being intermediate. Colonies are also most elastic to the age-dependent increase in forager mortality in winter and least elastic in summer, with spring/fall elasticity being intermediate but closer to that of summer. Note that to make seasonal differences more visible, the y-axis scale is larger in this figure than that in Figure 1. For full parameter values, see Supplementary Information, Table S1.

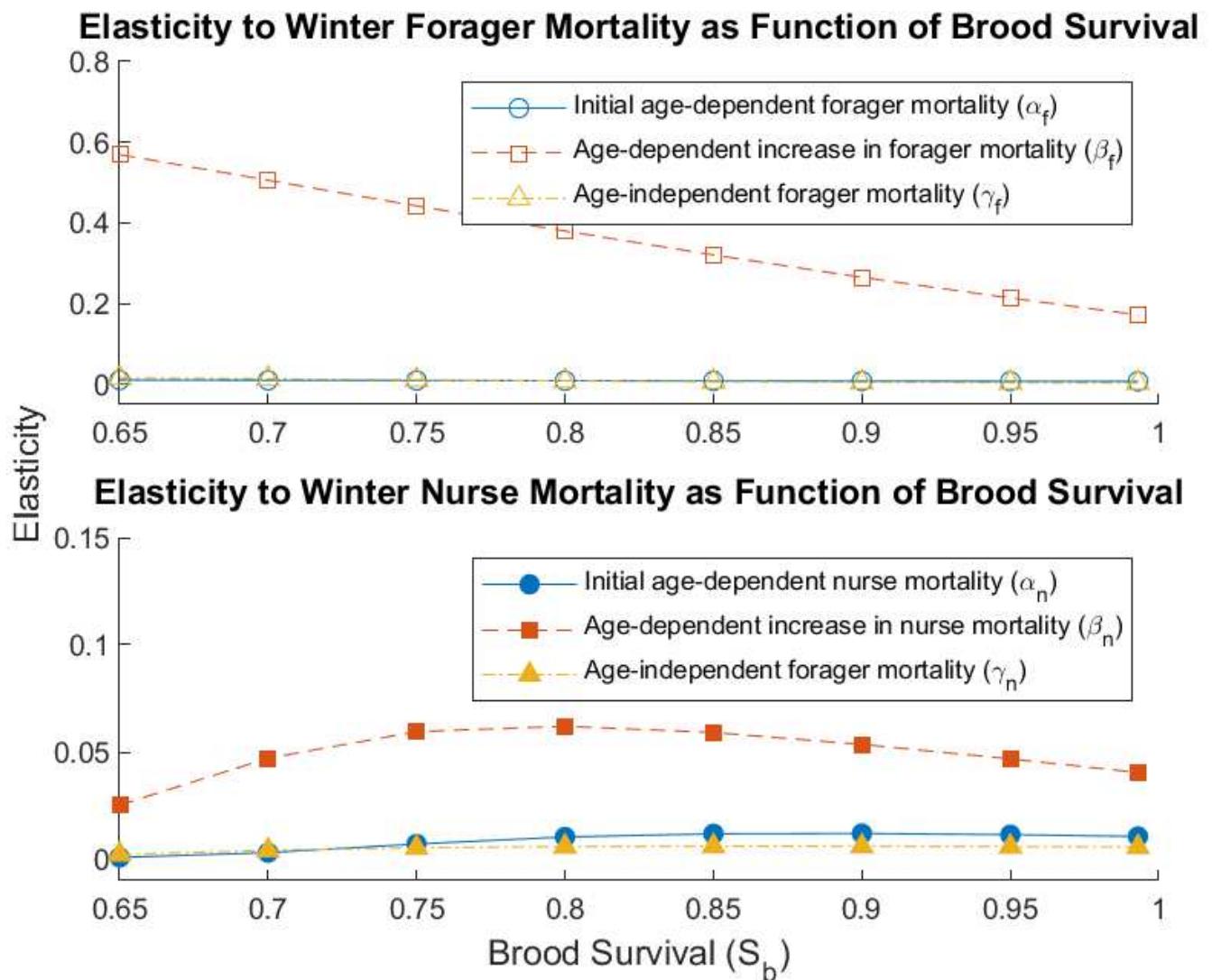


Figure 3

Elasticity of colony growth rate to worker mortality as a function of brood survival. To estimate how colony growth responds to changes in adult worker mortality, we calculated the elasticity for six parameters: age-independent forager mortality (γ_f), age-dependent forager mortality (α_f), age-dependent increase in forager mortality (β_f), age-independent nurse mortality (γ_n), age-dependent nurse mortality (α_n), age-dependent increase in nurse mortality (β_n). To examine whether reduced brood survival in winter influences the colony's sensitivity to adult worker mortality, we re-calculated the elasticities for various values of brood survival (S_b) with all other parameters set to winter levels (Table S1). Open markers show results for forager mortality parameters, while solid markers show results for nurse mortality parameters. Note that bottom panel has a smaller scale than top panel to make lines more visible.