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1 The concept of critical age group for density dependence: bridging the gap  
2 between demographers, evolutionary biologists and behavioral ecologists

3

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12

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14 populations’.

15

16

17 **Abstract**

18 Density dependence plays an important role for population regulation in the wild. It involves a  
19 decrease in population growth rate when the population size increases. Fifty years ago,  
20 Charlesworth introduced the concept of “critical age group”, denoting the age classes in  
21 which variation in the number of individuals most strongly contribute to density regulation.  
22 Since this pioneering work, the use of this concept has remained scarce. In light of  
23 Charlesworth’s concept, we discuss the need to develop work between behavioral ecology,  
24 demography and evolutionary biology to better understand the mechanisms acting in density-  
25 regulated age-structured populations. We highlight demographic studies that explored age-  
26 specific contributions to density dependence and discuss the underlying evolutionary  
27 processes. Understanding competitive interactions among individuals is pivotal to identify the  
28 ages contributing most strongly to density regulation, highlighting the need to move towards  
29 behavioral ecology to decipher mechanisms acting in density-regulated age-structured  
30 populations. Because individual characteristics other than age can be linked to competitive  
31 abilities, expanding the concept of critical age to other structures (e.g. sex, dominance rank)  
32 offers interesting perspectives. Linking research fields based on the concept of the critical age  
33 group is key to move from a pattern-oriented view of density regulation to a process-oriented  
34 approach.

35 **Keywords:** age-structured populations, density regulation, dominance rank, competition,  
36 personality, senescence, sociality, stage-structured populations, viability selection

## 37        **1. Introduction**

38            Understanding fluctuations in population size over time is a major goal in both  
39 conservation and evolutionary ecology. Density-independent and density-dependent factors  
40 both shape fluctuations in population size over time [1]. Their relative importance has long  
41 been debated [2–5], but empirical evidence from a wide variety of taxa shows that both  
42 processes contribute to fluctuations in population size [6–8].

43            Density dependence generates fluctuations in population size around a mean value, the  
44 carrying capacity [9], and thus plays an important role in population regulation. From a  
45 demographic viewpoint, negative density dependence (hereafter called density dependence)  
46 describes the negative relationship between a population’s growth rate and the number of  
47 individuals currently present or at an earlier time step [4,10–13]. This decrease in population  
48 growth rate when the population increases in numbers may be explained by several factors.  
49 For instance, at high population sizes, contests for the access to critical resources or space, or  
50 higher risk of disease transmission [14] can negatively influence reproduction and survival  
51 [15] with cascading effects on the growth rate of the whole population.

52            Assessing density dependence by exploring the strength of the negative relationship  
53 between population growth rate and population size relies on several assumptions, one of  
54 them being that all individuals are expected to have the same competitive effects on other  
55 individuals [16]. However, in age-structured populations, this assumption may be violated.  
56 Individuals may differently contribute to the density regulation according to their age. In the  
57 1970’s, Charlesworth introduced the concept of “critical age group” in a model with density-  
58 dependent selection. In his seminal works in 1972 and 1973 [17,18], he wrote: “*In any*  
59 *particular case, this density regulation must occur in response to the number of individuals in*  
60 *a specific group of ages, which I shall call the “critical age group”. The critical age group*  
61 *might, for example, be composed of individuals in the first age class only, or of all individuals*

62 *of reproductive age, or of any other combination of age classes, depending on the exact mode*  
63 *of density regulation in the population under consideration. Mortality at all or some ages will*  
64 *be increased and/or fecundity decreased in relation to the number of individuals existing in*  
65 *the critical age group, either at the present time, or at a specific time in the past, or over a*  
66 *whole range of past times.”*

67         This pioneering work on density-dependent selection was primarily rooted in  
68 evolutionary studies of natural selection in populations with overlapping generations. Beyond  
69 density-dependent selection, the definition of “critical age group” given in Charlesworth’s  
70 studies [*“this density regulation must occur in response to the number of individuals in a*  
71 *specific group of ages”*] can be more broadly interpreted in the context of density-dependent  
72 regulation. Until recently, the use of this important concept in demographic studies has  
73 remained scarce [19,20], which is surprising as it can shed light on the underlying  
74 mechanisms acting on density-regulated age-structured populations. Similarly, this concept  
75 has to our knowledge not been explored by behavioral ecologists. This field has a long history  
76 of studying biotic interactions and can therefore provide key insights on the behavioral  
77 processes determining the critical age group. Linking evolution, demography and behavior  
78 based on the concept of the critical age group is particularly relevant to move from pattern-  
79 oriented view of density regulation to a process-oriented approach in age-structured  
80 populations (Figure 1).

81         In the first part of this paper, we thus discuss some of the empirical demographic  
82 studies that explored age-specific contributions to density dependence in light of  
83 Charlesworth’s concept of the critical age group. We discuss the implications for accurate  
84 predictions of fluctuations in population size over time. In the second part, we discuss how the  
85 critical age group has been included in evolutionary biology and describe the processes that  
86 may affect the evolutionary consequences of variation in the critical age class. In the third

87 part, we discuss some of the behavioral mechanisms that could explain age-specific  
88 contributions to density dependence, including age-related changes in personality traits and  
89 dominance rank. Improved understanding of competitive interactions among individuals can  
90 be useful in identifying which age or group of ages will contribute the most strongly to the  
91 strength of density dependence. Finally, in the last part of the paper, we discuss the need to  
92 improve the interactions between behavioral ecology, population dynamics, demography and,  
93 ultimately evolutionary biology to address the concept of critical age group in a more  
94 comprehensive way across research fields. We conclude by discussing some new exciting  
95 research perspectives.

96

## 97 **2. The concept of critical age group for density dependence in demographic studies**

98 In age-structured populations, individuals may have different contributions  
99 (“weights”) to density regulation, depending on their age. In other words, adding one  
100 individual of age  $i$  in a population is not necessarily equivalent to adding one individual of  
101 age  $j$  in terms of negative effects on the vital rates of other individuals in the population.  
102 Surprisingly, age-specific contributions to density dependence have been rarely investigated  
103 in demographic studies [11,21,22]. Gamelon et al. [19] considered age-specific population  
104 sizes  $N_i$  instead of the total population size  $N_{tot}$  to explore the influence of density dependence  
105 on the dynamics of a great tit (*Parus major*) population. Partitioning the contribution of  $N_{tot}$   
106 into the age-specific contributions  $N_i$  allows identifying the age(s) contributing the most to  
107 density regulation by estimating the “per capita” effects on density dependence. In other  
108 words, partitioning the contribution of  $N_{tot}$  allows answering the question: “what is the  
109 density-dependent effect of an individual of a certain age on the vital rates of other  
110 individuals?”. With such an approach focusing on the per capita effects, the critical age group  
111 is not necessarily the largest age class. They found that the number of females in their first

112 year of breeding had the strongest negative effects on survival and recruitment of all ages, and  
113 concluded that the youngest females were the critical age class (sensu Charlesworth).

114 More recently, Lande et al. [20] expanded this approach and provided a general  
115 framework to quantify age-specific contributions to density dependence in (st)age-structured  
116 populations. In this study, density dependence in vital rates is exerted by a function called  
117  $g(N)$ , of a weighted sum of stage abundances,  $N$ . In accordance with the previous study on  
118 great tits, they found that in this great tit population, the estimated relative weights of stage  
119 abundances decrease strongly for the older stages. Therefore, 1-year olds had the strongest  
120 impact on density regulation.

121 Strikingly, some demographic studies have assessed the influence of the number of  
122 individuals in a specific group of age on density regulation acting on individuals' vital rates  
123 (survival, reproduction) or on the population growth rate, but did not explicitly use the term  
124 "critical age group". For instance, in their empirical study on Alpine plants, Cotto et al. [23]  
125 developed an eco-evolutionary model in which the survival probability of seedlings depends  
126 specifically on the number of adult individuals previously established. Similarly, Schmid et al.  
127 [24] simulated contrasting life history strategies, and assumed a decline of juvenile survival  
128 due to intraspecific competition, with increasing adult number for overlapping generations,  
129 and with juvenile number for non-overlapping generations. These examples highlight that  
130 despite not always been mentioned explicitly, the concept of critical age group for density  
131 dependence is growing in use in demographic studies. These density-dependence models  
132 imply that a group of age instead of all ages drives density regulation, and are thus more  
133 biologically realistic, depending strongly on the biology of the species.

134 Identifying the critical age group is key to unravel the demographic mechanisms  
135 leading to density regulation at the population level, but it is also crucial for accurately  
136 predicting fluctuations in population size over time. Gamelon et al. [25] identified the age(s)

137 contributing the most to density regulation in 12 great tit populations and in 12 blue tit  
138 (*Cyanistes caeruleus*) populations in Europe. They found that a density-dependence model  
139 with age-specific contributions to density dependence significantly improves predictions of  
140 fluctuations in population size, compared to the “classical” density-dependence model  
141 including only the total population size  $N_{tot}$ . Accordingly, including age in demographic  
142 analyses of density dependence seems particularly relevant in a management or in a  
143 conservation context to identify the age groups limiting the most the population growth rate  
144 and make accurate predictions of fluctuations in population size.

145 While a few demographic studies have started to apply the concept of critical age group,  
146 its roots reside in evolutionary biology [17]. Therefore, unsurprisingly, this is in this research  
147 field that the term “critical age group” has been used more frequently (about fifty times)  
148 compared to demographic and behavioral studies. Putting more broadly the concept of critical  
149 age group back into the evolutionary theatre will improve our understanding of the  
150 evolutionary causes and consequences of the critical age class.

151

### 152 **3. The concept of critical age group for density dependence in evolutionary biology**

153 Evolutionary studies that coin the term “critical age group” have primary focused on  
154 density-dependent selection, not on density-dependent population regulation [18,26,27].  
155 However, different evolutionary processes may result in age classes differing in their  
156 competitive ability and therefore in their relative contribution to density regulation (Figure 2).

157 Age-specific contributions to density regulation may be underpinned by phenotypes  
158 with different competitive abilities either appearing in or disappearing from the population in  
159 a particular sequence. For instance, viability selection can cause changes in the phenotypic  
160 composition of different ages. This has been extensively studied in the context of selective  
161 disappearance, a form of viability selection whereby specific phenotypes are selected for,



162 creating a change in phenotypic composition across ages [28]. Selective disappearance of a  
163 given phenotype can result in older classes being composed of individuals with a larger or a  
164 lower impact on density regulation. For instance, figure 2A depicts a hypothetical example in  
165 which phenotype A has high competitive ability and high survival, whereas phenotype D has  
166 opposite characteristics (but possibly high reproductive output). Viability selection can  
167 therefore cause phenotypes D (frail) to be less common in older age classes, leading the  
168 average competitive ability of the different age classes to be higher in the older age classes,  
169 and the variance in competitive ability to be lower for the older age classes (Figure 2B). In  
170 this hypothetical scenario, the older age classes have a stronger per-capita effect on population  
171 growth rate (Figure 2C). The same reasoning applies when a phenotype has high competitive  
172 ability, enabling it to better acquire resources for reproduction at the expense of low survival.  
173 In this scenario, viability selection will cause phenotypes with lower competitive abilities to  
174 be more common in older age classes, the youngest age classes thus having a stronger per-  
175 capita effect on the population growth rate (Figure 2D, E, F).

176         Age-related changes in competitive ability and therefore age-specific variation in the  
177 contribution to density regulation can be also caused by senescence. This is a within-  
178 individual decline with age in residual reproductive value owing to deteriorating survival  
179 probability and reproductive performance, caused by a progressive loss of physiological and  
180 cellular function late in life [29,30]. Evidence for within-individual phenotypic deterioration  
181 is accumulating for various traits across a range of animal taxa [31]. In the hypothetical  
182 scenario where senescence causes a similar decline in competitive ability with age for all  
183 individuals (depicted in different colors on Figure 2G), i.e. same senescence rates, the average  
184 competitiveness decreases with age (Figure 2H), leading to a lower per-capita effect on the  
185 population growth rate for the older age classes (Figure 2I). Note that different phenotypes  
186 can have contrasting senescence patterns (e.g. different slopes, shapes, onsets) possibly

187 resulting in complex relationships between competitive ability and age. The mounting  
188 evidence of a decline in trait values that may reflect competitive ability with age suggests that  
189 senescence can shape the contribution to density regulation of the different age classes.

190 Both senescence and selective disappearance through viability selection can happen at  
191 the same time: competitive ability can decline within an individual's lifespan, and individuals  
192 with specific competitive abilities may disappear from the older age classes. This can result in  
193 complex non-linear relationships between the average competitive ability and age (Figures  
194 2H, K), as well as with the per-capita effect on the growth rate and age (Figure 2I, L).  
195 Accordingly, population-level patterns do not necessarily provide insights into within-  
196 individual processes such as senescence [32], or age-specific changes in the phenotypic  
197 composition of a population, per se. For instance, selective disappearance of poor-quality  
198 individuals has been found to partly mask age-specific declines in reproductive performance  
199 measures in roe deer *Capreolus capreolus* [28] and mute swans *Cygnus olor* [33]. It is thus of  
200 key importance to separate these two processes in order to understand how evolution may  
201 affect the critical age class and its phenotypic characteristics.

202 Concomitantly to Charlesworth's concept of critical age group for density dependence,  
203 the idea that several phenotypes with different competitive strategies co-exist and interact was  
204 introduced in the 70's. Indeed, in their seminal article [34], published at the early stages of the  
205 evolutionary game theory, Maynard Smith and Price introduced the concept of evolutionary  
206 stable strategy (ESS) that became an important tool for studying animal contests [35] in both  
207 evolutionary and behavioral studies. However, to the best of our knowledge, "conflicts"  
208 among individuals within the evolutionary game theory framework have not been studied in  
209 light of age-specific abilities to compete and Charlesworth's concept of critical ages.

210 Moving from population to individual level may help understand why some ages are  
211 more "critical" than others for the density regulation in age-structured populations. Important

212 knowledge can be gained from behavioral studies, that have long been interested in biotic  
213 interactions in natural populations.

214

#### 215 **4. Insights from behavioral studies on the critical age group**

216 To our knowledge, the term “critical age group” has not been used yet in behavioral  
217 studies to describe the age class contributing the most to density regulation. This is surprising  
218 as behavioral ecologists have extensively explored among-individual differences in  
219 competitive abilities in animals to get access to food resources, territory, mating partners, etc.  
220 [36,37] and the consequences on their vital rates [38] and the population growth rate.  
221 Competitive abilities can be related to personality traits (or temperament, [39]), like  
222 aggressiveness, exploration, problem-solving performance, etc. [40]. These traits can be under  
223 selection [41], and may have strong influence on density regulation and thus on population  
224 dynamics [42,43].

225 Personality traits related to competitive abilities can be age-specific, changing over an  
226 individual lifespan due to senescence [44], as mentioned earlier (Figure 2G). In a study on  
227 blue tits, Class and Brommer [46] explored age-related changes in two traits, aggression and  
228 breath rate within individuals’ lifespan, and found evidence for a decline in aggression with  
229 increasing ages. This observation of a decrease in performance of an individual with age may  
230 indicate senescence. This means that some traits associated with competitive capacity could  
231 decline with age, possibly weakening the contribution of older ages to density dependence. If  
232 traits associated with competitive abilities may decline over an individual lifespan, they can,  
233 in contrast, improve as individuals become older through social learning for instance  
234 [40,47,48] + [Hasenjager & Fefferman, this issue](#). In that case, expectations are opposite to  
235 Figures 2G, H, I, with a positive relationship between competitive ability and age resulting in  
236 an increase in per-capita effect on population growth rate with age. For instance, in beef cattle

237 (*Bos taurus*), social dominance and thus the access to critical resources is mostly explained by  
238 age, that prevails over body mass in the structuring of the dominance network [49]. Similarly,  
239 in zebra (*Equus burchelli*), the social rank of mares increases with age, and mares with higher  
240 social rank appear to be the ones that have access to resources and have higher reproductive  
241 success [50]. Thus, older individuals may have the highest contribution to density regulation  
242 in this specific case. Note however that some personality traits related to competitive abilities  
243 can remain stable within life stages (see [51] for a review). This is the case for the yellow-  
244 bellied marmots (*Marmota flaviventris*), for which docility is established early in life and is a  
245 good predictor of docility at adulthood [52]. Similarly, in horses (*Equus caballus*), the social  
246 rank of an individual throughout its life is determined by the social rank of its mother [53].  
247 Therefore, age-related changes in personality traits associated with competitive abilities can  
248 strongly differ among species. These species-specific patterns may provide a crucial  
249 explanation for the role played by different critical age classes in their population dynamics.

250 Another important factor that could explain age-specific contributions to density  
251 dependence is social organization. Coulson and Godfray [15] contrasted two main types of  
252 competition . In the *contest* type, a few individuals are able to monopolize critical resources or  
253 space and exclude other individuals. In contrast, in the *scramble* competition type, resources  
254 are equally divided among the individuals in the population. In practice, most social systems  
255 are classified along a gradient between these two extremes. In their comparative study of  
256 altricial birds mostly regulated by territorial behavior, Sæther et al. [54] showed that in long-  
257 lived species in which adults may breed in the same territory for several years, the number of  
258 new recruits was negatively related to the return rate of adults from the previous breeding  
259 season. This indicates a contest type of social organization, with consequences for the  
260 definition of critical age group.

261 The patterns of space use of species can also shed light on which ages are more likely to  
262 contribute to density dependence. Spatial assortment by age can lead to age-based social  
263 groups or hierarchies. Within these groups, individuals of similar ages may interact more  
264 frequently. For instance, assortative mating by age is commonly documented and one of the  
265 explanations is that individuals with similar ages are more likely to be in the same location  
266 [55]. Alternatively, older individuals may interact more with younger individuals, for instance  
267 individuals without a territory are generally younger and are constantly interacting with older  
268 territory owners to gain access to their territory [56]. In some vertebrate species, individuals  
269 use different habitat types sequentially throughout their life span to maximize fitness. This is  
270 known as ontogenetic niche shift in habitat use [57,58]. This could also result in non-random  
271 spatial distribution with age that can potentially affect the critical age class. More generally,  
272 patterns of non-random association of different age groups can result in both stronger or  
273 weaker density-dependent effects on population growth as compared to scenarios where  
274 interactions are at random.

275

## 276 **5. Concluding remarks and perspectives**

277 Since the 1930's and Nicholson's pioneering work [59], density dependence has been  
278 intensively studied both theoretically and empirically in several fields of research, including  
279 demography, behavioral ecology and evolutionary biology. In demography, this is an  
280 important mechanism contributing to population size regulation. In behavioral ecology, this is  
281 a key aspect of biotic interaction, involving competition and cooperation (in case of positive  
282 density dependence)(see [Woodman et al., this issue](#)). In evolutionary biology, this is often  
283 studied in the context of density-dependent selection shaping phenotypic traits in natural  
284 populations [60–66] and affecting the rate of genetic drift [67]. As discussed earlier, there are  
285 many ecological situations that can lead to age-specific contributions to density dependence.

286 Despite important advances and the seminal work of Charlesworth [17,18], it still remains an  
287 open question: which are the ages contributing the most to density regulation. Whether the  
288 critical age groups depend on the age-specific responses to density dependence (Box 1), the  
289 species life history strategy, climate conditions (Box 2), or other factors remain to be carefully  
290 explored. Addressing these questions is critical to identify general principles of how density  
291 regulation affects the eco-evolutionary dynamics of age-structured populations.

292         Some methodological challenges can explain the lack of studies on this topic:  
293 quantifying the age-specific contributions to density dependence requires knowing the  
294 number of individuals in each age class [21], which is notoriously difficult as both  
295 determining individuals' age and counting individuals in the wild is a real challenge. Some  
296 new methodological tools such as integrated population models IPM [68,69] now allow  
297 accurately estimating age-specific population sizes from demographic data, while accounting  
298 for imperfect detection. Once age-specific population sizes are estimated, another  
299 methodological challenge is to quantify the age-specific contributions to density regulation.  
300 Indeed, partitioning the contribution of  $N_{tot}$  into the age-specific contributions  $N_i$  increases the  
301 degrees of freedom and thus requires more data. Again, IPMs can be a suitable framework.

302         After having identified “which are” the critical age classes, the question then becomes:  
303 why do some ages contribute more than others to density regulation? To interpret and  
304 understand the role played by the critical age group for density dependence, behavioral  
305 studies bring important insights. We argue that there is a clear need to fill the gap between  
306 demography, behavioral ecology and evolutionary biology. Such a transdisciplinary  
307 framework would deepen our understanding of the role played by age in biotic interactions  
308 (processes) and their consequences on population dynamics (patterns) (Figure 1).

309         The need to bring together demography, behavioral ecology and evolution to explore  
310 the concept of age group for density dependence is even clearer when going back to

311 Charlesworth's work [17]: "*the critical age group might, for example, be composed of all*  
312 *individuals of reproductive age, or of newborn individuals, depending on the biology of the*  
313 *population*". Thus, the critical group is not necessarily an age class but more broadly a group  
314 of individuals, depending on the biology of the population. Age is obviously one key  
315 structuring factor in natural populations, possibly associated with contrasting abilities to  
316 compete. Furthermore, other individual characteristics than age can be closely linked to  
317 competitive abilities, as previously demonstrated by behavioral ecologists: body mass, sex,  
318 etc. For instance, in the common lizard (*Lacerta vivipara*), the number of males specifically  
319 reduces female's survival and reproduction, due to female's aggression [70]. Therefore,  
320 density dependence in that specific example seems primarily driven by the number of  
321 reproductive males. To what extent the pioneering work of Charlesworth [17,18] can be  
322 expanded to two-sex age-structured populations, or even generalized to other type of traits  
323 (behavioral, morphological, etc.) offers exciting research perspectives. Thus, instead of  
324 focusing on the female segment of the population as classically done in demographic studies,  
325 one should include age- and sex-structured models to assess density regulation acting on the  
326 population growth rate.

327         While Charlesworth's work [17,18] preliminary focused on intraspecific density  
328 dependence, individuals do not live in isolation but interact with other species within a  
329 community. Since the 1920's and the demographic models of competition between two  
330 species of Lotka [71] and Volterra [72], it is well accepted that the density of species *A* may  
331 influence the population growth rate of species *B*, and vice versa. In behavioral ecology too,  
332 there is a large amount of literature including field and experimental studies, providing  
333 evidence for competition between species (see e.g. [73,74]). Expanding the concept of critical  
334 age group for density dependence to interspecific density dependence would shed light on  
335 density regulation acting in age-structured populations within a community. In that case, the

336 number of individuals in a given age class for species *A* would influence not only the  
337 demographic performances of individuals of certain ages of species *A*, but also of species *B*,  
338 and vice versa. Gamelon et al. [25] developed such a demographic model and applied it on  
339 two competing species, the great tit and the blue tit living in sympatry. They considered that  
340 the number of great tits in four different age classes may influence the demographic  
341 performances of great tit and also the vital rates of blue tit, and vice versa. They found that  
342 blue tits (this species is smaller than great tits) were strongly influenced by the number of  
343 great tits, whereas great tit populations were mostly regulated by intraspecific density  
344 dependence. However, great and blue tits live in a community with other potential  
345 competitors, and expanding the approach to more than two competing species is a natural next  
346 step [75]. Here as well, knowledge gained by behavioral ecologists will help to understand  
347 biotic interactions among multiple species within a community, and help building realistic  
348 demographic models to characterize the critical age group for density dependence.  
349



350

351 **Box 1: What about age-specific response to density dependence?**

352           Until now, age-specific responses to density (i.e. who is more strongly affected by an  
353 increase in density in its vital rates?) have received more interests in both theoretical and  
354 empirical studies than age-specific contributions to density regulation (i.e. who is affecting  
355 the most the vital rates of others?). In the first case (i.e. who is more strongly affected by an  
356 increase in density in its vital rates?), it means for instance that increasing the total population  
357 size  $N_{tot}$  affects the survival rates  $S$  of all ages  $i$  differently:

358           
$$\text{logit}(S_{i,t}) = \alpha_i + \beta_{N_{tot} i} \times N_{tot,t} \quad (1),$$

359 the  $\beta$  coefficients assessing the strength of density dependence acting on the survival of each  
360 age  $i$ . Importantly, density regulation can act on various vital rates (e.g. survival,  
361 reproduction), differently according to the age of the individuals, with potentially different  
362 (non-linear) forms. In the second case (i.e. who is affecting the most the vital rates of others?),  
363 it means for instance that increasing the number of individuals in age class  $j=1$  does not have  
364 the same effect on survival rate than increasing the number of individuals in age class  $j>1$ :

365           
$$\text{logit}(S_t) = \alpha + \sum_{j=1}^{j=\text{number of age groups}} \beta_j \times N_{j,t} \quad (2)$$

366 We define the age classes  $j$  with the largest negative  $\beta_j$  as the critical age groups. More  
367 complex density regulation patterns can exist. For instance, an increase in the number of  
368 individuals in a given age group  $j$  can differently affect the survival rates of individuals  
369 according to their age (mixture of Eq. 1 & 2):

370           
$$\text{logit}(S_{i,t}) = \alpha_{i,j} + \sum_{j=1}^{j=\text{number of age groups}} \beta_{i,j} \times N_{j,t} \quad (3)$$

371           In age-structured populations, all individuals do not equally respond to an increase in  
372 density (Eq. 1). Since the 70's, it is well known that some ages are more strongly influenced  
373 in their vital rates (survival, reproduction) than others. The pioneering work of Eberhardt [76]  
374 for instance predicts sequential demographic responses to an increase in density, with first an

375 increase in mortality rate for immatures, followed by a change in reproductive rate of adult  
376 females and finally an increase in adult mortality rate. This means that adults are affected by  
377 density only when the population reaches the carrying capacity, whereas the youngest  
378 individuals seem to be the first age group affected by density dependence [77]. Since then,  
379 this theoretical model has been supported by empirical studies (e.g. [77–81]). More generally,  
380 there is increasing empirical evidence that individuals, depending on their age, are not equally  
381 influenced by an increase in density (see e.g. [7,22,82]). Another striking example of age-  
382 specific response to increasing density has been reported in a German great tit population, in  
383 which low density favors fast explorer individuals that are the youngest ones, whereas high  
384 densities rather select for slower explorers generally the oldest ones [44,83]. This adds to the  
385 spate of studies highlighting that depending on their age, individuals may not equally respond  
386 to an increase in density. Furthermore, it has been shown that the evolutionary dynamics of  
387 species depend on the life stage on which density is acting [84]. How does this age-specific  
388 response to density interact with the critical age group? Let's consider that age class  $j$  is the  
389 critical age group. One can expect that an increase in the density of age group  $j$  could lead to  
390 different density-dependent patterns at the population level if i) individuals of different ages  
391 do not respond equally to such an increase in density; ii) all individuals in the population  
392 equally respond to increasing density; iii) only individuals of age class  $j$  are influenced by an  
393 increase of the density in their own age class. Exploring more deeply this question would  
394 offer interesting insights into the role played by age in density regulation, not only in terms of  
395 contribution but also in terms of response to density regulation.

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401 **Box 2: The concept of critical age group for density dependence in the context of climate**  
402 **change**

403 Density dependence in age-structured natural populations is a dynamical process, its  
404 strength is expected to vary across space and time in relation to climatic conditions. For  
405 instance, empirical evidence for stronger strength of density dependence under harsh  
406 environmental conditions is accumulating in the literature (see e.g. [85–87]). This means that  
407 climate conditions can mediate competitive abilities and, thus, density dependence [88],  
408 which is important in the current context of global changes. Critical age groups make no  
409 exception: within a species, the critical age group for density dependence varies among  
410 populations, depending on environmental conditions. For instance, in their study involving  
411 multiple great tit and blue tit populations across Europe, Gamelon et al. [25] found that even  
412 if young females consistently contribute to density regulation, older individuals also play an  
413 important role in one-third of the populations. They concluded that the fact that some ages  
414 appear to be important in driving density regulation at some sites but not others could be  
415 attributed to differences in local environmental conditions. Accordingly, the critical age class  
416 can be driven by local abiotic conditions and can change over habitat types, i.e. across space.  
417 Along the same line, one can expect that the critical age group during a period of time may  
418 change if environmental conditions are changing. Assessing to what extent age-specific  
419 contributions to density dependence depends on climate conditions offers exciting research  
420 perspectives, especially now, while climate is changing at an unprecedented rate.

421 Further support for the key role of climate conditions in mediating biotic interactions is  
422 provided in behavioral studies. Some have explored the influence of climate conditions on  
423 personality traits potentially related to competitive abilities. For instance, environmental  
424 temperature during early life has been shown to shape the personality of mosquitofish

425 (*Gambusia affinis*) [89], namely shyness and exploration as well as activity, exploration,  
426 sociability and boldness of southern rainforest sunskinks (*Lapropholis similis*) [90]. Similarly,  
427 daily temperature increases of few degrees had important effects on aggressiveness, activity  
428 and boldness in two species of coral reef fish [91]. Remarkably, the rank order of individual  
429 scores on each of these personality traits changed as a function of temperature [91]. This  
430 indicates that temperature-induced changes in personality traits related to competitive abilities  
431 could ultimately have implications for the critical age group contributing the most to density  
432 regulation.

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649

650

651 **Figure legends**

652

653 **Figure 1**

654 Schematic summary of the unified approach integrating evolution, behavior and demography  
655 to study density regulation in age-structured populations. On the left, the “classical” view of  
656 density dependence is pattern-oriented. The total population size ( $N$ ) negatively influences  
657 mean vital rates (e.g. survival, reproduction), that in turn influence the population growth rate.  
658 On the right, the suggested process-oriented framework linking demography, evolution and  
659 behavior. The total population size is divided into age-specific population sizes ( $N_i$ ) (example  
660 with 4 age classes black, blue, orange and green), that negatively influence age-specific vital  
661 rates more or less strongly depending on their competitive abilities, driven by senescence,  
662 learning, sociality, etc. In turn, age-specific demographic rates influence the population  
663 growth rate. The critical age group corresponds to the age(s) contributing the most to the  
664 density regulation acting on the population growth rate.

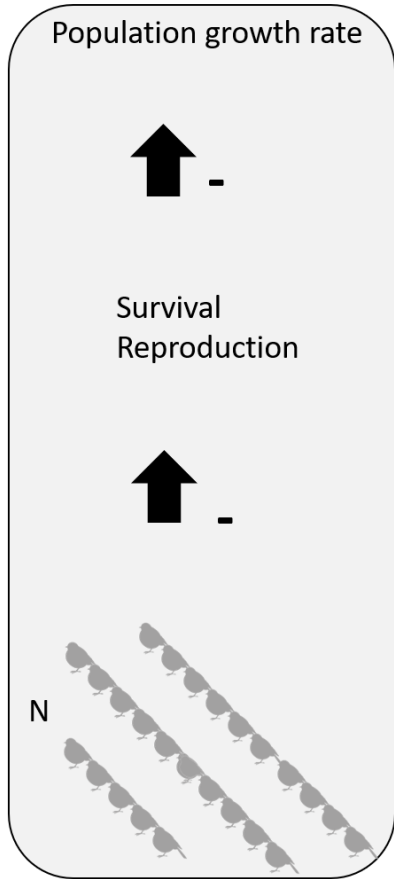
665

666 **Figure 2**

667 Simplified hypothetical scenarios leading to different critical age groups. Each color  
668 corresponds to one phenotype. The first row (A, B, C) corresponds to a scenario of selective  
669 disappearance of phenotypes with the lowest competitive abilities, resulting in higher  
670 competitive abilities and per-capita effect on growth rate for older age classes (age 4 is the  
671 critical age group). The second row (D, E, F) corresponds to a scenario of selective  
672 disappearance of phenotypes with the highest competitive abilities, resulting in lower  
673 competitive abilities and per-capita effect on growth rate for older age classes (age 1 is the  
674 critical age group). The third row (G, H, I) corresponds to a scenario of senescence with equal  
675 rate for all phenotypes, resulting in lower competitive abilities and per-capita effect on growth

676 rate for older age classes (age 1 is the critical age group). The fourth row (J, K, L)  
677 corresponds to a scenario in which both senescence and selective disappearance of  
678 phenotypes with the lowest competitive abilities happen, resulting in complex non-linear  
679 relationships between competitive ability and age (age 3 is the critical age group).

*Pattern-oriented approach*



*Process-oriented approach*

