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1 **Asynchrony of actuarial and reproductive senescence: a lesson from an**  
2 **indeterminate grower**

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15

16 Running head: **Senescence in an indeterminate grower**

17

18 **Abstract**

19

20 Aging evolutionary theories predict that patterns of actuarial and reproductive senescence should  
21 be aligned, with a common onset of senescence set at the age of first reproduction. However, a few  
22 empirical studies reported asynchrony between actuarial and reproductive senescence. This  
23 asynchrony is expected to be particularly pronounced in organisms with indeterminate growth. Yet,  
24 this process is still poorly documented due to the lack of long-term demographic data on known-  
25 aged individuals. We investigated the asynchrony of actuarial and reproductive senescence in the

42 **Introduction**

43

44 Although a few studies have challenged the idea of an inevitable senescence in nature (e.g. Martinez  
45 1998, Cayuela et al. 2020), it is now broadly recognized that senescence, the decline in the  
46 contribution to fitness with increasing age, is a widespread phenomenon across the animal kingdom  
47 (Nussey et al. 2013; Gaillard & Lemaître 2020). Senescence can be due to an age-specific decrease  
48 in survival probabilities (i.e., actuarial senescence) and/or reproductive performance (i.e.,  
49 reproductive senescence), two processes usually anchored in the same theoretical framework  
50 (Gaillard & Lemaître 2017). Evolutionary theories predict that patterns of actuarial and  
51 reproductive senescence should be aligned (Williams 1957, Maynard-Smith 1962), with a common  
52 onset of senescence at the age of first reproduction (Williams 1957). However, few recent studies,  
53 performed in both laboratory and free-ranging conditions, reported asynchrony between actuarial  
54 and reproductive senescence patterns (reviewed in Gaillard & Lemaître 2017). The factors  
55 modulating the degree of synchrony are still poorly understood.

56 The asynchrony between actuarial and reproductive senescence could be particularly  
57 pronounced in organisms with indeterminate (i.e., continuous) growth (e.g., fishes, amphibians,  
58 and reptiles) where survival and reproductive traits (e.g., fecundity, offspring survival) are often  
59 positively correlated with maternal body size, and thus indirectly determined by female age  
60 (Hoekstra et al. 2020). This asynchrony could result from non-linear relationships between fitness  
61 components and age. The fecundity of females with indeterminate growth recurrently increases  
62 with body size and age in a linear way (e.g., in reptiles, Jenkins et al. 2009, Setser et al. 2010, Rose  
63 et al. 2018), whereas the strength and the form of the relationship between mortality and age after  
64 sexual maturity can be highly variable among species (Colchero et al. 2019, Cayuela et al. 2019a)  
65 and populations (Cayuela et al. 2020).

66 To date, the asynchrony of actuarial and reproductive senescence in indeterminate growers  
67 is still poorly documented, mainly due to the lack of long-term demographic data on known-aged

94 day lasting from 0800 to 1800), by two or three people who searched intensively for snakes in the  
95 dilapidated building and neighbouring area of about 100× 80 m. Snakes were captured by hand,  
96 and individually marked by ventral scale clipping for future identification. At their first capture,  
97 female snakes were measured for snout-vent-length (SVL). We did not measure them on further  
98 captures to minimize disturbance and hence risks of their departure from the nesting area, as  
99 permanent emigration would bias capture-recapture inferences. We were able to assess the age of  
100 16 females that were captured at juvenile stage over the capture-recapture survey. Detailed  
101 information about the number of captures performed each year is given in **Table S1**.

102 Several females (N = 16) on their first capture were palpated in the abdomen to verify their  
103 pregnancy status and to count the number of eggs (Filippi et al. 2007). We also captured 44  
104 additional females in the surroundings of the study area to increase the number of observations of  
105 egg clutch size (N = 60 in total).

106

#### 107 *Reproductive senescence: assessing age-dependent variation in clutch size*

108

109 First, we verified that SVL was a good proxy of female age by quantifying the correlation between  
110 age and SVL in a small set of females for which the age was known (N = 16). Then, we examined  
111 how annual egg clutch size was associated with SVL in a larger sample of females (N = 60). In  
112 both cases, we used regression models where SVL or egg clutch size were included as the response  
113 variable and body size or age were included as explanatory variables. We compared null (i.e.  
114 without covariate), linear, and polynomial models using their AIC. We graphically verified the fit  
115 of the model by examining model residuals. The analyses were conducted in R program (R  
116 Development Core Team 2018).

117

#### 118 *Modeling age-dependent mortality using BaSTA*

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146

147 *Reproductive senescence pattern*

148

149 Our results confirmed that female SVL linearly increased with age (**Fig.1A** and **Table S2** for model  
150 selection procedure) and was thus a robust proxy of their age ( $R^2 = 0.43$ ). Next, we showed that  
151 annual egg clutch size increased with SVL (**Fig.1B**). Although the polynomial model was close  
152 (less than 2 AIC points between the two models), the linear model was selected  $R^2$  (0.74) (**Table**  
153 **S3**). Overall, our analyses highlighted that female annual fecundity increased linearly with SVL  
154 and age.

155

156 *Actuarial senescence pattern*

157

158 BaSTA models revealed that capture-recapture data were best described by a logistic function  
159 without any refinement of the shape (**Table 1**). The cumulative probability of surviving was 0.75  
160 until age six, 0.50 until age seven, and 0.25 until age eight (**Fig.1C**). Furthermore, the model  
161 showed a strong positive effect of age on hazard rate (**Fig.1D**), which indicates an early and strong  
162 actuarial senescence in *H. viridiflavus*.

163

## 164 **Discussion**

165

166 Using capture-recapture data collected over a 29-year period, we showed that *H. viridiflavus* female  
167 did not experience any fecundity loss late in life, suggesting a negligible reproductive senescence.  
168 In contrast, they suffered from an early and severe actuarial senescence. Taken together, those  
169 results revealed a pronounced asynchrony in the senescence process of two main fitness  
170 components.

197 general inferences about the ecological and biological factors modulating the asynchrony between  
198 aging components. At the intraspecific level, abiotic factors such as temperature and habitat  
199 predictability regulate lifespan and actuarial senescence (Sears 2005, Hjernquist et al. 2012, Zhang  
200 et al. 2018, Cayuela et al. 2019b), as well as reproductive investment (Morrison et al. 2003, Cayuela  
201 et al. 2016, Hughes et al. 2019), in ectotherm vertebrates with an indeterminate growth, which could  
202 ultimately modify the asynchrony of senescence patterns. In our study system, the low abundance  
203 of natural predators compared to other habitats occupied by *H. viridiflavus* (Philippi et al. 2007)  
204 could also buffer actuarial senescence by reducing predation-induced mortality late in life, which  
205 might lead to intraspecific variation in the degree of asynchrony between aging components.  
206 Furthermore, covariation between mortality patterns and several phenotypic traits of indeterminate  
207 growers could result in interspecific variation in the asynchrony of actuarial and reproductive  
208 senescence. In particular, the magnitude of the asynchrony could be diminished in species with  
209 size-dependent fecundity and negligible or even “negative” actuarial senescence (*sensu* Vaupel et  
210 al. 2004, Jones & Vaupel 2017) allowed by high regeneration capacities (e.g., salamanders, Cayuela  
211 et al. 2019a), or chemical (e.g., venomous snakes, Cayuela et al. 2019a, Colchero et al. 2019) and  
212 armour protection (e.g., turtles, Warner et al. 2016). Overall, our study raises important questions  
213 about the ecological and evolutionary mechanisms allowing the uncoupling of reproductive and  
214 actuarial senescence processes.

215

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218

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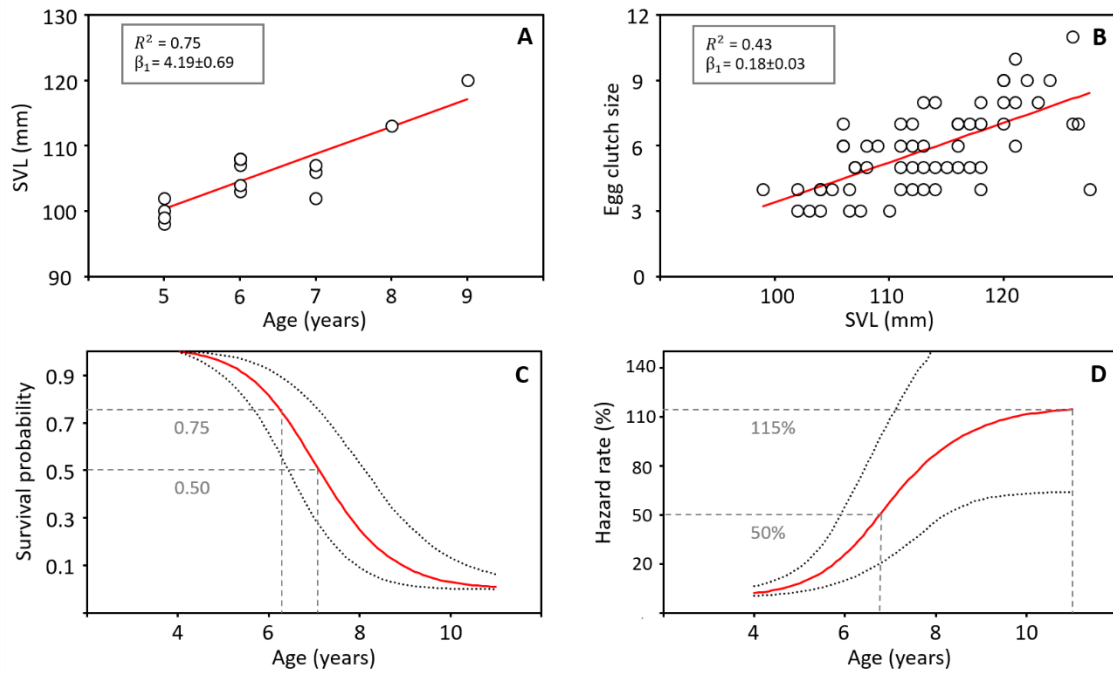
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329

330 **Fig.1.** Reproductive and actuarial senescence in females of *Hierophis viridiflavus*. (A) Linear  
 331 relationship between snout-vent-length (SVL) and age. (B) Linear relationship between egg clutch  
 332 size and SVL. (C) Relationship between survival and age described by a logistic function. (D)  
 333 Relationship between hazard rate and age described by a logistic function.

334

335