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1 **Population dynamics and age-dependent mortality processes in tropical**

2 **reptiles**

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19

20 **Abstract**

21

22 Understanding age-dependent mortality processes is a critical challenge for population biologists.

23 Actuarial senescence appears to be a common process across the tree of life. Senescence patterns

24 are highly variable in pluricellular organisms: senescence can be gradual or sharp and its onset may

25 be early or delayed. By contrast, studies revealed that organisms may also not experience

26 senescence at all while others display a "negative senescence"; i.e. a decrease of mortality rate with

27 age. To date, studies on senescence have largely focused on human and other endotherm

28 vertebrates, limiting our understanding of senescence in amniotes as a whole. By contrast, few have

29 examined the diversity of senescence patterns in ectotherm vertebrates as reptiles. Here, we

30 examined population dynamics and age-dependent mortality patterns in three tropical tortoises

31 (*Kinixys erosa*, *Kinixys homeana*, *Kinixys nogueyi*) and snakes (*Bitis gabonica*, *Bitis nasicornis*,

32 *Causus maculatus*). Our study revealed that tortoises of *Kinixys* genus had a higher survival and a

33 lower recruitment than snakes of the genera *Bitis* and *Causus*, indicating that they have a slower

34 life history. Furthermore, we showed that survival more slowly decreased with age in tortoises than

35 in snakes. In addition, we highlighted contrasted patterns of age-dependent mortality in the three

36 genera. In *Kinixys*, the relationship between mortality rate and age was positive and linear,

37 suggesting gradual senescence over tortoise lifetime. By contrast, the relationship between

38   mortality rate and age was negative and sharp in *Bitis* and *Causus*, possibly due to a "negative

39   senescence" starting early in life. Our study highlighted various age-dependent mortality patterns

40   in tropical reptiles. It also contributed to extend our knowledge of senescence in ectotherm

41   vertebrates whose the demography is still poorly understood. In addition, while negative

42   senescence has never been reported in endotherm vertebrates, our results showed that it can be

43   common phenomenon in ectotherms.

44

45   **Keywords**: age-dependent mortality, senescence, survival, recruitment, reptile

46

Introduction

The ageing theories state that an organism's survival should decrease with age, a phenomenon called actuarial senescence (hereafter senescence) (Hamilton 1966, Monaghan et al. 2008). In the 1950s, Medawar introduced the mutation accumulation theory that predicts that the strength of natural selection decreases with age after the primiparity. It states that the efficiency of the purging of deleterious mutations – having a detrimental effect on fitness components including survival – diminishes with age. Simultaneously, Williams (1957) proposed the theory of antagonistic pleiotropy postulating that senescence is a by-product of selection: an allelic variant conferring a selective advantage at early stage may lead to a decreased survival later in life. In the 1970s, Kirkwood (1977) introduced the theory of disposable soma that poses that senescence results from a trade-off between an early reproduction and somatic maintenance. A decrease in the energy allocation in somatic maintenance for the benefit of reproduction leads to lower survival-related performances and senescence.

More recently, studies suggested that senescence is a common process across the tree of life (Baudisch et al. 2013, Jones et al. 2014, Colchero et al. 2019; but see Jones & Vaupel 2017). Senescence patterns are highly variable in pluricellular organisms: it can be gradual or sharp and its onset may be early or delayed (Jones et al. 2014, Colchero et al. 2019). Studies showed that the onset of senescence is usually associated to species position along the fast-slow continuum of life histories (Stearns 1992, Oli 2004, Bielby et al. 2007). Species at the slow end of the continuum – with a long lifespan, a low fecundity, and a delayed maturity – usually have a delayed senescence (Jones et al. 2008, Kiørboe et al. 2015, Salguero-Gómez & Jones 2017). However, several species do not experience senescence at all (Jones et al. 2014, Jones & Vaupel 2017, Colchero et al. 2019). Moreover, other organisms may have a "negative senescence" (Vaupel et al. 2004, Jones & Vaupel 2017), a phenomenon that usually occurs in species exhibiting large body size variation over life and size-dependent survival. Mortality increases as body size decreases and size increases with age, which results in a negative relationship between mortality and age (see several cases in Jones et al. 2014).

To date, studies dealing with age-dependent mortality processes and senescence in amniotes have broadly focused on human and other endotherm vertebrates (Nussey et al. 2013, Fridlyanskaya et al. 2015, Shefferson et al. 2017). By contrast, the senescence patterns of ectotherm vertebrates as reptiles have been overlooked for a long time (Robert & Bronikowski 2010, Colchero et al. 2019), thus limiting our understanding of senescence processes to a restricted set of amniotes. The reptile class is the second most species-rich group of amniotes after birds and hosts 32% of the

81   tetrapod diversity (Pincheira-Donoso et al. 2012, IUCN 2019). To date, few studies suggested that

82   senescence patterns could be highly variable in reptiles: three of them indicated that senescence

83   may occur or not in squamates and turtles (Robert & Bronikowski 2010, Warner et al. 2016,

84   Colchero et al. 2019) while another one showed that negative senescence can be found in tortoises

85   (Jones et al. 2014). Yet, the small number of studies focusing on this topic is insufficient to reflect

86   the potentially high diversity of senescence patterns in reptiles.

87   Here, we examined population dynamics and age-dependent mortality patterns in three

88   tropical testudinid tortoises (*Kinixys erosa*, *Kinixys homeana*, *Kinixys nogueyi*) and viperid snakes

89   (*Bitis gabonica*, *Bitis nasicornis*, *Causus maculatus*). The six species were surveyed using capture-

90   recapture method over a 16-years period in a tropical forest of western Africa (Nigeria). First, we

91   quantified adult survival and recruitment in the six species of tortoises and snakes. Based on

92   previous studies on the demography of testudines (Gibbons 1987; Congdon et al. 1993, 1994), we

93   expected (1) tortoises to have slow life histories (i.e. higher adult survival and lower recruitment).

94   By contrast, we did not have any precise expectations for *Bitis* and *Causus* snakes (their

95   demographic parameters are unknown as in most of tropical snakes), even if the lifespan measured

96   in captivity suggests a long lifespan for *Bitis* species. Second, we examined age-dependent survival

97   and mortality rate. After showing that tortoises have slower life histories than snakes, we

98   hypothesized that (2) survival should decrease more slowly with age in tortoises than in snakes.

99   We also hypothesized that (3) if senescence occurs in both tortoises and snakes, tortoises should

100   have a more delayed senescence.

101

102   **Materials and methods**

103

104   *Studied species*

105

106   *Kinixys homeana, K. erosa* and *K. nogueyi* are omnivorous tortoises inhabiting the forested areas

107   and the forest-plantation mosaics of West Africa. They feed essentially on mushrooms and

108   invertebrates, and are rapidly declining because of habitat loss and overharvesting for local

109   consumption (Luiselli & Diagne 2013, 2014). They occur in sympatry in several forest zones of

110   the Niger Delta and of the Togo hills (Luiselli & Diagne 2013, 2014).

111   *Bitis gabonica* and *Bitis nasicornis* are two massive viper species (usually longer than 130

112   cm), with a wide distribution across the Guinea-Congolian forest belt, where they inhabit forest

113   and forest-plantation mosaics (Chippaux 2013). Their diet is based essentially on rodents, and, in

114   southern Nigeria, it is very similar in sympatric conditions (Luiselli & Akani 2003). *Causus*

115   *maculatus* is a small viper species (up to 60 cm in length), nocturnal in habits, that feed mainly of

116   frogs and inhabit forest patches as well as highly disturbed areas and plantations in West Africa

117   (Chippaux, 2013).

118

119   *Study area and capture-recapture surveys*

120

121   The field study was performed in the Port Harcourt area of the Niger Delta, Rivers State, south-

122   eastern Nigeria. The study area is heavily populated with hundreds of villages interspersed by

123   patches of forests and cultivated lands (yam, cassava and pineapples). The climate of the study

124   region is tropical, with well-delineated dry (from November to March) and wet (from April to

125   October) seasons. Mean annual rainfall averages around 4000 mm, making it one of the wettest

126   areas in Africa. The wet season peaks in July, and the dry season peaks in January and February.

127   Relative humidity rarely dips below 60% and fluctuates between 90% and 100% for most of the

128   year. During most of the rainy season cloud cover is nearly continuous, with about 1500 mean

129   annual sunshine hours and an average annual temperature of approximately 28°C. Both vipers and

130   tortoises are particularly active above-ground by wet season whereas they spend most of the dry

131   season months hidden, with only nocturnal activity on occasion (Luiselli 2003a, 2006a).

132   The survey was conducted between 2000 and 2016: tortoises were surveyed over the

133   complete period while snakes were monitored from 2000 to 2007. M-array matrices documentig

134   the mark-recapture process in the six species is provided in Supplementary material, Table S1-S4.

135   Most of the surveys were done between 0630-1030 hour and at 1730-2230 hour (Lagos standard

136   time). Field research was suspended during the central daylight hours because of too much hot, and

137   therefore no activity above-ground of these reptiles. Snakes and tortoises were studied

138   simultaneously, as they were sympatric and syntopic inside the same forest patch. These reptiles

139   were searched for by means of different surveying procedures: (i) random searching along all

140   appropriate forest micro-habitats, (ii) pitfalls with drift fences checked every day, and (iii)

141   examination of specimens just captured by local people that were employed by us to help in getting

142   more individuals from the field. Overall, random searching was done during 911 different days,

143   518 during the wet season (May to September), and 393 during the dry season (October to April).

144   Every tortoise was identified to species, sexed and individually marked by unique sequences of

145   notches filed into the marginal scutes. Each snake individual was permanently marked by ventral

146   scale clipping. Tortoises were generally easier to locate than vipers because they exhibited more

147   clear-cut microhabitat preferences: they were almost always hidden into leaf litter of well

148   vegetated, wet and shady spots inside the rainforest, usually in the surroundings of spots with plenty

149   mushrooms. On the other hand, microhabitat characteristics of vipers were less defined (Luiselli

150   2006a). For the six species of tortoises and snakes, juvenile data were removed from further

151   analyses because of the scarcity of observations at this life stage.

152

153   *Goodness-of-fit tests*

154

155   We examined transience and trap-dependence using U-CARE program (Choquet et al. 2009a). We

156   performed the TEST3.SR, TEST3.SM, TEST2.CT, and TEST2.CL for the six reptile species. The

157   tests TEST3.SR was significant for *K. erosa* and *K. homeana* (two species with a very similar

158   ecology; see Luiselli & Diagne 2013, 2014), which indicates an excess of transients in these species

159   (Supplementary material, Table S5). The other tests were non-significant in all species.

160

161   *Modeling survival and recruitment*

162

163   We examined survival using Cormack-Jolly-Seber models. For tortoises in which an excess of

164   transient was detected we considered a model with three states: transient (T), resident (R), and dead

165   (D). At their first capture, individuals can be in the state T or R. In the following vector probability,

166   individuals may thus be transient with a probability ψ_T or resident with a probability $1 - \psi_T$:

167         $$[\psi_T \quad 1 - \psi_T \quad 0]$$

168   Then, at each time step, resident individuals may survive with a probability φ_R or die with a

169   probability $1 - \varphi_R$ while the survival of transient individual is fixed at 0. This results in the

170   following state-state transition matrix (state at time t-1 in rows, state at t in columns):

171         $$\begin{bmatrix} 0 & 0 & 1 \\ 0 & \varphi_R & 1 - \varphi_R \\ 0 & 0 & 1 \end{bmatrix}$$

172   The last component of the model links field observations to underlying states. At each capture

173   session, transient and resident individuals can be captured with a probability p_T and p_R, leading

174   to the following matrix:

175         $$\begin{bmatrix} 1 - p_T & p_T \\ 1 - p_R & p_R \\ 1 & 0 \end{bmatrix}$$

176   We examined recruitment using Pradel capture-recapture model (1996) in which

177   recruitment is modeled by reversing capture histories and analyzing them backwards. For tortoises,

178   we considered a transient excess and used a modified version of the Pradel model. Recruitment

179   probability was estimated as the probability that an individual present at t was not present at t-1,

180   i.e. the proportion of "new", resident individuals in the population at t. The model had the same

181   structure than the survival model. However, the survival matrix was replaced by the recruitment

182   matrix. At each time step, resident individuals may be recruited with a probability δ_T or not with a

183   probability $1 - \delta_T$, leading to the following matrix:

184
$$\begin{bmatrix} 0 & 0 & 1 \\ 0 & 1 - \delta_R & \delta_R \\ 0 & 0 & 1 \end{bmatrix}$$

185   The survival and recruitment models were implemented in program E-SURGE (Choquet

186   et al. 2009b). As the number of years and the study period differed for tortoises and snakes, we

187   analyzed the datasets of tortoises and snakes separately. We ranked models using the second order

188   AIC and its quasi-likelihood counterpart (QAICc) and Akaike weights (w). If the Akaike weight of

189   the best supported model was less than 0.90, we used model-averaging to obtain parameter

190   estimates. The 95% CI were calculated using the delta-method (Royall 1986). For tortoises, we

191   tested our hypotheses about transience, survival, recapture probabilities, from the following general

192   model: [ψ(species), φ(species), p(species + t)] in which species was included as discrete covariate.

193   We also hypothesized that recapture probability varied among years (t). The model for snakes was

194   [i(.), φ(species), p(species + t)]. We tested all the possible combinations of effects, leading to the

195   consideration of 16 and eight competitive models for tortoises and snakes respectively.

196   For tortoises, we tested our hypotheses about recruitment, transience, and recapture from

197   the model [ψ(species), δ(species), p(species + t)]. For snakes, we considered the model [i(.),

198   δ(species), p(species + t)]. All the possible combinations of effects were considered, leading to 16

199   and eight candidate models for tortoises and snakes respectively.

200

201   *Modeling age-dependent survival and mortality rates*

202

203   We investigated age-dependent patterns of survival and mortality using Bayesian survival

204   trajectory analyses implemented in the R package BaSTA (Colchero et al. 2012a, 2012b). BaSTA

205   allowed us to account for imperfect detection, left-truncated (i.e., unknown birth date) and right-

206   censored (i.e., unknown death date) capture-recapture data in our analysis. The model allows the

207   estimation of two age-dependent parameters: survival until age x and the proportion of individuals

208   dying at age x (i.e. mortality rate, or hazard rate).

209   We focused our analysis at the genus level (the data of *Bitis* species and *Kinixys* species

210   were merged) to increase the statistical power of the analyses. It was not possible to examine age-

211   dependent processes in each species of tortoises and snakes due to the relatively low number of

212   individuals marked; models estimates were too imprecise. We therefore merged the capture-

213   recapture data of the different species of *Kinixys* and *Bitis*. In this regard, it should be considered

214   that *B. gabonica* and *B. nasicornis* are ecologically and morphologically very similar (Luiselli

215   2006a, 2006b), and the same is true for *K. erosa*, *K. nogueyi*, and *K. homeana* (Luiselli & Diagne

216   2013, 2014), thus making our merging of the data as *ecologically* relevant. We analyzed the data

217   of the three genera separately. For tortoises, we removed transient individuals by excluding the first

218   observation in capture-recapture histories. Given the results of the survival models (**Table 1**), we

219   allowed recapture probabilities to vary among years. The proportion of unknown birth date was 0%

220   in *Kinixy*s and 13% in *Bitis*, and 12% in *Causus*. The proportion of unknown death date was 4% in

221   *Kinixy*s, 0% in *Bitis*, and 1% in *Causus*.

222   We considered the four mortality functions implemented in BaSTA: exponential,

223   Gompertz, Weibull and logistic. For the three last functions, we considered three potential shapes:

224   *simple* that only uses the basic functions described above; *Makeham* (Pletcher 1999); and *bathtub*

225   (Silver 1979). As individuals usually reach sexual maturity at eight years in *Kinixys* (Coulson &

226   Hailey 2001) and at three years in *Bitis* and *Causus* (Luiselli, unpublished data) genera, we

227   conditioned the analyses at a minimum age of eight in tortoise models and three in snake models.

228   Four MCMC chains were run with 50,000 iterations and a burn-in of 5,000. Chains were thinned

229   by a factor of 50. Model convergence was evaluated using the diagnostic analyses implemented in

230   BaSTA, which calculate the potential scale reduction for each parameter to assess convergence.

231   Models that did not converge were not considered in the procedure of model selection. We used

232   DIC to compare the predictive power of each mortality function and its refinements (Spiegelhalter

233   et al. 2002, Colchero et al. 2012b).

234

235   **Results**

236

237   We made a total of 1071 captures (843 tortoises and 228 snakes). In tortoises, we identified 231

238   individuals of *K. erosa*, 281 individuals of *K. homeana*, and 57 individuals of *K. nogueyi*. In snakes,

239   we identified 35 individuals of *B. gabonica*, 34 individuals of *B. nasicornis*, and 68 individuals of

240   *C. maculatus*. For more detailed information about capture-recapture data, see m-array matrices in

241   Supplementary material, Table S1-S4.

242

243   *Modeling transience, survival and recruitment*

244

245   For tortoises, the best-supported model was [ψ(species), φ(species), p(species+t)] (**Table 1**); its

246   QAICc weight was 0.36 and we therefore model-averaged the estimates. Recapture probabilities

247   varied according to species and time (Supplementary material, Fig.S1). Recapture probability was

248   the highest in 2013: it was 0.95 (95% 0.82-0.99) in *K. erosa*, 0.90 (95% 0.68-0.98) in *K. homeana*,

249   and 0.90 (95% 0.67-0.97) in *K. nogueyi*. By contrast, recapture probability was the lowest in 2004:

250   it was 0.48 (95% 0.24-0.72) in *K. erosa*, 0.29 (95% 0.14-0.51) in *K. homeana*, and 0.29 (95% 0.10-

251   0.59) in *K. nogueyi*. Moreover, the transience rate differed among species (**Fig.1B**): it was the

252   highest in *K. erosa* (0.79, 95% 0.72-0.85) while *K. homeana* had an intermediate transience rate

253   (0.53, 95% 0.62-0.72), and *K. nogueyi* had the lowest one (0.30, 95% 0.11-0.60). This result is

254   congruent with the GOF tests (Supplementary material, Table S5) that have detected an excess of

255   transience in *K. erosa* and *K. komeana* but not in *K. nogueyi*. Furthermore, survival probability

256   differed between species (**Fig.1A**): *K. erosa* had higher survival (0.83, 95% 0.73-0.90) than *K.*

257   *homeana* (0.70, 95% 0.62-0.77) and *K. nogueyi* (0.73, 95% 0.56-0.85). The best-supported

258   recruitment model was [ψ(species), δ(.), p(species+t)] (w = 0.23; **Table 2**). Recruitment probability

259   was relatively similar among tortoise species (**Fig.1C**): it was 0.28 (95% 0.22-0.35) in *K. erosa*,

260   0.28 (95% 0.22-0.34) in *K. homeana*, and 0.33 (95% 0.25-0.42) in *K. nogueyi*.

261
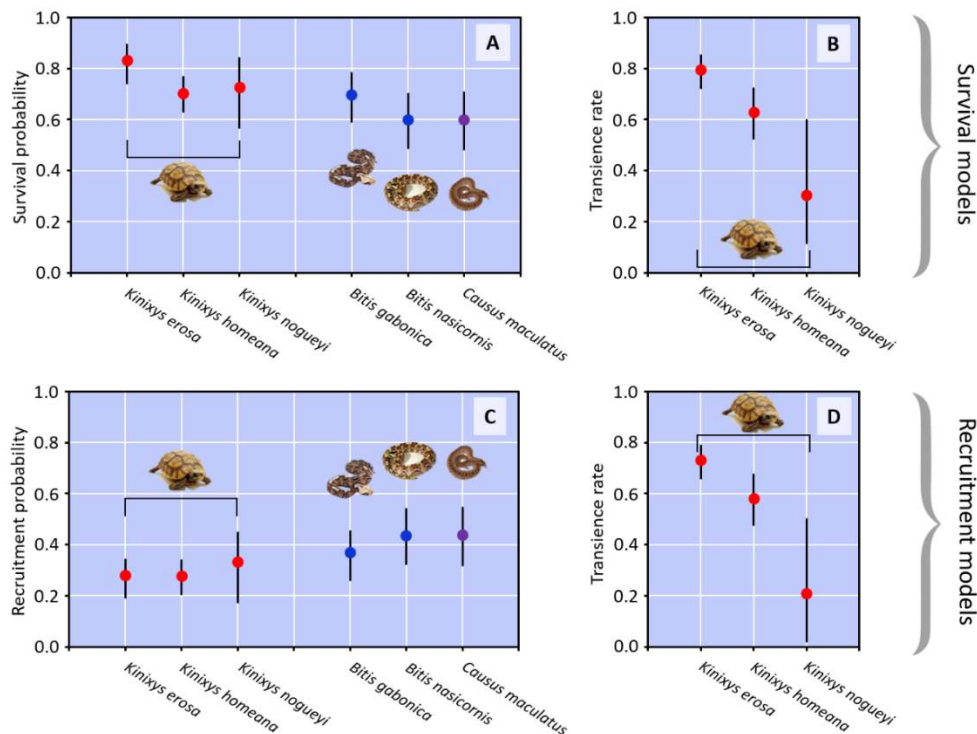
262

263   **Fig.1**. Estimates of survival, recruitment, and transience in three tropical tortoises (*Kinixys erosa*,

264   *Kinixys homeana*, *Kinixys nogueyi*) and snakes (*Bitis gabonica*, *Bitis nasicornis*, *Causus*

265   *maculatus*).

266   For snakes, [i(.), φ(species), p(species)] was the best supported model (w = 0.59, **Table 1**).

267   The recapture probability marginally varied among years (Supplementary material, Fig.S1).

268   However, it markedly differed among species: *C. maculatus* had a higher recapture probability

269   (e.g., 2003: 0.93, 95% CI 0.67-0.99) than *B. gabonica* (2003: 0.83, 95% CI 0.56-0.95) and *B.*

270   *nasicornis* (2003: 0.61, 95% CI 0.29-0.85). Moreover, survival rate slightly varied among species:

271   *B. gabonica* (0.70, 95% CI 0.59-0.78) had a higher survival rate than *B. nasicornis* (0.60, 95% CI

272   0.48-0.70) and *C. maculatus* (0.61, 95% CI 0.49-0.71). The best-supported recruitment model was

273   [i(.), δ(.), p(species+t)] (w = 0.23; **Table 2**). Recruitment probability was relatively similar among

274   snake species (**Fig.1C**): it was 0.37 (95% 0.29-0.47) in *B. gabonica*, 0.44 (95% 0.33-0.55) in *B.*

275   *nasicornis*, and 0.44 (95% 0.33-0.55) in *C. maculatus*.

276
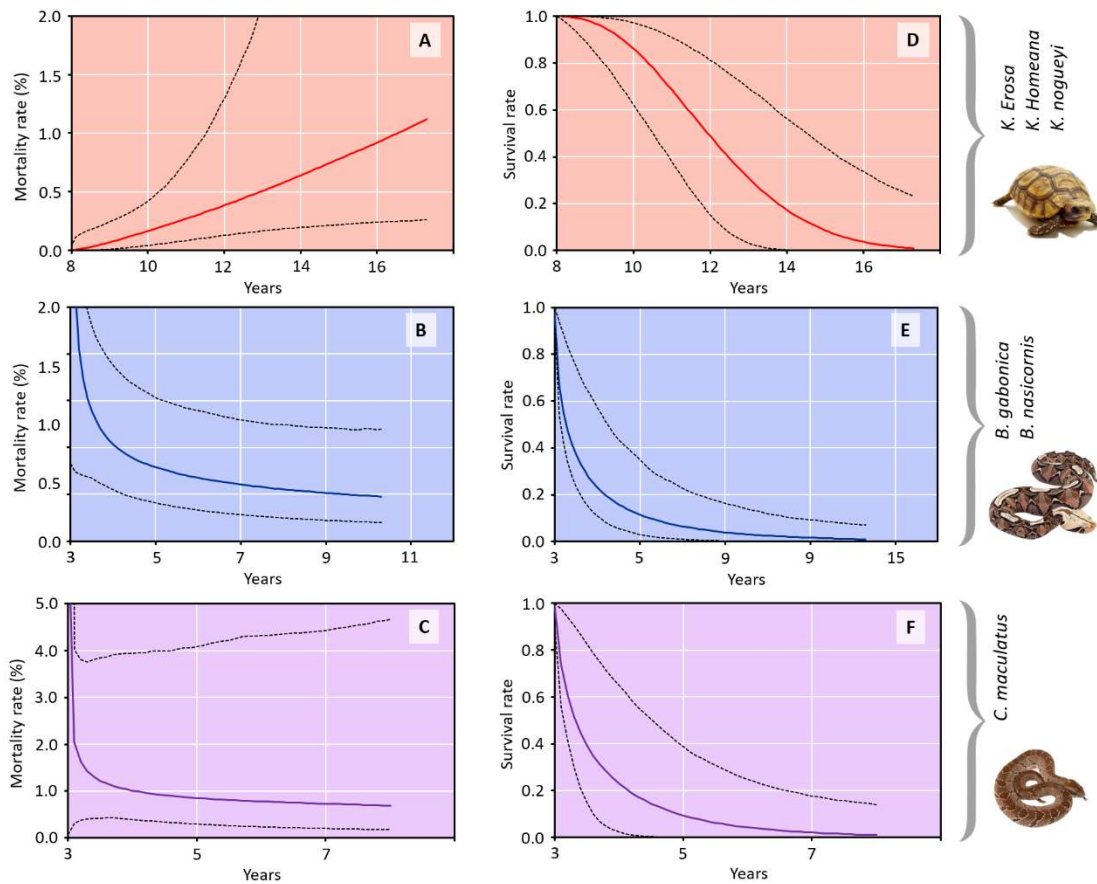
277

278   **Fig.2.** Age-dependent survival and mortality (i.e., hazard) rate in the genera *Kinixys*, *Bitis*, and

279   *Causus*.

280

281

282 **Table 1**. Model selection procedure for survival models in snakes (*Bitis gabonica*, *Bitis nasicornis*,

283 *Causus maculatus*) and tortoises (*Kinixys erosa*, *Kinixys homeana*, *Kinixys nogueyi*). r = model

284 rank, k = number of parameters, Dev. = residual deviance, QAICc = quasi-likelihood AICc,

285 ΔQAICc = difference of QAICc points with the best-supported model, w = QAICc weight.

r	Model	k	Dev.	QAICc	w
Snake					
1	$i(.)$, φ(species), p(species)	6	345.56	357.94	0.59
2	$i(.)$, $\varphi(.)$, p(species)	4	351.25	359.43	0.28
3	$i(.)$, φ(species), $p(.)$	4	353.09	361.27	0.11
4	$i(.)$, φ(species), p(species+t)	12	340.45	365.90	0.01
5	$i(.)$, $\varphi(.)$, p(species+t)	10	346.08	367.09	0.01
6	$i(.)$, φ(species), $p(t)$	10	348.71	369.72	0.00
7	$i(.)$, $\varphi(.)$, $p(.)$	2	365.37	369.42	0.00
8	$i(.)$, $\varphi(.)$, $p(t)$	8	360.81	377.47	0.00
Tortoises					
1	ψ(species), φ(species), p(species+t)	24	1195.63	1245.10	0.36
2	ψ(species), $\varphi(.)$, p(species+t)	22	1201.14	1246.37	0.19
3	ψ(species), φ(species), $p(t)$	22	1201.93	1247.16	0.13
4	ψ(species), φ(species), p(species)	9	1228.49	1246.71	0.16
5	ψ(species), $\varphi(.)$, $p(t)$	20	1206.99	1248.01	0.08
6	ψ(species), $\varphi(.)$, p(species)	7	1234.05	1248.18	0.08
7	ψ(species), φ(species), $p(.)$	7	1241.77	1255.90	0.02
8	ψ(species), $\varphi(.)$, $p(.)$	5	1247.78	1257.86	0.00
9	$\psi(.)$, $\varphi(.)$, $p(t)$	18	1223.17	1260.00	0.00
10	$\psi(.)$, $\varphi(.)$, p(species+t)	20	1220.16	1261.18	0.00
11	$\psi(.)$, φ(species), $p(t)$	20	1221.27	1262.30	0.00
12	$\psi(.)$, φ(species), p(species+t)	22	1217.88	1263.11	0.00
13	$\psi(.)$, $\varphi(.)$, p(species)	5	1254.33	1264.40	0.00
14	$\psi(.)$, φ(species), p(species)	7	1251.77	1265.90	0.00
15	$\psi(.)$, φ(species), $p(.)$	5	1262.91	1272.98	0.00
16	$\psi(.)$, $\varphi(.)$, $p(.)$	3	1267.14	1273.16	0.00

286

287

288 **Table 2**. Model selection procedure for recruitment models in snakes (*Bitis gabonica*, *Bitis*

289 *nasicornis*, *Causus maculatus*) and tortoises (*Kinixys erosa*, *Kinixys homeana*, *Kinixys nogueyi*). r

290 = model rank, k = number of parameters, Dev. = residual deviance, QAICc = quasi-likelihood

291 AICc, ∆QAICc = difference of QAICc points with the best-supported model, w = QAICc weight.

r	Model	k	Dev.	QAICc	w
	Snakes				
1	$i(.), \delta(.), p(species)$	4	371.62	379.80	0.55
2	$i(.), \delta(species), p(species)$	6	368.47	380.85	0.32
3	$i(.), \delta(species), p(.)$	4	375.10	383.28	0.10
4	$i(.), \delta(.), p(.)$	2	382.49	386.55	0.02
5	$i(.), \delta(.), p(species+t)$	10	368.29	389.31	0.00
6	$i(.), \delta(species), p(species+t)$	12	365.25	390.70	0.00
7	$i(.), \delta(species), p(t)$	10	371.60	392.62	0.00
8	$i(.), \delta(.), p(t)$	8	378.87	395.53	0.00
	Tortoises				
1	$\psi(species), \delta(.), p(species+t)$	22	1254.18	1299.41	0.23
2	$\psi(species), \delta(.), p(species)$	7	1284.84	1298.98	0.28
3	$\psi(species), \delta(species), p(species+t)$	24	1251.52	1300.98	0.10
4	$\psi(species), \delta(species), p(species)$	9	1281.62	1299.83	0.18
5	$\psi(species), \delta(.), p(t)$	20	1259.64	1300.66	0.12
6	$\psi(species), \delta(species), p(t)$	22	1256.39	1301.62	0.07
7	$\psi(species), \delta(.), p(.)$	5	1296.18	1306.25	0.01
8	$\psi(species), \delta(species), p(.)$	7	1293.03	1307.17	0.00
9	$\psi(.), \delta(.), p(t)$	18	1275.02	1311.85	0.00
10	$\psi(.), \delta(species), p(t)$	20	1273.69	1314.71	0.00
11	$\psi(.), \delta(.), p(species+t)$	20	1273.83	1314.85	0.00
12	$\psi(.), \delta(.), p(species)$	5	1304.33	1314.40	0.00
13	$\psi(.), \delta(species), p(species+t)$	22	1272.06	1317.30	0.00
14	$\psi(.), \delta(species), p(species)$	7	1302.66	1316.79	0.00
15	$\psi(.), \delta(.), p(.)$	3	1314.02	1320.05	0.00
16	$\psi(.), \delta(species), p(.)$	5	1313.33	1323.40	0.00

292

293   *Modeling age-dependent survival and mortality rates*

294

295   In the genus *Kinixys*, data were best described by a Weibull function (Supplementary material,

296   Table S2). The model indicated the mortality rate was age-dependent: it increased gradually with

297   age (**Fig.2A**). Survival probability was 0.95 until nine years, 0.50 until 12 years, 0.25 until 13 years,

298   and was below than 0.05 until 16 years (**Fig.2D**).

299   As well, the Weibull function was the best supported one in the genus *Bitis* (Supplementary

300   material, Table S2). The model showed that mortality rates decreased with age (**Fig.2B**): it dropped

301   dramatically and then the decrease tended to be less strong. Survival probability was 0.95 until 3

302   years, 0.50 until 3.5 years, 0.25 until 4 years, and was below than 0.05 until 7 years (**Fig.2E**).

303   In the genus *Causus*, exactly as in the two previous genera, data were best described by a

304   Weibull function (Supplementary material, Table S2). Mortality rate was age-dependent although

305   the 95% CI were very large (**Fig.2B**). Mortality rate decreased brutally and then remained stable.

306   Survival probability was 0.95 until three years, 0.50 at 3.5 years, 0.25 until 4 years, and was below

307   than 0.05 until 5.5 years (**Fig.2E**).

308

309   **Discussion**

310

311   We validated two out of our three hypotheses of departure. First, we showed that tortoises of the

312   *Kinixys* genus had a higher survival and a lower recruitment than snakes of the genera *Bitis* and

313   *Causus*, indicating that they have a slower life history (*hypothesis 1*). Second, we showed that

314   survival more slowly decreased with age in tortoises than in snakes (*hypothesis 2*). Third, we

315   highlighted contrasted age-dependent mortality rate patterns in the three genera. In *Kinixys*, the

316   relationship between mortality rate and age was positive and linear, suggesting gradual senescence

317   over tortoise lifetime. By contrast, the relationship between mortality and age was negative and

318   sharp in *Bitis* and *Causus*, suggesting negative senescence starting early in life. Therefore, we did

319   not validated *hypothesis 3* (i.e., a more delayed senescence in *Kinixys* with slow life histories) as

320   only tortoises likely experienced "positive" senescence.

321

322   *Population dynamics and species position along the fast-slow continuum*

323

324   The tortoises of the genus *Kinixys* had slower life histories (i.e. longer lifespan and lower

325   recruitment) than the three snake species. The total lifespan obtained by adding the pre-maturity

326   lifespan (8 years, Lawson 2001) and the adult lifespan (calculated using survival φ estimates;

327 lifespan = 1-/ln(φ)+ 8) was 13 years in *K. erosa* , and 11 years in *K. homeana* and *K. nogueyi*.

328 Those estimates are congruent with the lifespan (10 years) calculated using scale ring counting in

329 *Kinixys spekii* (Coulson & Hailey 2001). In snakes, the total lifespan was 6 years in *B. gabonica*

330 and 5 years in *B. nasicornis* and *C. maculatus*. The lifespan of the *Bitis* species is far lower than

331 the one reported in captivity (around 18 years). First, this could be due to methodological

332 limitations: in capture-recapture studies, survival can be biased by permanent emigration from the

333 study area (Lebreton et al. 1992). Large *Bitis* species such as *B. gabonica* or *B. nasicornis* can

334 exhibit looping excursions well outside their home ranges (Linn et al. 2006), which may lead to

335 apparent survival if they die before returning to their home range. Yet, this explanation does not

336 seem completely satisfactory as recapture probability is relatively high in *B. gabonica* and GOF

337 test 3SR did not indicate an excess of transient, which does not suggest a high permanent emigration

338 from the study area. Alternatively, the low survival of snakes may be due to a high mortality in

339 natural conditions. Small adults could experience predation but anthropogenic factors (road killing,

340 voluntary destruction due to snake harmfulness, human hunting for subsistence) might also

341 negatively affect survival. Indeed, *Bitis gabonica* is one of the most intensely hunted snakes in the

342 Niger Delta region for the bushmeat trade (Eniang et al. 2006, Akani et al. unpublished data). Since

343 these vipers are actively searched for by hunters, it is likely that their mortality risks are high (given

344 also the high density of settlements and population around the forested patches), and this might

345 have substantially reduced the life expectancy of these vipers locally. For *B. nasicornis* it is the

346 same, but this latter species occurs less frequently than *B. gabonica* in the local bushmeat markets

347 (Eniang et al. 2006, Akani et al. unpublished data).

348   In parallel, recruitment was lower in tortoises than in snakes. Recruitment probability was

349 relatively similar (around 0.30) among the tortoises of the *Kinixys* genus. By contrast, the

350 recruitment probability was slightly higher in the three snake species (around 0.40) and did not

351 markedly differed between the genera *Bitis* and *Causus*. The lower recruitment in *Kinixys* than in

352 *Bitis* and *Causus* likely resulted from a variation in female fecundity. Females of *K. erosa* and *K.*

353 *homeana* lay from 4 and 8 eggs (Akani et al. 2004) while females of *B. gabonica* and *B. nasicornis*

354 produce 18 and 25 young respectively after a gestation of one year.

355   .

356 *Footprints of positive and negative senescence*

357

358 We only detected the footprint of (positive) senescence in tortoises. In the *Kinixys* genus,

359 individuals appear to experience a gradual senescence: the relationship between mortality rate and

360 age was almost linear and reached 100% at 17 years. This pattern markedly differs from the one

361 reported (i.e. negative senescence) by Jones et al. (2014) for the desert tortoise *Gopherus agassizii*.

362 However, *Kinixys* and *Gopherus* have very contrasted ecological characteristics: *Gopherus* are

363 burrowers, vegetarian species from dry, moderately vegetated up to semidesertic areas (e.g. Ashton

364 & Ashton, 2007), whereas *Kinixys* are above-ground active, omnivorous species from very wet,

365 forested areas (Luiselli & Diagne 2013, 2014). In addition, age-dependent survival patterns strongly

366 differ between *Kinixys* and *Gopherus* tortoises. In *Gopherus agassizii*, juveniles experience a high

367 mortality while adult have very high survival ($\varphi > 0.95$, Tuberville et al. 2008), which results in a

368 very long lifespan (around 40 years, Curtin et al. 2009) in few individuals and a negative senescence

369 pattern. By contrast, our study and a previous one (Coulson & Hailey 2001) indicated that *Kinixys*

370 tortoises have a shorter lifespan (13-10 years) likely associated with a progressive senescence over

371 individual lifetime.

372   The age-dependent mortality pattern found in *Bitis* and *Causus* vipers strongly suggests a

373 negative senescence (Vaupel et al. 2004). In the genus *Bitis*, the mortality rate sharply decreases

374 between three and five years and then tends to slow down. In *Causus*, mortality dramatically

375 dropped between three and four years and then stabilized. This indicates that vipers experience a

376 high mortality during a period (few years) following sexual maturity. Mortality tends to decrease

377 after that allowing few individuals to have a relatively long lifespan (possibly more than 10 years).

378 In those snakes, negative senescence likely results from large variation of body size over snake

379 lifetime and size-dependent survival. In *B. gabonica* for instance, newborns have a body size of

380 0.30 m and body mass of 0.05 kg while large adults can reach a size of 2.2 meters and a mass of 10

381 kg (Bonnet et al. 2001). It is possible that young adults (3-4 years) with a relatively small body size

382 (0.80-1.10 m) experience a high mortality due to extrinsic factors such as predation while a large

383 size may better protect old individuals from those factors. Cobras frequently eat on vipers and other

384 snakes (Luiselli et al. 2002, Filippi & Petretto 2013, Maritz et al. 2019) and two species, *Naja*

385 *melanoleuca* and *Naja nigricollis*, are common at the study area. The pattern of negative senescence

386 found in *Bitis* and *Causus* strongly differs from the one reported for *Vipera aspis*, a small viperid

387 from temperate regions that seems to do not experience either positive or negative senescence

388 (Colchero et al. 2019).

389

390 **Conclusion**

391

392 To our knowledge, the present study was the first to investigate age-dependent mortality processes

393 in tropical squamates and contributed to extend our knowledge of senescence in amniotes in a more

394 general way. Our results, and those of Jones et al. (2014), indicate that negative senescence that

395   was initially ruled out by the Hamilton's model (Hamilton 1966) seems to be a common pattern in

396   reptiles while it has not been reported so far in mammals and birds. They also indicate that reptiles

397   with contrasted life histories and population dynamics may have highly divergent senescence

398   patterns. We strongly encourage further studies to use capture-recapture data available in a broader

399   range of ectotherm amniotes to expand our understanding of senescence in the living world.

400

401   **Acknowledgements**

402

410

411   **References**

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551

552 # Supplementary material

553

554 **Fig.S1**. M-array matrix for *K. erosa*.

K. erosa	Total_released	t2	t3	t4	t5	t6	t7	t8	t9	t10	t11	t12	t13	t14	t15	t16	t17	Total_recapt
R1	14	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
R2	14		2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	4
R3	12			2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
R4	21				2	2	0	0	0	0	0	0	0	0	0	0	0	4
R5	19					1	0	0	0	0	0	0	0	0	0	0	0	1
R6	17						5	0	0	0	0	0	0	0	0	0	0	5
R7	15							5	0	0	0	0	0	0	0	0	0	5
R8	18								6	1	0	0	0	0	0	0	0	7
R9	18									3	1	1	0	0	0	0	0	5
R10	17										4	1	1	0	0	0	0	6
R11	25											4	0	0	0	0	0	4
R12	18												7	0	1	0	0	8
R13	23													10	0	0	0	10
R14	21														9	1	2	12
R15	24															8	2	10
R16	24																14	14

555

556 **Fig.S2**. M-array matrix for *K. homeana*.

K. homeana	Total_released	t2	t3	t4	t5	t6	t7	t8	t9	t10	t11	t12	t13	t14	t15	t16	t17	Total_recapt
R1	23	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7
R2	27		7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	9
R3	31			5	4	2	1	0	0	0	0	0	0	0	0	0	0	12
R4	22				2	4	1	1	0	0	0	0	0	0	0	0	0	8
R5	28					3	1	3	0	1	0	0	0	0	0	0	0	8
R6	26						3	1	0	0	0	0	0	0	0	0	0	4
R7	27							3	5	0	0	0	0	0	0	0	0	8
R8	30								7	1	1	0	0	0	0	0	0	9
R9	35									5	2	0	0	0	0	0	0	7
R10	24										6	2	0	0	0	0	0	8
R11	24											4	1	1	0	0	0	6
R12	20												9	1	0	0	0	10
R13	24													9	0	0	0	9
R14	19														6	1	0	7
R15	17															3	1	4
R16	14																7	7

557 **Fig.S3**. M-array matrix for *K. nogueyi*.

K. nogueyi	Total_released	t2	t3	t4	t5	t6	t7	t8	t9	t10	t11	t12	t13	t14	t15	t16	t17	Total_recapt
R1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R2	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R3	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R4	0				0	0	0	0	0	0	0	0	0	0	0	0	0	0
R5	0					0	0	0	0	0	0	0	0	0	0	0	0	0
R6	0						0	0	0	0	0	0	0	0	0	0	0	0
R7	0							0	0	0	0	0	0	0	0	0	0	0
R8	0								0	0	0	0	0	0	0	0	0	0
R9	0									0	0	0	0	0	0	0	0	0
R10	9										2	1	1	0	0	0	0	4
R11	11											3	4	0	0	0	0	7
R12	15												6	1	0	0	0	7
R13	17													11	1	0	0	12
R14	18														5	2	0	7
R15	14															6	1	7
R16	16																8	8

558

559

560 **Fig.S4**. M-array matrix for the three snake species.

B. gabonica	Total_released	t2	t3	t4	t5	t6	t7	t8	Total_recaptured
R1	4	3	0	0	0	0	0	0	3
R2	8		4	2	0	0	0	0	6
R3	9			5	1	0	0	0	6
R4	9				3	2	1	0	6
R5	8					4	1	0	5
R6	11						6	1	7
R7	13							6	6

B. nasicornis		t2	t3	t4	t5	t6	t7	t8	
R1	11	2	1	0	0	0	0	0	3
R2	10		2	2	0	0	0	0	4
R3	11			4	2	0	0	0	6
R4	12				2	0	1	0	3
R5	13					3	1	0	4
R6	8						2	1	3
R7	18							3	3

C. maculatus		t2	t3	t4	t5	t6	t7	t8	
R1	6	3	0	0	0	0	0	0	3
R2	7		3	1	0	0	0	0	4
R3	7			4	0	0	0	0	4
R4	9				4	0	0	0	4
R5	5					2	1	0	3
R6	8						3	0	3
R7	9							5	5

561

562 **Fig.S5**. Goodness-of-fit tests (TEST3.SR, TEST3.SM, TEST2.CT, and TEST2.CL) performed in the
563 program U-CARE for the six species of reptiles.

Species	TEST3.SR	TEST3.SM	TEST2.CT	TEST2.CL
Snakes				
Bitis gabonica	df = 6, χ^2= 2.98, p = 0.81	df = 5, χ^2= 0.71, p = 0.98	df = 4, χ^2= 0.00, p = 1.00	Unsuccessful
Bitis nasicornis	df = 6, χ^2= 2.31, p = 0.88	df = 5, χ^2= 0.00, p = 1.00	df = 5, χ^2= 0.71, p = 0.98	Unsuccessful
Causus maculatus	df = 6, χ^2= 1.51, p = 0.96	df = 2, χ^2= 0.00, p = 1.00	Unsuccessful	Unsuccessful
Tortoises				
Kynixys erosa	df = 15, χ^2= 87.46, p < 0.001	df = 7, χ^2= 2.79, p = 0.90	df = 7, χ^2= 5.11, p = 0.65	Unsuccessful
Kynixys homeana	df = 15, χ^2= 58.47, p < 0.001	df = 13, χ^2= 4.12, p = 0.98	df = 12, χ^2= 10.61, p = 0.56	df = 5, χ^2= 2.45, p = 0.78
Kynixys nogueyi	df = 6, χ^2= 4.67, p < 0.58	df = 5, χ^2= 0.62, p = 0.63	df = 5, χ^2= 0.00, p = 1.00	Unsuccessful

564

565

566 **Table S6**. Age-dependent survival and mortality rate in the genus *Kinixys*. Deviance information
567 criterion (DIC) for each of the mortality function. We considered the four mortality functions
568 implemented in BaSTA program: exponential (EXP), Gompertz (GOM), Weibull (WEI) and logistic
569 (LOG). For the three last functions, we considered three potential shapes: simple that only uses
570 the basic functions described above ("simple"); Makeham ("make"); and bathtub ("bath").

	Simple	*Bath*	*Makeham*
Logistic	1660.15	1648.95	1657.82
Exponential	1753.58	-	-
Gompertz	Not converged	Not converged	1640.35
Weibull	1631.98	1652.27	1668.54

571

572 **Table S7**. Age-dependent survival and mortality rate in the genus *Bitis*.

	Simple	*Bath*	*Makeham*
Logistic	601.03	Not converged	611.46
Exponential	599.11	-	-
Gompertz	Not converged	Not converged	Not converged
Weibull	584.10	592.71	Not converged

573

574 **Table S8**. Age-dependent survival and mortality rate in the genus *Causus*.

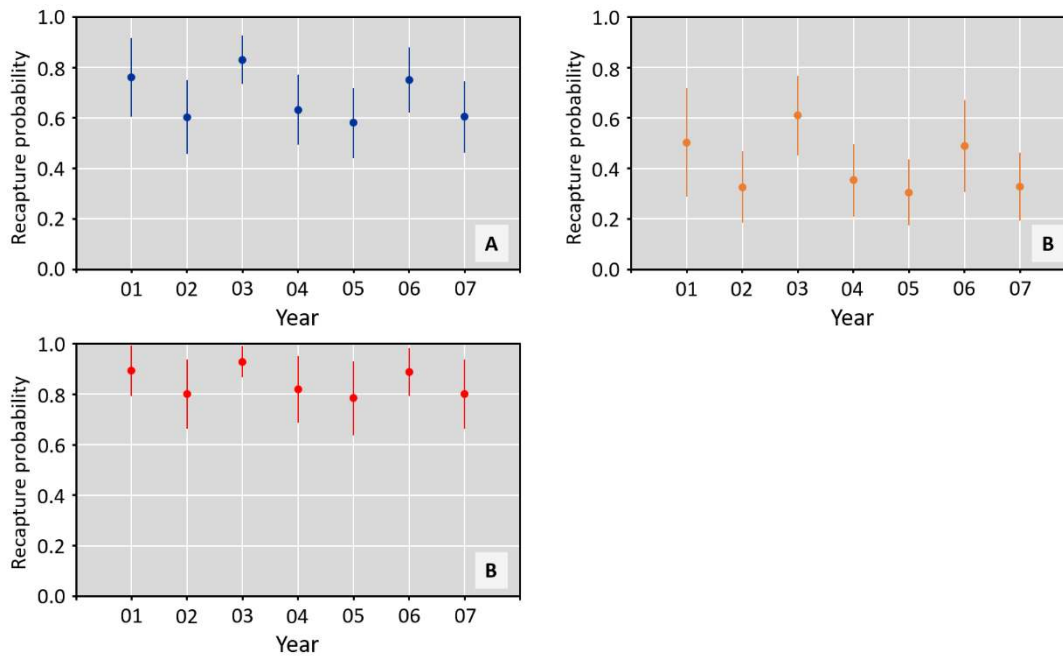|	*Simple*	*Bath*	*Makeham*
Logistic	402.59	Not converged	Not converged
Exponential	370.63	-	-
Gompertz	Not converged	Not converged	Not converged
Weibull	231.96	238.54	Not converged

575

576
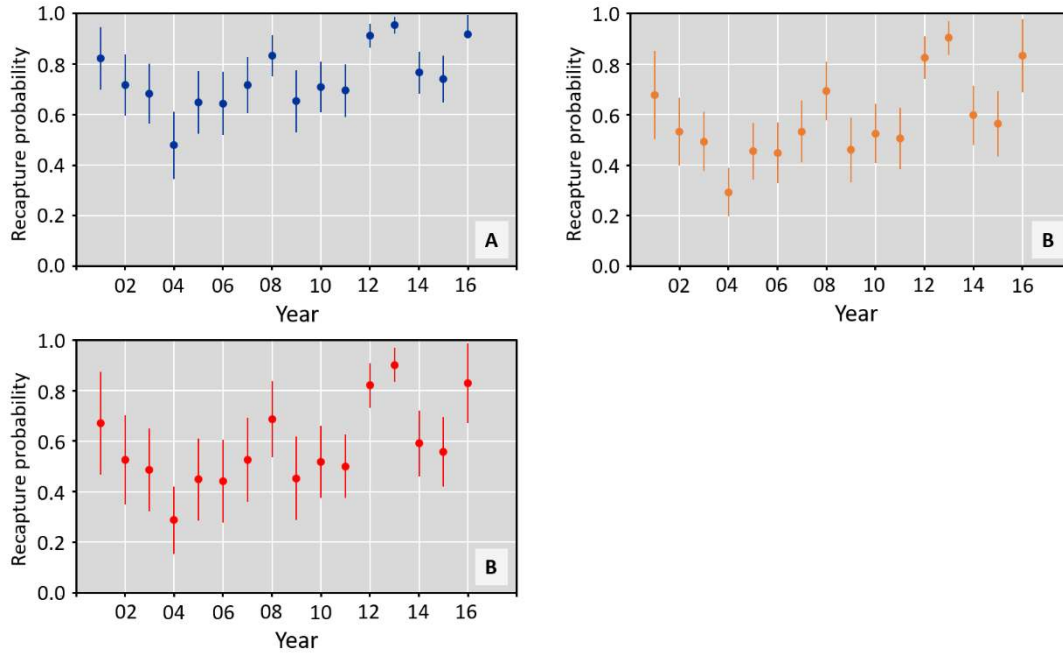
577
578 **Fig.S1.** Recapture probability of *Kinixys erosa*, *Kinixys homeana*, and *Kinixys nogueyi* over the
579 period 2001-2016. Model-averaged estimates and standard errors.
580
581

582
583 **Fig.S2.** Recapture probability of *Bitis gabonica*, *Bitis nasicornis*, and *Causus maculatus* over the
584 period 2001-2007. Model-averaged estimates and standard errors.
585
586