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► To cite this version:

Gopal Billy, Christophe Barbraud, Magali Dahirel, Xavier Bonnet. Does strict protection status harm snake populations in a temperate forest?. *Journal for Nature Conservation*, 2024, 81, pp.126683. 10.1016/j.jnc.2024.126683 . hal-04704031

HAL Id: hal-04704031

<https://hal.science/hal-04704031v1>

Submitted on 26 Sep 2024

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1 Does strict protection status harm snake populations in a temperate
2 forest?

3

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5

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14 **Keywords:** forest management; habitat closing; snake decline; snake monitoring; Strict

15 Nature Reserve (SNR)

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16 **Abstract**

17 Intensive agriculture causes landscape homogenization and massive defaunation. The
18 creation of Strict Nature Reserves (SNR) where management is proscribed aims to stem this
19 trend; this is the case for SNR forests in Western Europe. Yet, unmanaged forests are
20 subjected to rapid habitat closing; semi-open bushy habitats that are essential to many
21 thermophilic organisms can be squeezed between industrial agriculture and high timber
22 forests. Long-term capture-mark-recapture monitoring of snake populations (~27 years; 3,447
23 individuals) coupled with canopy closure monitoring conducted in a 2,579 ha forest amid a
24 landscape dominated by intensive agriculture in France provides an illustration of this threat.
25 Prior to SNR classification, logging maintained a mosaic of habitats (e.g., open, semi-open,
26 closed plots) favorable to snakes (*Hierophis viridiflavus*, *Zamenis longissimus*). SNR
27 classification promoted the growth of trees and rapid habitat closing, causing the
28 disappearance of open woodlands and a strong decline of snake abundance (~60% drop). The
29 impact was rapid in the most thermophilic species (*H. viridiflavus*) and delayed in the less
30 thermophilic species (*Z. longissimus*). This study provides robust and direct evidence that
31 habitat changes can entail a drastic decrease of snake abundance. Unintendedly, applying the
32 most protective conservation status to temperate forests might be less valuable in terms of
33 snake abundance and diversity than a status where limited conservation management actions
34 are permitted.

35

36 **Keywords:** forest management; habitat closing; snake decline; snake monitoring; Strict
37 Nature Reserve (SNR)

38 **Introduction**

39 Habitat loss is the main cause of defaunation (Cox et al., 2022; Young et al., 2016). On land,
40 this notably involves urbanization, the development of transport infrastructures and landscape
41 simplification (Tilman et al., 1994). Habitat homogenization, likely the main threat for
42 biodiversity, is largely associated with sprawling intensive agriculture and forest destruction
43 (DeFries et al., 2010; Foley et al., 2005; Karp et al., 2012). For example, in Europe several
44 millions of km of agricultural hedgerows have been uprooted and replaced by immense
45 monoculture fields during the past decades, causing large scale destruction of rich terrestrial
46 ecosystems (Holden et al., 2019; Montgomery et al., 2020). The disappearance of woodlands,
47 especially well-preserved old forests which host large amounts of threatened biodiversity, is a
48 strong conservation concern (Watson et al., 2018).

49 Protected areas have been created to mitigate the loss of natural habitats (Watson et al.,
50 2014). They pertain to six main IUCN categories plus several subcategories corresponding to
51 the respective degree of protection they confer against human alteration (International Union
52 for Conservation of Nature, Dudley 2008). The category 1a or Strict Nature Reserve - SNR
53 hereafter - is the most restrictive; a total ban of the exploitation of wildlife, minimal public
54 access and minimal intervention are key operational targets. SNR are primarily designed to
55 limit the erosion of endangered biodiversity and are considered as wildlife sanctuaries.

56 In temperate biomes, the SNR status is critical to protect the few remaining old temperate
57 forests (e.g., that exceed 250 years in age), especially to retain old tree formations along with
58 the wide range of species they host (Watson et al., 2018). However, imposing strict rules and
59 constraining policies generates conflicts against private interests (Shafer, 2020).

60 Consequently, SNR forests cover very small surfaces and most are limited to isolated patches
61 usually owned by countries or states (Cantú-Salazar & Gaston, 2010; Ficko et al., 2019;

62 Niemelä et al., 2005). Augmenting the area and connectivity of strictly protected forests is an
63 objective shared by many countries (Dudley, 2008).

64 There is another side to consider, however. The complexity of forest habitats, including
65 open and semi-open spaces, correlates with animal diversity (Eggers et al., 2010; Hanberry et
66 al., 2020; Kopecký et al., 2013). As the basic needs of heliophilous organisms cannot be met
67 in very closed forests, opening up the canopy by restoring traditional coppices favours
68 heliophilous species, thus promoting animal biodiversity (Hamřík et al., 2023; Perlík et al.,
69 2023). Thus, a lack of management in forests designated as SNR reserves may lead to habitat
70 homogenization and decreasing local biodiversity (Hanberry et al., 2020; Sebek et al., 2015).
71 In the absence of drastic events such as storms or fires, a lack of intervention favours canopy
72 growth and forest closing at the expense of herbaceous layers, shrubs and bushes (Hanberry
73 et al., 2020). Mosaic landscapes that combine dense old forests, open woodlands, bushy
74 habitats and meadows are essential to many organisms (Paillet et al., 2010; Pike et al., 2011).
75 In Europe, although the total surface of forests is currently increasing (Palmero-Iniesta et al.,
76 2021), biodiversity is still declining at worrying rates (Felton et al., 2010; Pimm et al., 2014;
77 Raven & Wagner, 2021). One possible reason for this discrepancy is that the increase of
78 forested surfaces does not result from conservation management policies; instead, it results
79 from the mere abandonment of traditional agricultural lands (Benayas et al., 2007).
80 Traditional complex semi-open cultivated areas are now squeezed between growing uniform
81 industrial agriculture, forest closure and urbanization. Review articles and field experiments
82 show that non-intensive farming and sustainable forest exploitation substantially contribute to
83 the maintenance of complex and biologically rich habitats (Paillet et al., 2010; Sebek et al.,
84 2015; Tinya et al., 2021). In this context, assessing the effectiveness of SNR forests to protect
85 vulnerable biodiversity is important, especially when strictly protected forests are surrounded
86 by degraded and homogeneous habitats (e.g. industrialized crops, urbanized areas). Yet,

87 recurrent deficiency of data linking habitat changes and animal diversity in protected areas
88 pose difficulties to propose guidance for the maintenance of local biodiversity (Gaston et al.,
89 2008).

90 Comparing unexploited *versus* harvested forests provides a straightforward means to
91 examine the effect of habitat management on the status of animal populations (Paillet et al.,
92 2010). Several conditions may facilitate the investigation of causalities. A) An experimental
93 design with replicates of contrasted habitats, notably open woodlands, closed woodlands,
94 closing and opening spots (i.e. increase/decrease in canopy closure) would provide a robust
95 background. B) Long term monitoring is essential to analyse the influence of habitat changes
96 on animal populations, especially to filter out short-term (e.g. annual) fluctuations. C)
97 Focusing on sedentary animals limits blurring effects of dispersal of individuals among forest
98 plots. D) Mark recapture design (CMR) offers a means to accurately estimate abundance in
99 different habitats.

100 Such conditions were almost entirely fulfilled in the current study, which aims to assess
101 the influence of habitat closing (i.e. forest or canopy closing) on snake populations in a
102 temperate SNR forest. The studied forest is amid a deeply degraded landscape (most
103 hedgerows have been destroyed) and it shelters snake populations that have been largely
104 extirpated from the surrounding environment during the last decades (Reading et al., 2010).
105 More generally, reptiles, including the species under focus, suffer from drastic global decline
106 largely provoked by habitat homogenization (Cox et al., 2022; Doherty et al., 2020; Reading
107 et al., 2010). This is also valid for a wide array of plants and animal species (many
108 invertebrate taxa) that are affected by the disappearance of semi-open forests and hedgerows
109 in agricultural and urbanized landscapes (Lecq et al., 2017, 2018). The studied SNR forest
110 represents a biodiversity sanctuary in a highly degraded landscape. Before SNR
111 classification, clear-cut geometric parcels were exploited for wood production, creating a

112 quasi-experimental background with contrasted plots (e.g. open vs closed plots). During the
113 last 27 years, populations of two snake species, the western whip snake (*Hierophis*
114 *viridiflavus*) and the Aesculapian snake (*Zamenis longissimus*) have been continuously
115 monitored using CMR in different habitats spread across the forest; broadly 11 years before
116 and 16 years after SNR classification. Most snakes are sedentary mesopredators that use
117 complex micro-habitats to find their prey, open spots for sun basking, or thick vegetation as
118 refuges (Beaupre, 1995; Pringle et al., 2003; Row & Blouin-Demers, 2006). Accordingly, it
119 has been suggested that reptiles represent appropriate organisms to assess important segments
120 of local biodiversity (Lewandowski et al., 2010). Overall, the study design permitted the
121 examination of a major question with a high spatial resolution: does a lack of management
122 prescribed by the SNR status necessarily favour the maintenance of globally declining
123 snakes?

124 Although *H. viridiflavus* and *Z. longissimus* are often found in syntopy, they exhibit
125 different ecologies. The former species is a thermophilic racer that regularly consumes
126 terrestrial lizards while the second species is a semi-arboreal and more thermo-conforming
127 snake that regularly feeds on nesting birds (Lelièvre et al., 2011, 2012). We hypothesized that
128 the intensity of habitat closing should provoke a proportional decline of snake abundance,
129 expectedly more pronounced for the most thermophilic species.

130 To address these issues, we combined canopy surveys and snake population monitoring.
131 We measured the canopy cover and described the ground vegetation in all forest plots from
132 1996 to 2020; this provided a dynamic view of canopy closure, notably following the
133 cessation of logging. From 1995 to 2021 we analysed long term CMR data to estimate annual
134 abundance of two snake species in three habitat types characterised by contrasted degree of
135 canopy closure. This design enable us to assess the effect of canopy closure on snake
136 abundance.

137

138 **Material and methods**

139 Study site

140 The Chizé forest (4,775 ha, 46.14°N, 0.42°W; Figure 1), located in a vast agricultural plain in
141 western France, is primarily represented by deciduous species (oaks [*Quercus robur*, *Q.*
142 *petraea*, *Q. pubescens*, *Q. Ilex*] 38%, beech trees [*Fagus sylvatica*] 35%, other deciduous
143 trees [*Carpinus betulus*, *Sorbus torminalis*, *Fraxinus excelsior*, *Acer monpessulanum*] 17%).
144 A dense network of agricultural hedgerows connected to the forest has been replaced by large
145 intensively managed crops (see online Appendix, Fig. A1). In this state forest, wood
146 harvesting is under the authority of the Office National des Forêts (ONF). Geometric parcels
147 (typically 5 to 20 ha) were exploited. More than half of the forest (~2,600 ha) was classified
148 in 1973 as a hunting reserve. Wood exploitation continued along with hunting of wild boar
149 (*Sus scrofa*) and roe deer (*Capreolus capreolus*).

150 In 1999, two exceptionally strong storms hit the forest (Rivière et al., 2010). Over 10,000
151 trees fell. Habitat openness was maximal in 2000 (Figure 1b). The excessive stock of timbers
152 induced a strong reduction of logging. Tree growth due to minimal forest management
153 promoted habitat closing (Vild et al., 2013). The year 2000 represents a milestone in the
154 management history of the forest, especially regarding canopy closure level.

155 In 2006 the status of most of the hunting reserve (2,579 ha; ~99%) was upgraded to the
156 maximal protection level: strict nature reserve (SNR). This status is equivalent to the 1a
157 IUCN category (i.e. Integral Biological Reserve, RBI, for the ONF). The Chizé Forest is the
158 largest continental SNR in metropolitan France and one of the largest in Europe. The official
159 decree (#DEVN0650590A) stipulates that forest management and harvesting are prohibited,
160 except for road maintenance and to control ungulate populations. It also specifies that a key
161 objective of the RBI is to maintain or increase biodiversity. Two enclaves, a meadow of 15.1

162 ha and a partly urbanized area of 6.4 ha, were not classified as SNR (Figure 1); habitat was
163 maintained open via regular shredding of wild vegetation.

164 From 2000 to 2021, we monitored canopy growth in different types of parcels (i.e., closed
165 with dense overstorey, open herbaceous with small bushes, semi-open herbaceous bushy; see
166 below). The legacy of timber harvesting by plots offered a quasi-experimental design to
167 survey the influence of canopy closing on reptile populations. We did not consider the
168 unprotected part of the Chizé forest (~2,200 ha) because logging precluded systematic snake
169 population survey. This study therefore focuses on the 2,661 ha of protected forest with
170 restricted access (2,579 ha of SNR plus small enclaves and several paths).

171

172 Forest management and habitat closing

173 We used three complementary sources of information: timber harvesting records, a time
174 series of aerial views of the forest, and photos taken from the ground. It enabled us to see if
175 the habitat category defined using aerial view provided coherent results when considered
176 from the ground level (i.e. where the snakes are living). The timber harvesting records
177 enabled us to see whether each of the habitats defined by aerial views resulted from
178 contrasting timber harvesting regimes.

179

180 *Timber harvesting records:* The ONF provided access to the annual catalogues of wood
181 exploitation from 1968 until harvesting cessation in 2005. Each year, in each exploited
182 parcel, the total timber volume harvested (m^3 and $m^3 \cdot ha^{-1}$) was available.

183

184 *Aerial views:* National Geographic Institute (IGN, geoportail.gouv.fr) offers a public access
185 of aerial images of the vegetation cover. Periods when deciduous plants do not have foliage
186 were excluded (e.g. mid-winter). We used images taken in 1996, 2000, 2007, 2011 and 2020,

187 almost fully covering the period of snake population monitoring (1995-2021). We
188 georeferenced aerial images (QGIS Development Team 2020). In each image, a pixel
189 represented 0.7m². This precision was sufficient to distinguish the canopy from the
190 herbaceous and bushy elements. In 2020, image gravimetry enabled us to estimate vegetation
191 height (Kiani, 2020).

192 Canopy cover, the surface covered by a vertical projection of the canopy (Jennings et al.,
193 1999), was visually evaluated. We classified each parcel as Open (O), Intermediate (I) or
194 Closed (C) in a given year (Figure 1b; Appendix, Section A1). We validated this procedure
195 using automatized analyses (Appendix, Section A1).

196 Habitat closing was a key dynamic variable in this study. Therefore, we further classified
197 each parcel, according to its cover change from 2000 (maximal forest openness) to 2020, into
198 three main categories of habitat closing, named “habitat categories” hereafter (Figure 1a):

- 199 • Open-Open: canopy never covered more than 30% of the surface. Only the two
200 managed enclaves belonged to this habitat category.
- 201 • Closed-Closed: canopy always covered more than 70% of the surface.
- 202 • Open-Closed: canopy cover increased during the study, shifting from habitat (O) to
203 (I), from (I) to (C), or from (O) to (I) then to (C).

204

205 *Photos taken from the ground:* In aerial views, ground vegetation was masked by tall
206 crowned trees hampering the characterization of (un-)favourable microhabitats for reptiles.
207 Similarly, the possibility for sun rays to cross the canopy and to contribute to snake
208 thermoregulation could not be gauged. Therefore, we used wide angle photographs taken
209 from the ground to analyse sky view and ground vegetation cover (Appendix, Section A1).

210

211 Snake survey

212 *Species:* The western whip snake (*Hierophis viridiflavus*) and the Aesculapian snake
213 (*Zamenis longissimus*) are medium-sized snake species (adult snout vent length ~0.9 m;
214 Bonnet et al., 1999). They occur in syntopy and rely on shrubby open microhabitats where
215 they find their main prey (voles, field mice and shrews); *H. viridiflavus* also regularly feeds
216 on reptiles (~20%) and *Z. longissimus* on nestling birds (~10%) (Lelièvre et al., 2012).
217 Radio-tracking revealed substantial differences in habitat use, and strong differences in
218 thermoregulation and associated locomotor performances. *H. viridiflavus* is a terrestrial
219 thermophilic racer that selects high body temperature; *Z. longissimus* is a partly arboreal,
220 relatively slow moving, highly secretive and largely thermo-conforming snake (Lelièvre et
221 al., 2011, 2013). *H. viridiflavus* was expected to be more dependent on open microhabitats
222 compared with *Z. longissimus* that can exploit arboreal strata.

223 These two species are the most abundant and widespread snakes in the studied forest, so
224 they were suitable to assess the impact of canopy closing. Grass snakes (*Natrix helvetica*) and
225 aspic vipers (*Vipera aspis*) that also occur in the studied forest are more scattered and much
226 less abundant, and the viper belongs to a different lineage making comparison difficult.

227

228 *Population monitoring:* A network of geo-located corrugated concrete slabs (120 x 80 cm)
229 was deployed in the forest to facilitate captures (Bonnet et al., 1999). Snakes were almost
230 impossible to detect without the slab network. This network was divided into 12 sub-
231 networks (=12 searching sites), each one assigned to one of the three habitat categories
232 defined above (Figure 1a). During surveys, the slabs of a sub-network were successively
233 lifted. Uncovered snakes were captured by hand. Most of the time, the 12 sub-networks could
234 not be checked during a single day; thus, we followed a rotation plan.

235 The total number of slabs and surveys increased over time, reaching a total of 798 slabs in
236 2021 (Appendix, Fig. A2). Snakes use slabs occasionally, spending most of their time in

237 other habitats, foraging or sheltered in bushes (Lelièvre et al., 2010). To better encompass
238 snakes' home ranges, we considered a buffer zone of 125 m on both sides of the line joining
239 successive slabs in a given survey (Figure 1a). Taking into account this buffer zone, in 2020
240 the density of slabs per ha was respectively 3.2 in the Open-Open category, 1.4 in the Closed-
241 Closed category and 1.9 in the Open-Closed category. Whatever the category, the total slab
242 surface covered less than 0.03% of the surface of the buffer zone.

243 Field work was performed during the active season, from April to October. Individuals
244 were sexed, measured (snout to vent length), photographed, permanently marked (scale rows
245 were superficially burned following a code, triggering a stable color change) and released at
246 the exact place of capture (Bonnet et al., 2016).

247

248 *Snake fidelity to study sites*: Frequent movements of snakes among the three habitat closing
249 categories would complicate analyses and blur interpretations. Many individuals were located
250 more than once (either within or among years). We noted the snakes that moved across sub-
251 networks, possibly shifting among habitat category, and we measured the straight-line
252 distance between the two locations involved. Such occurrences were negligible (see results),
253 and we discarded the rare individuals found in more than one habitat category. Thanks to this
254 exclusion, we assigned all individuals to one of the six main groups: 2 snake species
255 combined with 3 habitat categories.

256

257 Model selection and snake abundance

258 Snakes are elusive in forest habitats and raw numbers (Appendix, Fig. A6) imperfectly reflect
259 their abundance. Therefore, capture-mark-recapture (CMR) analyses were performed to
260 estimate abundance and demographic parameters (Mazerolle et al., 2007). Because the
261 monitoring scheme was based on slab network monitoring, individuals may temporarily leave

262 searching sites (i.e. sub-networks) and become unavailable for capture. These behaviors
263 result in temporary emigration, i.e. individuals are alive but not available for capture.
264 Temporary emigration may vary spatially and temporally, and its occurrence violates key
265 assumptions for CMR models, resulting in biased estimates (Kendall, 2023). Furthermore, for
266 individuals available for capture, several factors such as age, reproductive status, habitat
267 characteristics, climatic conditions or time of the day may affect their capture probability
268 (Bonnet & Naulleau, 1996). These factors are known to bias abundance estimates obtained
269 from methods assuming equal catchability. Moreover, through time, inherent characteristics
270 of open populations (i.e. births, deaths, immigration, and emigration) influence population
271 size and thus abundance in complex ways. Provided that a suitable data set is available (i.e.
272 intensive prolonged monitoring of marked individuals), robust design modelling offers a
273 means to avoid these major difficulties (Kendall, 2023; Kendall & Pollock, 1992). Although
274 we potentially considered using the Jolly Seber model to estimate abundance, we chose the
275 robust design due to substantial advantages despite the extra sampling effort required:
276 increased precision of estimates, relaxing assumptions such as homogeneity in capture
277 probabilities, estimating additional parameters (Kendall, 1999; Kendall et al., 1995, 1997;
278 Koper & Brooks, 1998; Pollock, 1982; Pollock et al., 1990; Seber, 1982; Williams et al.,
279 2002). We used the program MARK (White & Burnham, 1999) to conduct the Robust design
280 modelling, which relies on multiple capture sessions sufficiently close in time so that the
281 population can be considered as closed (e.g. survival rate close to 1 during short time
282 intervals) (Kendall, 2023). In practice, survival, recruitment, immigration or emigration can
283 be explicitly modeled and tested to relax the assumption of equal catchability (details
284 provided in Appendix, Section A2).

285 As snakes were monitored during the whole activity period, it was possible to divide each
286 yearly session into sub-sessions to estimate abundance using a Huggins robust design model.

287 From early 1995 to late 2021 we obtained 27 primary sampling sessions (i.e., 27 years). Each
288 primary session was set from April 1 to July 30 to limit the influence of annual recruitment
289 (hatching occurs in late summer). Each primary session was then divided into secondary
290 sessions of 2 weeks. The number of secondary sessions varied from 5 to 8 per year due to
291 climatic conditions; for example, snakes remained invisible during cold weather in early April.
292 We tested for possible effects of trap-response behavior and time-related variations on capture
293 (p) and recapture (c) probabilities. We also modelled temporary emigration (the probability of
294 an individual not being available for trapping during one or more primary sampling periods),
295 transience (the probability that a newly captured individual was just passing through the study
296 area, with a near-zero chance of returning to the study area and to be recaptured during the
297 study), and apparent survival (the probability of surviving from one primary period to the next
298 and of staying in the study area). The number of individuals not captured was modelled for
299 each primary period as time dependent or constant and added to the number of individuals
300 known to be in the population to provide an estimate of population size (\hat{N}_t). Capture and
301 recapture probabilities were modelled on an annual scale, and were either year dependent, $p(t)$
302 and $c(t)$, or constant, $p(\cdot)$ and $c(\cdot)$. We first attempted to estimate parameters for each primary
303 period and for each secondary period. Due to sample size limitation in the first years of the
304 study, several parameters were not estimated. To reduce this problem, all secondary sessions
305 belonging to a given primary period were set constant. We tested the effect of time among
306 primary sessions for recapture and capture parameters only, to further reduce estimation
307 problems. Temporary emigration was modelled with two parameters: $\gamma'(\cdot)$ was the probability
308 that a snake was absent from the study area at time t if absent at time $t-1$, and $\gamma''(\cdot)$ was the
309 probability that a snake was absent from the study area at time t if present at time $t-1$.
310 Temporary emigration was also modelled as either random $\gamma'(\cdot)=\gamma''(\cdot)$, or Markovian $\gamma'(\cdot)\neq\gamma''(\cdot)$.

311 The robust design modelling was implemented for each species (*Hierophis viridiflavus*,
312 *Zamenis longissimus*) and habitat category (Open-Open, Closed-Closed, Open-Closed). We
313 did not implement the habitat category as an annual covariate of each study site because with
314 only 12 study sites the power of analyses would have been low, and because canopy cover
315 was not measured annually. Instead, we derived the estimated abundance for each habitat
316 category, and explored the pattern of abundance in each category.

317 We used an information theoretic approach to select the most appropriate model for the
318 data based on ecologically sound hypotheses and based on the small-sample modification
319 (AICc) (Anderson & Burnham, 2002). In *H. viridiflavus* the sample size used for the AICc
320 (corresponding to the number of individuals retained for the robust design matrix) was
321 respectively 404, 97 and 627 for Open-Open, Closed-Closed and Open-Closed categories. In
322 *Z. longissimus*, it was respectively 589, 394 and 798 for Open-Open, Closed-Closed and
323 Open-Closed categories. A model was preferred to a competing model when the AICc of the
324 model was lower than the AICc of the competing model by at least two units. When the AICc
325 difference between two models was less than 2, the difference in deviance (Δdev) and the
326 difference in number of parameters K multiplied by two ($\Delta 2K$) were explored (Arnold, 2010;
327 Leroux, 2019). If $\Delta 2K < \Delta dev$, the model with the lower deviance was selected. When $\Delta 2K \approx$
328 Δdev the most parsimonious model (i.e. which used fewer parameters) was selected.
329 Confidence intervals (95% CI) of parameters between models were also inspected. If a time
330 dependent parameter had similar CI among primary periods, then the constant parameter
331 (most parsimonious) was retained.

332 We assessed the fit of our initial model using program U-CARE (Choquet et al., 2009).
333 For this, individual sighting histories were pooled for all the secondary sampling periods
334 keeping only one sighting occasion per primary sampling period. Hence, we assessed the fit
335 of the Cormack-Jolly-Seber model corresponding to our dataset. TEST 3.SR provided a test

336 for transients (Choquet et al., 2005, 2009). Transients were defined as “individuals having a
337 zero probability of local survival after their initial capture” (Genovart & Pradel, 2019). True
338 transients crossing through but not belonging to the study population should be distinguished
339 from individuals that die after a single reproductive bout or from individuals that die (or
340 emigrate) following marking (Genovart & Pradel, 2019). We excluded the two last
341 possibilities because *Hierophis viridiflavus* and *Zamenis longissimus* reproduce more than
342 once during their lifetime and our marking technique had no detectable effect on the survival
343 of snakes (Fauvel et al., 2012). Therefore, detecting significant transience will suggest that a
344 substantial proportion of marked individuals do not settle in the sub-network of slabs where
345 they have been marked. When transience was detected, it was explicitly modelled by
346 considering 2 apparent age-classes for survival (Genovart & Pradel, 2019; Pradel et al.,
347 1997). These age classes were apparent in the sense that they gave a means to model
348 transience effect when TEST 3.SR was significant. We have not performed real age models
349 (e.g. juveniles vs adults) in the present manuscript due to the many parameters already
350 involved in the robust design. However, real age models were the subject of a second paper
351 that targets the underlying mechanisms of potential declines due to canopy closure. No cohort
352 models (i.e. using age classes) were conducted in this study.

353 The starting model was $S(.) \gamma''(.) \gamma'(.) p(t) c(t)$ or $S(a1, a2) \gamma''(.) \gamma'(.) p(t) c(t)$ in case of
354 transience, where $(.)$ and (t) respectively represent an absence or the presence of time effect
355 among primary sessions. We modelled the effect of time on capture and recapture
356 probabilities and the type of temporary emigration and used the best supported models to
357 obtain annual estimates of snake abundance (\hat{N}_t). We also sequentially tested if linear trends
358 occurred on each parameter issued from the best supported model. We built models where the
359 demographic parameter θ was modelled as $\text{logit}(\theta) = \alpha + \beta \times T$, where α is an intercept
360 parameter, β is a slope parameter and T is a linear temporal trend. When $\beta > 0$ the parameter

361 increases through time, whereas it decreases when $\beta < 0$. We used ANODEV to test for linear
362 trends (Grosbois et al., 2008). In case of a significant ANODEV test, the slope confidence
363 interval (CI) was checked. If 0 belonged to the slope CI, we rejected the hypothesis of a trend
364 even if the ANODEV test was significant. Linear trend was tested for each parameter and
365 slope estimates are reported on the logit scale (see Table A4.).

366 Table 1 shows the results of the model selection, and Table A6 gives the parameters of the
367 models shown in Table 1. Table 2 provides parameters derived from simple models for each
368 habitat and species to facilitate comparison with other snake studies.

369 The number of slabs checked (thereafter NSC) increased over time: we extended the slab
370 network (hence the surface prospected but not the density of slabs in the given place) and
371 augmented the number of surveys (Appendix, Fig. A2). The number of slabs checked during
372 surveys represented an integrative measure of searching area for each habitat category and for
373 each species. The change of NSC was known (= number of slabs lifted/habitat category/year)
374 and thus it was easy to factor out to scale abundance estimates to the area patrolled. Thus,
375 number of slabs, which is directly related to the surface prospected, was used as a post-hoc
376 correction, to weight the abundance estimation derived in MARK program. Practically we
377 divided annual estimates of snake abundance (\hat{N}_t) by the NSC. Resulting values \hat{N}_{NSC} were
378 very low because no snake was captured below most slabs during a given survey. To
379 represent snake abundance more realistically (instead of fractions of individuals), we adjusted
380 \hat{N}_{NSC} (Adjusted \hat{N}_t) using the ratio between mean \hat{N}_t and mean \hat{N}_{NSC} calculated between 1995
381 and 2021:

$$382 \quad \text{Adjusted } \hat{N}_t = \hat{N}_{NSC} * (\text{mean } \hat{N}_t / \text{mean } \hat{N}_{NSC})$$

383 Each \hat{N}_t was randomly sampled from a log normal distribution with 10,000 iterations per
384 year (t) to obtain mean adjusted \hat{N}_t and their 95% confidence intervals extracted from their
385 respective log normal distribution. This adjustment was equally applied to all categories and

386 thus had no impact on the results; instead, it was explicitly designed to facilitate
387 interpretations. We used R 4.0.3 (R core team, 2020) and Rstudio 2022.12.0.353 to perform
388 iterations. In Closed-Closed and Open-Closed categories, 1995 and 1996 estimates were
389 based on small sample sizes and were imprecise ($N = 2$) or unavailable ($N = 6$). Importantly,
390 snake abundance was estimated as a function of searching area and was limited to searching
391 sites which varied over time. Thus, the estimates provide relative values of abundance.
392 Indeed, most of the surface of the forest was not monitored and thus was not considered,
393 especially until 2002 before the strong increase of slab network. Estimating snake density
394 (snakes/ha, considering their home ranges) was out of scope of this study. To further assess
395 temporal trends, we also estimated population growth rates (λ) over time in each habitat
396 category (Appendix, Section A2).

397 For *H. viridiflavus* we predicted lower survival values in the Closed-Closed category than
398 in the Open-Open category. In the Closed-Closed category, we expected a higher survival
399 value for the less thermophilic *Z. longissimus* than for *H. viridiflavus*. In the Open-Closed
400 category, we expected a negative trend in *H. viridiflavus* survival as the canopy closed, but no
401 trend in *Z. longissimus*. We expected no trend for temporary emigration in the Open-Open
402 and Closed-Closed categories for either species. However, we expected a positive temporal
403 trend in *H. viridiflavus* for temporary emigration (γ') in the Open-Closed category, with
404 snakes likely to be less and less present under slabs as the canopy closed over time. For the
405 Open-Closed category, we expected a negative trend in capture and recapture rates for *H.*
406 *viridiflavus*, but no trend for *Z. longissimus*.

407 Ethic statement

408 Non-invasive capture-recapture surveys were performed in accordance with French
409 regulations (permits and ethical approvals# DREAL/2021D/8647, 09/346/DEROG,
410 DBEC/004/2022, A79-001 and 79-157).

411

412 **Results**

413 Forest management and habitat closing

414 *Timber harvesting records.* Logging was more intensive in Open-Closed parcels compared
415 with Closed-Closed parcels, especially from 1989 to 1992 (Appendix, Fig. A3; ANOVA with
416 the annual volume of wood extracted as the dependent variable and habitat type as the
417 independent variable; $F_{1, 132}=14.827, p < 0.001$). Logging was limited after 2000 and ceased
418 after 2003. Only one value was recorded in the Open-Open parcels, ($113 \text{ m}^3.\text{ha}^{-1}$ in 1992).

419

420 *Visual analyses of aerial images.* Open habitats expanded from 1996 to 2000 ($\chi^2 = 56.892, 12$
421 $\text{df}, p < 0,001$; Figure 1b; Appendix, Table A1). This trend reversed from 2000 to 2020 with
422 continuous habitat closing ($\chi^2 = 610.21, 3 \text{ df}, p < 0,001$). Two sub-networks belonged to the
423 Open-Open category, four to the Closed-Closed category, and six to the Open-Closed
424 category (Figure 1a). The forest was largely open in 2000 and was almost totally closed
425 twenty years later. Two small open enclaves and very few semi-open parcels persisted in
426 2020.

427

428 *Photographs taken from the ground.* Sky views revealed strong differences among habitats:
429 mean (SD) canopy closure (% of sky obscured) was respectively 4% (7), 87% (3.5) and 39%
430 (21) in the (O), (C) and (I) habitat types (ANOVA with canopy closure as the dependent
431 variable and habitat as a factor, $F_{2, 18}=50.27, p < 0.001$). These values matched the criteria
432 used to define habitats: canopy closure remained below 30% in open habitat and above 70%
433 in closed habitat (Appendix, Table A2). Photographs taken toward the ground revealed thick
434 herbaceous layers with abundant shrubs in open habitat (Appendix, Fig. A5). Closed habitat
435 was essentially characterized by forest litter. Intermediate habitat was characterised by a

436 combination of herbaceous layer, various bush formations and sparse trees of various size.
437 Horizontally taken photographs showed similar kinds of surrounding vegetation but they
438 included further elements (Appendix, Fig. A5).

439 Overall, aerial categorization and ground assessment of habitat openness were congruent.
440 Open habitats offered abundant microhabitats, sunny spots and shelters to snakes; closed
441 habitats were essentially inhospitable.

442

443 Snake survey

444 *Population monitoring.* A total of 1,357 *H. viridiflavus* and 2,090 *Z. longissimus* were
445 marked; 424 *H. viridiflavus* and 588 *Z. longissimus* were recaptured at least once providing a
446 total of 1,258 and 1,598 recaptures respectively. The number of *H. viridiflavus* individuals
447 retained for the robust design matrix is respectively 404, 97 and 627 for Open-Open, Closed-
448 Closed and Open-Closed categories. The number of *Z. longissimus* individuals retained for
449 the robust design matrix is respectively 589, 394 and 798 for Open-Open, Closed-Closed and
450 Open-Closed categories.

451

452 *Snake fidelity to study sites.* Sixty *H. viridiflavus* (4% of marked individuals) were observed
453 in more than one searching site. Five individuals (0.4%) shifted among habitat categories.
454 The straight-line distance travelled between searching sites ranged from 100 m to 5,500 m (N
455 = 47 individuals). Forty-one *Z. longissimus* (2% of marked individuals) were observed in
456 more than one searching site and none shifted among habitat categories. The straight-line
457 distance travelled between searching sites ranged from 100 m to 2,400 m (N = 30).

458

459 Model selection and snake abundance

460 In the three habitat categories and for both snake species, global goodness-of-fit tests were
461 not significant (Appendix, Table A3). Test 3.SR GOF components were significant for *Z.*
462 *longissimus* and *H. viridiflavus* in Open-Open and Closed-Closed categories indicating
463 transience (*H. viridiflavus*, Open-Open: $z = 2.742$, $p = 0.003$; *H. viridiflavus*, Closed-Closed:
464 $z = 2.903$, $p < 0.002$; *H. viridiflavus*, Open-Closed: $z = 0.613$, $p = 0.270$; *Z. longissimus*,
465 Open-Open: $z = 3.647$, $p < 0.001$; *Z. longissimus*, Closed-Closed: $z = 2.479$, $p < 0.007$; *Z.*
466 *longissimus*, Open-Closed: $z = 4.936$, $p < 0.0001$; Appendix, Table A3). The best supported
467 models differed among habitat categories and snake species (Table 1).

468 In the Open-Open category and in both species, abundance fluctuated over years (i.e.
469 primary sessions) but declined during the study period (*H. viridiflavus* -51% and *Z.*
470 *longissimus* -31%, Figure 2). In 2005, a prolonged summer drought hampered recaptures in
471 *Z. longissimus* (the less thermophilic species), generating an imprecise estimate and excessive
472 SD. For *Z. longissimus*, survival rate remained constant in the transient group but increased in
473 the resident group (all subsequent $F_{\text{constant/trend/time}}$ tests from ANODEV: respectively $F =$
474 5.560 , $p < 0.007$; slope S_{a1} (SE) = -0.0005 (0.020); slope S_{a2} (SE) = 0.064 (0.019); Appendix,
475 Table A4). For *H. viridiflavus*, recapture probability and temporary emigration increased over
476 time (respectively, $F = 4.198$, $p = 0.051$, slope (SE) = 0.041 (0.014); $F = 7.717$, $p < 0.011$,
477 slope (SE) = 0.084 (0.039); Appendix, Table A4).

478 In the Closed-Closed category, *H. viridiflavus* abundance was below 10 on average and
479 lower than 3 after 2012 (Figure 2); capture probability decreased over time ($F = 8.401$, $p <$
480 0.008 ; slope (SE) = -0.122 (0.037); Appendix, Table A4). *Z. longissimus* abundance was
481 higher (68 on average, Figure 2), capture and recapture probabilities increased over time ($F =$
482 4.952 , $p = 0.035$; slope (SE) = 0.064 (0.019); Appendix, Table A4), and survival rate
483 remained constant in the transient group but increased in the resident group (respectively $F =$

484 5.128, $p < 0.010$; slope S_{a1} (SE) = -0.126 (0.081); slope S_{a2} (SE) = 0.110 (0.041); Appendix,
485 Table A4).

486 In the Open-Closed category and in both species, estimated abundances were elevated
487 during the first eight years of the study (>200 on average in both species) and then declined
488 sharply (71 for *Z. longissimus* and 39 for *H. viridiflavus* on average since 2003; Figure 2). A
489 steep drop in 2003 was partly due to the deployment of new searching networks (snakes need
490 time to familiarize themselves with new slabs). Disregarding this issue and focusing on the
491 last 15 years, a strong and continuous decline with accurate estimates (low SD) occurred in
492 *H. viridiflavus*. *H. viridiflavus* abundance remained below 25 after 2014 (Figure 2).
493 Temporary emigration decreased ($F = 21.465$, $p < 0.001$, slope (SE) = -29.842 (13.255);
494 Appendix, Table A4). For *Z. longissimus*, following the 2001-2003 drop, abundance
495 increased slightly and remained above 75 after 2014.

496 Overall, in both species and in the 3 habitat categories abundance declined over time
497 (Figure 2). Snakes became more difficult to find, especially *H. viridiflavus* in the Open-
498 Closed category (Figure 2; Appendix, Fig. A2). Population growth rates (λ) reflect these
499 results: λ fluctuated in Open-Open category and declined in the Closed-Closed and Open-
500 Closed categories, especially for *H. viridiflavus* (Appendix, Fig. A7).

501

502 **Discussion**

503 Increasing the surface and protection status of natural reserves is essential (Rodrigues et al.,
504 2004; Shafer, 2020), for example to safeguard large mammals (Ferreira et al., 2020).

505 However, SNR is not necessarily the best option to stem biodiversity loss. Some practices of
506 habitat management and exploitation of natural resources can be beneficial for many species;
507 it would be judicious to select protection status on a case-by-case and precisely assessed basis
508 (Elleason et al., 2021; Oldekop et al., 2016).

509 Our results show that a cessation of logging in a SNR temperate forest amid an intensively
510 cultivated landscape entailed the rapid disappearance of open woodlands with negative
511 consequences on two species of snakes. Concurrent long-term monitoring of canopy cover
512 and of snake populations provides precise information to interpret the effect of past
513 management and to forecast possible consequences of forest closing.

514

515 Canopy closing

516 Aerial and ground images provided convergent results. Thick herbaceous layer and abundant
517 shrubs were dominant in open parcels but were almost totally absent in closed parcels.
518 Intermediate (semi-open) habitats contained a mosaic of microhabitats with dense shrub
519 formations and various trees. Hence, the categorisation based on aerial images provided a
520 suitable proxy of the availability of microhabitats that are essential to snakes in temperate
521 ecosystems (Bruton et al., 2016; Pringle et al., 2003; Blouin-Demers & Weatherhead, 2001).

522 During the first decade of the study (1995-2006), various habitats ranging from meadows
523 (O) to closed stands (C) were all well represented (Figure 1b). This situation resulted from
524 past logging regime, (O) parcels eventually covered 17% of the forest surface in 2000. Small
525 trees (<2m tall) were abundant in all open parcels in 2000. Between 2000 and 2007, due to
526 tree growth 20 parcels shifted from (O) to (I) status and 13 parcels from (I) to (C) status. SNR
527 status triggered the inevitable disappearance of open woodlands. In 2020, two small (O)
528 enclaves (<1% of the surface) plus eight (I) parcels remained while closed habitats (C)
529 covered more than 95% of the forest.

530

531 Snake decline and population fragmentation

532 Despite increasing searching effort, snakes became more difficult to find (raw numbers
533 declined over time, especially for *H. viridiflavus*). Accordingly, snake abundance estimated

534 using robust design modelling adjusted to searching effort dropped drastically. Averaging
535 abundances on three periods to smooth inter-annual fluctuations illustrates the magnitude of
536 the decline: mean abundance shifted from 104 (SD 56) individuals (species and habitats
537 pooled) before logging cessation (1995-1999) to 65 (SD 27) during the following decade
538 (2000-2010) and to 42 (SD 12) during the next decade (2011-2021). This suggests a 60%
539 global decrease. This appraisal is minimal because most open and semi-open parcels (>600
540 ha in 2000) disappeared but were never sampled: our relative abundance estimates do not
541 account for the massive loss of most of the favourable habitats. Likely, forest closure
542 decreased most, albeit unsampled, snake populations.

543 In Open-Open and Closed-Closed categories habitats were relatively stable, nonetheless
544 snake abundance declined. This may be due to continuous tree growth; in many Closed-
545 Closed parcels canopy closure increased from 70% to 100% (pers. obs.). In large timber
546 parcels there is a lack of shelters that are essential to snakes (Bonnet et al., 2013). Eventually,
547 Closed-Closed parcels became excessively hostile (Figure 2) and the two Open-Open
548 enclaves fully isolated (Figure 1). Even partly arboreal *Z. longissimus* avoid high timber
549 zones in Poland forests (Kurek et al., 2018).

550 The most relevant pattern was observed in Open-Closed category where canopy closing
551 was rapid and strong (Figure 1). The decline of *H. viridiflavus* abundance was drastic (-88%
552 using the three periods mentioned above). *Z. longissimus* decline was less marked (-52%) and
553 followed an uneven trajectory with a slight increase since 2012 and an unexplained peak in
554 2016.

555 Transience detected in both species in the three habitat categories (except *H. viridiflavus*
556 in Open-Closed) suggests that a substantial proportion of the snakes were not resident,
557 possibly moving away from closing habitats. Continuous canopy growth increased
558 fragmentation, separating favourable albeit shrinking patches and making long displacements

559 risky. The very small proportion of snakes shifting among sub-networks of slabs supports this
560 hypothesis; successful dispersal events might be rare in a rapidly closing forest.

561

562 Alternative explanations for snake decline

563 Several alternative causes could hypothetically explain the decline we have observed, such as
564 predation, invasive species, disease, and climate change (Clark et al., 2011; Lorch et al.,
565 2016; Phillips et al., 2003; Pomara et al., 2014; Todd et al., 2010; Winton et al., 2020). In
566 temperate forests, wild boar outbreaks can have a dramatic impact on snakes (Graitson et al.,
567 2018), but boar populations were regulated in the SNR forest. We did not observe any sign of
568 illness or epizooty and to our knowledge no invasive species preying or competing with the
569 two snake species are present in the SNR. Changes in climatic conditions, such as rainfall,
570 can be ruled out as they cannot affect only certain habitat categories and not others given the
571 spatial extent of our study site. On the other hand, variations in the availability of prey may
572 be a determining factor. In fact, the closure of the canopy may have led to the disappearance
573 of microhabitats favourable to the prey of snakes (lizards and small mammals). Interestingly,
574 an experiment performed in a zone initially devoid of snakes and adjacent to the south eastern
575 part of the forest showed that the creation of favourable habitats (0.9 hectare fitted with 9
576 artificial hedgerows in 2011) bolstered *H. viridiflavus* and *Z. longissimus* snake numbers: the
577 reptiles dispersed from the forest and rapidly colonized the experimental site (Lecq et al.,
578 2018). Habitat change is therefore the most plausible explanation for the strong snake
579 decline, especially in the forest parcels subjected to intense closing, concomitant to a
580 population rise in a contiguous newly created open bushy zone.

581

582 Snake species sensitivity to canopy closure

583 If habitat closing mainly impacts the most thermophilic species, possible confounding effects
584 are less likely to play a role. *H. viridiflavus* and *Z. longissimus* occur in syntopy (often
585 captured under the same slabs), they are philopatric, their diets largely overlap, and thus they
586 experience similar environmental conditions. The decline was stronger for the more
587 thermophilic racer (*H. viridiflavus*, 79% global decline) compared with the more thermo-
588 conforming slow moving species (*Z. longissimus*, 36% decline). *H. viridiflavus* select
589 elevated body temperatures (>25°C). Because of its higher preferred body temperature
590 compared to *Z. longissimus*, *H. viridiflavus* relies much more on open habitats to bask
591 (Lelièvre et al., 2011, 2013). As expected, closed habitats were relatively favourable to *Z.*
592 *longissimus* but not to *H. viridiflavus* (Figure 2). Yet, habitat closing may reach a deleterious
593 limit for *Z. longissimus* over time. In the Closed-Closed category, the canopy closure tended
594 to be closer than 100% at the end of the study. This perhaps explains why the abundance in *Z.*
595 *longissimus* became lower after 2015 (Figure 2).

596 The linear trends in temporary emigration parameters provides complementary insight
597 relative to the effect of canopy cover on slab use. In the Open-Open category, *H. viridiflavus*
598 were less and less observable following events of temporary emigration, contrary to our
599 prediction (Table 3, Appendix, Table A4). Open-Open category became strongly enclosed
600 with time and *H. viridiflavus* probably moved from the edge towards the core of these areas,
601 which is proportionally less equipped with slabs than the open area adjacent to the edge. *H.*
602 *viridiflavus* may have therefore remained more and more in the unobservable state (i. e.
603 increase of $\gamma''=\gamma'$).

604 In the Open-Closed category, *H. viridiflavus* returned more often under slabs following
605 temporary emigration (Table 3 and A4), contrary to our prediction. No such trend was
606 detected on *Z. longissimus* according to our prediction. We suspect that the slabs became
607 more and more favorable for *H. viridiflavus* in the category Open-Closed as the habitat

608 became less attractive: snakes relied more often on the slabs in this species. In *Z. longissimus*,
609 closure of habitat being less constraining than for *H. viridiflavus*, individuals did not tend to
610 return more often under slabs.

611 Finally, we have identified some limitations of the studies. First, we did not consider age
612 as a factor potentially affecting demographic parameters and how age-specific abundance
613 varied. This has prevented us to consider potentially sharp differences between naïve
614 neonates and experienced snakes (i.e. aged one year or more). This perhaps explains why we
615 found similar survival estimates among habitat categories. Nevertheless, the generally similar
616 survival between the different habitat categories may mask survival differences of newborns
617 between each habitat category. Second, despite our efforts to describe population abundance
618 at a fine scale (i.e. woodland plot), a finer scale (i.e. microhabitat) could be more relevant to
619 characterize habitat changes within woodland plots, especially to better describe woodland
620 plot spatial heterogeneity. Third, the unequal surfaces among the three habitat categories was
621 partly a limitation, although relative to snake's home ranges other studies showed that snake
622 populations were viable in 1 ha (Lecq et al., 2018). Thus, even the smaller habitat category
623 (Open-Open) was large enough to reflect the pattern observed due to canopy closure.

624 Conclusion and recommendations

625 Two decades after the cessation of logging almost all open parcels were closed in this
626 temperate SNR forest. A canopy cover 5 m above ground was sufficient to inhibit the
627 development of herbaceous and bushy layers. Habitat closing was fast, occurring long before
628 climax (i.e. parcels with old >15 m timbers) (Dobbertin et al., 2013). Concomitantly, snake
629 abundance declined sharply. Overall, forest closing was detrimental to the populations of two
630 snake species, especially the most thermophilic, and likely to many other organisms that
631 depend on open habitats (Kopecký et al., 2013; Košulič et al., 2016; Sebek et al., 2015)

632 In non-exploited temperate forests, the scarcity of disturbance factors (e.g., fires, grazing
633 by mega-herbivores) means that natural clearing is generally limited to small surfaces and
634 cannot provide enough open habitats needed for the maintenance of large snake populations.
635 In SNR forests, the combined lack of natural disturbance factors with the lack of management
636 is likely to create a very shady environment. Recent reviews suggest that forestry practices
637 such as coppice management are very efficient options to restore “the full range of
638 interconnecting growth stages” (Buckley, 2020) and the whole forest complexity which in
639 turn sustains the highest plant and animal biodiversity in European forests (Amori et al.,
640 2021; Buckley, 2020). Unfortunately, these practices are hampered by highly mechanized
641 wood industry that involves the promotion of continuous canopy cover and ephemeral open
642 areas with clear cut harvesting plus monospecific replanting. Mature forests that combine old
643 timbers and exploited semi-open woodlands are vanishing due to the intensification of
644 industrial forestry (Miklín & Čížek, 2014). In this general context, residual populations might
645 not be capable of adapting to climatic changes and to other threats.

646 A field experiment showed that limited management is efficient to bolster reptile
647 populations (Bonnet et al., 2016). Protected forests where limited management is permitted
648 may represent a complementary option to create biodiversity sanctuaries. For example, in the
649 SNR forest of Chizé, maintaining 10% of the surface (approximately 250 ha) as open or
650 semi-open habitats through the selection of several interconnected parcels might be sufficient
651 to host large populations of heliophilous organisms, including the two studied species and
652 other reptiles. This implies a modification of the current status of the reserve: unchanged
653 SNR for 90% of the surface and shifting to conservation through active management for 10%
654 (category IV of the IUCN classification, Dudley 2008). A partial reassessment of the SNR
655 status of forests subjected to strong closing with regard to their species diversity and
656 functional ecological relationships would be a wise option (Shafer, 2020).

657 **Open Research statement:** data are shared privately on Figshare using the active link:
658 <https://figshare.com/s/0b3f9927eeb022b5ce57>). Data will be publicly and permanently
659 archived if the paper is accepted for publication.

660

661 **Funding.** This research did not receive any specific grant from funding agencies in the public,
662 commercial, or not-for-profit sectors.

663

664 **Supporting Information:** additional supporting information may be found in the online
665 version of the article at the publisher's website.

666

667 **CRedit authorship contribution statement**

668 Gopal Billy: Data curation, Formal analysis, Writing - original draft, Writing - review &
669 editing. Christophe Barbraud: Formal analysis, Supervision, Writing – review & editing,
670 Methodology. Magali Dahirel: Data curation, Formal analysis. Xavier Bonnet:

671 Conceptualization, Data curation, Supervision, Writing – original draft, Writing – review &
672 editing, Methodology, Formal analysis.

673

674 **Declaration of competing interest**

675 The authors declare that they have no known competing financial interests or personal
676 relationships that could have appeared to influence the work reported in this paper.

677

678 **Data availability**

679 Data will be publicly and permanently archived if the paper is accepted for publication

680

681

682 **Acknowledgments**

683 We warmly thank G. Fosseries, J.M. Ballouard and the many students who contributed to
684 data collection. We would also like to thank L. Lorrain-Soligon and T. Schneider-Bruchon
685 for their help during analyses. We are grateful to the Office National des Forêts for
686 permission to work in the Chiz'è forest and to G. Naulleau who pioneered snake studies at
687 the Centre d'Etude Biologique de Chiz'è. We are grateful to two referees, Ross Goldingay
688 and Brian J. Halstead, who provided many valuable comments to improve the manuscript.
689

690 **Author's contributions.** XB initiated and managed long-term snake surveys. XB and GB
691 conceived this study, collected and handled the data. GB, MD and XB performed habitat
692 analyses. GB and CB performed demographic analyses. GB and XB wrote the first draft. All
693 authors contributed to writing, editing and approved the final version.

694

695 **Appendix A. Supplementary data**

696 Supplementary data to this article can be found online at
697 <https://doi.org/10.1016/j.jnc.2024.126683>.

698

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965

966 Table 1. Best supported Huggins Robust Design model derived from model selection
 967 performed in the program MARK. Sp: snake species (*H. viridiflavus*: *Hierophis viridiflavus*;
 968 *Z. longissimus*: *Zamenis longissimus*). S, apparent annual survival; γ'' , temporary emigration;
 969 γ' , temporary immigration; p, capture probability; c, recapture probability; a1, first year after
 970 initial capture; a2, >1 year after initial capture; t, year (primary session) effect; (.), no time
 971 effect.

Sp	Habitat category	Best model
<i>H. viridiflavus</i>	Open-Open	$S(a1,a2)\gamma''(.)=\gamma'(.)p(t)c(t)$
	Closed-Closed	$S(a1,a2)\gamma''(.)=\gamma'(.)p(.)c(.)$
	Open-Closed	$S(.)\gamma''(.)\gamma'(.)p(.)c(.)$
<i>Z. longissimus</i>	Open-Open	$S(a1,a2)\gamma''(.)=\gamma'(.)p(t)c(t)$
	Closed-Closed	$S(a1,a2)\gamma''(.)=\gamma'(.)p(t)=c(t)$
	Open-Closed	$S(a1,a2)\gamma''(.)\gamma'(.)p(.)c(.)$

972

973 Table 2. Estimation of parameters and SE derived from the constant Huggins Robust Design
 974 model, $S(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$ or $S(a_1, a_2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$. The modelling was performed in the
 975 program MARK. Sp: snake species (*H. viridiflavus*: *Hierophis viridiflavus*; *Z. longissimus*:
 976 *Zamenis longissimus*). Cat: habitat category. S, apparent annual survival; γ'' , temporary
 977 emigration; γ' , temporary immigration; p, capture probability per primary session; c,
 978 recapture probability per primary session; a1 first year after initial capture; a2, >1 year after
 979 initial capture; (\cdot), no time effect.

Sp	Cat	S (SE)	$\gamma''(\cdot)$ (SE)	$\gamma'(\cdot)$ (SE)	p(\cdot) (SE)	c(\cdot) (SE)
<i>H.</i> <i>viridiflavus</i>	Open-Open	Sa1 0.485 (0.047)	0.467 (0.057)	0.534 (0.094)	0.702 (0.042)	0.363 (0.024)
		Sa2 0.689 (0.028)				
	Closed-	Sa1 0.240 (0.084)	0.245 (0.194)	0.791 (0.322)	0.535 (0.119)	0.150 (0.049)
	Closed	Sa2 0.753 (0.119)				
	Open-	S(\cdot) 0.648 (0.032)	0.168 (0.084)	0.700 (0.217)	0.423 (0.046)	0.327 (0.020)
	Closed					
<i>Z.</i> <i>longissimus</i>	Open-Open	Sa1 0.439 (0.040)	0.313 (0.078)	0.543 (0.134)	0.578 (0.050)	0.284 (0.020)
		Sa2 0.671 (0.028)				
	Closed-	Sa1 0.472 (0.076)	0.131 (0.087)	0.557 (0.279)	0.261 (0.042)	0.361 (0.029)
	Closed	Sa2 0.766 (0.047)				

Open-	Sa1 0.501	0.211	0.587	0.433	0.244
Closed	(0.038)	(0.083)	(0.172)	(0.047)	(0.017)
	Sa2 0.774				
	(0.026)				

980

981 Table 3. Temporal linear trends of temporary emigration parameters among categories and
 982 species. Linear trend were tested by ANODEV test (see Material and methods, and Table A4
 983 for more details). Movement is specified as either random $\gamma'(\cdot)=\gamma''(\cdot)$, or Markovian
 984 $\gamma'(\cdot)\neq\gamma''(\cdot)$. Sp: snake species (HV: *Hierophis viridiflavus*; ZL: *Zamenis longissimus*); Cat:
 985 habitat category; γ'' trend, temporary emigration trend; γ' , temporary immigration trend; +
 986 means positive trend; - means negative trend.

Sp	Cat	Random/Markovian movement	γ'' trend	γ' trend	Biological interpretation	Possible explanation
HV	Open-Open	random	+	+	HV more & more unobservable.	Open-Open Category landlocked: snakes tend to move inland, away from the edges of the category
	Closed-Closed	random	No trend	No trend		
	Open-Closed	Markovian	No trend	-	Unobservable HV more and more observable	HV rely more often in slabs because of canopy closure
ZL	Open-Open	random	No trend	No trend		
	Closed-Closed	Random	No trend	No trend		
	Open-Closed	Markovian	No trend	No trend		

987

988 **Figure captions**

989

990 Figure 1.

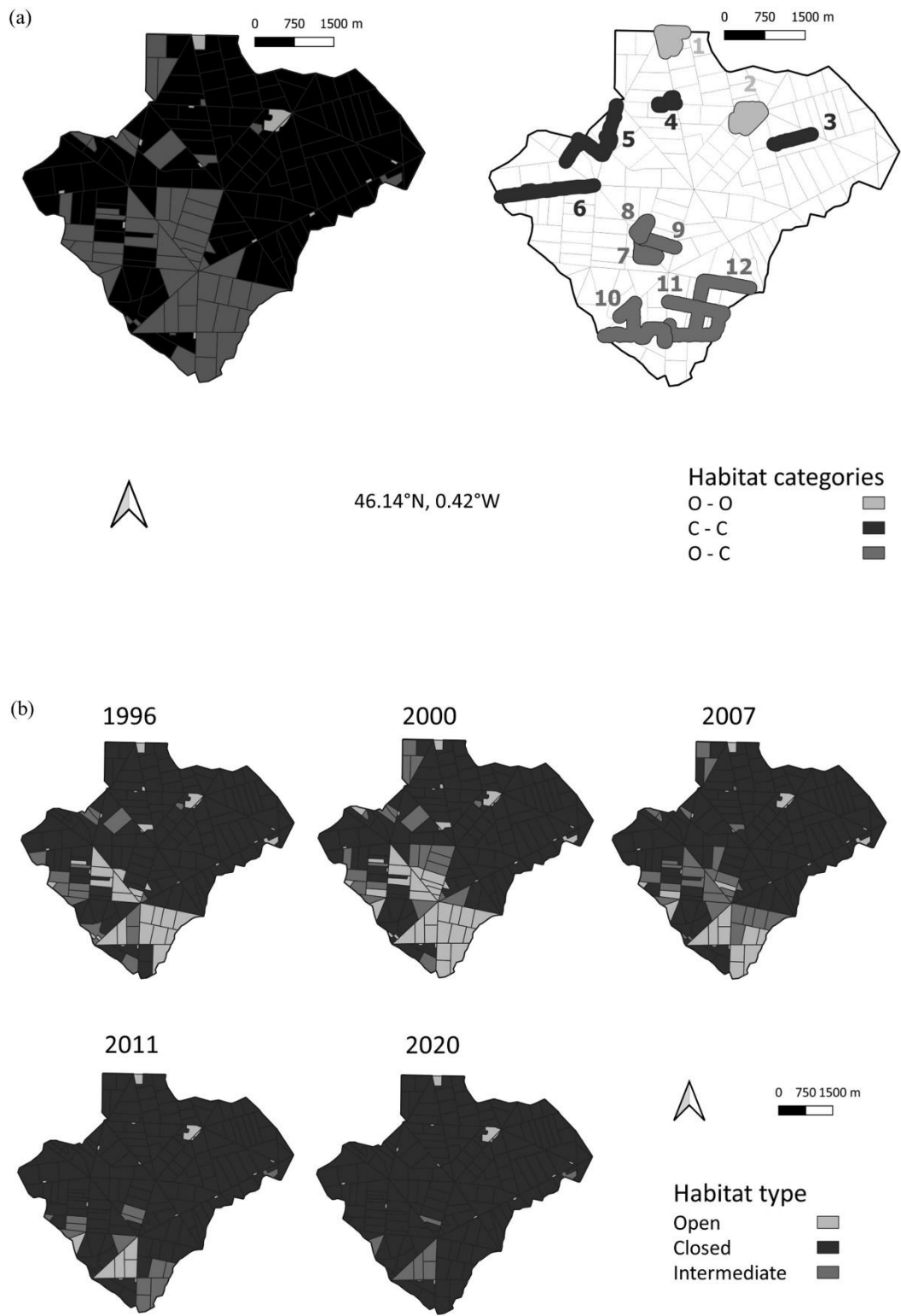
991 (a) Spatial distribution of the three habitat categories in the Chizé SNR forest (left) and of
992 the twelve sub-networks of slabs used to monitor snakes (right). The three habitat categories
993 (O-O, Open-Open; C-C, Closed-Closed and O-C, Open-Closed) were assigned to each
994 geometric parcel retrospectively in 2020 (changes from 2000 to 2020). Open-Open stands for
995 the parcels that remained open (light grey); Closed-Closed for parcels that remained closed
996 (dark grey); Open-Closed for parcels subjected to strong closing (middle-grey). In the sub-
997 networks, a buffer area of 250m along each survey track was applied (the slabs, <1m², are not
998 visible, sub-networks are numbered from 1 to 12).

999 (b). Canopy cover changes over time analyzed using aerial images from 1996 to 2020. Light
1000 grey indicates open parcels (O), where canopy covers 0% to 30% of the surface; dark grey
1001 closed parcels (C), where canopy covers 71% to 100% of the surface); middle grey indicates
1002 semi open or intermediate habitats (I), where canopy covers 31% to 70% of the surface.

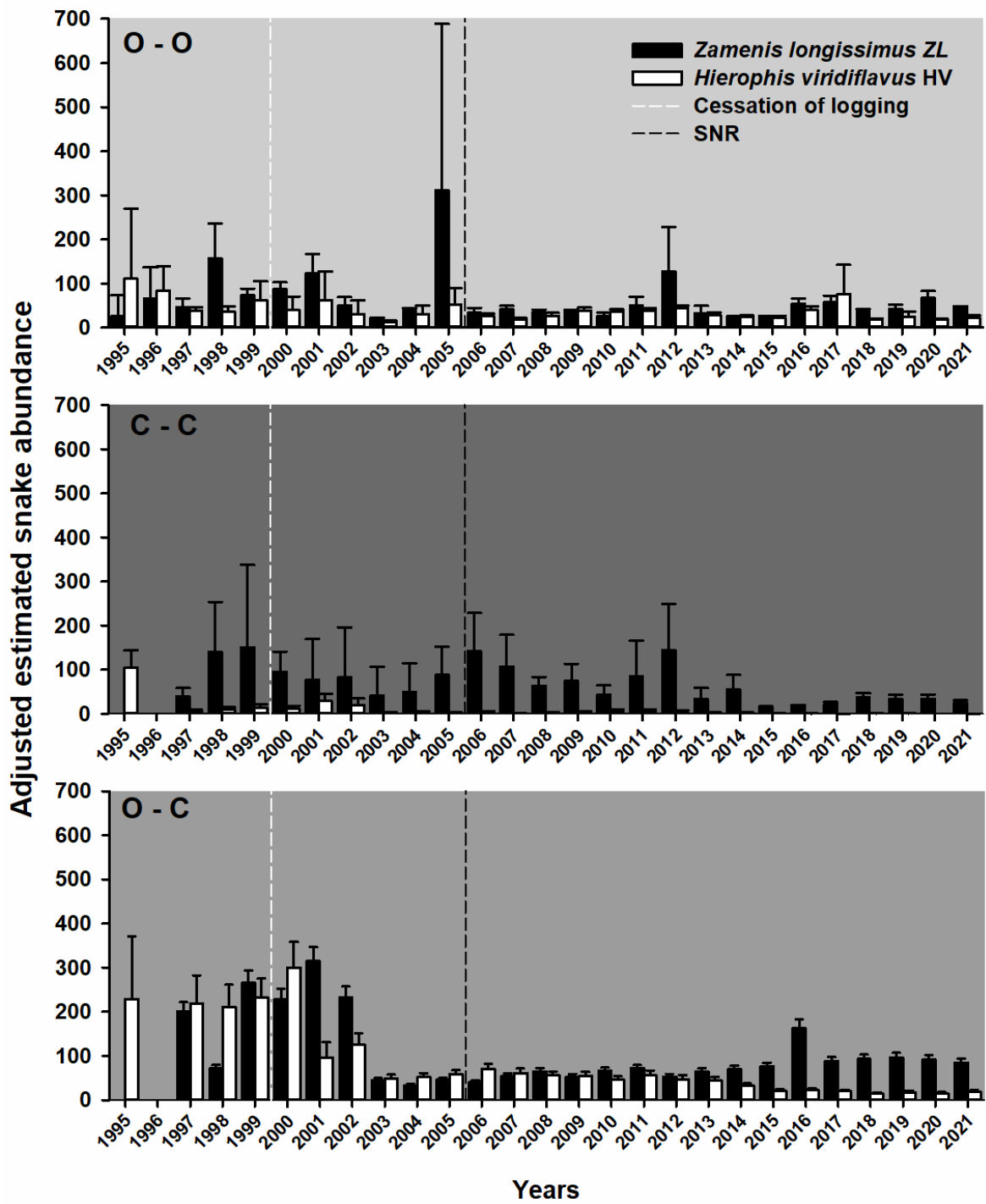
1003

1004 Figure 2.

1005 Annual changes of snake abundance (SD) in each habitat category (O-O, Open-Open; C-C,
1006 Closed-Closed and O-C, Open-Closed) for each snake species (*H. viridiflavus* and *Z.*
1007 *longissimus* are respectively represented by white and black bars). The white vertical dashed
1008 line indicates logging cessation in 2000. The black vertical dashed line indicates the
1009 classification of the forest as strictly protected nature reserve (SNR).



1013 Figure 2



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SUPPLEMENTARY MATERIAL

1020

1021 Does strict protection status harm snake populations in a temperate

1022 forest?



1023

1024 **Figure A1.** Habitat homogenization of the landscape around Chizé forest from 1950's (top
1025 photography, exact date unknown) to 2021 (bottom photography, Google Earth). Aerial images
1026 include a small area of the western part of the forest (lower right corner in both pictures) and
1027 surrounding agricultural landscape plus several roads and buildings. The dense network of
1028 hedgerows (several are indicated with white arrows) and small fields initially present was
1029 eliminated, replaced by large industrial homogeneous crops.

1030 **Section A1. Habitat closing survey**

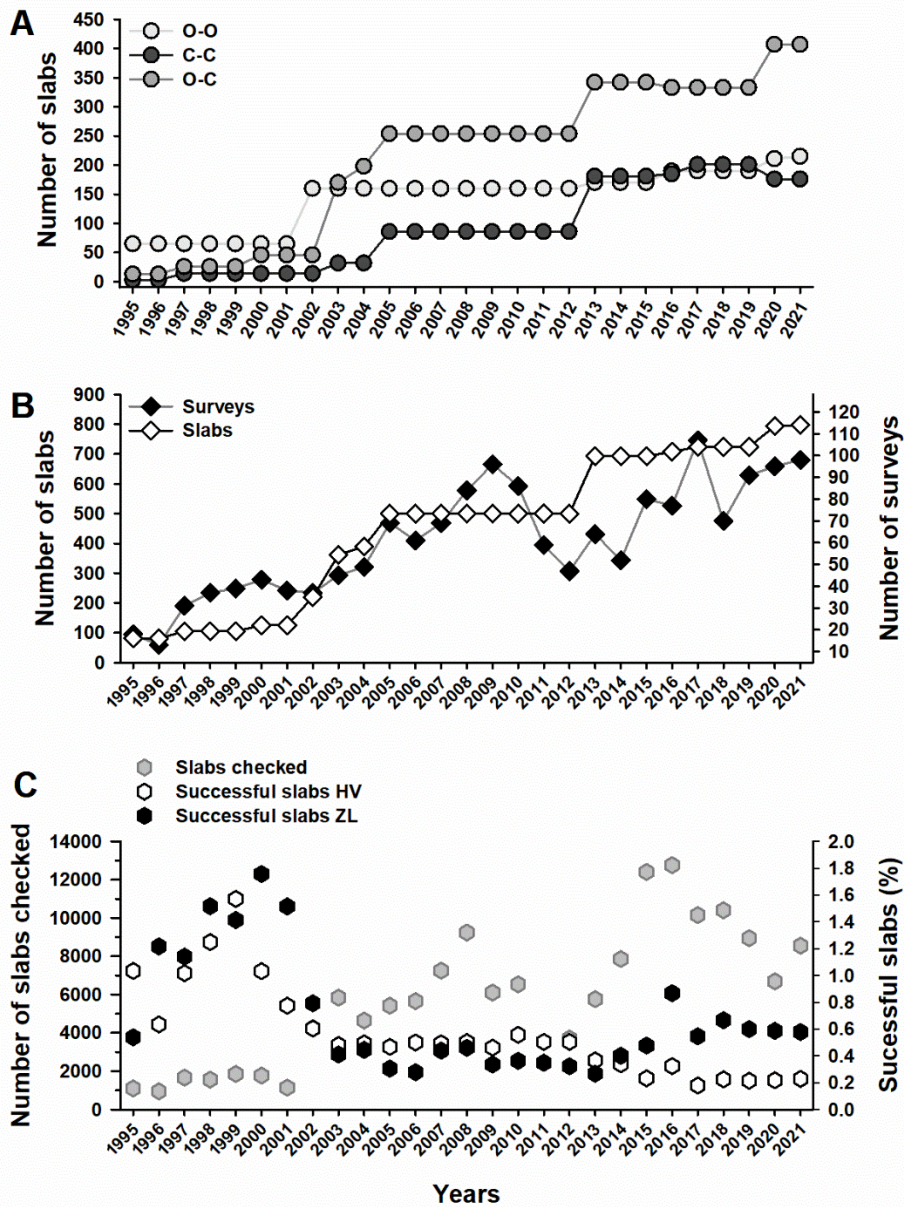
1031 *Aerial view:* aerial images were georeferenced (QGIS Development Team 2020). In each image
1032 we considered that canopy cover was represented by tall crowned trees while open habitats
1033 were represented by bushy and herbaceous covers. We distinguished three main types of
1034 habitats in function of the surface covered by the canopy (%). Open (O): 0 to 30%; Intermediate
1035 (I): 31 to 70%, and Closed (C): 71 to 100%. This categorization was straightforward in fully
1036 closed or fully open parcels. However, visual estimation might be imprecise in parcels with
1037 well-developed semi open habitats. Thus, in 2000 and 2020 the canopy cover of each parcel
1038 was quantified using ImageJ software (Schneider et al., 2012). To automatically calculate the
1039 canopy surface, B&W thresholds were applied. Threshold adjustment was performed by
1040 targeting a group of tall trees with a houppier in crown (approximately 10 trees in six different
1041 areas spread across the SNR). We set the threshold value once the tree crowns were precisely
1042 captured. Threshold value was adjusted each year depending upon input images. In 2020,
1043 gravimetric information provided a mean to assess the elevation of the vegetation above and
1044 below the B&W threshold. We used a 4.5 ha zone characterized by a complex habitat, mixing
1045 herbaceous layer, bushy areas, and trees (small and large). The discriminant value obtained
1046 was of 3 m: a maximum vegetation height of 3 m defined open habitat, higher values defined
1047 closed habitat. ImageJ automatically provided the surface covered by the canopy in each parcel,
1048 subsequently labelled as (O), (I) or (C).

1049 Automatized analyses led to slightly different results without impacting the categorization of
1050 the parcels associated with the 12 searching sites: figure 1 b *versus* figure A4 below page 14).

1051

1052 *Photos taken from the ground:* in September 2022, we randomly selected several parcels in
1053 each habitat category Open-Open, Closed-Closed and Open-Closed. From approximately the
1054 middle of each parcel, we took 3 kinds of wide angle photographs (GoPro H9, shooting angle

1055 107°, N=76 pictures) with the camera held approximately 1.75 m above the ground: a)
1056 Toward the zenith to evaluate canopy closure (the proportion of the sky masked by vegetation
1057 when viewed from a single point at ground level; Jennings et al. 1999), b) Approximately 45°
1058 toward the soil to evaluate ground vegetation cover, c) Horizontally to evaluate surrounding
1059 vegetation. Canopy closure was analyzed using Gap Light Analyzer (N=21 photos pointing
1060 toward the sky, Frazer et al. 1999). Photos pointing toward the soil or taken horizontally were
1061 visually analyzed: the occurrence of a thick herbaceous layer, scrubs (e.g. blackthorns, *Prunus*
1062 *spinosa*; brambles, *Rubus fruticosus*; dogroses, *Rosa canina*) and trees was noted. Photographs
1063 were taken in 2022, two years after the last evaluations based on aerial views, closing level was
1064 thus possibly slightly overestimated.



1065

1066 **Figure A2.** A) Number of corrugated slabs used to monitor snakes that have been deployed in the
 1067 forest over time in each closing category (Open-Open [O-O]: light grey, Closed-Closed [C-C]: dark
 1068 grey and Open-Closed [O-C]: middle-grey). B) Total number of slabs deployed over time (left Y-axis,
 1069 open diamonds) and total number of surveys performed over time (right Y-axis, black diamonds). C)
 1070 Searching effort (SEF, number of slabs checked, left Y-axis, grey hexagons) from 1995 to 2021 versus
 1071 searching success per slab (proportion of successful slabs, i.e. with at least one snake observed,
 1072 right Y-axis, HV, *Hierophis viridiflavus*: open hexagons; ZL, *Zamenis longissimus*: black
 1073 hexagons).

1074 **Section A2. Modelling details**

1075 Snakes are elusive animals and their activity level is strongly influenced by climatic conditions
1076 (Mazerolle et al., 2007). These factors and other causes such as survival, temporary emigration
1077 or attractiveness for the capture slabs may generate strong time and spatial heterogeneity in
1078 capture and recapture probabilities that may bias estimates (Kendall, 1999; Kendall et al., 1995,
1079 1997; Koper & Brooks, 1998; Pollock, 1982; Pollock et al., 1990; Seber, 1982). Therefore, we
1080 used a Huggins robust design with 27 primary sessions (i.e. years of study) and 5 to 8 secondary
1081 sessions of 2 weeks each (depending on climatic conditions that determine the duration of the
1082 active season).

1083 We tested for possible effects of trap-response behavior and time-related variations on
1084 capture (p) and recapture (c) probabilities. We also modelled temporary emigration (the
1085 probability of an individual not being available for trapping during one or more primary
1086 sampling periods), transience (the probability that a newly captured individual was just passing
1087 through the study area, with a near-zero chance of returning to the study area and to be
1088 recaptured during the study), and apparent survival (the probability of surviving from one
1089 primary period to the next and of staying in the study area). The number of individuals not
1090 captured was modelled for each primary period as time dependent or constant and added to the
1091 number of individuals known to be in the population to provide an estimate of population size
1092 (\hat{N}_t). Capture and recapture probabilities were modelled on an annual scale, and were either
1093 year dependent, $p(t)$ and $c(t)$, or constant $p(\cdot)$. We first attempted to estimate parameters for
1094 each primary period and for each secondary period. Due to sample size limitation in the first
1095 years of the study, several parameters were not estimated. To reduce this problem, all secondary
1096 sessions belonging to a given primary period were set constant. We tested the effect of time
1097 among primary sessions for recapture and capture parameters only, to further reduce
1098 misestimation. Temporary emigration was modelled with two parameters: $\gamma'(\cdot)$ was the

1099 probability that a snake was absent from the study area at time t if absent at time t-1, and $\gamma''(.)$
1100 was the probability that a snake was absent from the study area at time t if present at time t-1.
1101 Temporary emigration was also modelled as either random $\gamma'(.)=\gamma''(.)$, or Markovian $\gamma'(.)\neq\gamma''(.)$.

1102 All these models were implemented in MARK program (White & Burnham, 1999) for each
1103 species (*Hierophis viridiflavus*, *Zamenis longissimus*) and habitat category (Open-Open,
1104 Closed-Closed, Open-Closed). We used an information theoretic approach to select the most
1105 appropriate model for the data based on ecologically sound hypotheses and based on the small-
1106 sample modification (AICc) (Anderson & Burnham, 2002). In *H. viridiflavus* the sample size
1107 used for the AICc (corresponding to the number of individuals retained for the robust design
1108 matrix) is respectively 404, 97 and 627 for Open-Open, Closed-Closed and Open-Closed
1109 categories. In *Z. longissimus*, the sample size used for the AICc is respectively 589, 394 and
1110 798 for Open-Open, Closed-Closed and Open-Closed categories. A model was preferred to a
1111 concurrent model when the AICc of the model was lower than the AICc of the concurrent
1112 model by at least two units. When the AICc difference between two models was less than 2,
1113 the difference in deviance (Δdev) and the difference in number of parameters K multiplied by
1114 two ($\Delta 2K$) were explored. If $\Delta 2K < \Delta dev$, the model with the lower deviance was selected.
1115 When $\Delta 2K \approx \Delta dev$ the most parsimonious model (i.e. which used fewer parameters) was
1116 selected. Confidence intervals (95% CI) of parameters between models were also inspected. If
1117 a time dependent parameter had similar CI among primary periods, then the constant parameter
1118 (most parsimonious) was retained.

1119 We assessed the fit of our initial model using program U-CARE (Choquet et al., 2009). For
1120 this, individual sighting histories were pooled for all the secondary sampling periods keeping
1121 only one sighting occasion per primary sampling period. Hence, we assessed the fit of the
1122 Cormack-Jolly-Seber model corresponding to our dataset. TEST 3.SR provided a test for
1123 transients (Choquet et al., 2005, 2009). Transients were defined as “individuals having a zero

1124 probability of local survival after their initial capture” (Genovart & Pradel, 2019). True
1125 transients crossing through but not belonging to the study population should be distinguished
1126 from individuals that die after a single reproductive bout or from individuals that die (or
1127 emigrate) following marking (Genovart & Pradel, 2019). We excluded the two last possibilities
1128 because *Hierophis viridiflavus* and *Zamenis longissimus* reproduce more than once during their
1129 lifetime and our marking technique had no detectable effect on the survival of snakes (Fauvel
1130 et al., 2012). Therefore, detecting significant transience will suggest that a substantial
1131 proportion of marked individuals do not settle in the sub-network of slabs where they have
1132 been marked. When transience was detected, it was explicitly modelled by considering 2
1133 apparent age-classes for survival (Genovart & Pradel, 2019).

1134 The starting model was $S(.) \gamma''(.) \gamma'(.) p(t) c(t)$ or $S(a1,a2) \gamma''(.) \gamma'(.) p(t) c(t)$ in case of
1135 transience, where $(.)$ and (t) respectively represent an absence or the presence of time effect
1136 among primary sessions. We modelled the effect of time on capture and recapture probabilities
1137 and the type of temporary emigration, and used the best supported models to obtain annual
1138 estimates of snake abundance (\hat{N}_t). We also sequentially tested if linear trends occurred on each
1139 parameter issued from the best supported model. We built models where the demographic
1140 parameter θ was modelled as $\text{logit}(\theta) = \alpha + \beta \times T$, where α is an intercept parameter, β is a
1141 slope parameter and T is a linear temporal trend. When $\beta > 0$ the parameter increases through
1142 time, whereas it decreases when $\beta < 0$. We used ANODEV to test for linear trends (Grosbois
1143 et al., 2008). In case of a significant ANODEV test, the slope confidence interval (CI) was
1144 checked. If 0 belonged to the slope CI, we rejected the hypothesis of a trend even if the
1145 ANODEV test was significant. Linear trend was tested for each parameter and slope estimates
1146 are reported on the logit scale (see Table A4.).

1147 Finally, we used abundance estimates to calculate population growth rates (λ) for each of
1148 the six groups (2 snake species and 3 habitat categories). To facilitate interpretation of trends

1149 and to attenuate the effects of large inter-annual variations of \hat{N}_t on λ estimates, we pooled the
1150 years in seven time periods: 1995-1997; 1998-2001; 2002-2005, 2006-2009, 2010-2013, 2014-
1151 2017, 2018-2021. From these seven time periods i, six abundance estimates (λ_1 to λ_6) were
1152 calculated:

$$1153 \quad \lambda_i = (\text{Mean Adjusted } \hat{N}_t \text{ of time period } i) / (\text{Mean Adjusted } \hat{N}_t \text{ of time period } i-1)$$

1154 Since each adjusted \hat{N}_t was already linked to a log normal distribution, it was possible to extract
1155 the mean, the lower confidence interval (LCI) and the upper confidence interval (UCI) from
1156 each resulting log normal distribution of λ . Robust design matrix are shared privately on
1157 Figshare using the active link: <https://figshare.com/s/0b3f9927eeb022b5ce57>

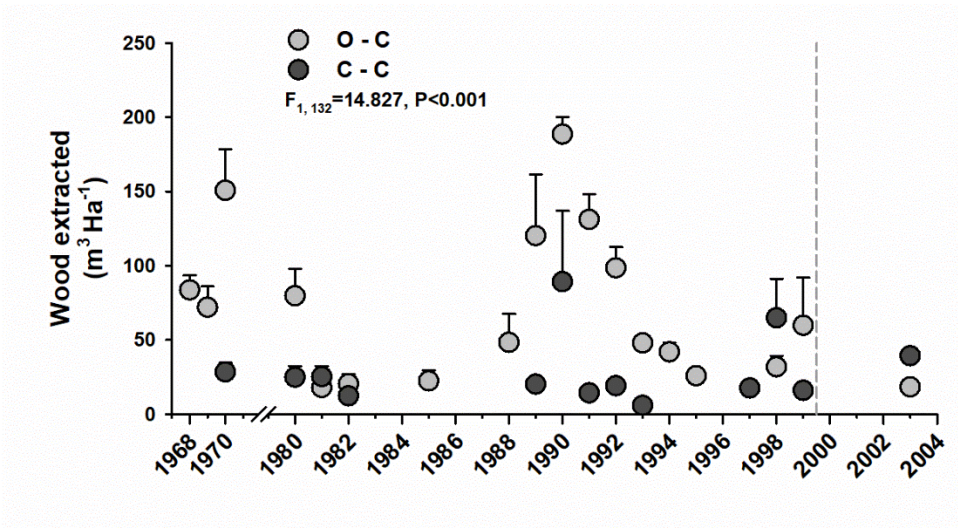
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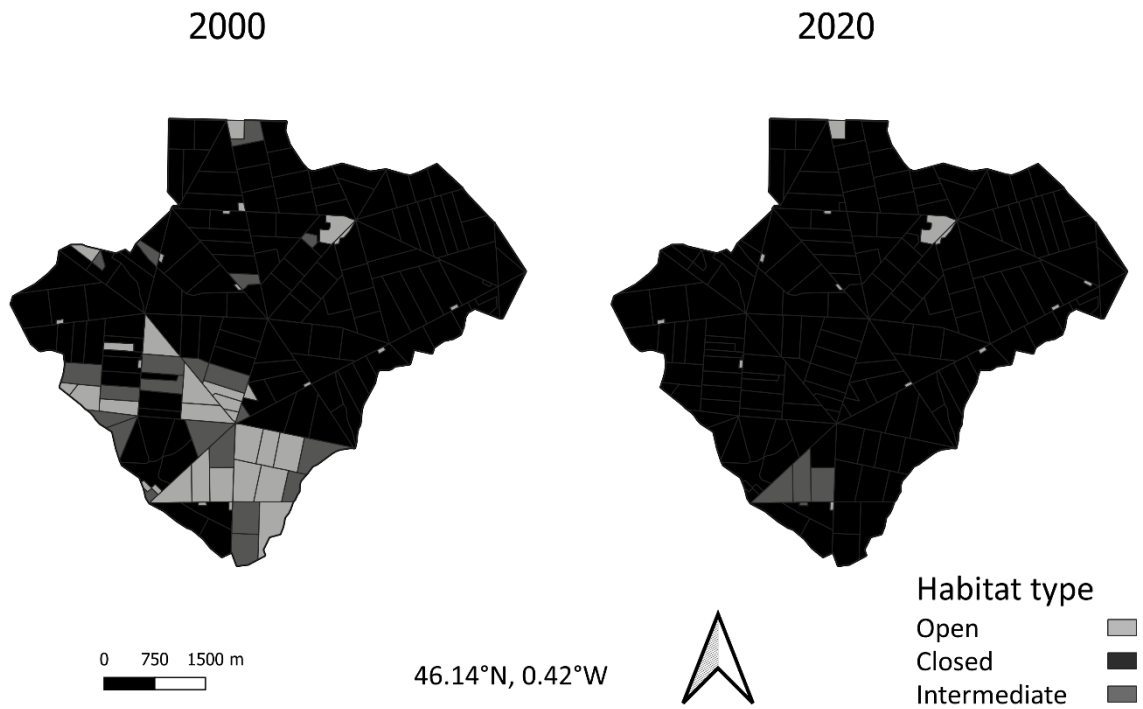
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1208 **Figure A3.** Logging history from 1968 to 2004 in the Closed-Closed (C-C, black circles) and
 1209 Open-Closed (O-C, grey circles) categories. The mean volume (SD) of wood extracted in each
 1210 parcel was expressed in $\text{m}^3 \cdot \text{ha}^{-1}$ (Y-axis). In late 1999 (vertical dashed line) two strong storms
 1211 provoked the fall of more than 10,000 trees and the almost total cessation of logging.

1212 **Table A1.** Habitat specific areas (ha) from visual analyses using the QGIS software over time
1213 (QGIS Development Team 2020). Canopy cover was evaluated qualitatively each year (see
1214 text). Habitat types are classified in three group: Open (canopy covering 0% to 30% of parcel
1215 surface); Closed (canopy covering 71% to 100% of a parcel surface); Intermediate (canopy
1216 covering 31% to 70%).

Years	Open	Closed	Intermediate
1996	336.46	2119.63	205.03
2000	461.17	1884.18	315.77
2007	230.12	2078.66	352.34
2011	111.56	2372.06	177.5
2020	27.96	2535.54	97.62

1217



1218

1219

1220 **Figure A4.** Comparison of canopy cover (surface covered by a vertical projection of the
 1221 canopy, Jennings et al. 1999) quantified using ImageJ software in 2000 and 2020 (Schneider
 1222 et al., 2012). The same aerial images were used for visual quantification (see Figure 1b). Light
 1223 grey indicates open habitat type (O) where canopy covers 0% to 30% of the parcel surface;
 1224 dark grey indicates closed habitat type (C, canopy covers 71% to 100% of the surface); middle
 1225 grey indicates semi open or intermediate habitat (I, canopy covers 31% to 70% of the surface).

1226 **Table A2.** Statistics describing the canopy closure rate (Canopy Openness, %) derived from
1227 the GLA software (Frazer et al., 1999). Pictures were taken toward the zenith (GoPro H9,
1228 shooting angle 107°, N = 21 pictures) to evaluate canopy closure from several parcels randomly
1229 selected among each closing category (Open-Open, Closed-Closed and Open-Closed).

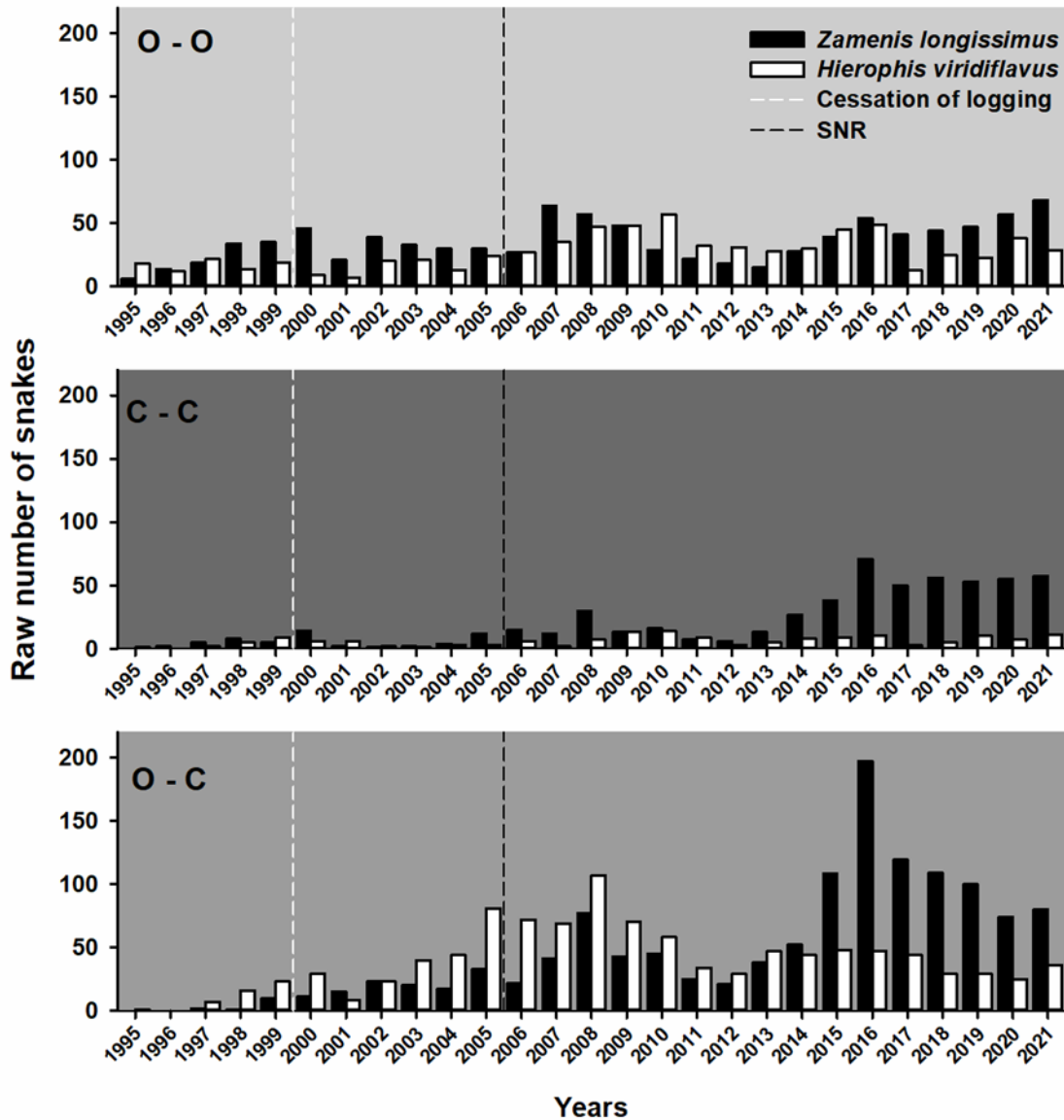
Category	mean	SD	min	max
Open-Open	4.00	7.15	0.02	14.70
Closed-Closed	87.04	3.52	82.91	92.68
Open-Closed	39.03	20.72	2.33	77.34

1230



1231

1232 **Figure A5.** Ground photographs of the three main types of habitats. First row: open habitat
1233 (O), second row: closed habitat (C), third row: intermediate or semi-open habitat (I). First
1234 column: photo taken toward the zenith to evaluate canopy closure, second column photo taken
1235 45° toward the soil to assess ground vegetation, third column photo taken horizontally to assess
1236 surrounding vegetation. Photos taken by the authors.



1237

1238 **Figure A6.** Raw numbers of snakes found each year in each habitat category (*O-O*, *Open-Open*;
 1239 *C-C*, *Closed-Closed*; *O-C*, *Open-Closed*), from 1995 to 2021. Whip snakes (*HV*, *Hierophis*
 1240 *viridiflavus*) and Aesculapian snakes (*ZL*, *Zamenis longissimus*) are respectively represented
 1241 by white and black bars. Only one observation per individual is considered each year. The
 1242 white vertical dashed line indicates a milestone in the management history of the forest. Timber
 1243 harvesting ceased almost totally in 2000 (see Figure A3) and canopy closure attained its lowest
 1244 level. The black vertical dashed line indicates the classification of the forest as strictly protected
 1245 nature reserve (SNR).

1246 **Table A3.** Goodness-of-fit test (GOF) applied on each species and category. Sp: snake species
 1247 (HV: *Hierophis viridiflavus*; ZL: *Zamenis longissimus*). Cat: habitat category.

Species	Cat	GOF (global)	TEST 3.SR	GOF (without TEST 3.SR)
HV	Open-Open	$p=0.782$ $\chi^2=67.127$ df=77	$p=0.2137$ $\chi^2=30.288$ df=25	$p=0.945$ $\chi^2=36.839$ df=52
	Closed-Closed	$p=0.949$ $\chi^2=8.721$ df=17	$p=0.190$ $\chi^2=8.721$ df=6	$p=1$ $\chi^2=0$ df=11
	Open-Closed	$p=0.807$ $\chi^2=64.265$ df=75	$p=0.647$ $\chi^2=18.034$ df=21	Not concerned
ZL	Open-Open	$p=0.887$ $\chi^2=60.528$ df=75	$p=0.027$ $\chi^2=39.024$ df=24	$p>0.999$ $\chi^2=21.505$ df=51
	Closed-Closed	$p=0.839$ $\chi^2=38.365$ df=48	$p=0.444$ $\chi^2=15.106$ df=15	$p=0.896$ $\chi^2=23.259$ df=33
	Open-Closed	$p=0.379$ $\chi^2=84.291$ df=81	$p=0.002$ $\chi^2=44.874$ df=21	$p=0.982$ $\chi^2=39.417$ df=60

1248

1249 **Table A4.** Testing for linear temporal trends on parameters issued from the best supported Huggins Robust Design model (Best model). Slope
1250 estimates are reported on the logit scale. Sp: snake species (HV: *Hierophis viridiflavus*; ZL: *Zamenis longissimus*). Cat: habitat category. Sign
1251 means sign trend. Probability p was obtained using ANODEV. S, apparent annual survival; γ'' , temporary emigration; γ' , temporary immigration;
1252 p , capture probability; c , recapture probability; a_1 first year after initial capture; a_2 , >1 year after initial capture; t , year (primary session) effect;
1253 (.), no time effect; TR, significant linear temporal trend; LCI, lower confidence interval; UCI, upper confidence interval; *, significant interaction.

Sp	Cat	Best model	Sign	p	Slope	LCI	UCI	
HV	Open-Open	$S(a_1, a_2)\gamma''(\text{TR})=\gamma'(\text{TR})p(t)c(\text{TR})$	$\gamma''=\gamma'$	< 0.011	0.084	0.008	0.159	
			c	0.051	0.041	0.014	0.068	
	Closed-Closed	$S(a_1, a_2)\gamma''(\cdot)=\gamma'(\cdot)p(\text{TR})c(\cdot)$	p	< 0.008	-0.122	-0.195	-0.049	
	Open-Closed	$S(\cdot)\gamma''(\cdot)\gamma'(\text{TR})p(\cdot)c(\cdot)$	γ'	0.0001	-29.842	-55.821	-3.862	
ZL	Open-Open	$S(\text{TR}*_a_1, a_2)\gamma''(\cdot)=\gamma'(\cdot)p(t)c(t)$	Sa1	< 0.007	-0.0005	-0.040	0.039	
			Sa2	< 0.007	0.064	0.027	0.100	
	Closed-Closed	$S(\text{TR}*_a_1, a_2)\gamma''(\cdot)=\gamma'(\cdot)p(\text{TR})c(\text{TR})$	$p=c$	0.035	0.064	0.026	0.103	
			Sa1	< 0.010	-0.126	-0.285	0.033	
				Sa2	< 0.010	0.110	0.030	0.189
	Open-Closed	$S(a_1, a_2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$	No trend					

1254

1255

1256 **Table A5.** Huggins Robust Design model selection for each species and habitat category. In each case, the starting model is in italics, and the best
1257 model is in bold. In case of competitive models ($\Delta AICc < 2$) we have discarded the model with noninformative parameters (Arnold, 2010; Leroux,
1258 2019) (see “Model selection and snake abundance” in the methods of the manuscript). Sp: snake species (HV: *Hierophis viridiflavus*; ZL: *Zamenis*
1259 *longissimus*); Cat: habitat category; S: apparent annual survival; γ'' : temporary emigration; γ' : temporary immigration; p: capture probability; c:
1260 recapture probability; a1: first year after initial capture; a2: >1 year after initial capture; t: year (primary session) effect; (.): no time effect; Par:
1261 number of parameters.

Sp	Category	Model	AICc	Delta AICc	AICc Weights	Par	Deviance
HV	Open-Open	S(a1,a2)γ''(.)=γ'(.)p(t)c(t)	4608.192	0.000	0.529	57	2910.435
		<i>S(a1,a2)γ''(.)γ'(.)p(t)c(t)</i>	4608.537	0.345	0.445	58	2908.431
		S(a1,a2) γ'' (.) γ' (.)p(.)c(t)	4615.319	7.127	0.015	32	2974.152
		S(a1,a2) γ'' (.) γ' (.)p(t)c(.)	4615.912	7.720	0.011	32	2974.744
		S(a1,a2) γ'' (.)= γ' (.)p(.)c(.)	4625.238	17.046	0.000	5	3040.927
		S(a1,a2) γ'' (.) γ' (.)p(.)c(.)	4626.808	18.616	0.000	6	3040.465
		S(a1,a2) γ'' (.) γ' (.)p(t)=c(t)	4633.826	25.634	0.000	31	2994.840
		S(a1,a2) γ'' (.) γ' (.)p(.)=c(.)	4652.833	44.641	0.000	5	3068.523

1262

Table A5. (Continued)

Sp	Category	Model	AICc	Delta AICc	AICc Weights	Par	Deviance
HV	Closed-Closed	S(a1,a2)$\gamma''(\cdot)=\gamma'(\cdot)p(\cdot)c(\cdot)$	693.993	0.000	0.613	5	226.023
		S(a1,a2) $\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$	695.037	1.044	0.364	6	224.825
		S(a1,a2) $\gamma''(\cdot)\gamma'(\cdot)p(\cdot)=c(\cdot)$	702.239	8.246	0.010	5	234.269
		S(a1,a2) $\gamma''(\cdot)\gamma'(\cdot)p(t)c(\cdot)$	741.976	47.983	0.000	32	192.799
		S(a1,a2) $\gamma''(T)\gamma'(\cdot)p(\cdot)c(\cdot)$	745.305	51.313	0.000	31	200.151
		S(a1,a2) $\gamma''(\cdot)\gamma'(T)p(\cdot)c(\cdot)$	758.819	64.826	0.000	30	217.585
		S(a1,a2) $\gamma''(\cdot)\gamma'(\cdot)p(t)c(t)$	881.514	187.521	0.000	58	171.246
HV	Open-Closed	S(\cdot) $\gamma''(\cdot)\gamma'(\cdot)p(t)c(\cdot)$	6894.436	7.174	0.025	31	5379.796
		S(\cdot)$\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$	6895.041	7.779	0.019	5	5434.275
		S(\cdot) $\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(t)$	6895.722	8.460	0.013	31	5381.082
		S(\cdot) $\gamma''(\cdot)=\gamma'(\cdot)p(\cdot)c(\cdot)$	6896.554	9.293	0.009	4	5437.808
		S(\cdot) $\gamma''(\cdot)\gamma'(\cdot)p(\cdot)=c(\cdot)$	6897.560	10.298	0.005	4	5438.813
		S(\cdot) $\gamma''(\cdot)\gamma'(\cdot)p(t)c(t)$	6897.915	10.653	0.004	57	5326.601

Table A5. (Continued)

Sp	Category	Model	AICc	Delta AICc	AICc Weights	Par	Deviance
ZL	Open-Open	$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)c(t)$	5902.887	0.000	0.517	58	3706.808
		$S(a1,a2)\gamma''(\cdot)=\gamma'(\cdot)p(t)c(t)$	5903.070	0.182	0.472	57	3709.254
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)c(\cdot)$	5910.450	7.563	0.012	32	3771.658
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$	5921.279	18.391	0.000	6	3836.666
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(t)$	5926.140	23.253	0.000	32	3787.349
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)=c(t)$	5929.480	26.593	0.000	31	3792.829
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)=c(\cdot)$	5945.710	42.823	0.000	5	3863.122
ZL	Closed-Closed	$S(a1,a2)\gamma''(\cdot)=\gamma'(\cdot)p(t)=c(t)$	3559.259	0.000	0.652	30	2135.358
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)=c(t)$	3560.632	1.372	0.329	31	2134.502
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(t)$	3566.364	7.104	0.019	32	2137.998
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$	3574.916	15.656	0.000	6	2202.191
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)=c(\cdot)$	3581.071	21.812	0.000	5	2210.388
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)c(t)$	3596.569	37.310	0.000	58	2107.124

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Table A5. (Continued)

Sp	Category	Model	AICc	Delta AICc	AICc Weights	Par	Deviance
ZL	Closed-Closed	$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)c(\cdot)$	3599.682	40.423	0.000	32	2171.317
ZL	Open-Closed	$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(\cdot)$	8169.661	0.000	0.495	6	7527.509
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)c(t)$	8170.211	0.550	0.376	32	7474.385
		$S(a1,a2)\gamma''(\cdot)=\gamma'(\cdot)p(\cdot)c(\cdot)$	8172.361	2.700	0.128	5	7532.229
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)=c(t)$	8185.755	16.093	0.000	31	7492.035
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)c(\cdot)$	8186.220	16.558	0.000	32	7490.393
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(t)c(t)$	8186.836	17.175	0.000	58	7434.981
		$S(a1,a2)\gamma''(\cdot)\gamma'(\cdot)p(\cdot)=c(\cdot)$	8188.882	19.221	0.000	5	7548.750

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1267

1268 **Table A6.** Parameter estimates issued from the best supported Huggins Robust Design model (best model in Table A5). Sp: snake species (HV:
1269 *Hierophis viridiflavus*; ZL: *Zamenis longissimus*); Category: habitat category; S: apparent annual survival; γ'' : temporary emigration; γ' : temporary
1270 immigration; p: capture probability per primary session; c: recapture probability per primary session; a1: first year after initial capture; a2: >1 year
1271 after initial capture; (.): no time effect; SE: standard error; LCI: 95% lower confidence interval; UCI: 95% upper confidence interval.

Species	Category	Parameter	Mean	SE	LCI	UCI
HV	Open-Open	Sa1	0.522	0.051	0.429	0.626
		Sa2	0.671	0.027	0.620	0.727
		$\gamma''(.)=\gamma'(.)$	0.492	0.046	0.399	0.578
		p (1)	0.439	0.277	0.000	0.819
		p (2)	0.401	0.196	0.000	0.711
		p (3)	0.724	0.139	0.380	0.914
		p (4)	0.625	0.178	0.189	0.870
		p (5)	0.487	0.249	0.000	0.828
		p (6)	0.426	0.269	0.000	0.805
		p (7)	0.422	0.319	0.000	0.849
		p (8)	0.507	0.264	0.000	0.856
		p (9)	0.843	0.112	0.552	0.971
		p (10)	0.450	0.261	0.000	0.808
		p (11)	0.350	0.186	0.000	0.648
		p (12)	0.745	0.143	0.384	0.931
		p (13)	0.823	0.107	0.552	0.956
p (14)	0.678	0.130	0.366	0.867		
p (15)	0.757	0.106	0.501	0.908		
p (16)	0.772	0.079	0.587	0.894		

1272 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	LCI	UCI
HV	Open-Open	p (17)	0.885	0.093	0.637	0.985
		p (18)	0.819	0.081	0.620	0.934
		p (19)	0.787	0.148	0.405	0.962
		p (20)	0.902	0.073	0.710	0.984
		p (21)	0.826	0.105	0.562	0.957
		p (22)	0.687	0.118	0.407	0.864
		p (23)	0.185	0.105	0.000	0.375
		p (24)	0.938	0.055	0.793	0.993
		p (25)	0.580	0.267	0.000	0.909
		p (26)	0.900	0.094	0.646	0.991
		p (27)	0.698	0.166	0.284	0.915
		c (1)	0.256	0.144	0.000	0.503
		c (2)	0.241	0.190	0.000	0.560
		c (3)	0.224	0.131	0.000	0.454
		c (4)	0.484	0.184	0.053	0.763
		c (5)	0.219	0.124	0.000	0.437
		c (6)	0.247	0.198	0.000	0.573
		c (7)	0.245	0.198	0.000	0.572
		c (8)	0.375	0.135	0.077	0.603
		c (9)	0.536	0.121	0.262	0.733
		c (10)	0.200	0.154	0.000	0.464
		c (11)	0.219	0.162	0.000	0.495
		c (12)	0.284	0.119	0.026	0.493
		c (13)	0.417	0.106	0.186	0.600
		c (14)	0.629	0.091	0.426	0.780
		c (15)	0.395	0.094	0.196	0.561
		c (16)	0.448	0.089	0.255	0.605

1273 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
HV	Open-Open	c (17)	0.177	0.087	0.000	0.335
		c (18)	0.314	0.103	0.094	0.497
		c (19)	0.385	0.122	0.121	0.594
		c (20)	0.369	0.104	0.146	0.552
		c (21)	0.328	0.096	0.124	0.500
		c (22)	0.638	0.077	0.467	0.769
		c (23)	0.391	0.177	0.000	0.673
		c (24)	0.458	0.105	0.229	0.637
		c (25)	0.737	0.104	0.491	0.892
		c (26)	0.283	0.117	0.033	0.490
		c (27)	0.326	0.117	0.074	0.530
HV	Closed-Closed	Sa1	0.218	0.066	0.116	0.372
		Sa2	0.705	0.081	0.527	0.837
		$\gamma''(\cdot)=\gamma'(\cdot)$	0.136	0.345	0.001	0.980
		p (1)	0.467	0.168	0.077	0.731
		p (2)	0.369	0.141	0.059	0.609
		p (3)	0.468	0.167	0.083	0.731
		p (4)	0.509	0.177	0.093	0.777
		p (5)	0.510	0.177	0.095	0.778
		p (6)	0.421	0.155	0.075	0.675
		p (7)	0.368	0.141	0.058	0.608
		p (8)	0.468	0.167	0.079	0.731
		p (9)	0.509	0.177	0.095	0.777
		p (10)	0.510	0.176	0.097	0.777
p (11)	0.511	0.176	0.095	0.777		
p (12)	0.468	0.167	0.081	0.731		
p (13)	0.510	0.177	0.091	0.777		

1274 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
HV	Closed-Closed	p (14)	0.510	0.175	0.100	0.775
		p (15)	0.510	0.176	0.095	0.775
		p (16)	0.509	0.177	0.091	0.776
		p (17)	0.467	0.167	0.078	0.730
		p (18)	0.469	0.166	0.086	0.733
		p (19)	0.420	0.155	0.071	0.674
		p (20)	0.468	0.167	0.085	0.731
		p (21)	0.469	0.166	0.086	0.730
		p (22)	0.468	0.167	0.079	0.730
		p (23)	0.509	0.177	0.091	0.777
		p (24)	0.509	0.177	0.093	0.777
		p (25)	0.421	0.155	0.070	0.674
		p (26)	0.421	0.155	0.072	0.674
		p (27)	0.509	0.177	0.091	0.776
		c (1)	0.147	0.048	0.048	0.239
		c (2)	0.108	0.036	0.035	0.177
		c (3)	0.147	0.049	0.048	0.239
		c (4)	0.166	0.054	0.056	0.267
		c (5)	0.166	0.054	0.056	0.267
		c (6)	0.128	0.042	0.042	0.209
		c (7)	0.108	0.036	0.035	0.177
		c (8)	0.147	0.048	0.049	0.238
		c (9)	0.166	0.054	0.055	0.267
		c (10)	0.166	0.054	0.058	0.267
		c (11)	0.166	0.054	0.055	0.267
		c (12)	0.147	0.048	0.048	0.238
		c (13)	0.166	0.054	0.056	0.267

1275 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
HV	Closed-Closed	c (14)	0.166	0.054	0.055	0.268
		c (15)	0.166	0.054	0.056	0.267
		c (16)	0.166	0.054	0.056	0.268
		c (17)	0.147	0.048	0.050	0.239
		c (18)	0.147	0.048	0.049	0.238
		c (19)	0.128	0.042	0.043	0.208
		c (20)	0.147	0.048	0.050	0.239
		c (21)	0.147	0.048	0.049	0.238
		c (22)	0.147	0.048	0.049	0.239
		c (23)	0.166	0.054	0.056	0.268
		c (24)	0.166	0.054	0.056	0.267
		c (25)	0.128	0.043	0.042	0.209
		c (26)	0.128	0.042	0.042	0.208
		c (27)	0.166	0.054	0.055	0.267
HV	Open-Closed	S(.)	0.648	0.032	0.582	0.708
		γ' (.)	0.168	0.084	0.058	0.397
		γ (.)	0.700	0.217	0.235	0.947
		p (1)	0.418	0.046	0.324	0.504
		p (2)	0.321	0.038	0.244	0.393
		p (3)	0.418	0.046	0.324	0.503
		p (4)	0.461	0.048	0.361	0.550
		p (5)	0.461	0.049	0.360	0.551
		p (6)	0.371	0.042	0.285	0.451
		p (7)	0.321	0.038	0.244	0.393
p (8)	0.418	0.046	0.324	0.503		
p (9)	0.461	0.049	0.360	0.551		
p (10)	0.461	0.049	0.361	0.550		

1276 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
HV	Open-Closed	p (11)	0.461	0.049	0.360	0.552
		p (12)	0.418	0.046	0.324	0.503
		p (13)	0.461	0.049	0.360	0.551
		p (14)	0.461	0.049	0.361	0.551
		p (15)	0.461	0.049	0.361	0.551
		p (16)	0.461	0.048	0.360	0.550
		p (17)	0.418	0.046	0.324	0.504
		p (18)	0.418	0.046	0.324	0.503
		p (19)	0.372	0.042	0.285	0.451
		p (20)	0.418	0.046	0.324	0.503
		p (21)	0.418	0.046	0.324	0.504
		p (22)	0.418	0.046	0.324	0.504
		p (23)	0.461	0.049	0.361	0.551
		p (24)	0.461	0.049	0.359	0.551
		p (25)	0.372	0.042	0.286	0.451
		p (26)	0.372	0.043	0.285	0.452
		p (27)	0.461	0.048	0.361	0.550
		c (1)	0.322	0.020	0.282	0.361
		c (2)	0.243	0.016	0.211	0.274
		c (3)	0.322	0.020	0.282	0.361
		c (4)	0.359	0.022	0.315	0.401
		c (5)	0.359	0.022	0.315	0.401
		c (6)	0.284	0.018	0.247	0.319
		c (7)	0.243	0.016	0.211	0.274
		c (8)	0.322	0.020	0.282	0.361
		c (9)	0.359	0.022	0.315	0.401
		c (10)	0.359	0.022	0.315	0.401

1277 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
HV	Open-Closed	c (11)	0.359	0.022	0.315	0.401
		c (12)	0.322	0.020	0.283	0.361
		c (13)	0.359	0.022	0.315	0.401
		c (14)	0.359	0.022	0.315	0.401
		c (15)	0.359	0.022	0.315	0.400
		c (16)	0.359	0.022	0.316	0.401
		c (17)	0.322	0.020	0.282	0.361
		c (18)	0.322	0.020	0.282	0.361
		c (19)	0.284	0.018	0.247	0.319
		c (20)	0.322	0.020	0.282	0.361
		c (21)	0.322	0.020	0.282	0.361
		c (22)	0.322	0.020	0.282	0.361
		c (23)	0.359	0.022	0.316	0.401
		c (24)	0.359	0.022	0.316	0.400
ZL	Open-Open	c (25)	0.284	0.018	0.247	0.319
		c (26)	0.284	0.018	0.247	0.319
		c (27)	0.359	0.022	0.315	0.401
		Sa1	0.438	0.038	0.367	0.514
		Sa2	0.655	0.026	0.605	0.707
		$\gamma''(\cdot)=\gamma'(\cdot)$	0.382	0.054	0.271	0.479
		p (1)	0.523	0.378	0.000	0.941
		p (2)	0.526	0.247	0.000	0.860
		p (3)	0.569	0.196	0.094	0.847
		p (4)	0.355	0.148	0.025	0.603
p (5)	0.676	0.122	0.388	0.859		
p (6)	0.799	0.112	0.517	0.944		
p (7)	0.436	0.144	0.114	0.672		

1278 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
ZL	Open-Open	p (8)	0.448	0.134	0.150	0.670
		p (9)	0.867	0.093	0.626	0.975
		p (10)	0.730	0.109	0.470	0.889
		p (11)	0.117	0.090	0.000	0.281
		p (12)	0.581	0.164	0.192	0.823
		p (13)	0.701	0.113	0.432	0.869
		p (14)	0.681	0.090	0.475	0.826
		p (15)	0.850	0.078	0.656	0.954
		p (16)	0.617	0.152	0.255	0.839
		p (17)	0.537	0.203	0.042	0.825
		p (18)	0.223	0.118	0.000	0.433
		p (19)	0.376	0.169	0.000	0.650
		p (20)	0.902	0.079	0.695	0.988
		p (21)	0.860	0.092	0.621	0.970
		p (22)	0.574	0.109	0.328	0.754
		p (23)	0.520	0.130	0.225	0.730
		p (24)	0.824	0.116	0.525	0.962
		p (25)	0.672	0.139	0.335	0.872
		p (26)	0.520	0.104	0.288	0.696
		p (27)	0.825	0.067	0.665	0.925
		c (1)	0.780	0.242	0.122	0.992
		c (2)	0.516	0.189	0.069	0.799
		c (3)	0.506	0.166	0.122	0.765
		c (4)	0.531	0.132	0.227	0.744
		c (5)	0.322	0.107	0.092	0.511
		c (6)	0.194	0.075	0.040	0.331
		c (7)	0.330	0.149	0.000	0.581

1279 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI		
ZL	Open-Open	c (8)	0.461	0.113	0.211	0.654		
		c (9)	0.415	0.098	0.203	0.586		
		c (10)	0.314	0.117	0.060	0.519		
		c (11)	0.156	0.112	0.000	0.357		
		c (12)	0.312	0.128	0.032	0.533		
		c (13)	0.163	0.065	0.029	0.284		
		c (14)	0.440	0.094	0.237	0.604		
		c (15)	0.292	0.085	0.111	0.447		
		c (16)	0.460	0.121	0.191	0.662		
		c (17)	0.190	0.109	0.000	0.385		
		c (18)	0.239	0.139	0.000	0.479		
		c (19)	0.512	0.217	0.000	0.820		
		c (20)	0.179	0.086	0.000	0.337		
		c (21)	0.373	0.089	0.182	0.532		
		c (22)	0.516	0.090	0.322	0.671		
		c (23)	0.218	0.092	0.023	0.386		
		c (24)	0.307	0.080	0.140	0.453		
		c (25)	0.251	0.089	0.062	0.412		
		c (26)	0.347	0.106	0.119	0.533		
		c (27)	0.229	0.069	0.086	0.357		
		ZL	Closed-Closed	Sa1	0.410	0.059	0.307	0.530
				Sa2	0.743	0.035	0.677	0.813
				$\gamma'(\cdot)=\gamma(\cdot)$	0.237	0.104	0.036	0.429
				p(1)=c(1)	0.799	0.500	0.000	1.000
				p(2)=c(2)	0.458	0.363	0.000	0.894
				p(3)=c(3)	0.594	0.213	0.067	0.881
				p(4)=c(4)	0.321	0.178	0.000	0.612

1280 **Table A6.** (Continued)

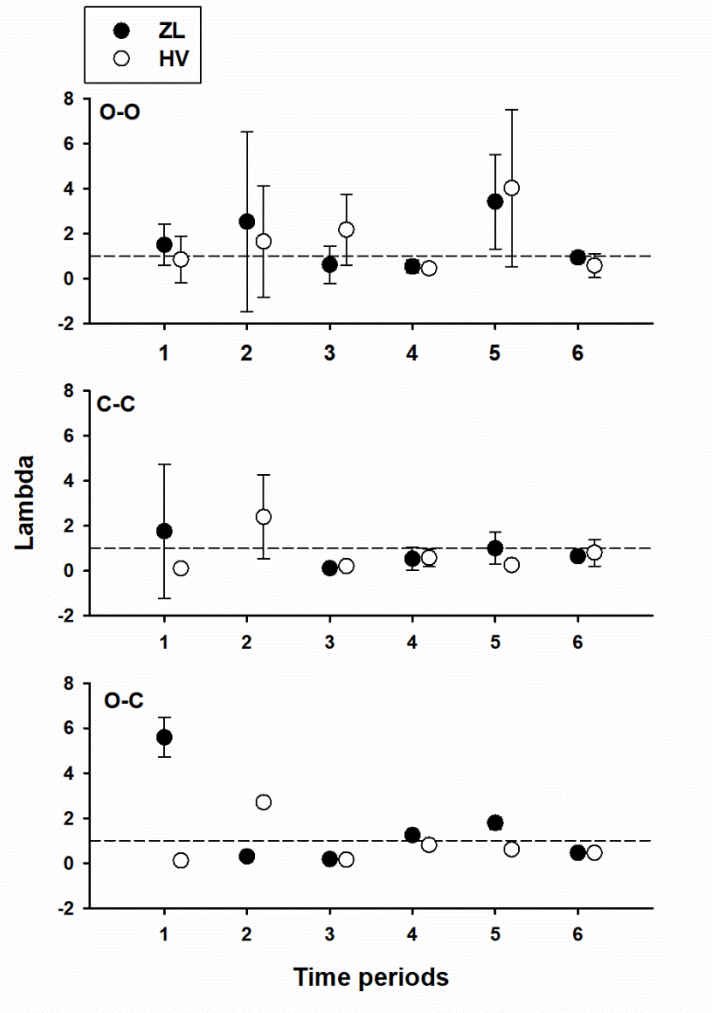
Species	Category	Parameter	Mean	SE	95% LCI	95% UCI		
ZL	Closed-Closed	p(5)=c(5)	0.234	0.199	0.000	0.560		
		p(6)=c(6)	0.455	0.172	0.058	0.725		
		p(7)=c(7)	0.292	0.290	0.000	0.716		
		p(8)=c(8)	0.434	1.670	0.000	1.000		
		p(9)=c(9)	0.405	0.374	0.000	0.860		
		p(10)=c(10)	0.319	0.244	0.000	0.690		
		p(11)=c(11)	0.275	0.158	0.000	0.542		
		p(12)=c(12)	0.261	0.125	0.000	0.479		
		p(13)=c(13)	0.243	0.126	0.000	0.463		
		p(14)=c(14)	0.373	0.093	0.174	0.538		
		p(15)=c(15)	0.241	0.101	0.029	0.422		
		p(16)=c(16)	0.293	0.109	0.059	0.485		
		p(17)=c(17)	0.143	0.090	0.000	0.307		
		p(18)=c(18)	0.155	0.096	0.000	0.330		
		p(19)=c(19)	0.212	0.108	0.000	0.404		
		p(20)=c(20)	0.196	0.085	0.018	0.353		
		p(21)=c(21)	0.499	0.085	0.316	0.648		
		p(22)=c(22)	0.580	0.058	0.456	0.684		
		p(23)=c(23)	0.434	0.068	0.290	0.559		
		p(24)=c(24)	0.364	0.064	0.231	0.482		
		p(25)=c(25)	0.320	0.065	0.186	0.439		
		p(26)=c(26)	0.336	0.069	0.190	0.462		
		p(27)=c(27)	0.462	0.072	0.310	0.591		
		ZL	Open-Closed	Sa1	0.501	0.038	0.429	0.578
				Sa2	0.774	0.026	0.724	0.830
				$\gamma'(\cdot)$	0.211	0.083	0.048	0.367
				$\gamma(\cdot)$	0.587	0.172	0.216	0.923

1281 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
ZL	Open-Closed	p (1)	0.320	0.038	0.243	0.392
		p (2)	0.370	0.042	0.284	0.448
		p (3)	0.370	0.042	0.284	0.449
		p (4)	0.459	0.048	0.359	0.548
		p (5)	0.416	0.046	0.322	0.501
		p (6)	0.416	0.046	0.323	0.501
		p (7)	0.416	0.046	0.322	0.500
		p (8)	0.416	0.046	0.321	0.501
		p (9)	0.459	0.048	0.359	0.548
		p (10)	0.459	0.049	0.359	0.548
		p (11)	0.459	0.048	0.360	0.548
		p (12)	0.416	0.046	0.323	0.501
		p (13)	0.459	0.048	0.359	0.549
		p (14)	0.459	0.048	0.358	0.548
		p (15)	0.459	0.048	0.359	0.548
		p (16)	0.459	0.048	0.359	0.548
		p (17)	0.459	0.048	0.359	0.548
		p (18)	0.459	0.049	0.359	0.549
		p (19)	0.416	0.046	0.323	0.501
		p (20)	0.370	0.042	0.283	0.450
		p (21)	0.459	0.048	0.359	0.548
		p (22)	0.416	0.046	0.322	0.501
		p (23)	0.459	0.049	0.359	0.549
		p (24)	0.459	0.048	0.359	0.549
		p (25)	0.459	0.048	0.358	0.548
		p (26)	0.459	0.048	0.359	0.549
		p (27)	0.459	0.048	0.359	0.549

1282 **Table A6.** (Continued)

Species	Category	Parameter	Mean	SE	95% LCI	95% UCI
ZL	Open-Closed	c (1)	0.173	0.013	0.147	0.197
		c (2)	0.203	0.015	0.174	0.232
		c (3)	0.203	0.015	0.174	0.232
		c (4)	0.261	0.018	0.225	0.297
		c (5)	0.233	0.017	0.200	0.265
		c (6)	0.233	0.017	0.200	0.265
		c (7)	0.233	0.017	0.200	0.265
		c (8)	0.233	0.017	0.200	0.265
		c (9)	0.261	0.018	0.225	0.297
		c (10)	0.261	0.018	0.225	0.297
		c (11)	0.261	0.018	0.225	0.296
		c (12)	0.233	0.017	0.200	0.265
		c (13)	0.261	0.018	0.225	0.297
		c (14)	0.261	0.018	0.225	0.297
		c (15)	0.261	0.018	0.225	0.297
		c (16)	0.261	0.018	0.225	0.297
		c (17)	0.261	0.018	0.225	0.297
		c (18)	0.261	0.018	0.225	0.296
		c (19)	0.233	0.017	0.200	0.265
		c (20)	0.203	0.015	0.174	0.232
		c (21)	0.261	0.018	0.225	0.297
		c (22)	0.233	0.017	0.200	0.265
		c (23)	0.261	0.018	0.225	0.297
		c (24)	0.261	0.018	0.225	0.297
		c (25)	0.261	0.018	0.225	0.297
		c (26)	0.261	0.018	0.225	0.297
		c (27)	0.261	0.018	0.225	0.297



1284

1285 **Figure A7.** Changes in population growth rates (Lambda, λ with lower and upper confidence
 1286 intervals) in each habitat category (O-O, Open-Open; C-C, Closed-Closed; O-C, Open-
 1287 Closed), and for each snake species (HV, *Hierophis viridiflavus* and ZL, *Zamenis longissimus*
 1288 respectively represented by white and black circles). To attenuate the effects of large inter-
 1289 annual variations, λ were calculated using seven time periods: 1) from 1995-1997 to 1998-
 1290 2001; 2) from 1998-2001 to 2002-2005, 3) from 2002-2005 to 2006-2009, 4) from 2006-2009
 1291 to 2010-2013, 5) from 2010-2013 to 2014-2017, 6) from 2014-2017 to 2018-2021. The dashed
 1292 line indicates stable population ($\lambda = 1$).

1293