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Repeated use of high risk nesting areas in the European whip snake, *Hierophis viridiflavus*

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Oviparous snakes deposit their egg clutches in sites sheltered from predation and from strong thermal and hydric fluctuations. Appropriate laying sites with optimum thermal and hydric conditions are generally scarce and are not necessarily localised in the home range. Thus, many gravid females undertake extensive trips for oviposition, and many may converge at the best egg laying sites. Dispersal mortality of neonates post-hatching is also a critical factor. Assessing the parameters involved in this intergenerational trade-off is difficult however, and no study has succeeded in embracing all of them. Here we report data indicating that gravid females of the highly mobile European whip snake, *Hierophis viridiflavus* exhibit nest site fidelity whereby they repeatedly deposit their eggs in cavities under sealed roads over many decades. These anthropogenic structures provide benefits of relative safety and suitable incubation conditions (due to the protective asphalted layer?), but they expose both females and neonates to high risk of road mortality. Artificial laying sites constructed at appropriate distances from busy roads, along with artificial continuous well protected pathways (e.g. dense hedges) that connect risky laying sites to safer areas, should be constructed.

Keywords: *Hierophis viridiflavus*, road mortality, cost of reproduction, reptiles, anthropogenic landscape, forest

INTRODUCTION

Although females of several snake species are able to excavate their own nest in soft ground (Burger & Zappalorti, 1991; Cunnington & Cebek, 2005), most exploit existing cavities in rocky areas or in trees to deposit their eggs. The attraction of certain sites for nesting can be considerable and many females, sometimes from different lineages of squamates, converge toward communal nesting places (Graves & Duvall, 1995; Filippi et al., 2007). Empirical and experimental studies, as well as intuition, suggest that these repeatedly used sites offer excellent environmental conditions for embryonic development (review in Doody et al., 2009). Guided by environmental and social clues (e.g. empty shells of previous hatchlings, Brown & Shine, 2005a; Meek, 2017) and using their spatial memory, gravid females search underground tunnels or cavities for localities with stable ambient temperatures of around 30 – 35 °C and high moisture levels, which produce optimal conditions for embryo development (Shine et al., 1997; Aubret et al., 2005; Brown & Shine, 2005b; Löwenborg et al., 2010, 2011; Ramesh & Bhupathy, 2010; Stahlschmidt et al., 2011; Meek, 2017). Such conditions can be represented by large partly rotting logs, hollow trees, thick leaf litters,

underground insect nests or the burrows of various animals (Carman-Blazquez & Villafuerte, 1990; Madsen & Shine, 1999; Pearson et al., 2003; Velásquez-Múnera et al., 2008; Ramesh & Bhupathy, 2010; Nagy et al., 2017; Meek, 2017; Alexander, 2018).

However, in landscapes shaped by anthropogenic activity, oviparous reptiles frequently use artificial structures as laying sites. The selection of artificial structures by gravid females is likely underpinned by adaptive mechanisms that operate in natural settings, and it is probably driven by the rarity of suitable natural nesting sites (Doody et al., 2009). For example, in cool climates, incubation success in the grass snake (*Natrix helvetica*) depends strongly on fermenting compost or dung heaps associated with livestock farming, especially in northern Europe (Löwenborg, 2012) to the extent that the disappearance of open manure heaps during the past decades has resulted in snake population declines across Sweden (Hagman et al., 2012). Besides this well documented example of the reliance of a snake on artificial laying sites, there are many other instances where gravid females use human constructions for oviposition, even in tropical countries. Egg laying sites under roads have been associated with snakes in Australia (Covacevich & Limpus, 1972), Europe (Capula et

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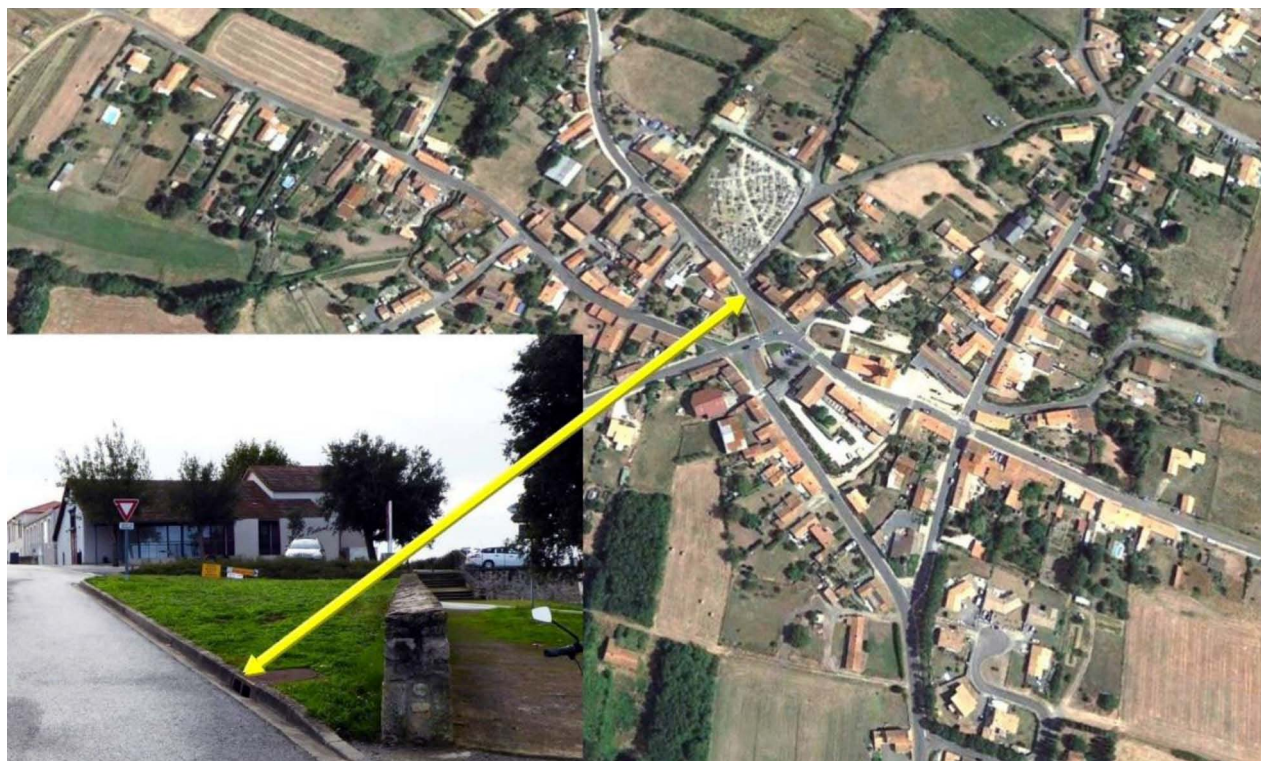


Figure 1. Google Earth map showing the village of St Denis du Payre and the location of the drain where hatchling *H. viridiflavus* emerge (inserted photograph).

al., 1997; Meek, 2017 and unpublished data) and Brazil (Braz & Manço, 2011). Additionally, snakes reportedly nest in railroad sleepers, artificial snake dens, in hollow retaining walls, old partly demolished buildings and in walls in a cement culvert (Albuquerque & Ferrarezzi, 2004; Filippi et al., 2007; Zappalorti & Mitchell, 2008; Shine & Bonnet, 2009; Hanslowe et al., 2016). Indeed, there are more documented examples of artificial than of natural sites, but there are few reports of long term repeated nesting in anthropogenic structures (Filippi et al., 2007).

We do not know if females prefer anthropogenic to natural laying sites or vice-versa; but it is likely that in anthropogenic environments, the scarcity of suitable natural sites constrain females to use artificial sites. Answering these questions is important for conservation managers, especially to instigate mitigation measures to restore or improve habitats, for example to remove those laying sites that attract gravid females but that are actually deadly traps for huge numbers of snakes. Conversely, it might be useful to construct artificial laying sites at suitable distances from high-risk high traffic roads (Bonnet et al., 1999). In the context of habitat fragmentation, sprawling urbanisation, and global snake decline, it is therefore crucial to attract or retain snakes in well protected areas instead of directing them toward dangerous zones. In oviparous species, road mortality may heavily impact reproductive females during round trips to laying sites, and males tracking females often suffer the same fate (Bonnet et al., 1999; Meek, 2015). Therefore for snake conservation in anthropogenic landscapes we need key information (e.g. mortality assessment, site preference) to assess the risk of artificial

laying sites situated in high risk zones, roads or urbanised areas.

In eight zones, long term-monitoring of living snakes and of road-kills provided a means to address the following questions: Are natural versus artificial nesting areas associated with differential long term frequenting by gravid females? Is there any evidence that neonate mortality is particularly high in anthropogenic areas? Would high usage of artificial laying sites, when associated with high neonate mortality, suggest a possible lethal trap effect?

METHODS

Study species

The European whip snake *Hierophis viridiflavus* is a medium-sized European oviparous colubrid snake with a maximal recorded snout to vent length (SVL) in the study localities of ~139 cm in males (163 cm total length) and ~108 cm (145 cm total length) in females. It inhabits a range of environments with an extensive home range and a life span that may reach 20 years (Scali et al., 2008; Lelièvre et al., 2011; Fornasiero et al., 2016). Mean egg clutch size varies geographically and broadly ranges from 4 to 8 eggs (Luiselli, 1995; Zuffi et al., 2007a). In the study areas, on average, mating occurs from mid-May to mid-June, oviposition from late June to early July, and then hatching in late August to September; this phenology is influenced by climate and latitude across the distribution range of the species (Bonnet & Naulleau, 1996; Capula et al., 1997; Filippi et al., 2007).

Study areas and surveys

Two main areas were monitored in central west France; respectively situated in Vendée and Deux-Sèvres districts and separated from each other by a straight-line distance of ~74 km.

Vendée: The nest site was located in a roadside drain in the centre of a village of St Denis du Payré (42° 19' N, 1° 16' W; Fig. 1). The locality is almost 300 m from the nearest natural area of woodland (Fig. 1) and for a snake accessing the site the route is almost devoid of cover - for example there are no hedgerows or other low risk movement pathways (Fahrig, 2007). During the active season (April – October), the locality was observed regularly with a minimum of between 4 and 6 monthly surveys undertaken at around 4 day intervals by a single observer (RM). Surveys were normally mid-week and at weekends. Road traffic volume recorded on the main route entering and leaving the village (D60) was just over 60 vehicles per hour during daylight hours (Meek, 2009). Data collected at the den was mostly hatchling mortalities (SVL < 30 cm) and 2 adult females (SVL = 67 cm) found at or within 4-5 m of the den entrance. All snakes were measured for SVL along with the dates they were found.

Deux-Sèvres: Seven sites were compared in this study area in the forest of Chizé (46° 07' N, 0° 24' W; Fig. 2). Five sites are situated in relatively natural areas in the integral biological reserve (RBI). Two other sites are in relatively urbanised areas next to busy roads (D1 and D53) that transect the forest. One (LABO) is a small 4 ha enclave at the northern limit of the RBI that contains a research campus (e.g. CNRS and University). The other (MUDB) is in the garden of a private property adjacent to the exploited forest. The seven sites differ in total area (from 0.3 to 50 ha; Fig. 2), terrain and degree of openness of the habitat (open meadows vs mature forest; Fig. 2).

Long-term mark-recapture monitoring from 1990 to 2019 (+episodic data collected from 1981 to 1988) showed that very few individuals move between sites, and that these exchanges are largely limited to adjacent zones (e.g. ZOSE vs CHEP, Fig. 2). Consequently, the seven sites were considered as independent, at least in terms of population functioning. In addition to the main sites, other natural sites and scattered locations in the RBI provided data on reproduction of female whip snakes and hatchlings (data pooled).

The networks of roads that connect the sites were also systematically surveyed for road killed snakes. In the

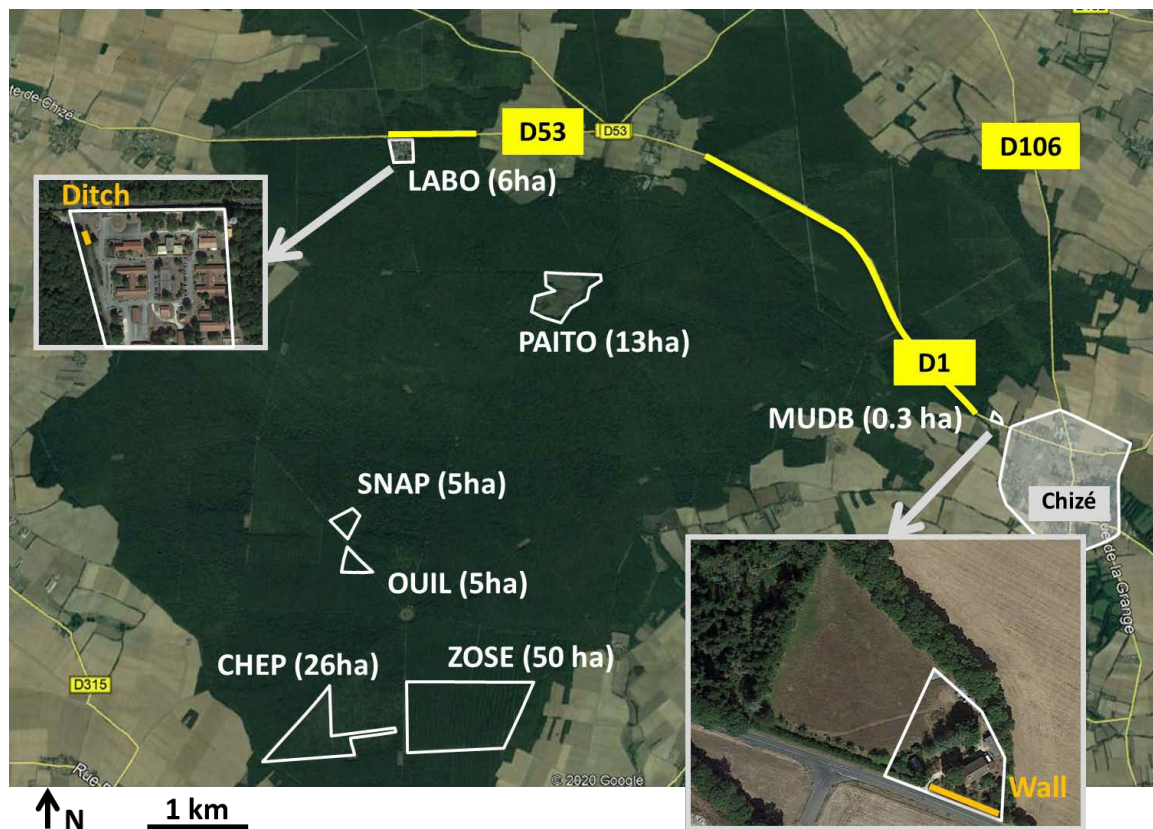


Figure 2. Modified Google Earth map showing seven sites monitored in the forest of Chizé. South of the D53 and D1, the forest is strictly protected (integral biological reserve, RBI) with no public admittance (RBI limits not visualized to limit overload). The north-eastern part of the forest (partly visible here) is open to the public and exploited for wood. Five natural sites are in the RBI (PAITO, SNAP, OUIL, CHEP and ZOSE). The two urbanised sites (LABO, MUDB) not included in the RBI are respectively adjacent to two busy roads, D53 and D1. The grey area shows a village (Chizé). Enlargements are provided for LABO and MUDB (grey arrows) to identify the main nesting site entrances in orange (ditch and stone wall). The dense network of roads inside the RBI is not visible at this scale, busy roads (all out of the RBI are highlighted); the thick yellow sections indicate where >70% of road kill snakes have been collected.

RBI, the roads are rarely used; but D1 and D53 are busy. Roads were surveyed by car driving at low speed (<50 km/h), cycling, and walking. The two main busy-roads (D1 & D53) were surveyed cycling and/or driving (XB). Additional roads (e.g. D106) were mostly surveyed by normal speed driving (70 to 90 km/h).

In the seven sites, snakes were searched for presence under corrugated slabs (>800 slabs deployed; fibrocement, roughly 120x80 cm, undulation height 6 cm) where if present they were captured by hand, measured (SVL), marked (individual code using heat-branded scales with medical cautery units; Winne et al. 2006) and released. Sex was determined by inspection of the tail. Females were considered as adults if larger than the smallest individuals with enlarged follicles (SVL=67 cm). Females do not reproduce every year (Capula et al., 1997), thus populations contain both reproductive and non-reproduce individuals. In order to determine the reproductive status of each female, we restricted analyses to the period during which abdominal palpation can reveal the presence of eggs (enlarged follicles), or evidence of recent egg-laying (extensive skin folds, distended sub-cloacal scale). Following emergence from hibernation, from March to mid-April, reproductive females cannot be distinguished from non-reproductive females by palpation. Similarly, from late summer until hibernation (August to late October), post-laying females cannot be distinguished from non-reproductive females. Consequently, analyses were restricted to the periods from 25th April to 30th July. Data from all years was pooled, but we included only one observation per individual per year.

Individuals were considered as neonates when SVL<30 cm, even if they were measured weeks or months after the hatching period (e.g. following hibernation). All road-kills were collected and measured for body size (SVL). For several snakes, information was incomplete (e.g. date or exact location), generating slight variations of sample size in the analyses (contingency table statistical tests were performed with Statistica 13.5.0.17, 2018 TIBCO Software).

RESULTS

Vendée

The entrance of the Vendée nest was first detected in 2005 in the centre of the village of St Denis du Payré in a roadside drain (42°19'N, 1°16'W; Fig. 1). Observations of nesting activity were made in 12 of the 15 (80 %) years between 2005 and 2019. Hatchling emergence was between 26th August (recorded 2016) and 27th September (recorded 2017) with annual hatchling count over the 12 years ranging from 1 – 9 (mean = 4.1 ± 2.4 std. dev.). Additional hatchlings were found between 2nd and 22nd April at the entrance during the springs of 2015 (n = 2), 2017 (n = 2) and 2018 (n = 1). These were likely the previous year's hatchlings that overwintered at the site. Only two adult females were found at the site, on 17th and 30th June of 2010 and 2013 respectively. Figure 3 shows the annual counts. The broken line represents an expected probability of equality of annual counts derived

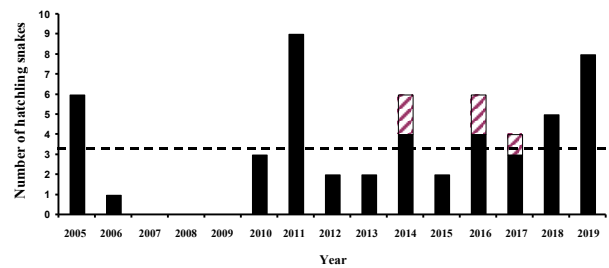


Figure 3. Annual numbers of hatchling *H. viridiflavus* found between 2005 and 2019 at St Denis du Payré. Cross hatched areas represent snakes found in April of the following year but here shown as year of hatching. The broken line represents expected snake numbers if annual counts were equal. See text for details.

from: $\text{Expected} = 1/N_1 * N_2$, where N_1 is number of years and N_2 the total sample size. This gave an expected value of 3.3 hatchling snakes per year when years with zero counts are included in the calculation. This indicated that snake numbers at the site in 2011 and 2019 were 2.73 and 2.42 times greater than expected.

Deux-Sèvres

The proportion of reproductive versus non-reproductive females varied significantly among the seven sites ($\chi^2=103.96$, $df=6$, $p<0.001$; Fig. 4). Compared to the 5 natural sites, the 2 urbanised sites (LAB & MUDB) showed the highest proportion along with highest absolute numbers of gravid females (Fig. 4). Each year, approximately 50 % of the individuals observed at natural sites were reproductive, this proportion reached 70 % and 90 % in the urbanised sites.

Gravid females were observed spatially scattered and mixed with non-reproductive females in natural sites. But, in the two urbanised sites, almost all females were gravid and were captured in highly localised places: under the tiles covering a small stone-wall that borders the D1 road in the MUDB site; under few corrugated fibrocement slabs placed in a ditch at the LAB site. The MUDB stony wall is directly connected to under road cavities resulting from partial land filling before asphaltting; the ditch is connected to deep cavities under the D53 sealed road via a pipe partly obstructed by rocks. The clutches have not been discovered (it is impossible to excavate public roads). Yet, many gravid females were found at the entrance of the sites and they were recaptured a few days later with an empty abdomen and extensive skin folds indicating recent oviposition. We also found one male whip snake killed on the road just above this site with recently ingested conspecific eggs in the stomach; this species being occasionally known for oophagy and cannibalistic behaviour (Schmidlin et al., 1996; Capula et al., 2014). No adult female was found road-killed inside the RBI. Several reproductive and a few non-reproductive females were found road-killed on the roads in the exploited part of the forest and in other roads of the district (n = 54 reproductive vs 8 non-reproductive females; 9 vs 1 focusing on the forest

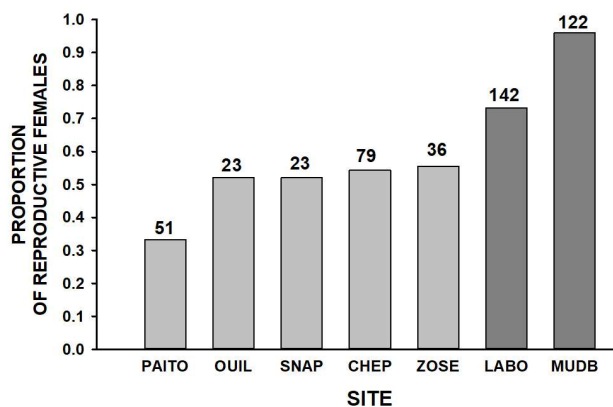


Figure 4. Proportion of reproductive females (gravid or shortly after egg laying) compared to non-reproductive females in different populations (i.e. site) of *H. viridiflavus*. Absolute numbers are provided above each bar. Light grey bars indicate sites situated in natural environments (fully protected natural reserve); dark grey bars indicate urbanised sites adjacent to busy roads.

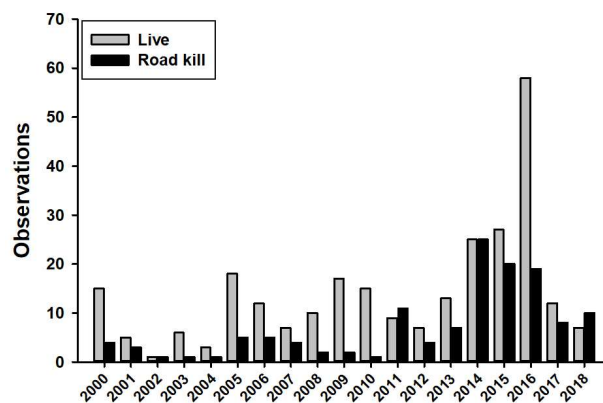


Figure 5. Annual numbers of hatchling whip snakes (*H. viridiflavus*) observed between 2000 and 2018 in the forest of Chizé. Living snakes were found under corrugated slabs; road kills were found on asphalt covered roads, essentially the D1 and D53.

Table 1. Live hatchling whip snakes and road killed hatchlings found in different sites on the road network in the forest of Chizé and surroundings areas. In addition to the 7 main sites used in the analyses (Fig. 2) we pooled observations collected in various other places in the forest of Chizé (n=13). Five sites situated in the fully protected part of the forest (RBI) were considered as natural. Two urbanised sites (LABO and MUDB) are juxtaposed to the roads D1 and D53. Other busy roads are on the south and east part of the forest.

Site	Status	Live	Roadkilled	Total
PAITO	Natural	70	1	71
OUIL	Natural	2	0	2
SNAP	Natural	8	0	8
CHEP	Natural	38	0	38
ZOSE	Natural	23	1	24
Other Natural sites	Natural	108	2	110
LABO	Urbanised	87	3	90
MUDB	Urbanised	9	0	9
D1	Road	0	50	50
D53	Road	0	17	17
Other local busy roads	Road	0	14	14
Sum		345	88	433

section of D1 and D53 roads).

Many living neonates were found under corrugated slabs in all the seven sites (Table 1), especially in a large meadow (PAITO, a natural site) and in one urbanised site (LABO). Most live hatchlings (62 %, n = 340) were observed following emergence from hibernation, from late March to late May, while most road-killed hatchlings (63 %, n = 82) were observed after nest emergence from late August to late September; generating significant temporal difference between the two categories of hatchlings ($\chi^2=106.2$, df=1, $p<0.001$). Living and road-killed hatchlings were observed continuously over a prolonged time period, 6.5 ± 6.7 per year on average (Fig. 5). Data collected before 2000 are not shown in Figure 5 because the D1 and D53 roads that transect the forest were not regularly surveyed by cycling. Cycling survey intensified over time, corrugated slab surveys also increased over time. In combination with demographic

variations (unpublished data), these factors caused inter-annual fluctuations. We did not analyse such annual changes because different data sources are involved (e.g. increasing but variable searching effort); disentangling their respective effect was outside the scope of this study.

DISCUSSION

The two study areas (Vendée and Deux-Sèvres) provided complementary information. Some results were confirmatory for example, the frequent use of certain sites associated with long-term fidelity. Others were novel: our analyses indicate *Hierophis viridiflavus* female preference for artificial sites and evidence of associated increased mortality risk. Together, these results suggest high and continuous mortality associated with artificial nesting sites and thus a possible behavioural trap effect

that requires adequate management options to mitigate mortalities.

1) Long term nest site fidelity: In Vendée, gravid females used under the road sites in the centre of St Denis du Payré, for a period of at least over 15 years and continuously for at least 10 years (Fig. 1). Similarly, in Deux-Sèvres, gravid females used the LABO and MUDB under road sites during 30 and 12 years of monitoring of each site respectively. Moreover, in both areas, other snake species used under road artificial sites. In Vendée, this observation is supported by data from a roadside nesting area around 3 km from the study site that is repeatedly used by wide foraging grass snakes *Natrix helvetica* (Meek, 2017). In Deux-Sèvres, Aesculapian (*Zamenis longissimus*) and grass snakes, regularly used LABO and MUDB artificial sites during the entire monitoring period of this study (unpublished data).

Long term monitoring of individual snakes (e.g. decades) indicate that different cohorts of females are involved and that nest site fidelity crosses generations; reproductive lifespan of females is relatively short (usually 3 to 6 years, unpublished data) and does not exceed 10 years (max observed = 9 years, unpublished data). Long term nest site fidelity and communal nesting has previously been documented in the western whip snake *H. viridiflavus* in Italy (Capula & Luiselli, 1995; Filippi et al., 2007; Rugiero et al., 2012); our paper presents additional observations in two localities in central west France, close to the northernmost limit of the species range. The observation that *H. viridiflavus* may also enter urban areas for nesting is of interest and makes a valuable comparison with nest site fidelity in more natural habitats. However, in the absence of recaptures of marked individuals we do not know if individuals exclusively used a preferred site or alternated between different sites.

2) Mortality risk of artificial nesting sites: For different reasons, mortality risk assessed with road mortality severely underestimates actual numbers of animals that are victim of a collision, including snakes (Slater, 2002; Santos et al., 2011; Antworth et al., 2005; Hastings et al., 2019). Firstly, persistence of carcasses is low, especially in forest sites where scavengers are numerous (e.g. various birds, foxes and cats) that patrol roads in search of fresh road kills (Schwartz et al., 2018). Unsurprisingly, almost all hatchlings we collected were flat and dry, probably because they were killed during traffic peaks, which limits the opportunities for scavengers to pick them up (Slater, 2002). Secondly, small animals are difficult to spot and hence the associated underestimation is particularly strong for very small individuals, <8 g for *H. viridiflavus* hatchlings (Teixeira et al., 2013). Nevertheless we accumulated large numbers of road killed hatchlings, which represent minimal counts.

Disregarding the underestimate issues, the numbers of annual hatchling mortalities we recorded were small, maximal annual count was nine hatchlings in Vendée and 25 in Deux-Sèvres, which compares with a broad average

clutch for a single female (6-8 eggs) or for three females in some years. This may suggest either a low-cost impact by road traffic if numerous females are using the site at the same time or, conversely, substantial mortality of only a few gravid females at each site each year. In the first case, many hatchlings must have escaped road traffic, in the second case many did not and were killed. In Vendée, only two females were found road killed over a 15 year period at a cross roads in a village centre providing support to the second possibility. In Deux-Sèvres, road mortality was concentrated at two artificial nesting sites (Table 1). The mean annual number of reproductive females at these sites (calculated from 2000 to match the Fig. 5 timescale) was 9.0 ± 8.6 , leading to a crude estimate of 63 hatchlings per site per year. Given that hatching success is not generally 100 %, and that annual numbers of road mortalities are strongly underestimated, our results suggest that road mortality was significant in the surveyed areas, impacting a high proportion of hatchlings from urbanised artificial sites (e.g. ~25 %). Even limited road traffic can generate substantial snake mortalities (Hartmann et al., 2011). Thus, the very small number of road-killed hatchlings found on the rarely used roads connecting natural sites (over four decades) suggests that the strictly protected reserve (RBI) was a low cost environment in terms of road mortalities.

Frequent use of artificial laying sites

The high number of reproductive females found close to artificial road sites strongly suggests that reproductive females are particularly likely to use these sites in the absence of good egg laying sites elsewhere, often resulting in high neonate road mortality during the post-hatchling dispersal phase. Adult males follow the pheromone trails of females, and hence they may converge to the best laying sites (Bonnet & Naulleau, 1996; Zuffi et al., 2007b). This was particularly apparent at MUDB, which is too small to sustain any population of medium sized snakes. Many gravid females from the adjacent forest visited the stone wall specifically during the mating and laying period, and they were accompanied by high numbers of adult males during the mating season (unpublished data).

Why do gravid females persistently and intensively nest under roads? In oviparous snakes, where offspring develop independently from the female, the location of egg-laying sites with optimal thermal and hydric conditions, that also limit accessibility to predators, are key factors in their ecology (Ackerman & Lott, 2004; Birchard, 2004; Filippi et al., 2007). It is probable that these artificial nesting areas offer easy access to appropriate conditions for incubation, for example the protective cover of road surfaces limits dehydration (no roots and thus evapotranspiration), indeed stable and warm ambient temperatures have been recorded in under road sites (Lelièvre et al., 2010). Asphalt is not only resistant to evapotranspiration but it is also periodically renewed and hence artificial sites under roads probably offer favourable and stable conditions over decades. If such sites are also minimally disturbed

during times when not used for egg development, they may be used repeatedly. Locating optimal nesting sites may require well-developed orientation abilities in species that operate a wide ranging foraging strategy. In Europe several species of snake are known to employ this lifestyle, including the European whip snake *H. viridiflavus* (Luiselli, 2006).

Management proposal

In this paper we have shown that gravid females tend to use artificial sites situated next to busy roads over prolonged periods of time, which entails high risk both for adults (Bonnet et al., 1999) and for their offspring (this study). Animal abundance is known to be impacted by altered levels of predation risk in fragmented anthropogenic landscapes (e.g. Evans, 2004), especially when wildlife enters urban areas and faces increased risk from domestic predators. Frequent use of artificial nesting sites means that *Hierophis viridiflavus* often enter these areas where they suffer mortalities from dogs, cats and humans (Bonnet et al., 1999; Rugiero & Luiselli, 2004; Meek, 2012). It is conceivable that females may not be able to fully evaluate all these risks. Similar data are available for Aesculapian, grass and viperine snakes: many were collected as road kill or killed by humans and domestic pets during the hatchling season, along with many reproductive females and large males during mating and laying seasons (Bonnet et al., 1999). Thus the phenomenon observed with whip snakes may well apply to many oviparous snakes especially those species operating a wide foraging movement strategy.

Following hibernation, we observed many small snakes (i.e. hatchlings, n=249) in the natural sites. Many juveniles (SVL>30 cm) were also observed in the RBI (unpublished data). This suggests that those snakes living in the well-protected areas of the forest, situated away from the busy roads, can achieve their reproductive cycle in relatively safe places.

Importantly, our data do not show that artificial nesting sites are not useful for the maintenance of endangered snake populations, especially when no alternative exists. Instead, our results reveal high mortality risks; thus, appropriate management should target these risks.

From an evolutionary perspective snakes are probably able to evaluate that open patches present a high mortality risk, and thus might be reluctant to use them while preferring to follow sheltered pathways (e.g. hedgerows) when available (e.g. Fahrig, 2007; Naulleau et al., 1997). Therefore, we suggest three main nonexclusive actions: (1) Building suitable artificial laying sites in well protected areas where many snakes are observed (Bonnet et al., 1999), especially because such sites offer excellent refuges during hibernation and aestivation (Zappalorti & Reinert, 1994; Shine & Bonnet, 2009; Burger et al., 2012); (2). When possible, moving the highest risk sites (e.g. MUDB) to safer places (i.e. long distances from busy roads); and (3) Building low risk movement corridors to channel gravid females and hatchlings away from high risk laying sites toward safer locations, for example thick hedgerows with abundant ground shelters (e.g. stone piles), represents another

option. In addition, management planning should pay attention to preserving older artificial sites, for example old building, roads, esplanades that are often perceived as undesirable by managers for aesthetic reasons and demolished. These structures often offer valuable refuges to a wide range of animals, notably reptiles (Lecq et al., 2017).

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Contribution

RM and XB initiated the study, performed the analyses and wrote the first version of the manuscript. JMB and GB provided comments and approved the successive versions. All authors intensively participated to the acquisition of field data.

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