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Forest management bolsters native snake populations in urban parks

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ABSTRACT

Within a mosaic of agricultural and urbanized landscapes, shrub habitats are important refuges that help maintain biodiversity. Unfortunately, these habitats have been dramatically altered over the past several decades for practical and esthetic reasons. Continued rapid growth of suburban areas has accelerated this shift in habitat quality. Management strategies that promote shrub habitat within developed areas are rarely greeted with public acceptance because bushy thickets (e.g. *Rubus* brambles) shelter undesired species of animals (e.g. snakes, small mammals) and are typically associated with a lack of property maintenance. We conducted an experiment in a heavily impacted suburban habitat (population density of ~2700 humans/km^2). Our study site, containing forest and meadow habitats, was adjacent to a large city (~320,000 inhabitants) and visited by >70,000 people annually. We manipulated the forest habitat by removing trees, and through active maintenance, thereby promoting the growth of brambles. Within six years, we observed that newly-created shrub habitat was rapidly colonized by snakes, notably *Vipera aspis*. The total number of detected individuals increased markedly over time. Numerous advertising and educational activities about snake ecology were conducted in parallel, especially with school children. Complaints from the public were absent which demonstrates that management strategies that favor unpopular organisms are feasible, even in densely populated areas.

1. Introduction

Urbanization is typically viewed as having negative impacts on landscapes, from disrupting the functioning of ecosystems to reducing biodiversity (Gilbert, 1989). Given the rapid pace of landscape alterations, the incorporation of natural elements (e.g. “green spaces,” parks) within urbanized developments is essential for wild populations. For example, these elements provide key habitats and improve connectivity across a fragmented urbanized landscape (Fahrig, 2003). Patches of natural habitat that occur within urban settings also serve to enhance human well-being and contribute to public understanding of the importance for conservation efforts when educational materials or signage are present (Miller and Hobbs, 2002; Alvey, 2006). Indeed, green spaces within a mosaic of urban habitat provide the opportunity for inhabitants to experience an encounter with nature.

Not all green spaces are created equal. They can be relatively contrived, populated by a monoculture of tolerant or non-native species, and therefore of limited interest for conservation or environmental education. Furthermore, well-kept, open parks require intensive maintenance, including frequent mowing and pesticide application, making these habitats unsuitable for a variety of wildlife (Fenn et al., 1998; Ma et al., 2000). In contrast, efforts in some inner-city parks have successfully protected the native flora and fauna while promoting public education. These latter examples gained significant international reputation for scientific research and conservation (e.g. http://www.bgpa.wa.gov.au/kings-park). We are unaware of any comparisons of the ecological and educational benefits associated with these two strategies for maintaining green spaces (a surrogate biota representing a few species versus a relatively natural community). Thus, assessing and promoting biodiversity in patches of natural habitat both within and immediately adjacent to urban areas are of paramount importance. We predict, however, that complex and diverse habitats are more valuable for conservation when compared to green spaces that are intensively maintained to comprise a small and artificial community. Green spaces that accommodate populations of threatened species and offer opportunities to observe free ranging animals have a greater conservation and educational impact (Ballouard et al., 2011).

One way to promote the establishment of green spaces that are themselves environmentally friendly (e.g. require minimal maintenance) is to demonstrate the feasibility of the required management operations, and highlight the success of practical outcomes that follow. This study describes a management strategy applied to forest habitats in a suburban landscape that is designed to promote native snake populations. This study faced a number of challenges. Indeed, the study area is not only visited by thousands of people annually, but is inhabited by snakes, species that usually trigger negative reactions from the public. In addition, the most abundant snake species,

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Vipera aspis, is venomous, further complicating the success of the project. Indeed, recent changes (2007) in French legislation now allow for the killing of this previously-protected snake species; without permits, people may now destroy snakes or complain to local authorities to have them removed. Finally, our study design adopted a management approach that promoted, via tree removal, the growth of large brambles. This type of vegetative landscape contrasts with the widely held public opinion that green spaces should be manicured, easily accessible, and contain large trees that offer ample shaded areas (Lindhagen and Hörnsten, 2000; Tyrväinen et al., 2003). For most people, mature forests better represent nature than dense thickets of thorny shrubs, and consequently these esthetic aspects prevail over the ecological value of forests and green spaces (Jim and Chen, 2006; Gundersen and Frivold, 2008).

Although not measured in this study, public acceptance provided the conceptual framework for the project. Indeed, public acceptance can determine the success or failure of conservation landscape management (Clark et al., 2002; Schenk et al., 2007). Several studies have removed canopy cover to create open habitats suitable for reptile communities have been carried out in remote forest areas where possible conflicts with human interests were limited (Greenberg, 2001; Pike et al., 2011a,b). Transferring this experimental approach to an oft-visited urban park is novel, especially with the intent of increasing populations of animals that typically elicit fear responses from humans (Burghardt et al., 2009). Studies report declines in snake populations worldwide (e.g., Reading et al., 2010) including relatively common species, such as the four taxa that occur in this study region. Because alteration and fragmentation of suitable habitat are the leading causes attributed to global losses of biodiversity (Fahrig, 2003; Opdam and Wascher, 2004), generating suitable habitats could help mitigate declines.

During the past 50 years, the abandonment of traditional farming practices has altered previously-open habitats that were characterized by mosaics of meadows and dense networks of hedgerows (Woodhouse, 2010). Therefore, the management employed in our study partly represents restoration to a historic condition. Our primary objective was to replace closed-canopy forest with shrub habitat in order to bolster snake populations. In temperate climates, removal of closed-canopy forest increases opportunities for thermoregulation in ectothermic reptiles like snakes, and thus enhances physiological processes such as digestion or reproduction (Huey, 1982). Consequently, this management approach is expected to favor colonization of the open patches (Edgar et al., 2010). Here we focus on the dynamics of snake occurrence within four experimentally modified habitats in an urban park used intensively for recreational purposes.

2. Material and methods

2.1. Study site

The study site is situated in western France (47°59′25″N, 0°14′47″E; 50–75 m above sea level; 450 ha) and includes a suburban public forest (350 ha) interspersed with several small meadows and orchards (100 ha). The study site borders the city of Le Mans (~320,000 people), and is fully surrounded by an urban mosaic composed of smaller cities and transportation infrastructure (Fig. 1). The forest is managed for wood production, and is transected by many paths that connect various recreational areas (e.g. jogging and cycling trails, large lawns, playgrounds, an educational farm, and an archery range) that are all part of a major city project led by the local authorities of Le Mans Métropole (www.lemans.fr/). This project, named the Ark of Nature (www.arche-nature.fr/), offers free services to approximately 70,000 visitors annually that participate in the educational activities at the park (e.g. registered schoolchildren), and an additional 500,000 non-registered visitors (e.g. joggers).

Most of the study site comprised a mature closed-canopy forest, and several patches are managed for timber production (~10% of the area is cleared annually). The canopy is nearly continuous and its average height ranges from 15 to 25 m; solar radiation does not easily reach the substrate. The dominant tree species include pines (*Pinus pinaster*; 60% of the forest area), chestnuts (*Castanea sativa*), oaks (*Quercus robur*), with additional species (e.g. *Salix caprea*) more sparsely distributed.

2.2. Experimental treatment of the habitat

We conducted this study from 2006 to 2012 and the habitat manipulation aspect of the project involved two separate phases. First, we removed canopy cover adjacent to several paths, orchards and meadows to create transects of recently opened habitat. Then, we applied different treatment regimes within the transects. Four species of spiny shrubs colonized the open habitats: mostly berry brambles (*Rubus fruticosus*; >80% of occurrence), but also gorse (*Ulex europaeus*), hawthorn (*Crataegus monogyna*), and dog-rose (*Rosa canina*). For simplicity, these bush species are collectively labeled bramble bushes hereafter. All forestry operations were completed in winter months when snakes were not active.

From 2006 to 2008 we established four replicate transects simultaneously in different locations (Fig. 1) in the park via the removal of canopy cover along preexisting paths frequented by park visitors. These transects consisted of open habitat extending 5–10 m in width beyond each path edge. Henceforth, we refer to these four transects created in 2006 as “initial transects.” The total length of all transects (i.e., sum of replicates) increased over time, from ~400 m in 2006, ~2500 m in 2007, to ~3700 m in 2008. Thus, a substantial increase of canopy removal occurred from 2006 to 2007 (6.3×), then a proportionally modest increase occurred from 2007 to 2008 (1.5×). The rate of increase in the length of the transects during 2006–2008 was comparable among transects. We adopted this gradual approach both for logistical reasons, and to increase acceptance by the public. Bramble bushes colonized the opened transects and developed rapidly (annual growth of 1–2 m).

From 2008 to 2012 we initiated phase two of the project where we actively managed segments within each initial transect to evaluate the effect of time on vegetative growth and snake colonization over four years. Based on this approach, we established 16 different experimental areas within the study site:

1) Stable unfavorable habitat (SU): we designated four transects of mature forest not managed during the study to serve as unfavorable habitat controls (total length = 555 m; 15% of total transect length). We never removed canopy in these SU areas.
2) Stable favorable habitat (SF): to prevent closure by fast-growing pioneer trees (e.g. *S. caprea*) in segments of the initial transects, we actively managed bramble bush height to remain below 2 m. We selected and maintained segments (total length = 1665 m; 45%) to remain open over the duration of the study in each of the four initial transects to serve as favorable habitat controls.
3) Transitional habitat from favorable to unfavorable conditions (FU): we selected segments (total length = 555 m; 15%) in each of the four initial transects where we did not actively maintain bramble bushes, thereby allowing for the establishment of pioneer trees and a gradually closing canopy.
4) Transitional habitat from unfavorable to favorable conditions (UF): we selected segments within each of the four initial transects where we removed additional tracts of mature forest (total length = 925 m; 25%) to create newly established areas of open habitat. These segments allowed us to evaluate if snakes rapidly used these newly opened areas. Note that we did not remove a few isolated large trees for esthetic reasons.

2.3. Snake monitoring

We conducted several initial surveys in 2006, and then instituted continual efforts for the duration of the project. Preliminary surveys

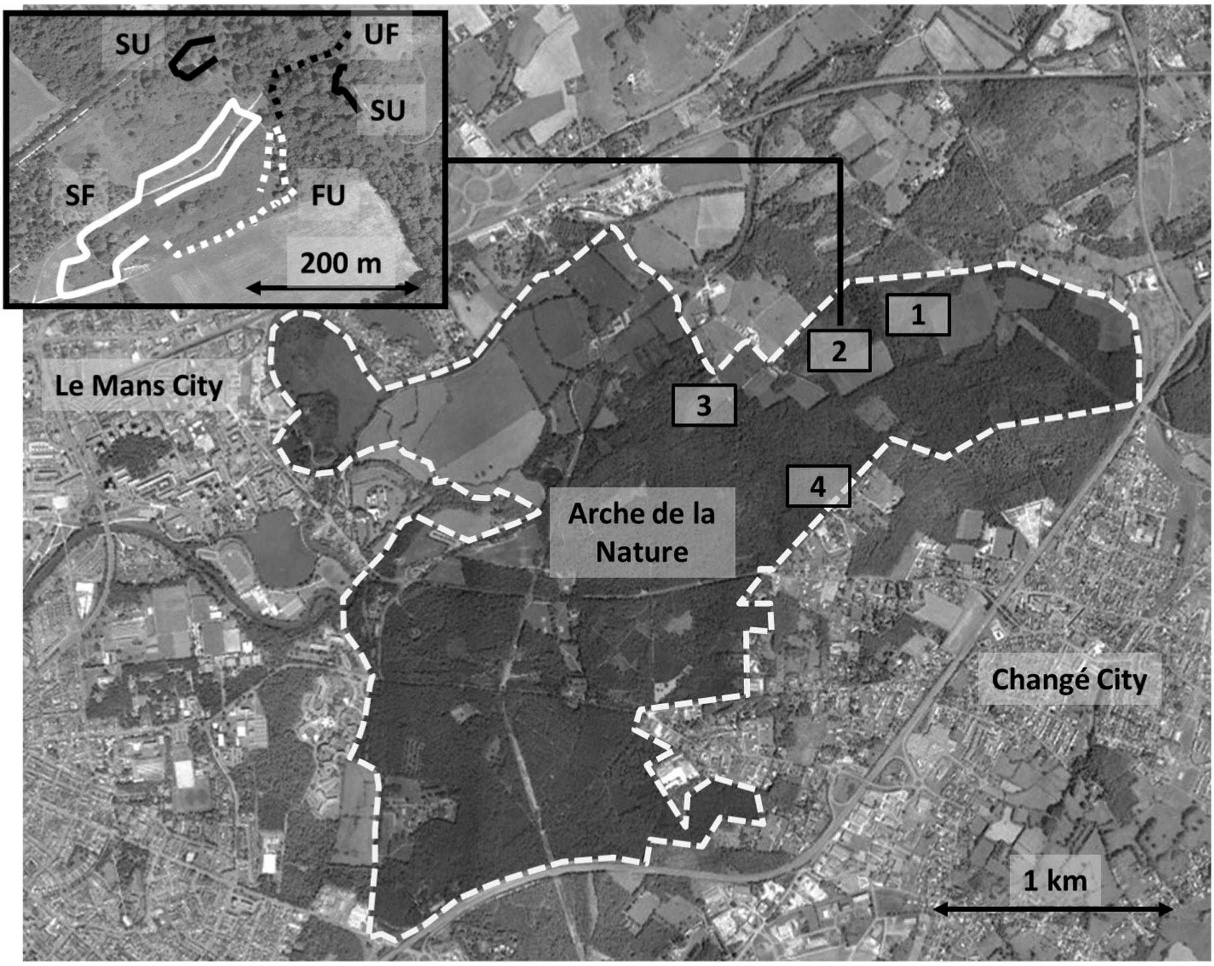

Fig. 1. Study site (extracted from Google earth images). The light-gray dashed line shows that the recreational green park, Ark of Nature, is bound by populated urban areas. Four experimental areas were established (boxes 1–4) where snakes were monitored along transects. The zone 2 is enlarged to provide an example of the segment-transects respectively associated with each of the four managed habitats: closed stable unfavorable (SU, black line); open stable favorable (SF, white line); opening canopy, unfavorable to favorable (UF, black dashed line); closing canopy, favorable to unfavorable (FU, white dashed line). At this scale, meadows and large trees are visible, but not small bushes. Transects were mainly established along paths and forest hedges.

were performed to assess snake occurrence and to obtain a crude index of their abundance within the study area, as such data were lacking. One to three people surveyed the hedges of meadows and forest along the four replicate transects. Following initial survey efforts, we deployed a standard trap system, from 2007 to 2008, consisting of corrugated fibrocement slabs (1.2×0.8 m, N = 76 slabs) placed linearly along each of the four initial transects. The slabs were placed in locations likely to provide shelter, cover and suitable conditions for thermoregulation (e.g. exposed small banks, near logs or thick vegetation; Bonnet et al., 1999; Ballouard et al., 2013b) with a mean interval between slabs of 25 m (range = 10–50 m). Slabs were regularly inspected during the period of snake activity (April–September) by 2–3 people (all slabs were inspected on the same day). Survey efforts varied across years, however, on account of variable availability of personnel: the number of days spent surveying was 33, 55, 57, 70, 59, 86 and 23, respectively, in each year from 2006 to 2012.

Each snake was captured, had its sex determined (visual inspection of tail shape), measured (snout to vent length [SVL], ± 0.5 cm) weighed (body mass, ± 1 g), and marked using a modified version of the scale-clipping technique (Brown and Parker, 1976), and then released at the point of capture. Although the snake species initially observed within the study area each exhibit some unique life-history traits (Vacher and Geniez, 2010), they are all constrained by low temperatures, and thus they should benefit from the thermoregulation opportunities associated with habitat manipulation.

In 2008 (prior to any survey effort for that year), we distributed an additional 126 slabs as follows: 17 slabs in the SU treatment, 41 in the SF treatment, 30 in the FU treatment, and 38 in the UF treatment. Even though a greater number of slabs were placed in the most favorable treatment segments (SF and UF), they were equally distributed among the 16 experimental areas (e.g. 4 to 5 slabs per replicate in the SU treatment, 10 to 11 slabs per replicate in the SF treatment; corresponding to proportionally longer transects in the favorable treatments). Therefore, we structured our analyses on the effect of treatment type.

In September 2011 (four years after the initial application of the experimental treatments), the vegetation was characterized within a 25 m^2 area surrounding each slab. We visually estimated the relative surface area covered by herbaceous layers, bramble bushes, shrubs (coppices and bushes) and trees; and we measured the mean height of trees and shrubs.

2.4. Analyses

2.4.1. Habitats

Habitat variables were not normally distributed (even following transformations); so we compared the values for vegetation surface area among the four treatments using Kruskal–Wallis tests.

2.4.2. Site occupancy analyses

One of our main objectives was to assess if snakes preferentially colonized the different habitat treatments, or simply any type of habitat.

Therefore, we analyzed the number of the snakes detected under the concrete slabs as a proxy for snakes associating with a specific vegetation. Snakes not captured under slabs were not included in these analyses. In practice, when cover objects become available, snakes tend to use them systematically during thermoregulation and they are very rarely detected away from cover (Lelièvre et al., 2010). Surveys performed over time enabled us to build the occupancy history of each slab. We merged consecutive searching-days into a single capture session to limit the inflation of columns in the matrix, thereby reducing the total number of capture sessions from 350 to 36 (6 sessions per year, from 2007 to 2012: 2 in spring [April–May], 2 in early summer [June–July] and 2 in late summer [August–September]; differences in the number of consecutive searching days that were combined into each session occurred because searching effort was lower in late summer). Importantly, this reduction followed the life-history patterns of the snake species studied: 1) spring, emergence, mating, vitellogenesis; 2) early summer, embryo development; 3) and late summer, hatching or birth. For simplicity, we coded the occurrence of a snake under a slab dichotomously: 0 (absent) and 1 (present). Therefore, we ignored the possibility that more than one snake could be observed at a given time. This approach was conservative because the slabs located in favorable sites often sheltered >1 snake (if snakes were present, we observed 1–10 individuals per slab per session). Therefore, detecting an effect of the experimental treatment of the habitat was not influenced by, for example, mating behaviors that tend to aggregate individuals.

For simplicity we focused on only *V. aspis* for site occupancy analyses: 1) this species is the most abundant in the study site; 2) it is the only venomous snake, thus the most problematic and challenging species to promote in anthropogenic areas; and, 3) the results of our site occupancy analyses did not change when all species were included. Indeed, whatever the snake species, individuals were observed more often in open habitats.

Site occupancy analyses enabled us to account for possible confounding variables and for imperfect detectability of snakes. For instance, differing amount of search effort (i.e. resulting from annual variation, or different transect lengths), or climatic conditions can influence the number of snakes captured and bias the probability of detection (p). Instead, site occupancy analyses provide unbiased probabilities of site occupancy (ψ) resulting from colonization (γ) and local extinction (ε) rates (MacKenzie et al., 2002, 2003). Using 6 survey periods per year to examine the impact of habitat treatment over the duration of the study enabled us to implement a robust design (Pollock, 1982; Pollock et al., 1990).

An important assumption of occupancy models is that the monitored population is demographically and geographically closed during secondary capture sessions. To test this assumption we used program CloseTest (Stanley and Burnham, 1999). Because we suspected variation in detection probabilities, and because survey effort is known to influence detectability in snakes (Durso et al., 2011), we used the number of days spent searching for snakes during each secondary capture sessions as a covariate of detection probability. Model selection was based on likelihood ratio tests based on Akaike's Information Criteria (AIC; following MacKenzie et al., 2002, 2003). To test for covariate effects, we used the ANODEV tests, and calculated the proportion of variance explained by covariates as the ratio of deviances of constant, time-dependent and covariate models (Grosbois et al., 2008). There is no goodness-of-fit test for multiseason occupancy models. Therefore, to assess the robustness of our inferences, we checked whether model selection was affected when the overdispersion parameter was set to 2 or 3. Analyses were performed using the program MARK (White and Burnham, 1999). Mean γ values were reported $\pm$ SE in those treatments where the habitat changed over time (UF and FU).

2.4.3. Absolute numbers of snakes

The number of snakes captured was used to illustrate the impact of the experimental treatments on all the species found in the study site. Specific site occupancy analyses were not presented because of the low numbers of individuals in some species (e.g. Aesculapian Snakes, *Zamenis* [*Elaphe*] *longissima*), or because they added no information compared to the population analyses involving vipers. Because this study focused on the impact of forest management on site occupancy (e.g. which habitat type is selected by snakes), we did not take into account captures versus recaptures (e.g. including individual recapture-history into the model to examine displacements). Output from site occupancy analyses poorly describes population trends and there is no surrogate to large sampling effort. Absolute numbers thus provide an additional value by which to gauge the robustness of our conclusions, and are also to better visualize the practical application of habitat management.

2.5. Ethical notes

No individual was mistreated or injured during this study. All procedures were performed in accordance with French guidelines and regulations.

3. Results

3.1. Habitat manipulation

In 2011, four years after initiating the experimental manipulation of the vegetation, important differences were observed among the four transects (Table 1, supplementary material). In closed and unfavorable areas (SU), trees and shrubs were tall (>10 m), and prevented the development of herbaceous layers and of bramble bushes. In areas managed for open habitat since 2006 (SF), small (height < 2 m) and thick bramble bush and herbaceous layers were dominant (e.g. 80% cover). Recently-opened areas (UF, first altered in winter 2007) were relatively similar to the SF areas. Because a few large trees were not removed, UF transects exhibited a greater average tree height compared to SF transects where large trees were very scarce or absent. Finally, the lack of management in the FU areas produced a greater % cover of trees and shrubs (Table 1; even though canopy height was not greater compared to other treatment areas) with a progressive reduction of the bramble bushes. Despite marked contrasts among treatments, the different transects of each habitat were not homogeneous (e.g. few large trees in

Table 1
Comparison of the status of measured vegetation components observed in a 25-m^2 area centered around each slab along four transects in late 2011 (four years after management of habitat). The percentages are reported as means $\pm$ 1 SD, and indicate the proportion of covered surface. Treatments: closed stable unfavorable (SU); open stable favorable (SF); closing canopy, favorable to unfavorable (FU); opening canopy, unfavorable to favorable (UF). H indicates the value of the Kruskal–Wallis test statistic, N = 120 (except N = 66 * and N = 53 **).

Vegetation	SU	SF	FU	UF	H	P
Herbaceous layer (%)	7.4 ± 10.9	32.1 ± 20.1	24.3 ± 18.5	31.1 ± 20.1	29.2	<0.001
Brambles (%)	10.6 ± 11.7	49.6 ± 20.0	36.4 ± 24.6	44.6 ± 19.3	32.5	<0.001
Shrubs (%)	11.7 ± 19.4	11.9 ± 17.3	22.0 ± 27.0	6.8 ± 12.0	5.5	0.136
Trees (%)	70.3 ± 29.8	6.4 ± 11.8	17.3 ± 24.8	17.5 ± 19.6	41.3	<0.001
Scrubs + trees (%)	82.1 ± 21.1	18.3 ± 20.4	39.3 ± 31.8	24.3 ± 21.1	40.9	<0.001
Tree height (m)	8.9 ± 6.0	4.1 ± 2.4	5.7 ± 3.1	5.4 ± 4.2	4.6*	0.198
Shrub height (m)	4.6 ± 5.1	1.6 ± 0.7	2.4 ± 1.2	2.5 ± 1.8	6.4**	0.092

open areas), and this was reflected by the large standard deviations associated with the means (Table 1).

Control transects (SU and SF) did not change over time; forest clearing in 2007 rapidly opened the habitat in the UF transects. The slight closing of the vegetation (not significant) was likely caused by the lack of management in the fourth category of transects (FU), but we acknowledge that more than four years are likely required to allow growing trees to produce a closed canopy.

3.2. Numbers of species and individuals detected

Four species of snakes were observed during the study. A total of 774 snakes were marked (+404 recaptures); vipers accounted for 68% of the observations. Ignoring species, most observations occurred in the open habitat treatments (SF and UF after 2008). During the 2006 initial surveys we observed and captured 126 snakes basking on vegetation: 102 Aspic Vipers (*V. aspis*), 13 Grass Snakes (*Natrix natrix*); and 11 Smooth Snakes (*Coronella austriaca*). Observations increased over time. Aspic Vipers (*V. aspis*) were the most common: 531 individuals were captured and marked (103 in 2006 before using slabs) and 721 observations were recaptures. Grass Snakes (*N. natrix*) and Smooth Snakes (*C. austriaca*) were regularly observed, with 116 marked individuals (+58 recaptures) and 111 marked individuals (+60 recaptures), respectively. Aesculapian Snakes (*Z.* [*Elaphe*] *longissima*) were rarely observed, with 16 marked individuals (+15 recaptures).

3.3. Effect of habitat management on site occupancy

The experimental manipulation of the habitat appeared to influence the presence of snakes under the slabs (Fig. 2). We detected relatively few snakes in closed forest habitat (SU) whereas snakes intensively used open habitat (SF). The opening of habitat (UF) triggered a rapid response: although few individuals were found before treatment, the numbers of captures increased linearly over three years (a 10-fold increase). In the progressively-closing habitat (FU), no clear trend was observed.

The patterns revealed by raw counts might have been influenced by two major sources of heterogeneity: variations in searching effort and the addition of 126 slabs before the 2008 search effort was initiated. Indeed, the number of vipers observed was correlated with the amount of

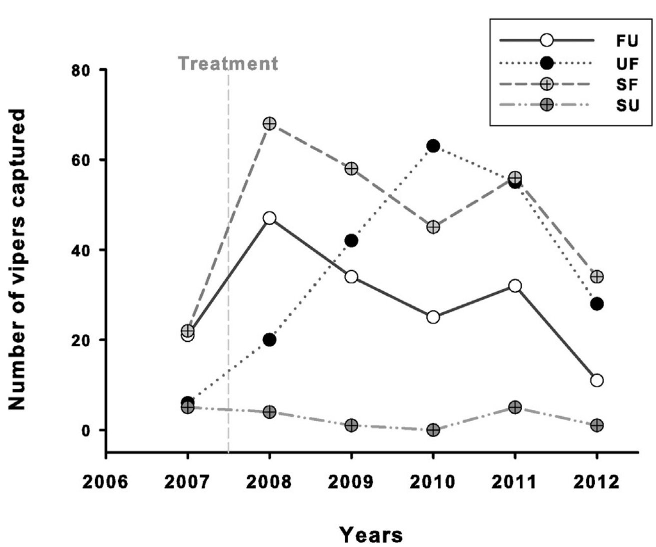

Fig. 2. Number of *Vipera aspis* captured under concrete slabs as a function of year (2007–2012) in each of four managed habitats: closed stable unfavorable (SU); open stable favorable (SF); opening canopy, unfavorable to favorable (UF); closing canopy, favorable to unfavorable (FU). Vertical dashed line (Treatment) indicates the winter during which the four treatments were applied.

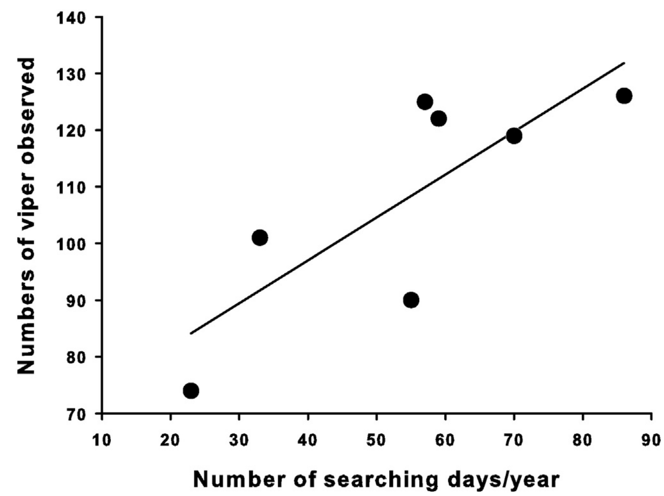

Fig. 3. Correlation between the total number of *Vipera aspis* observed each year (under slabs or basking in the sun) and searching effort ($r = 0.80$, $F_{1,5} = 8.63$, $P = 0.03$).

search effort (Fig. 3), and this might explain some of the interannual variation of captures within some of the treatments (Fig. 2).

The assumption of population closure within secondary capture sessions was met for most years (Table 2). Inspection of closure tests for the second primary period indicated that losses occurred at secondary session 2 (early summer), but no losses or gains were detected during other secondary capture sessions, indicating only a moderate violation of this assumption. Although the relative low number of observations in 2007 could not be taken into account into occupancy analyses (the model is weak with low numbers of observations), thereby removing an initial divergence between open and closed habitats (Fig. 2), model selection suggested that the detectability of vipers varied over time. Detectability was greater in late spring–early summer (Fig. 4a), but this seasonal trend was similar among the four habitat treatments (Table 3). Thus, it was possible to focus on the occupancy probability to compare the effect of habitat management. We detected an effect of capture effort and of its logarithm on detection probability (ANODEV: $F_{1,28} = 13.6$, $p = 0.001$ and $F_{1,28} = 21.8$, $p < 0.0001$, respectively). Variation in detectability was best explained by the logarithm of capture effort ($R^2 = 0.44$) and both were positively related (slope $= 0.89 \pm 0.09$; Fig. 4b). Thus, capture effort was kept as a covariate of detection probability when modeling local extinction and colonization probabilities.

The best supported models suggested differences in the rate of colonization between the four treatments (Table 3). In the top-ranked models, colonization rates were not different between two treatments (UF vs FU) but differed in the other comparisons. There was uncertainty about the effect of treatment on the local extinction rates because the AIC_c values were similar for a model where extinction rate was constant and one where extinction rates varied as a function of treatments. Group-specific estimators of extinction rate suggested that this value was higher in the SU treatment (0.66, 95% CI: 0.15–0.96) compared to other treatments (from 0.07 to 0.22). Thus, we suspect that model selection uncertainty was mainly attributable to a lack of precision in parameter estimates, possibly attributable to a lack of statistical power. All the

Table 2
Tests for population closure based on *Vipera aspis* capture history data. Analyses for closure tests were performed using program CloseTest (Stanley and Burnham, 1999) separately for the secondary sampling periods.

Primary period	χ^2	df	P
1	8.56	7	0.286
2	18.18	7	0.011
3	7.60	6	0.269
4	5.91	7	0.550
5	1.94	2	0.379

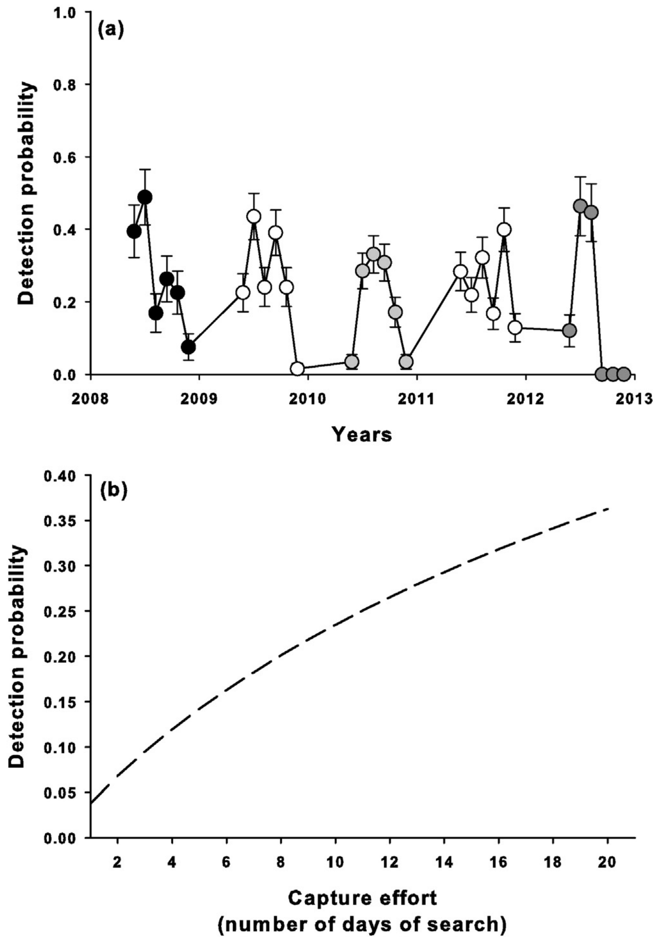

Fig. 4. Probability of detecting *Vipera aspis* over time. a) Estimates are represented in each year (distinguished by changes in shading pattern) based on a sampling effort of 6 surveys/year). The first 2 surveys were performed in spring (April–May), 2 in early summer (June–July) and 2 in late summer (August–September). b) Detection probability estimated as a function of capture effort. Mean values are shown ± 1 SE.

models tested by varying the parameters over time (i.e. to examine possible effect of the experimental treatments) were associated with important differences in AIC values (≫2), and therefore, were considered to be weakly relevant. Model selection remained unchanged when the overdispersion parameter was set to 2 or 3. Consequently, models where the extinction probabilities (ε) and colonization probabilities (γ) were influenced by treatment were the most likely (Fig. 5). The differences between groups for these parameters were not dependent on the year; thus, it was possible to combine ε and γ to estimate ψ across the duration of the study following MacKenzie et al. (2003):

$$\psi t = \psi_{t-1}(1-\varepsilon_{t-1}) + (1-\psi_{t-1})\,\gamma_{t-1}$$

The result provided a synthetic view of the impact of habitat management on the probability that snakes would occur in each habitat. Open habitats were more often occupied by snakes and, more importantly, opening the habitat (UF) triggered an increase in occupancy rate (Fig. 6).

4. Discussion

Whereas open habitats have been acknowledged as being favorable for reptiles (especially squamates from temperate climates; Edgar et al., 2010), an important finding of our study was the improved suitability of habitat for snakes achieved by reducing forest canopy, thus improving thermoregulation opportunities in a cool temperate climate (Greenberg, 2001; Pike et al., 2011a,b). Forest management also promoted the growth of bramble bushes that provide important shelters to the snakes, thereby broadening the application of opening the forest canopy. To our knowledge, the impact of experimental cross-manipulation (i.e. four crossed treatments) of habitat management has not been tested previously. Of equal importance, we have demonstrated the feasibility of this project in an intensively-used peri-urban park.

The experimental opening of the habitat followed by the growth of bramble bushes led to the colonization of these habitats by snakes. Although we did not account for the potential that the four transects were spatially autocorrelated, our results are among the first to quantify colonization rates and are not entirely surprising. Snakes in temperate climates regulate their body temperature via basking, an activity that is easiest to accomplish in open habitats. To enhance thermoregulatory precision, vipers must shuttle between exposed basking sites and cooler shelters. Appropriate refuges are equally important, especially because basking increases predation risk in the four studied species (Bonnet et al., 1999, 2013). The bramble bushes that grew in open and managed areas provided suitable microhabitats not only for the vipers, but also for their prey species (e.g. voles, field mice, lizards; Amo et al., 2007). Overall, our results indicate that forest management can be an efficient mechanism for promoting snake populations, and thus, a major tool to stem the population declines of major predators within this ecosystem.

Raw snake counts for each habitat treatment indicated similar trends compared to the site occupancy analyses (cf. Figs. 2 vs 6), but they differed in terms of statistical robustness of the information available (e.g. absolute numbers better exemplify snake abundance than

Table 3
Comparison of different models for estimating colonization (γ) and local extinction (ε) parameters for *Vipera aspis*. Writing gFU ≠ UF or gFU = UF indicates respectively if different or identical parameters were implemented for each group (g) of habitat treatment (see Fig. 2 and Table 1 heading for explanation of treatment codes). T stands for the year (2008–2012), t is the intra-annual catch session effect, Effort is the capture effort, lnEffort is the logarithm of capture effort and * means interactions. N indicates the number of parameters estimated in the model (initial settings and interactions).

Model	Hypothesis tested	AICc	δ AICc	N	Deviance
ε (g*T) γ (g*T) p(T,t)	No habitat effect on detectability	2445.6	0.0	66	1515.9
ε (.) γ (gFU = UF,gSF ≠ SU) p(lnEffort)	No habitat and year effect on extinction	2508.9	63.3	21	1683.4
ε (gFU ≠ UF,gSF ≠ SU) γ (gUF = FU,gSF ≠ SU) p(lnEffort)	No time effect on extinction	2508.9	63.3	23	1679.1
ε (gFU ≠ UF,gSF = SU) γ (gFU = UF,gSF ≠ SU) p(lnEffort)	No year effect on extinction in transitional areas	2512.5	66.9	22	1684.9
ε (g*T) γ (g) p(lnEffort)	No year effect on colonization	2519.7	74.1	29	1676.9
ε (g*T) γ (gFU = UF,gSF ≠ SU) p(lnEffort)	No habitat effect on colonization in transitional areas	2519.8	74.1	29	1676.9
ε (gFU ≠ UF*T,gSF = SU) γ (gFU = UF,gSF ≠ SU) p(lnEffort)	No habitat effect on extinction in stable areas	2522.8	77.2	24	1690.9
ε (g*T) γ (gFU ≠ UF,gSF = SU) p(lnEffort)	No habitat effect on colonization in stable areas	2529.4	83.8	29	1686.6
ε (g*T) γ (gFU ≠ UF*T,gSF ≠ SU) p(lnEffort)	No year effect on colonization in stable areas	2532.8	87.2	32	1683.3
ε (g*T) γ (gFU ≠ UF,gSF ≠ SU*T) p(lnEffort)	No year effect on colonization in transitional areas	2536.3	90.7	32	1686.8
ε (g*T) γ (g*T) p(lnEffort)	Effect of ln(capture effort) on detectability	2540.9	95.3	38	1677.9
ε (g*T) γ (g*T) p(Effort)	Effect of capture effort on detectability	2572.5	126.8	38	1709.5
ε (g*T) γ (g*T) p(g*T,t)	–	2629.3	183.7	156	1431.8
ε (g*T) γ (g*T) p(.,.)	Constant detectability	2664.5	218.8	37	1803.7

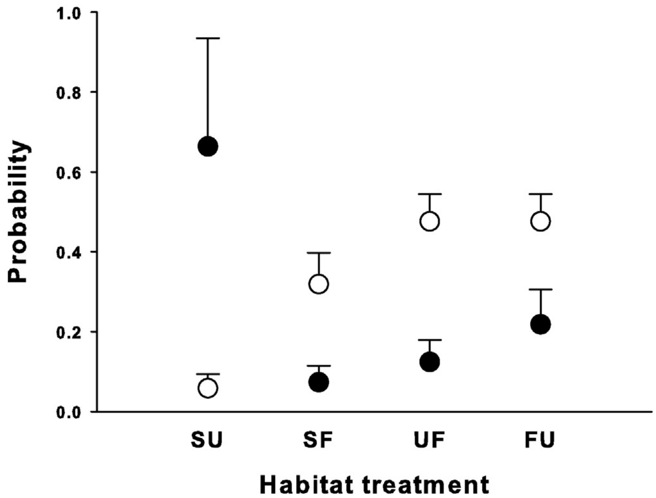

Fig. 5. Estimation of extinction (ε; filled circles) and colonization (γ; open circles) probabilities for *Vipera aspis* in each of the four habitat treatment groups (x-axis): closed stable unfavorable (SU); open stable favorable (SF); opening canopy, unfavorable to favorable (UF); closing canopy, favorable to unfavorable (FU). Mean values are shown + 1 SE.

detection probabilities). The occupancy analyses indicated that field work could be concentrated in several weeks during late spring–early summer, and thus minimize the logistic effort needed for similar projects in the future. These analyses also indicated that it is not necessary to devote equal survey effort across all areas within a study site. Instead, search effort can be biased towards the most favorable habitats without hampering the statistical inferences for the project. Importantly, because we accounted for heterogeneity in detectability, we obtained a dynamic view of the probability of occurrence. For example, the differing responses in the UF versus FU treatments (Fig. 6) show that habitat management must be maintained over time and should be factored into any long term planning.

The relative speed of snake responses to habitat manipulation indicates that many individuals captured in the newly opened areas were already present on our study site (e.g. the now-favorable habitats were colonized by dispersing snakes). Nonetheless, we found many new individuals in the course of the study, including juveniles, suggesting possible population size augmentation. The progressive increase in the snake numbers observed in open areas, combined with the fact that the favorable control areas (SF) did not experience a reduction in mean population size, indicates that the fecundity of adult females already present in the study site might have been positively influenced by food availability and thermal conditions. Although our analyses did not examine these parameters at the individual level, dispersal probabilities, maturity rates and fecundity have shown similarly rapid responses to changes in food availability in other viper populations (Madsen and Shine, 1992; Bonnet et al., 2001) and in other snake species (Shine and Madsen, 1997).

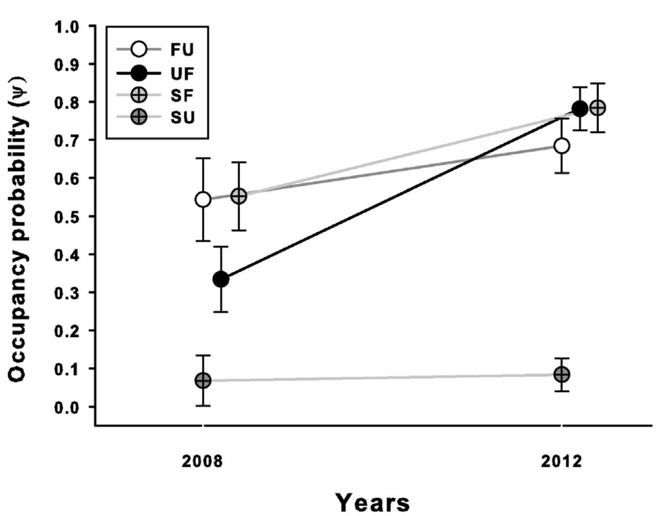

Fig. 6. Changes of the estimated occupancy probabilities (ψ) for *Vipera aspis* in each of the four habitat treatments from 2008 to 2012 (see text for details of calculations; treatment codes as described in Fig. 4). Mean values are shown ± 1 SE.

The duration of our experiment (seven years) was integral to our being able to assess acceptance of our methods by the general public. Providing suitable habitat for vipers, in the form of cutting down trees and promoting bramble bushes, in a frequently visited park might have been deemed incompatible with public use of the park. We preempted any negative perceptions through a combination of on-site outreach efforts, and through public conferences and media events. Different educational operations were conducted with schoolchildren, professional forest managers, firemen, hunters, police authorities and the general public (Ballouard et al., 2012, 2013a). The experiment was featured in local and national newspapers and television programs. In practice, most people questioned were interested in the research, understood the objective of the experiment, and declared a willingness to modify their attitude towards under-appreciated wildlife species. The magnitude of this positive effect was measured in schoolchildren (Ballouard et al., 2012). In addition to the park visitors who registered for pedagogic activities affiliated with our study, the park received another 500,000 patrons annually. These individuals could not easily avoid viewing information about our study (e.g. signs in the parking areas, on the concrete slabs), yet no complaints were registered. Vandalism was limited to very few cases (<10 slabs destroyed or stolen). The overall project cost was relatively low (e.g. <5000€ for logistics; two rangers involved approximately for 1/3 of their working time each year; 2–6 volunteers per year). Thus, the burden to the taxpayer was relatively small.

Attempting to re-establish or favor unpopular organisms does not conform to the flagship species paradigm, but educational progress requires changing public attitudes towards underappreciated species (Andelman and Fagan, 2000; Possingham et al., 2002; Veríssimo et al., 2013). We have demonstrated that a conservation operation that simultaneously educates the public can be conducted using non-charismatic species (snakes are among the most feared animals) in large urban green spaces. The validity and utility of the flagship concept combined with the focus on most threatened species is still under strong debate (Possingham et al., 2002; Veríssimo et al., 2013). Further studies on common and non-charismatic species are necessary to gauge the impact of conservation programs that can be conducted at field sites frequented by human populations, as opposed to those performed in restricted or remote sites where the likelihood of interacting with the public is low (Hungerford and Volk, 1990; Ferraro and Pattanayak, 2006). Finally, our research has provided a vehicle for improving the perception of disliked species (e.g. bramble bushes and snakes) among a public that already desires to protect loveable organisms.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.11.001.

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