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Effects of habitat management for small game species on bat activity in three French Mediterranean scrublands

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This study examines the impact of habitat management on the seasonal and spatial activities of bat species in Mediterranean scrublands of southern France. Three study sites, presenting managed and unmanaged scrublands, were sampled by acoustic recording to assess their ecological potential for bat conservation. General linear mixed models (GLMMs) were used to identify the key factors driving variation in activity patterns of these areas. A total of 16 bat species were recorded, and no significant differences in taxonomic composition were found between managed and unmanaged areas. Bats have an opportunistic tendency to explore different habitats over long distances. In addition to the strong seasonal dynamics observed in most species, we found evidence of a shift in activity rhythms suggesting species adaptation to seasonal thermal variations and prey availability. In this study, the impact of managed areas on activity patterns depends on the functional traits of each species. Level of activity differed considerably from one species to another, suggesting that the 'management' effect is not the only ecological parameter involved in conditioning bats' preferred occupancy patterns.

Key words: acoustic, species richness, season, habitat, conservation, France

INTRODUCTION

The order Chiroptera is a functional and diversified group of nocturnal flying mammal species occupying various trophic levels. Bats provide many ecosystem services, including reducing crop damage by regulating pest insects (Kunz *et al*., 2011; McCracken *et al*., 2012). In the temperate areas they are mainly insectivorous and rely on the diversity and abundance of insects (McCracken *et al*., 2012; Smirnov and Vekhnik, 2014; Russo *et al*., 2018; Vesterinen *et al*., 2018). They can be useful bioindicators because they are sensitive to the effects of anthropogenic pressures and mitigation actions on biodiversity (Jones *et al*., 2009; Van der Meij *et al*., 2015; O'Shea *et al*., 2016; Voigt and Kingston, 2016; Russo *et al*., 2021). Bats are threatened by forest management, intensive agriculture practices and increased fire frequency, consequences of global changes (Voigt and Kingston, 2016). Another major threat is the fragmentation of landscapes by human infrastructures such as wind turbines, alteration of movement corridors, disappearance and degradation of foraging areas (Hutson *et al*., 2001; Russo and Jones, 2003; Millon *et al*., 2015; Claireau *et al*., 2019; Froidevaux *et al*., 2021). On the opposite, some forest management and ecological agricultural practices benefit bat activity and species assemblages (Guldin *et al*., 2007; Bender *et al*., 2015; Puig-Montserrat *et al*., 2015). In Europe, some bat populations have benefited from forest management when it increases the vertical structure of the vegetation (Obrist *et al*., 2011), decreases structural clutter under the forest canopy (Berthinussen *et al*., 2014), and/or creates some openings, including water ponds (Lisón and Calvo, 2011). But sometimes, forest practices have a mixed impact on bat activity and species richness (Russo *et al*., 2010, 2016). In most cases, bat activity is greater in natural areas than in farmlands, and conservation of patches of natural or semi-natural habitat is important in intensive agricultural landscapes (Olimpi and Philpott, 2018).

Traditional landscapes of the Mediterranean basin are of great ecological value as they maintain

a high level of biological diversity in one of the world's biodiversity hotspots (Myers *et al*., 2000). However, this area, mostly in its European part, is highly concerned by a progressive abandonment of agricultural activity concealing the half-open Mediterranean landscapes of the past (Blondel and Aronson, 1999). This closure process can be a major threat to the survival of some bat species, by dramatically reducing their foraging areas and erase ecological corridors from the landscape (Safi and Kerth, 2004; Rainho, 2007). Even some of the most common species are currently experiencing population declines in the Mediterranean area according to the IUCN (Temple and Cuttelod, 2009).

In southern France, there are 31 migratory and sedentary bat species according to Arthur and Lemaire (2015). These include 16 of the 19 priority species for conservation listed in the National Action Plan 2016–2025 (Tapiero, 2017). These species are also listed in the regional action plans including the Mediterranean area (Bareille *et al*., 2018; Dentz *et al*., 2018) due to the regression of populations induced by the loss of habitats and the degradation of Mediterranean ecosystems. One of the main changes is the strong expansion of scrubland following the progressive drop of traditional agricultural practices that shaped the landscapes (Sirami *et al*., 2010). Scrubland expansion is recognized as a major driver of biodiversity loss in Mediterranean landscapes (Sirami *et al*., 2008; Vimal *et al*., 2017), including small game species (Delibes-Mateos *et al*., 2008; Ferreira *et al*., 2014). In order to favour the maintenance of these species, game managers employ various management devices that increase their habitat suitability and potentially the whole biodiversity (Arroyo and Beja, 2002). The effect of scrubland opening by game managers on other animal species has so far received little attention in the French Mediterranean region, despite possible conservation value (Martínez-Padilla *et al*., 2002). So, the impact of such management on bat assemblage and species activity has not been studied yet. This was the topic of our study which is part of a broader project aiming to evaluate the ecological effects of habitat management for small game species on various animal groups. We hypothesized (i) a higher bat species richness and (ii) a higher level of activity in managed areas (MA) when compared to unmanaged areas (UMA) of scrublands, according to the idea that MA are attractive for a larger number and variety of insects than are UMA. For testing these hypotheses, we recorded seasonal overnight bat echolocation calls in three 30-hectare scrublands of southern France.

MATERIALS AND METHODS

Study Sites

The three study sites belong to the large ecological region (GRECO) 'Mediterranean' (IGN, 2013), and thus share the climatic characteristics of this region, namely hot and dry summers (mean seasonal ca. 22°C), mild and wet winters (mean seasonal precipitation ± 800 mm). These three sites are mainly covered by scrublands (Fig. 1).

To prevent the decline of red-legged partridge (*Alectoris rufa*) and wild rabbit (*Oryctolagus cuniculus*) populations, game managers implement habitat management in 30 to 100 ha scrubland areas. This management includes restoring a mosaic environment by mechanical shredding, planting crops for wildlife, provisioning water bodies and sometimes, supplying additional cereals.

Bourg-Saint-Andéol (44°22'24"N, 4°38'39"E) is located in the vicinity of the Ardèche canyon and the Rhône valley. This area is covered by a succession of meso-Mediterranean holm oak (*Quercus ilex*) series to supra-Mediterranean vegetation (*Quercus pubescens* series, *Buxus sempervirens* coppice, matorrals, ...). In the MA, game managers maintain an impressive mesh of large linear openings by mechanical shredding and water retention via artificial ponds. There are also old ruins (dry stone walls, small stone shelters named capitelles) resulting from a long pastoral activity.

Lançon-Provence (43°35'36"N, 5°07'43"E) is located near to the brackish water lagoon named 'Etang de Berre', on the Fare mountain range near the Durance valley. The xeric landscape is made up of low scrubland (< 1.5 m) with kermes oaks (*Quercus coccifera*) and rosemary trees (*Salvia rosmarinus*), Ibero-Mediterranean limestone cliffs and rocky escarpments. The study site is highly vulnerable to fire and access is restricted during the summer. Several management practices (water ponds, artisanal feed hopper, crops for wildlife, opening of scrubland by mechanical shredding) are regularly achieved by game managers in the MA.

Montpeyroux (43°41'46"N, 3°30'25"E) is located on the foothills of the Cevennes, under the Mont Saint-Baudille at the extreme south-west of the southern slope of the Seranne. It includes vast limestone hills, covered by scrublands of *Quercus ilex* and various xeric species of bushes. The site is partly very closed with dense vegetation of *Quercus coccifera* and *Quercus ilex* trees, and partly made up of a series of loose rocky plots and lapiaz with a scattered vegetation. The management includes mechanical shredding of some parts of the scrubland and a few water holes and artisanal feed hoppers.

Data Collection

Bat acoustic activity was recorded simultaneously at different fixed points of each area (MA/UMA) of the three study sites during each season (spring, summer, autumn) in 2021 and 2022 (Table 1). We would like to highlight that our study is comparative, and we see no reason to believe that there would be variations in the likelihood of correct classification between MA and UMA at each site. Fixed points were sampled randomly on two consecutive full nights, twice per season at each study site
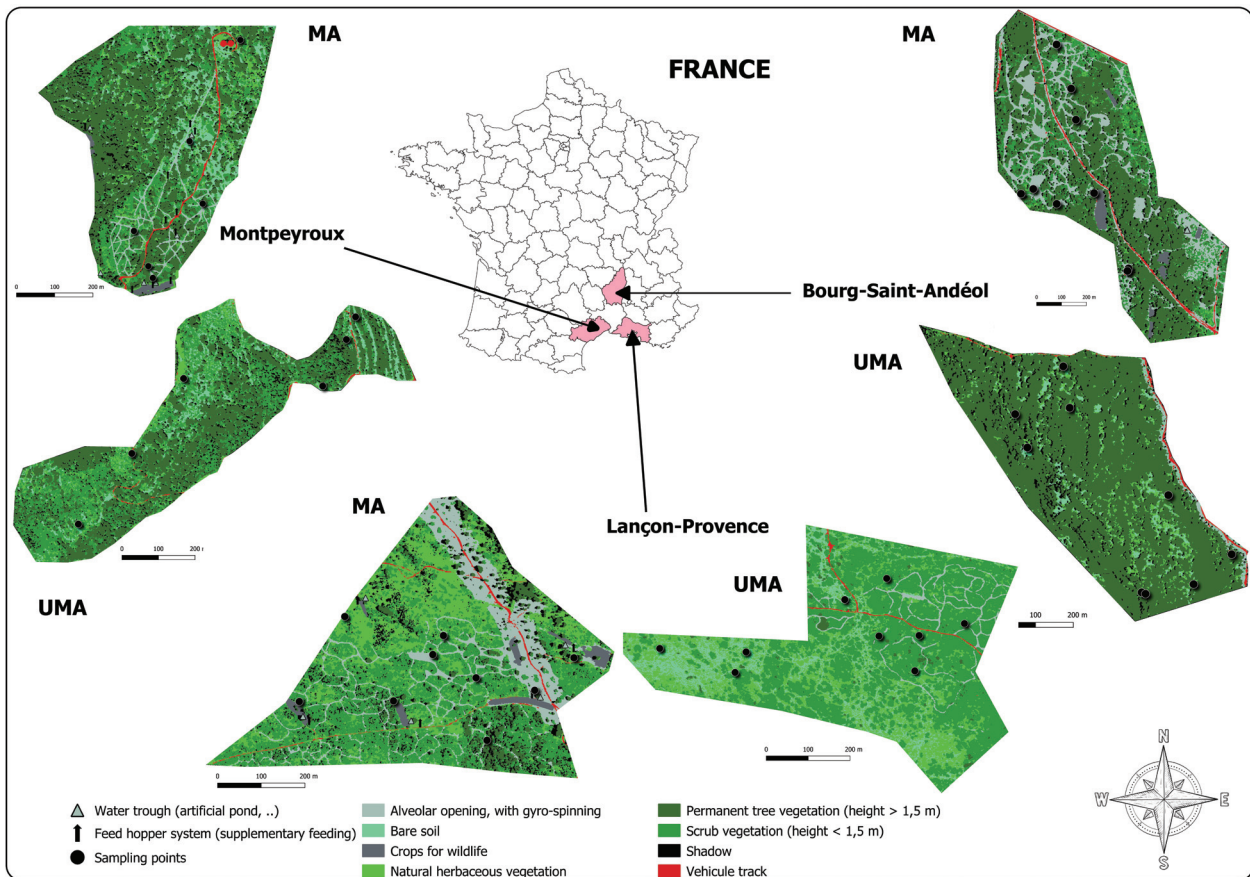
Fig. 1. Location of 46 fixed bat sampling points in three managed (MA) and unmanaged (UMA) scrublands of southern France: Bourg-Saint-Andéol [BSA; Ardèche, (BSA = 16)], Lançon-Provence [LP; Bouches-du-Rhône, (MP = 18)], and Montpeyroux [MP; Hérault, (MP = 12)]. MA BSA (44°23'06''N, 4°36'35''E), UMA BSA (44°22'27''N, 4°36'35''E), MA LP (43°34'35''N, 5°10'17''E), UMA LP (43°34'35''N, 5°10'17''E), MA MP (43°42'09''N, 3°31'27''E), UMA MP (43°42'50''N, 3° 30'52''E)

when weather conditions were favourable, i.e. no rain and wind under 30 km/h. The method was repeated in 2021 and 2022. A total of 46 nights were simultaneously sampled in both MA and UMA: 16 at BSA, 18 at LP and 12 at MP. During these surveys, poor weather conditions often disrupted sampling in MP. Each recording device consisted of an automatic echolocation call detector (BATLOGGER A+, Elekon, Switzerland) using a microphone (Elekon LG black ultrasonic microphone) that captures the high/low frequency sonar recorded calls emitted by bats when they are commuting or foraging. This method avoids the operator's presence in the field during the night and relies exclusively on the recording performance of the devices (Adams et al., 2012). Bat detectors were scheduled to turn on 30 minutes before sunset and turn off 30 minutes after sunrise. To limit interference with the vegetation, the microphone was set up a few centimetres from the vegetation and the canopy at the end of a pole, perpendicular to the axis of a trunk, usually about 2.5 m above the ground, as close as possible to an opening. The recordings were analysed using the licenses of SonoChiro® professional V5 (www.biotope.fr/fr/innovation/sonochiro) and Kaleidoscope® professional (www.wildlifeacoustics.com) sound analysis software. Following Haquart (2013) Sono-Chiro® classification process was preferred as it assigns with some probability each recorded sequence to a bat species or group of species. To overcome classification challenges, a bat

call expert for the French Mediterranean area AH provided reference recordings from sequences recorded in the three sites. Then, assignations by Sonochiro® were validated when the probability score was at least five. For lower probabilities, recordings were manually checked by the expert (see Supplementary Material). Kaleidoscope® professional software was used as a tool for independent manual checking of the original species groups assigned by SonoChiro®, using the reference sound resources of Barataud (2020), the shape and several parameters of calls such parameters as start frequency, end frequency, maximum energy frequency, pulse duration and pulse interval (Russo and Jones, 2002; Papadatou et al., 2008; Haquart, 2016; Russ, 2021). Due to foliage rubbing affecting the quality of recordings, some acoustic sequences could not be identified at the species level, and were excluded for further analyses.

TABLE 1. Seasonal sampling of bat activity in three scrublands of southern France

Season	BSA	LP	MP
Spring	1 * 2 nights	3 * 2 nights	3 * 2 nights
Summer	4 * 2 nights	2 * 2 nights	1 * 2 nights
Autumn	3 * 2 nights	4 * 2 nights	2 * 2 nights
Total	16 nights	18 nights	12 nights

Data Analyses

In order to evaluate the exhaustiveness of the recorded assemblages in each site rarefaction accumulation curves were calculated using the specaccum function (method = random") in the 'vegan' package. The sampling exhaustiveness is measured as the ratio between the maximum measured species richness and the maximum estimated species richness (Gotelli and Colwell, 2001). Difference of seasonal species richness between MA and UMA of the three sites was assessed using χ^2 tests.

Bat activity was measured using the acoustic activity index (AI) which is calculated by summing the number of one-minute time block for which the species was detected as being present (Miller, 2001). Dividing AI by the length of the night provides an hourly activity index (AIh) that allows comparisons among sites and seasons, and between MA and UMA. Such calculation was performed for measuring the whole bat activity, and each bat species activity for species recorded more than 100 minutes during the whole field campaigns.

To assess the sources of variation of bat activity, we built general linear mixed models (GLMMs) using AIh as response variable and site, area and season, and every interaction, as dependent variables. Fitted zero-truncated negative binomial GLMMs were performed with R (ver. 4.2.3) using the 'glmmTMB' (ver. 1.1.7) package (Bolker, 2023). The suggested error structure model is adapted to count data, where the response variable does not contain a zero value and when there is evidence of overdispersion (Zuur *et al*., 2009). The parameters of the model's distribution are estimated by the maximum likelihood. Candidate models were ranked according to the corrected Akaike information criterion (AICc), Akaike weights (AICcWt), and the 'best' model (i.e., with the lowest AICc and highter AICcWt) examined in detail with a type ANOVA associated with a χ^2 Wald test. In candidate models, we also included as random effects covariables year, julian day and hour of seasonal night surveyed. The size of the effects is translated by the coefficients of the selected GLMM by the ratio of logarithms of group means of tested covariates and their associated 95 % confidence intervals. They were summarized in a table with 'GGally', 'gtsummary' and 'ggstats' packages (Daniel *et al*., 2021; Larmarange, 2023). Ratio of logarithms were used to quantify and to compare the effects incorporated in the selected model on variation bat activity.

RESULTS

Bat activity was recorded during 5,475 minutes in the three sites and the two years of sampling. A total of 16 species were identified (Table 2). The eight most active species were: *Pipistrellus pipistrellus*, *P. kuhlii*, *P. nathusii*, *Hypsugo savii*, *Pipistrellus pygmaeus*, *Miniopterus schreibersii*, *Rhinolophus hipposideros*, and *Tadarida teniotis*. These species were recorded at all three sites in both MA and UMA. The eight less active species were: *Nyctalus leisleri*, *Plecotus austriacus*, *Eptesicus serotinus*, *Myotis emarginatus*, *Rhinolophus ferrumequinum*, *Myotis daubentonii*, *M. bechsteinii*, and *M. capaccinii*, the three last ones being recorded at one site only.

We recorded a representative sampling of the bat assemblage in each area (MA and UMA) of each study site (Fig. 2 and Table 3). The exhaustiveness of bat species richness in MAs and UMAs was around 88%. The species richness was lower at LP than at the two other sites, and lower in spring at BSA than in summer and autumn (Table 4), however no difference among areas and seasons was significant according to χ^2 tests ($\chi^2 = 0.108$, *d.f.* = 2, $P > 0.90$; $\chi^2 = 3.694$, *d.f.* = 4, $P > 0.25$).

Bat Activity

The key factors contributing most significantly to changes in bat activity were a three-way interaction area * season * site (Table 5 and Supplementary Table S1; truncated negative binomial GLMM, AICwt = 1, $\chi^2 = 16.95$, $P < 0.001$). The model highlights distinct patterns of bat activity between MA and UMA in the three study sites, with seasonal variations (Supplementary Table S1). The highest activity (AIh) was recorded in summer at all sites (Table 6). However, the seasonal patterns of bat activity differed from site to site, with a very high summer activity at BSA. Bats were more active in the MA at BSA, in spring only at LP and in the UMA of MP.

Six of the most frequently recorded bat species were more active in MAs than in UMAs (Fig. 3). The fitted GLMMs selected the area * season interaction and site effects for the most active one, *P. pipistrellus* (Supplementary Table S2). This species was very active in autumn in the UMA of MP, in summer in the MA of BSA (Table 6). For *P. kuhlii*, the triple interaction area * season * site was selected; this pipistrelle was the most active bat at LP in all seasons and very active in summer only at BSA and poorly active at MP in autumn, the area effect varied among seasons and sites. Then, models selected the interaction area * season for four species: *P. nathusii*, *H. savii*, *P. pygmaeus* and *R. hipposideros*. *Pipistrellus nathusii* was mostly recorded in summer in MA at BSA and in UMA at LP. *H. savii* was mainly active in summer in MA of BSA. *Pipistrellus pygmaeus* was detected at all sites but mainly active in UMAs during summer and conversely in autumn in MAs of LP and MP. *Rhinolophus hipposideros* was absent at LP and during spring at BSA, while it was very active in the MA of MP in spring. According to the selection of the variables site and area, *M. schreibersii* was more active at MP than at the two other sites and in MAs than in UMAs. The models failed to summarize the activity

TABLE 2. Bat activity per species in three managed (MA) and unmanaged (UMA) areas of scrublands in southern France. (A) Activity index (number of positive minutes) of recording activity per site, area and season. AIh: number of positive minutes per night hour. Seasons: Spr — Spring, Sum — Summer, Aut — Autumn; The French IUCN conservation status is given for each species: LC — Least Concern, NT — Near Threatened, VU — Vulnerable; Species: Pippip — *Pipistrellus pipistrellus*, Pipkuh — *P. kuhlii*, Pipnat — *P. nathusii*, Hypsav — *Hypsugo savii*, Pippyg — *P. pygmaeus*, Minsch — *Miniopterus schreibersii*, Rhihip — *Rhinolophus hipposideros*, Tadten — *Tadarida teniotis*, Nyclei — *Nyctalus leisleri*, Pleaus — *Plecotus austriacus*, Eptser — *Eptesicus serotinus*, Myoema — *Myotis emarginatus*, Rhifer — *Rhinolophus ferrumequinum*, Myodau — *Myotis daubentonii*, Myobec — *M. bechsteinii*, Myocap — *M. capaccinii*

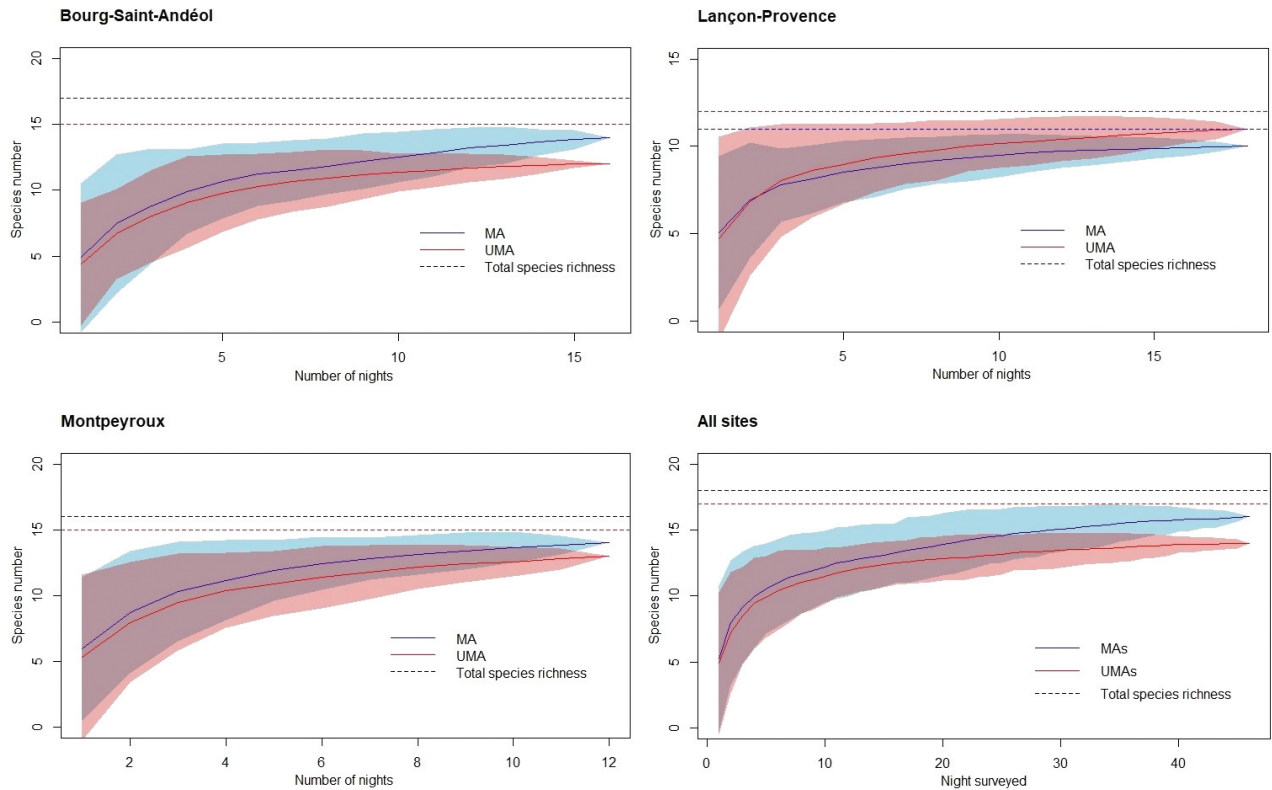| Bat species	Bourg-Saint-Andéol MA			Bourg-Saint-Andéol UMA			Lançon-Provence MA			Lançon-Provence UMA			Montpeyroux MA			Montpeyroux UMA			Total AI
	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	
Pippip (NT)	21	212	129	0	136	23	15	6	21	2	10	68	126	37	246	57	103	352	1,564
Pipkuh (LC)	3	153	4	3	138	8	96	176	169	67	220	190	19	72	4	61	54	16	1,453
Pipnat (NT)	0	143	8	0	64	4	16	50	41	6	42	291	27	12	11	32	23	32	802
Hypsav (LC)	2	194	4	3	72	9	3	24	5	6	26	37	32	13	3	4	21	9	467
Pippyg (LC)	4	26	7	0	27	8	3	6	63	2	27	48	6	6	77	5	26	44	385
Minsch (VU)	0	5	45	0	3	8	4	2	129	0	2	25	0	7	33	0	8	10	281
Rhihip (LC)	0	22	14	0	0	5	0	0	0	0	0	0	88	11	4	23	12	13	192
Tadten (NT)	3	25	29	0	0	17	0	18	3	0	21	12	11	0	7	3	0	12	161
Nyclei (NT)	0	4	11	0	1	3	0	7	9	3	17	4	6	2	6	0	0	7	80
Pleaus (LC)	0	0	13	1	1	9	0	0	4	0	0	6	0	0	4	5	0	7	50
Eptser (NT)	0	0	0	0	0	0	0	1	1	0	1	1	0	5	0	0	4	0	13
Myoema (LC)	0	1	0	0	0	0	0	0	0	0	2	0	0	3	2	0	0	2	10
Rhifer (LC)	0	0	1	0	1	2	0	0	0	0	0	0	0	1	0	1	2	0	8
Myodau (LC)	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Myobec (NT)	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Myocap (NT)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Seasonal AI	33	790	265	7	445	96	137	290	445	86	368	682	317	169	397	191	253	504	
AIh	1.65	10.97	3.14	0.35	6.18	1.14	2.20	8.05	3.70	1.43	10.22	5.67	5.28	9.38	6.61	3.18	14.05	8.40	
AI / area type		1,088			548			872			1,136			883			948		

FIG. 2. Species accumulation curves of bat species in managed (MA) and unmanaged (UMA) areas using the R package 'vegan'. Bourg-Saint-Andéol (16 sampling nights), Lançon-Provence (18 sampling nights), Montpeyroux (12 sampling nights) and all sites (46 sampling nights)

pattern of *T. teniotis*, possibly due to the numerous lacks of season and/or site recordings in both MAs and UMAs.

DISCUSSION

Sampling Conditions and Efforts

Bats were recorded in the three scrublands of southern France from spring to autumn, namely along their most active period in the Mediterranean region. Thus, the extent of the minimum survey effort required to robustly estimate bat richness was respected, taking care to account for the diverse factors of variation that are identified in the published literature (Fischer *et al*., 2009): such that prey resource availability (Murray *et al*., 2001; Fischer *et al*., 2009),

weather (Erickson and West, 2002), seasonality (Russ *et al*., 2003), the habitat (Vaughan *et al*., 1997; Russo and Jones, 2003), and detection materials used (Ahlén and Baagøe, 1999). We can rule out problems of spatial and temporal variance in the comparative study, since the devices were installed at the same time, in the same site, in the same type of habitat and for the same duration. This equipment has allowed for reliable assessment of species assemblage and quantification of bat activity in MA and UMA.

The asymptote of bat richness was reached after 20 sampling nights distributed along the seasons, which is comparable with previous surveys in the same area and more widely in France (Haquart, 2013; Dubos *et al*., 2021). However, more than 45 nights could be required to detect the rarest species, often those of greatest conservation concern (Skalak

TABLE 3. Species inventory exhaustiveness indicator for each managed (MA) and unmanaged (UMA) area of three scrublands of southern France, and for the three sites

Area	Bourg-Saint-Andéol		Lançon-Provence		Montpeyroux		All sites	
	MA	UMA	MA	UMA	MA	UMA	MAs	UMAs
Recorded species richness	14	13	10	11	14	13	16	15
Calculated species richness	17	15	11	12	16	15	18	17
Exhaustiveness (%)	82.4	86.6	90.9	91.7	87.5	86.6	88.9	88.2

TABLE 4. Species richness per site, area and season. Seasons: Spr — Spring, Sum — Summer, Aut — Autumn

Bat species	Bourg-Saint-Andéol MA			Bourg-Saint-Andéol UMA			Lançon-Provence MA			Lançon-Provence UMA			Montpeyroux MA			Montpeyroux UMA		
	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut
Sites		14						11						14				
Spring		6						7						11				
Summer		14						10						11				
Autumn		11						10						11				
Areas		14			13			10			11			14			13	
All Seasons	5	12	11	3	11	11	6	9	10	6	10	10	9	11	11	9	9	11

et al., 2012). This seems to be the case in our study, as we failed to record at least three priority species of the French action plan (Tapiero, 2017) living in the area: *Rhinolophus euryale*, *Nyctalus noctula* and *Myotis blythii* (Groupe Chiroptères Rhône-Alpes, 2014; LPO *et al.*, 2016). The absence of the noctule bat is surprising as this species, which emits loud echolocation calls, forages mostly in the open space (Lindecke *et al.*, 2023) and possibly over the sampled scrublands. For the two cave-dwelling bats, the lack of recording could be linked to the unfavourable foraging habitat coupled to low intensity echolocation calls, our results illustrating the low detection of bats of genera *Rhinolophus* and *Myotis*.

Bat Richness

A total of 16 bat species were detected during the field surveys, including mainly open space and edge foragers: *T. teniotis*, *M. schreibersii*, *E. serotinus*, *N. leisleri*, *H. savii*, *P. kuhlii*, *P. nathusii*, *P. pipistrellus*, and on a lesser extent *P. pygmaeus* (Dietz *et al.*, 2007). Those species were also the most often recorded in the three sites and along the three seasons in both MA and UMA. Two species are over water foragers, *M. daubentonii* and *M. capacinii*, whereas *R. ferrumequinum*, *R. hipposideros*, *P. austriacus*, *M. bechsteinii* and *M. emarginatus* are known to forage close to the vegetation (Dietz *et al.*, 2007). These species were also the least recorded presumably due their low intensity echolocation calls (Barataud, 2020). As a consequence, the effect of the habitat opening for small game species could not be tested on this guild, except on *R. hipposideros* which was quite active at two sites.

Apart from the priority species already mentioned, this list lacks some species which are not easily detectable (Barclay, 1999; Jaberg and Guisan,

TABLE 5. Statistics from the model averaging procedure based on General Linear Mixed Models, describing the seasonal bat activity patterns in managed and unmanaged areas of three scrublands in southern France. AIh: night hourly activity index per bat species; offset included number of nights surveyed (logit). Model ranking is based on differences in the corrected Akaike's Information Criterion (ΔAICc) and Akaike weights (AICcWt), K refers to the number of parameters. Candidate model in bold is selected for analysis

Models	K	AICc	ΔAICc	AICcWt
Fixed covariables(X)				
AIh ~ area * season * site + offset	**19**	**5773.19**	**0.00**	**1**
AIh ~ area + season * site + offset	11	5798.39	25.20	0
AIh ~ area + site * season + offset	11	5798.39	25.20	0
AIh ~ area * site + season + offset	9	5881.82	108.63	0
AIh ~ area * season + site + offset	9	5885.11	111.92	0
AIh ~ area + season + site + offset	7	5886.91	113.72	0
AIh ~ area * season + offset	7	5900.26	127.07	0
AIh ~ season + offset	4	5900.26	127.41	0
AIh ~ area + season + offset	5	5902.55	129.37	0
AIh ~ 1 + offset	2	5913.04	139.85	0
Mixed covariables				
AIh ~ X + (Year/hour) + julian day	**22**	**5661.62**	**0.00**	**1**
AIh ~ X + hour + julian day	21	5682.72	19.05	0
AIh ~ X + hour + Year + julian day	22	5683.30	19.62	0
AIh ~ X + Year + julian day	21	5696.47	32.79	0
AIh ~ X + julian day	20	5698.65	34.98	0

TABLE 6. Seasonal hourly activity indices (AIh) per night for the main eight bat species in three managed (MA) and unmanaged (UMA) areas of scrublands in southern France. (-) indicates an absent species. Acronyms of bat species are given in Table 2

Area and season	Total bats activity	Species							
		Pippip	Pipkuh	Pipnat	Hypsav	Pippyg	Minsch	Rhihip	Tadten
Bourg-Saint-Andéol									
spring	*1.95*	*1.05*	*0.30*	–	*0.25*	*0.20*	–	–	*0.15*
MA	1.65	1.05	0.15	–	0.10	0.20	–	–	0.15
UMA	0.30	–	0.15	–	0.15	–	–	–	–
summer	*67.78*	*19.34*	*16.17*	*11.50*	*14.78*	*2.94*	*0.44*	*1.22*	*1.39*
MA	43.33	11.78	8.50	7.94	10.78	1.44	0.28	1.22	1.39
UMA	17.65	7.56	7.67	3.56	4.00	1.50	0.17	–	–
autumn	*11.52*	*5.43*	*0.43*	*0.43*	*0.46*	*0.54*	*1.90*	*0.68*	*1.65*
MA	8.58	4.61	0.14	0.29	0.14	0.25	1.61	0.50	1.04
UMA	2.94	0.82	0.29	0.14	0.32	0.29	0.29	0.18	0.61
Lançon-Provence									
spring	*11.00*	*0.85*	*8.15*	*1.10*	*0.45*	*0.25*	*0.20*	–	–
MA	6.85	0.75	4.80	0.80	0.15	0.15	0.20	–	–
UMA	4.15	0.10	3.35	0.30	0.30	0.10	–	–	–
summer	*34.99*	*0.89*	*22.00*	*5.11*	*2.77*	*1.83*	*0.22*	–	*2.17*
MA	15.66	0.33	9.78	2.78	1.33	0.33	0.11	–	1.00
UMA	19.33	0.56	12.22	2.33	1.44	1.50	0.11	–	1.17
autumn	*36.73*	*2.97*	*11.96*	*11.07*	*1.40*	*3.70*	*5.13*	–	*0.50*
MA	14.37	0.70	5.63	1.37	0.17	2.10	4.30	–	0.10
UMA	22.36	2.27	6.33	9.70	1.23	1.60	0.83	–	0.40
Montpeyroux									
spring	*24.70*	*9.15*	*4.00*	*2.95*	*1.80*	*0.55*	–	*5.55*	*0.70*
MA	15.45	6.30	0.95	1.35	1.60	0.30	–	4.40	0.55
UMA	9.25	2.85	3.05	1.60	0.20	0.25	–	1.15	0.15
summer	*22.50*	*7.78*	*7.00*	*1.95*	*1.89*	*1.77*	*0.83*	*1.28*	–
MA	8.78	2.06	4.00	0.67	0.72	0.33	0.39	0.61	–
UMA	13.72	5.72	3.00	1.28	1.17	1.44	0.44	0.67	–
autumn	*29.09*	*19.93*	*0.66*	*1.44*	*0.40*	*4.04*	*1.43*	*0.56*	*0.63*
MA	12.83	8.20	0.13	0.37	0.10	2.57	1.10	0.13	0.23
UMA	16.26	11.73	0.53	1.07	0.30	1.47	0.33	0.43	0.40

2001; Adams *et al*., 2012; Dubos *et al*., 2021). For example, the widespread *Myotis crypticus*, as its sibling *M. nattereri*, is an aerial/trawling forager that tends to forage in cluttered habitats, gleaning arthropods from the vegetation or the ground (Razgour *et al*., 2023). The scrubland habitat is not suitable for the ground foraging *Myotis myotis* and for *Barbastella barbastellus* which mainly roosts in dense forests and forages often in the canopy, provided trees are sufficiently spaced out (Russo *et al*., 2023). The forest-dwelling *Nyctalus lasiopterus*, which can forage more than 50 km from its roost (Beucher *et al*., 2022), could reach at least two sites, without being detected if flying at high altitude. Finally, the study area stands at the margin of the range for *Myotis alcathoe*, *M. mystacinus* and *Plecotus auritus*.

Although a large number of recordings identify common and easily spotted bat species, these occupy several ecological niches, foraging at different altitudes, but mostly at the edge of trees and bush vegetation (Vaughan *et al*., 1997; Kalko *et al*.,

2008). Among the open space and edge foragers, the least recorded species were *N. leisleri*, possibly because it is only active for a short time at the beginning and end of the night (Rydell *et al*., 1996; Ruczyński *et al*., 2017; Gottwald *et al*., 2023), and *E. serotinus*, probably due to its habitat requirement of open landscapes including a high density of linear habitats (Martinoli *et al*., 2023). Among sites, the main difference is the lower bat richness at LP which is only significant by the absence of *R. hipposideros*, possibly due to the lack of roost, even if this bat shelters in a great number of different roost types (Schofield *et al*., 2023).

Bat Activity

Miller's index (2001) was an effective measure of overnight bat activity among seasons by avoiding difficulties of variable recording time, making comparisons among sites and areas achievable (Hayes, 1997; Haquart, 2013). Higher activity was recorded in the MA of BSA whenever the season, in spring
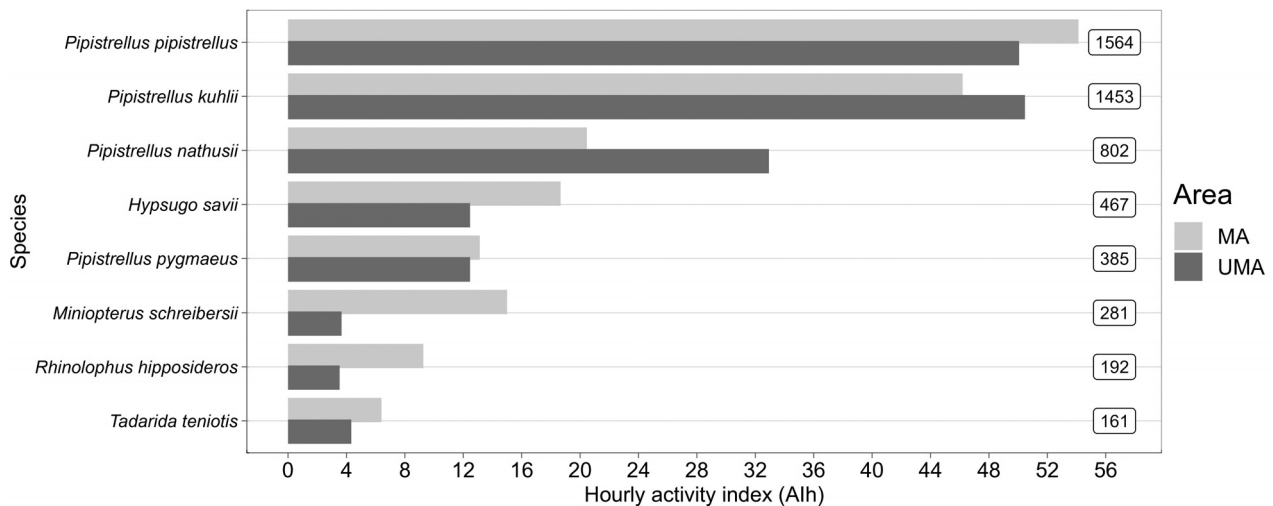
FIG. 3. Hourly activity indices (AIh, number of positive minutes per night hour) recorded for the eight main bat species in managed (MA) and unmanaged (UMA) areas of three scrublands in southern France

only at LP and MP. Several authors identify strong relationships between bat activity, habitat composition and structure in forest ecosystems (Adams *et al.*, 2009; Smith and Gehrt, 2010; Titchenell *et al.*, 2011; Charbonnier *et al.*, 2016; Carr *et al.*, 2020), or prey abundance (Müller *et al.*, 2012; Froidevaux *et al.*, 2021). Numerous bats require a mixed structurally heterogeneous landscape in which suitable sites for roosting, feeding and drinking can be found (Lookingbill *et al.*, 2010; Mendes *et al.*, 2014; Law *et al.*, 2016; Starik *et al.*, 2018; Tortosa *et al.*, 2023). For example, thinning management, that increased the amount of light in the canopy, was positively perceived by bats for daytime roost selection (Carr *et al.*, 2020). In open landscapes, such as agroecosystems, woody elements, riparian vegetation and water provide a multitude of benefits to bats (Froidevaux *et al.*, 2022). In a Mediterranean agricultural landscape Mendes *et al.* (2017) found that a higher number of patches per unit of area (patch density) favour the activity of species that forage in open habitats. Accordingly, in our study the MA features differed from one site to another, with a higher surface and number of scrubland openings at BSA inducing there the sole recorded higher activity than in the UMA whatever the season.

However, bat activity and habitat selection are species-specific and closely linked to foraging strategies (Altringham, 2011). In this regard, management practices for small game species had mixed effects on bat activity. Whereas *H. savii*, *P. pygmaeus*, *M. schreibersii*, *R. hipposideros* and *T. teniotis* were slightly more active in MAs, *P. pipistrellus* and *P. nathusii* were globally more active in UMAs

depending on sites and seasons. Such variations counterbalanced the activity of *P. kuhlii* in both area types. Except *R. hipposideros* and *T. teniotis* that were rarely recorded, these bat species are mid-range echolocators according to Schnitzler and Kalko (2001) or edge foragers according to Mendes *et al.* (2017). However, *H. savii* and *M. schreibersii* flying higher above the ground, faster and more directly than *Pipistrellus* species that remain closer to the vegetation (Dietz *et al.*, 2007) could benefit from openings of the MA for foraging. Verifying this possible link with resource abundance and hunting facilities should be further investigated.

Our results also showed that seasonal patterns of bat activity varied among species and sites making difficult to generalize them at the community level. Foraging in scrublands is likely linked to the flight capacities of each species including wing load and navigation senses. Some authors believe that the plasticity of echolocation signals is an adaptive biological trait that allows each species to make an opportunistic choice of foraging sites in the landscape (Kalko and Schnitzler, 1993; Russo and Jones, 2003). More generally, seasonality greatly influenced bat species activity among sites. The spring activity of *P. nathusii* at MP and LP, whereas this species was absent at BSA, could be related to its migratory behaviour and the location of the study site on a migratory route from Mediterranean hibernation roosts to the north-eastern breeding roosts (Hutterer *et al.*, 2005). *Pipistrellus kuhlii* and *H. savii* were more active in summer at the three sites, but the first one was also active in autumn at LP. Interestingly, bats were mainly active in summer

at BSA, which is the northernmost study site where the availability of prey could peak during a shorter period of time (McCracken *et al*., 2012). Resource availability could peak in autumn at MP, an hypothesis that should be tested later. It was shown that seasonal rhythms reflect a synchronization between foraging preferences and the optimization of prey resources to meet the specific energetic needs of bat species at the landscape scale (Erkert, 1982; Mendes *et al*., 2014). Each bat species is continually adjusting its foraging strategy in response to fluctuating nutritional requirements linked to seasonal variability and associated abiotic parameters (Charbonnier *et al*., 2016). Consequently, the seasonal activity rhythms, sometimes associated with longitudinal spatial movements, can be interpreted as an active search for resources to meet the nutritional or sexual requirements necessary for the survival of each species (Swift *et al*., 1985; Kusch and Idelberger, 2005; Bender *et al*., 2021).

Our field study in three scrublands of southern France, the first one in such habitats, did not support the hypotheses of a higher richness and activity of bats in areas managed for small game species. The small surface of these areas could be a major obstacle for revealing tiny differences between MA and UMA, together with the elusive behaviour of bats foraging in cluttered habitats, despite the positive results of exhaustiveness. Spatial and temporal variations including seasonal cycle and meteorological conditions, and life-history traits of bat species also affect their spatial behaviour and activity level. Also, the composition and structure of the vegetation of wooded areas at the landscape scale are recognized as factors of spatial segregation of bats, between those that can explore dense and homogeneous vegetation, from those that avoid them, except in a situation of substantial energy gain (Plank *et al*., 2012; Müller *et al*., 2013; Charbonnier *et al*., 2016). Beyond a closer sampling during the biological cycle of bats, further investigations should focus on the influence of vegetation within the sampled sites and also in their surroundings where acoustic surveys should be performed for comparison.

Finally, we believe that recommendations to improve bat richness and activity in scrublands and contribute to the conservation of threatened species should be based on management at a large scale, including promoting landscape heterogeneity, diversity and connectivity. Moreover, long-term monitoring should be encouraged to evaluate the impact of the re-opening of abandoned agricultural landscapes on bat communities, and more widely on the whole biodiversity.

SUPPLEMENTARY INFORMATION

Contents: Supplementary Tables: Table S1. Statistics relative to General Linear Mixed Models (GLMMs) investigating global bat activity in three scrublands of southern France. (A) ANOVAs estimate significant results are in bold. (B) Estimates (± confidence interval) of GLMM coefficients for the activity predictor (all species) per area, season, and site; Table S2. Statistics from the General Linear Mixed Models (GLMMs), describing the seasonal bat activity patterns in managed and unmanaged areas of three scrublands in southern France. (A) Candidate models per species. AIh: night hourly activity index per bat species; offset included number of nights surveyed (logit). Model ranking is based on differences in the corrected Akaike's Information Criterion (ΔAICc) and Akaike weights (AICcWt), K refers to the number of parameters. Candidate model in bold was selected for analysis. (B) ANOVAs estimate significant results are in bold. (C) Estimates (± confidence interval) of GLMM coefficients for the bat activity predictor per area, season, and site; Table S3. Habitat managements made by game managers in the three study sites of southern France. Supplementary Material. Acoustic criteria for species identification. Supplementary Information is available exclusively on BioOne.

AUTHOR CONTRIBUTION STATEMENT

NF: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; SA: research concept and design, data analysis and interpretation, writing, critical revision, and final approval of the article; AH: collection and/or assembly of data including bioacoustic analyses, and final approval of the article; MG: collection and/or assembly of data, data analysis and interpretation, and final approval of the article.

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