

Roost selection flexibility of European starlings aids invasion of urban landscape

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Abstract

The ability to shift habitat preferences is one of the characteristics of flexibility in a species and can be a key to the success of invasive species. Our objective in this paper was to analyse the possible behavioural flexibility of European starling (*Sturnus vulgaris*) through its rapid adjustment to changes in roost site availability. First we analysed the change of starling roost sites at regional (Brittany, 1973–1997, 87 sites) and at town scales (Rennes, 1983–2004, 59 sites) in western France. Site selection followed changes in habitat availability, switching from reed beds to conifer plantations regionally, and from hedges/bushes to trees, especially conifers, in Rennes. Secondly, we analysed urban roost sites measuring several characteristics of trees and neighbouring environment. Roost trees were taller and had a bole circumference and canopy larger than non-roost trees. Trees with a large amount of small branches were more selected by starlings. Among environmental features including landscape composition and configuration, only temperature was higher in roost sites. Starlings show great flexibility in choice of roost site characteristics which may in part explain their success as an invasive species and as urban colonists. Despite such flexibility, preferred roost site characteristics could be used to reduce urban nuisance by managing/creating sites in less sensitive locations.

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1. Introduction

The success of invasive species, i.e. introduced species or natural invasions (Williamson, 1996), can be related to (Labisky et al., 2003): (1) species-related factors such as reproductive (Pysek, 1998) or morphological (McLain et al., 1999) patterns, including competitive capacity and range of environmental tolerance (Ehrlich, 1989); (2) environmental factors, such as niche opportunities and type of ecosystem (Levine, 2000; Shea and Chesson, 2002); (3) human factors, such as landscape changes or introduction variables such as the number of releases and number of individuals released (Green, 1997). Among the life history traits that have been studied to explain why some animals are extremely successful invaders, behavioural flexibility has received little attention. This flexibility, in the form of rapid adjustment to new conditions, allows animals to respond more rapidly to changes in its environment. This ability to shift diet

or habitat preferences can consequently be an advantage when invading novel habitats. For example some recent works have emphasized the innovation frequency, i.e. the change in foraging techniques or diet items, in animal generalists and successful invaders (Sol et al., 2002; Prinzing, 2003; O'Brien et al., 2005).

Behavioural flexibility to spatial and temporal changes in landscape and habitat configurations could be a key of the success of some species such as European starling (*Sturnus vulgaris*). Relationships at European scale between the natural spread of starling and deforestation and grassland development have been observed over a long historical period (Feare, 1984). Since the 1950s, populations of the European starling have increased in many places in western Europe and have extended their breeding range, for example in the south of France (Clergeau, 1997). In winter, starlings were very abundant in western Europe until 1985 because of the presence of migrant birds from northern and eastern Europe; they decrease thereafter. The large numbers resulted in economic losses in agriculture, especially on crops and stored food products, and also caused new problems of fouling and excessive noise in

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towns (Feare, 1984; Clergeau, 1995, 1997). At the same time, the European starling, one of the 100 most invasive species throughout the world (IUCN, 2000), continues to be a pest in many countries where it has been introduced, such as the USA and Australia. In the evening, European starlings converge communally to roost sites from distances up to 20–25 km within the feeding area. These birds use reeds, conifers or evergreen hedges to roost (see review in Feare, 1984; Clergeau, 1997). However, the recent increase of roosting behaviour in new sites in rural areas and also in towns suggests that this bird is capable of responding rapidly to habitat change. Our objective in this paper was to analyse the possible behavioural flexibility of starlings through its rapid adjustment to changes in roost site availability.

We firstly predicted that roost site selection would shift in relation to landscape change at the regional level. Brittany, western France, was one of the regions most used by wintering starlings during the second part of 20th century (Clergeau and Fourcy, 2005) and starlings commonly roosted on reeds (Clergeau, 1997). However, the most important change in natural habitats of Brittany between the 1950s and 1980s has been the destruction of more than 70% of wetlands that have been drained for agricultural purposes and conifer plantations (Poncet, 1984; CRPF, 1992). We can analyse starling responses to these landscape changes.

We secondly predicted that the kind of roost used by starlings could change rapidly with recent changes in town green spaces. In towns, roosts of European starling were observed in UK from the beginning of the 20th century. However, large roosts (e.g. >20,000 birds) became very common in western and southern European towns only since the beginning of 1990s (especially in France, Italy and Spain) when the number of roosts decreased in rural areas (Clergeau, 1997); we now estimate that half of middle and large-sized towns are concerned by this problem in France. This recent invasion of towns by starlings also offers an opportunity to analyse flexibility in roost selection, independently of their abundance, as starling numbers have decreased in western Europe in the last 15 years. In Rennes, a town in Brittany, several practices of hedge management, such as development of pruning, and tree plantation, such as development of evergreen plantation, have been changed in the last decade (P. Lhoumeau, personal communication). We can also analyse starling choices at this scale.

We thirdly predicted that starlings selected some site characteristics irrespective of the tree species and consequently that active choice was involved. Indeed, even if rapid changes can be detected, the degree of flexibility is not clear: are starlings linked to particular site characteristics rather than to particular plant species? Do starlings select of roost sites according to decision rules (O'Brien et al., 2005) or random choice? Previous results have underlined the effect of temperature in the choice of the best night roost sites by various bird species (Kelty and Lustick, 1977; Yom-Tov et al., 1977; Jenni, 1991; Clergeau and Simonnet, 1996) and of day roost sites (Wang and Brigham, 1997; Fisher et al., 2004) but there have been few studies on roost site structures (Lyon and Caccamise, 1981). In urban areas, there are many plant and tree species over a small area and so

a comparison can be made between trees used by starlings and non-roost trees.

The results of analyses of these three predictions about changes in and the characters of roost sites can illustrate the behavioural flexibility, and can also assist the implementation of management programs, especially in the urban context.

2. Study area and methods

2.1. Roost site changes

Firstly, we analysed roost sites used by starlings in Brittany (27,000 km²), western France. The landscape was dominated by meadows and cereal fields, with the farms (for cattle and pig production) distributed relatively homogeneously throughout the country. This region had few large forests and wetlands. The sample was reduced to roosts (1) that were observed for 1 year or more during the period from 1973 to 1997, (2) that contained more than 50 000 starlings and (3) that existed from the beginning of November to the end of February to focus only on the migratory status (Clergeau, 1993). Roosts established on islands were not taken into account. Finally 293 starling roost observations involving 87 roost sites were included in this study.

Secondly, we analysed roost sites used by starlings within Rennes (pop. 270,000), a medium-sized town located in Brittany. This town is similar to other towns of France, with a pattern of concentric rings of decreasing urbanization out from the city centre. It has a temperate climate. The first large starling roost was observed in 1982 within Rennes and 64 urban sites have been used by starlings since this date (services of Rennes, pers. comm.; pers. obs.). Among 64 roost sites, we selected only those (1) that were observed during the period from 1983 to 2004, (2) that contained more than 1000 starlings, and (3) that existed from the beginning of November to the end of February, i.e. during the winter period. 119 observations were studied here from 59 selected sites.

In the two analyses, we retained one observation per site per winter and years were grouped in 5-year units. At the regional scale, we grouped the data into deciduous woods (especially *Quercus* sp. and *Castanea* sp.), conifer woods (especially *Picea* sp. and *Abies* sp.), bush–shrub (especially *Prunus* sp., *Salix* sp. and *Juniperus* sp.) and reeds (especially *Phragmites australis*). At the town scale, the categories used were deciduous trees (especially *Platanus* sp.), conifers (especially *Cupressus* sp.), bush–shrubs (especially *Crataegus* sp., *Rubus* sp. and *Salix* sp.) and hedges (especially *Laurus* sp.). Data on the changes of landscape and availability of wood, reed or shrub during our study period were not easy to obtain at Brittany and Rennes scales. However, the annual areas of conifer plantations that were encouraged since 1960s in some parts of Brittany were available (CRPF, 1992). Some of these sites planted with *Abies* sp. or *Picea* sp. became available as roost site 10 years after plantation when tree size permitted starlings to perch (B. Clément, pers. comm.). Consequently, we can compare the change in conifer plantation surfaces between 1968 and 1982 with change in roost selection by starlings between 1978 and 1992.

2.2. Characteristics of urban roost

This study was conducted at Rennes on a recent sample of roosts used by starlings. From the 59 roost sites, we selected only 14 starling roosts that were (1) tree sites (deciduous trees or conifers), (2) used between 1995 and 2003 and (3) accessible for immediate measure analysis.

We also randomly chose 15 non-roost sites using a GIS and aerial photographs of the city. These non-roost sites had to be far enough away from roost sites to avoid overlapping of landscape analysis zones. First we plotted every roost ($n = 64$) on a map of the town and drew a circular buffer area (500 m radius) around each of them using the Arcview “Buffer Theme Manager” script (O’Malley, 1999). Second, outside of these buffers but within the urban area, we generated 15 points using the “Random Point Generator” script (Hahn, 2002). The position of all 15 non-roost sites was adjusted to reach the nearest tree or group of trees.

The field study of the characteristics of roost and non-roost sites was carried out in Rennes in the winter period, from 15 January to 15 February 2004. To characterise trees, we measured total tree height, clear bole height, canopy height, canopy radius, bole circumference at breast height and an estimate of canopy volume. We also estimated the availability of small branches (<2 cm) using four photographs of canopy cover per tree (according to the recommendations of Mills et al., 1993) and classified the trees into four cover classes: 0 (<10%), 1 (11–25%), 2 (26–40%), 3 (>40%). We noted the form of canopy (0: ellipsoidal such as *Quercus*, 1: spherical such as *Platanus*, 2: conical such as *Pinus*), the kind of foliage (0: persistent, 1: deciduous) and the shape of plantation (0: linear such as hedge or avenue, 1: patch). We analysed all the trees available when there were only one, two or three, but sampled the three most representative trees when there were more.

In order to characterise the neighbouring environment, and following previous studies on bird roosts (Lyon and Caccamise, 1981; Peh and Sodhi, 2002; Yap et al., 2002), we made three replicate measurements in all the sites at the same time at the beginning of the night (three people working simultaneously) of the illumination level using a photometer (average of four readings around the roost), the noise level using a sound meter (average of 5 min recording), the temperature using instantaneous thermometers and a disturbance index of pedestrian presence within 10 m of the roost during 10 min (0 = 0–1 pedestrian, 1 = 2–10, 2 = 11–20, 3 > 20).

From a map of land use of Rennes previously constructed from several sources, we calculated the percentage of different land uses within a 150 m radius around each site, using Arcview GIS and Patch Analysis extension (Rempel and Carr, 2003). The land use classes were built-up areas, woods, lawns, water and others (especially roads). The landscape configuration was measured by the patch density (number of patches in the buffer zone) and edge density (perimeter/buffer area) of each land use classes.

We conducted a Mann–Whitney U -test corrected for ties and a χ^2 -test (pooling some categories to satisfy the requirement of the test) to determine whether there was a site preference by roosting starlings.

The variability of the data suggested that results should also be examined using a multi-factorial analysis. The quantitative variables were recoded into two classes (high, low) and a multiple correspondence analysis using the software program SPAD (Lebart et al., 2000) was applied to the data for 29 sites and 21 variables.

3. Results

3.1. Roost site changes

Rural roost sites used by starlings in winter showed a progressive change during the study period (Fig. 1). Reed bed roosts represented 52.0% of roosts in 1973–1977 but only 6.2% in 1993–1997 whereas roosts in conifer woods, especially *Picea* sp. plantations, increased from 20.0% in the first period to 70.1% in the latter. The area of new conifer plantations (especially *Picea* sp.) increased regularly from 1012 ha in 1968 to a total of 16,180 ha in 1982, providing sites suitable for roosting 10 years later. We obtained a positive correlation between the percent of starling roosts in conifer woods in 1978–1992 and the plantation area of conifers in 1968–1982 in Brittany (Spearman $r_s = 0.56$, $n = 14$ years, $P < 0.05$), and no correlation between the total number of roosts and the conifer area during these years.

In the town of Rennes, roosts used by starling also changed (Fig. 2) with a progressive decrease of hedge use, especially hedges of *Laurus nobilis*. After 2001, starlings deserted bush–shrub sites and used *Pinus* spp. for the first time in Rennes. In 2004 these conifers were used again. In the last period 2002–2004, 60.0% of roosts were in conifers whereas only

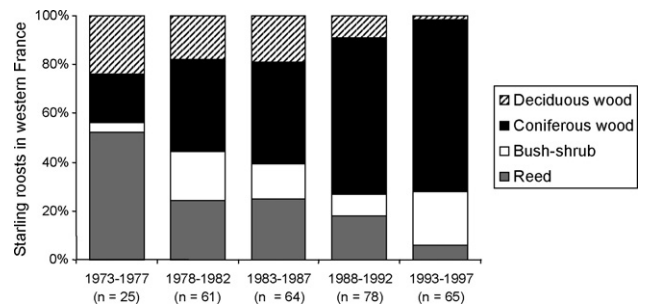


Fig. 1. Change of roost sites used by starlings in winter in Brittany between 1973 and 1997, showing the replacement of the traditional use of reed beds by roost in conifer woods (each roost > 50,000 birds).

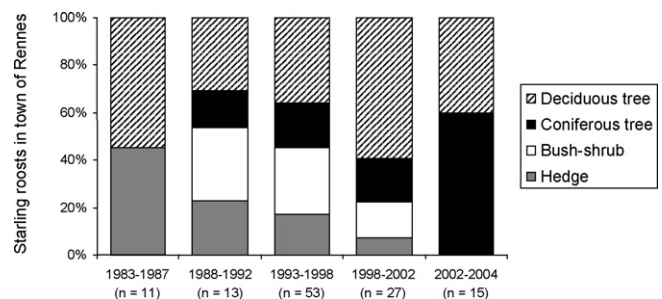


Fig. 2. Change of roost sites used by starlings within Rennes town between 1983 and 2004 (each roost > 1000 birds).

Table 1
Characteristics of 14 starling roost sites and 15 non-roost sites randomly selected in Rennes

	Roost site		Non-roost site		P
	Mean/classes	S.E.	Mean/classes	S.E.	
Tree characteristics					
Total tree height (m)	14.9	1.02	11.7	0.93	0.05 ^a
Clear bole height (m)	3.45	0.46	2.88	0.42	0.29 ^a
Canopy height (m)	11.46	1.11	8.94	0.75	0.11 ^a
Canopy radius (m)	5.38	0.35	3.93	0.29	0.01 ^a
Bole circumference (m)	1.77	0.18	1.15	0.13	0.01 ^a
Canopy volume (m ³)	814	151	413	91	0.04 ^a
	0=0		0=3		0.02 ^b
Small branch availability (0–3)	1=4		1=8		
	2=4		2=4		
	3=6		3=0		
	0=1		0=12		0.001 ^b
Canopy form (0–2)	1=9		1=2		
	2=4		2=1		
	0=8		0=13		0.08 ^b
Foliage (0 or 1)	1=6		1=2		
	0=7		0=7		0.86 ^b
Plantation shape (0 or 1)	1=7		1=8		
Environment					
Illumination (lux)	5.16	1.77	1.94	0.41	0.12 ^a
Noise (dB)	53.36	1.79	55.67	1.99	0.41 ^a
Temperature (°C)	4.23	0.12	3.72	0.11	0.008 ^a
	0=4		0=10		0.06 ^b
Disturbance index (0–3)	1=7		1=5		
	2=3		2=0		
Built-up area (%)	15.98	3.36	14.39	1.47	0.86 ^a
Woods (%)	9.22	1.14	10.62	1.03	0.22 ^a
Lawns (%)	15.23	2.08	14.83	1.17	0.89 ^a
Water (%)	0.92	0.65	3.62	2.09	0.44 ^a
Roads and others (%)	58.64	1.29	56.55	1.67	0.27 ^a
Patch density (n)	1304	50	1331	93	0.83 ^a
Edge density (m/ha)	3233	160	3465	197	0.26 ^a

^a Mann–Whitney *U*-test.

^b χ^2 -test.

15.4% were used in 1988–1992 and none in 1983–1987 on this kind of tree.

3.2. Characteristics of urban roosts

Roost and non-roost samples each included 9 tree species. Roost trees tended to be taller than non-roost trees (Table 1). They had bole circumference and canopy (height, radius, volume) larger than non-roost trees. Starlings avoided the ellipsoidal form of canopy and clearly selected trees with a large amount of small branches availability. The kind of foliage and the organisation of trees did not appear to be influential in our urban context.

Environmental features such as illumination, noise or level of human disturbance did not significantly distinguish roost from non-roost trees. Only temperature was higher in roost sites probably linked to the fact that roost sites were generally closer to building (external source of heat). Landscape composition and configuration were not different around the roost sites and around the non-roost sites (Table 1).

The multiple correspondence analysis applied to the data set of tree and environmental characteristics showed that the first two factorial axes explained 36% of the total inertia. On the first axis (F1), the most positive contributions were high total tree height (relative contribution RC = 8.77), high canopy height (RC = 9.38), conical canopy form (RC = 11.36) and persistent foliage (RC = 8.47). For negative contributions, the analysis gave opposite values of the same characteristics (respectively RC = 8.19, 7.62, 3.59, 3.23). On the second axis (F2), the most positive contributions were high temperature (RC = 9.75), spherical canopy form (RC = 10.64) and a high availability of small branches (RC = 7.39). The negative contribution was linked to the opposite value of the same characteristics (respectively RC = 7.92, 6.66, 5.03).

The mean coordinates of roost sites are in a positive location for F1 and F2 whereas the mean coordinates of non-roost sites are located in the negative part of F1 and F2 axes (Fig. 3). These results clearly opposed roost and non-roost sites on the first two factorial axes. In the factor analysis, the variables most explicative of roost site location were high small branch

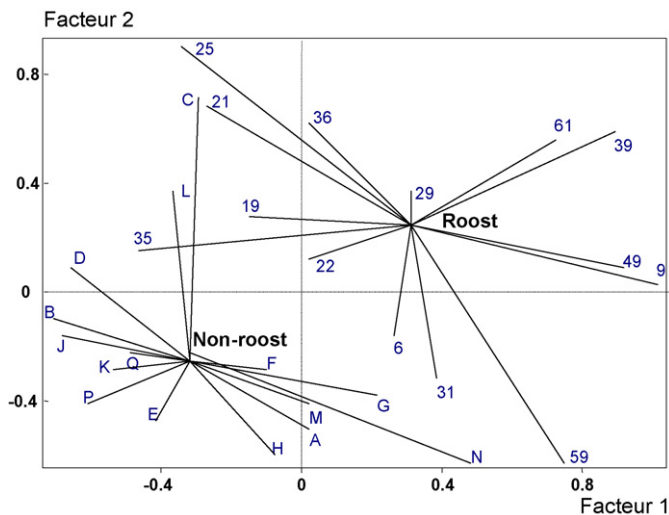


Fig. 3. Distribution of urban starling roost sites ($n=14$, figured by a number) and non-roost sites ($n=15$, figured by a letter) according to projection values on first axis (explaining 20.56% of the total inertia) and second axis (explaining 15.71% of the total inertia) (multiple correspondence analysis on 21 variables). On the first axis (F1), the most significant contributions were total tree height, canopy height, conical canopy form and persistent foliage. On the second axis (F2), the most significant contributions were temperature, spherical canopy form and availability of small branches.

availability, persistent foliage, large and non-ellipsoidal canopy and high temperature.

4. Discussion

Wintering starlings selected roost sites with certain physical attributes, but, in a changing environment and especially in the novel urban context they have invaded, birds shifted their roost site preferences.

Our results showed the change in roost site used by starling at the two scales studied. At regional scale, the shift in roost preferences followed the changes in the Brittany landscape. The ancestral starling roost site is the reed bed, cited in literature since the 17th century (see review in Feare, 1984; Clergeau, 1997). The most important change in natural habitats in Brittany during the last century has been the suppression of wetlands and especially coastal marshlands between the 1950s and 1980s that were drained for agricultural purposes (Poncet, 1984) and that were actively used by starling in the 1970s (our data from 1973 to 1977). The other change was the development of conifer plantations of several hectares, especially *Picea* sp. and *Abies* sp. with a peak of plantation in the 1970s (CRPF, 1992). The decrease in the availability of reed beds, the traditional roost site, has been progressively compensated for by the increase of conifer plantation availability that was quickly used by starlings. These two vegetation types have similar characteristics such as good protection from wind and high “small branch” availability, but are extremely different in their form. From earlier studies in Great Britain and Belgium, Feare (1984) also emphasized the change in roost selection between summer when deciduous woods are more selected and winter when starlings preferentially used conifers in Britain and ever-

greens in Belgium, probably according to the availability of site type.

The results of the urban roost study corroborate the capacities of starling to respond to changes in the resource availability, underlying the rapid adjustment to new conditions. Rennes Municipality Services (P. Lhoumeau, pers. comm.) observed that (1) in the 1980s the municipality actively encouraged the need to prune the hedges to avoid starling settlement, leading to many changes in the shape of *Laurus nobilis* hedges. The use of this kind of site by starlings clearly decreased after in the 1990s. (2) Green spaces and private gardens also underwent changes between 1960 and 1980, especially in the development of conifers and evergreen plantations. (3) After 2001, starlings deserted bush–shrub sites, i.e. fallow land in the suburbs, when some were redeveloped for buildings and starlings used new conifer sites the year after. A census of roost sites in other towns of western France over 20 years also showed a shift of species according to availability of plant species, for example many *Laurus nobilis* and *Thuja* sp. were used at the beginning of the 1990s and many *Magnolia* sp. and bamboos at the beginning of the 2000s (P. Clergeau, unpubl. data).

Our analysis of urban starling roost site characteristics showed the importance of the size of the trees (tree height, canopy volume) (see also May et al., 2004; Everding and Jones, 2006) and of the high availability of small branches of the trees selected by birds. The importance of canopy density was previously shown by Lyon and Caccamise (1981) for rural starling roosts and also in urban roosts of house crow *Corvus spendens* (Peh and Sodhi, 2002) and common myna *Acridotheres tristis* (Yap et al., 2002) in Singapore city. These authors emphasized the protection from wind, rain and exposure (see also Holmgren, 2004) but also suggested that a dense twig and perch configuration were preferred by some species of birds. In our study, the set of variables integrating both the size and the volume of canopy and the density of twigs, affected the capacity for accommodating high bird numbers. So, starlings could seek not only protection and branch size preference, but also available space to allow many birds to perch close together.

Among environmental characteristics, only temperature significantly differentiated roost and non-roost sites, corroborating the previous results obtained in various species (Jenni, 1991; Clergeau and Simonnet, 1996; Wang and Brigham, 1997; Fisher et al., 2004). The choice of the best site is clearly expressed when birds have to withstand more severe weather conditions and spent a longer time in the roost when the night is colder (Reeds, 1986). Surprisingly, illumination did not appear to be better in roost sites although it could allow birds to escape from disturbance by flying out during the night to a new site. The degree of illumination was identified by Yap et al. (2002) and Peh and Sodhi (2002) as a secondary factor in the choice of urban roost sites.

The landscape composition and configuration did not seem to influence roost site selection by the starling. The proximity of food resources such as lawns that are important starling feeding sites (Feare, 1984; Mennechez and Clergeau, 2001) was not identified as an important factor in the choice of roost site in Rennes. However, in an analysis of a large agricul-

tural region Clergeau and Fourcy (2005) showed relationships between landscape composition (especially pasture) and configuration (large patches) and roost locations. Observing the regular change of roost sites by starlings in a rural context, Caccamise and Morrison (1988) suggested that the roost site was linked to the availability of food resources: starlings could leave their diurnal feeding sectors for other distant food resources and establish a temporary roost in the proximity for the night. In urban roosts, we have never observed this behaviour; starlings feed together during the evening on the pastures nearest the town but not within the town in the proximity of the roost site.

Characteristics of urban starling roosts are the same as those obtained for other birds in urban context (Peh and Sodhi, 2002; Yap et al., 2002). Especially large trees with a high density of twigs allow large numbers of starlings to perch and benefit from wind protection. From these characteristics, we can recommend that homogeneous patches of tall trees with a high density of foliage and twigs should be avoided if urban roosts are undesirable. Pruning of trees could also be used to avoid the development of a high density of small branches. According to Clergeau (1997) and Peh and Sodhi (2002), we have to develop and exploit these results to encourage roosting birds to relocate to new roosting sites, for example at the periphery of the town where the starling impact can be low. These alternative roost sites have to be the most attractive (having the most favourable characteristics for roosting behaviour) and as stable as possible (having protection from external disturbances). Actually the better potentiality to reduce starling urban nuisance seems this creation/management of alternative sites in less sensitive locations. Although methods to put birds in a defined site are limited (Clergeau, 1997), roost habitat management have to be integrated in biodiversity policy (Savard et al., 2000) as a planning tool.

Starlings look for certain features in their roosting selection, i.e. they apply a general decision rule according to which they select better sites when searching for roosting sites. However, the plant species, the shape and even the environment of the perch can change with environmental availability. Starlings have shown a great capacity to shift in their roost sites. This behavioural flexibility has to be considered as an important reason for the success of the European starling, as it is also expressed in areas where it has been introduced (Lyon and Caccamise, 1981). Flexibility could account for the expansion of its natural range and its numerical success in many European regions (Feare, 1984) and in more or less recent colonisation of habitats such as towns (this study). Despite such flexibility, preferred roost site characteristics could be used to reduce urban problems, management responses being also flexible according to urban and landscape characters.

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