Distribution and characteristics of urban nesting sites of sympatric swifts

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Abstract - Distribution and nest locations of Common and Pallid Swifts are compared in two towns located in the Mediterranean zone, Bastia in Corsica and Nice on the French Riviera. Our goal is to evaluate whether nesting site selection by swifts on urban settings differs between the two locations. First, we noted an avoidance in the distribution between the two swifts in both towns. Secondly, our results show that Common and Pallid Swifts use different nesting sites to breed in Bastia, whereas the same structures are used by the two species in Nice. Requirement of each species differs between the two localities, suggesting that nesting site use is more locality dependent than species dependent.

Key words: Apodidae, competition, nesting site, sympatry.

Riassunto - Distribuzione e caratteristiche dei siti di nidificazione urbana dei rondoni comuni.

La distribuzione e i luoghi di di nidificazione dei rondoni comuni e dei rondoni pallidi sono stati confrontati in due città situate nella zona mediterranea, Bastia in Corsica e Nizza sulla Costa Azzurra. Il nostro obiettivo è valutare se la selezione dei siti di nidificazione da parte dei rondoni negli ambienti urbani differisce tra le due città. In primo luogo, abbiamo notato un evitamento nella distribuzione tra i due rondoni in entrambe le città. In secondo luogo, i nostri risultati mostrano che i rondoni comuni e i rondoni pallidi utilizzano diversi siti di nidificazione e che ciascuna specie differisce tra le due località, suggerendo che l'uso del sito di nidificazione dipenda più dalla località che dalla specie.

Parole chiave: Apodidae, competizione, simpatria, sito di nidificazione.

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INTRODUCTION

Colonial birds of closely related species often compete for habitats or breeding sites (*Sterna* spp.: Burger & Gochfeld, 1988; Ramos *et al*., 1995; *Uria* spp.: Birkhead & Nettleship 1987). On Mediterranean coasts, two swift species recently derived from a common ancestor (Randi & Boano, 1993; Pellegrino *et al*., 2017) − the Common Swift (*Apus apus*) and the Pallid Swift (*Apus pallidus*), breed in colonies in towns and very locally in cliffs, their respective range overlapping in the north of the Saharo-Arabian biogeographic zone (Cramp, 1985). More than half a century ago, Voous (1960) already notices that the two species bred in sympatry in a southern France town (Banyuls: Lack & Lack, 1951), whereas in North Africa the species did not form colonies on the same locality. Since then, several mixed swift colonies have been observed in Europe, with some differences noted on nest locations between the two species (Antonov & Atanasova, 2002; Cucco & Malacarne, 1987). Here, we compare the distribution and nest locations of the two species in two towns located in the Mediterranean zone, Bastia in Corsica and Nice on the French Riviera. Our goal is to evaluate whether nesting site selection by swifts on urban settings differs between the two locations. Numbers of both swift species are important: 10,000 pairs in Nice and more than 1,000 pairs in Bastia for the Common Swift; 2,000-2,500 pairs in Nice and more than 500 pairs in Bastia for the Pallid Swift. In both locations, Pallid Swift number has been increasing recently, whereas a decline has been noted for the Common Swift in Bastia (stable number for Nice) (C. Frelin pers. obs.; Thibault *et al*., 2022). At the European scale, the range of both species has been unchanged over the last decades (Keller *et al*., 2020) although the decreased numbers of Common Swifts led to a "Near Threatened" evaluation in Europe by BirdLife International (2021).

METHODS AND STUDY AREA

Identification of Common and Pallid Swifts, sometimes challenging because of their similar size and plumage, was based on difference of flying calls (Malacarne *et al.*, 1989), morphology, and plumage coloration (Vinicombe *et al*., 2014; Reyt & Duquet, 2020). In Nice (French Riviera; 341,032 inhabitants in 2018; range=72 km²), mapping and description of nesting-sites were conducted during the

autumn 2012, then from spring to autumn in 2013-2015. The town was divided into five districts (Paillon East, Paillon West, Nice-Nord, Carras, and Magnan), the first being the older; see Lemarchand & Frelin (2016) and Frelin (2016) for details on range and methods. In Bastia (Corsica Island; 48,044 inhabitants in 2018; range=19km²), prospecting took place from 2015 to 2020; there is an «old» district near the sea around which the town has expanded (see Thibault *et al*., 2022 for details). Because most swift nests are invisible, we used the movements of the adults during the breeding at the time of the incubation or the feeding of the young to locate them. The presence of prospectors -non-breeding birds displaying loudly near breeding sites at certain times of the day- facilitates this localization (Lack, 2018). The evidence researched is the entry of a swift into any location of nest supports. We used the term "nesting-site" for all the breeding sites, whether they refer to a colonial site or to isolated pairs. We geolocated 394 nesting-sites in Nice and 156 in Bastia, for which the architectural design was described in addition to the breeding species (Common Swift, Pallid Swift, or "mixed" when both species used the same building section). Figure 1 shows the nine types of nesting-site supports used by swifts. Information on the towns' architecture derived from Carti (2017) for Nice and Casta *et al*. (1996) for Bastia. The mapping was conducted using the software QGIS 3.16 (GGIS.org, 2021) with the OpenStreet map background. To appreciate whether a segregation exists between the two species distribution within each town, we used a 100x100m grid and counted within each square the number of sites occupied respectively by Common Swifts, Pallid Swifts, and mixed sites.

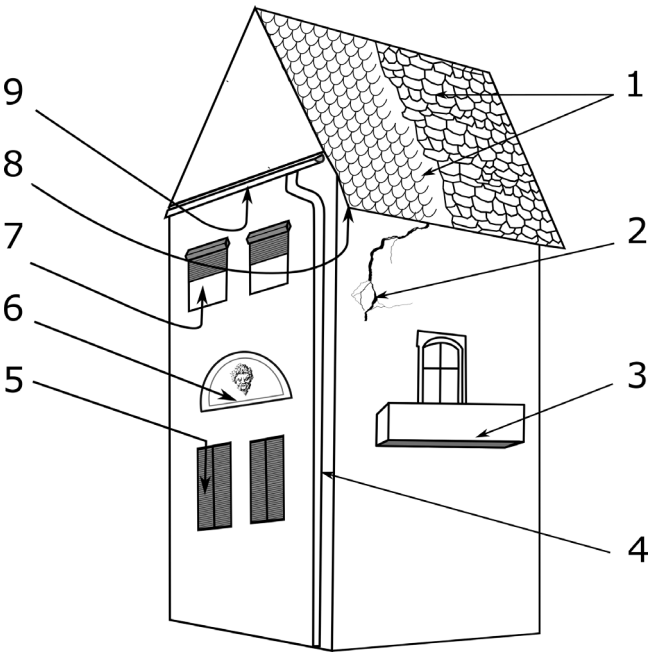

Fig. 1 - Location of the nine types of nest sites used by swifts in Bastia and Nice. 1) under stone slates or tiles, 2) in holes on walls, 3) in slots below balconies, 4) in vertical slots (often behind gutters), 5) on window sills behind closed shutters, 6) on mascarons (decorative ornaments), 7) within roller-shutter boxes, 8) under eaves or frames of the roof, 9) under horizontal gutters. / Ubicazione dei nove tipi di nidi utilizzati dai rondoni a Bastia e Nizza. 1) tetto in ardesia o piastrelle, 2) in fori sulle pareti, 3) in fessure sotto i balconi, 4) in fessure verticali (spesso dietro grondaie), 5) sui davanzali dietro le persiane chiuse, 6) su mascarons (ornamenti decorativi), 7) all'interno di avvolgibili, 8) sotto gronda o intelaiatura del tetto, 9) sotto grondaie orizzontali.

Comparative information on the presence and demography of the two swifts in both regions is presented in Table 1. The statistical analyses were carried out using the free software BioStaTGV (http://biostatgv.sentiweb.fr/) and the figures of the correspondence analysis (CA) carried out with RStudio (RStudio Team, 2020).

RESULTS

Distribution

In Nice, swifts occupy a large part of the town (Fig. 2). The western part shelters only Common Swifts (Carras and Magnan districts, a mosaic of modern buildings and older and traditional dwellings). The three other districts in the eastern part of the town shelter both species, but the number of nesting-sites is significantly different among them ($Chi^2_2 = 97.71$, $P<0.001$): the Common Swift predominates the Paillon-West and Nice-North and the Pallid Swift predominates Paillon-East (Tab. 2). Mixed sites accounted for only 6.3% of nesting-sites.

Bastia. Number of the Common Swift is higher than that of the Pallid Swift (Tab. 2). The respective breeding areas of the two species overlap throughout the town, from Toga, in north of Bastia, to Montesoru in the south (Fig. 2). However, several clusters with a high density of nesting sites are found in the town's center, with Common Swifts in the historical district and Pallid Swifts in the neighbourhood west of the new port. At the north of the town (Toga) and at the south (Lupinu, Montesoru), the distribution of the sites is less dense and no species are better represented than each other. Mixed sites represent 9% of the total number of sites.

Grid squares with a single species of swift (Figs. 2 and 3) represent 83.7% in Nice (210 squares over 251 in total) and 81.4% in Bastia (79/97), suggesting, similarly to the low numbers of mixed nesting-sites, an avoidance in the distribution between the two swifts in both towns.

Use of nesting-site supports

In Nice, the two swifts mainly locate their nests under eaves (Tab. 3), and to a lesser extent under horizontal gutters and in slots under balconies (these three represent 78% of locations for Common and 77% for Pallid). Holes in walls and mascarons are rather marginally occupied by the Common Swift. In Bastia a significant difference ($Chi^2_2=67.18$, $P<0.001$) was observed between the two species. Common Swifts mostly place their nests under stones late and in holes in walls, while Pallid Swift use mainly the roller shutter boxes and other supports (Tab. 3). These results are also visible on the correspondence analysis (Fig. 4), which shows clearly the different nesting sites uses of Common and Pallid swifts in Bastia, whereas the same structures are used by the two species in Nice. Interestingly, the requirement of each species differs between the two localities, suggesting that nesting site use is more locality dependent than species dependent.

Tab. 1 - Data on the breeding of the Common and Pallid Swifts in Nice and Corsica; double-broods in the Pallid Swift are documented in towns of Northern Italy (Boano & Cucco, 1989), Southern Iberia (Finlayson, 1992), North Africa (Isenmann & Moali, 2000, Thévenot *et al*., 2003); three-fold broods have been recorded at least two times in southern France (F. Dhermain in Barthélemy, 2015). Double-breeding of the Common Swift has been recorded in Switzerland (Maumary *et al*., 2007). / Dati sulla nidificazione dei rondoni comuni e dei rondoni pallidi a Nizza e in Corsica; doppie nidiate nel rondone pallido sono documentate nelle città del Nord Italia (Boano & Cucco, 1989), Iberia meridionale (Finlayson, 1992), Nord Africa (Isenmann & Moali, 2000, Thévenot *et al*., 2003); sono state registrate triple covate almeno due volte nel Sud della Francia (F. Dhermain in Barthélemy, 2015). La doppia nidificazione del rondone comune è stato registrato in Svizzera (Maumary *et al*., 2007).

	Bastia (this work, 2015-2019)	Nice (C. Frelin, 2013-2015)	Corsican Islets (Thibault *et al*, 1987)
Common Swift			
date of arrival on nesting-sites	Late March - 1st week of April	late March - 1st week of April	absent
date of laying	April-May	1st to 15 May	
number of breeding	one	one	
date of departure	mid to late July	mid July - 10th August	
Pallid Swift			
date of arrival on nesting-sites	8-19 April (2016-2021)	10-20 April	4th week of April
date of laying	May to August (extended to September)	May to September	June to July (extended to May and August)
number of breeding	Breeding period is spread, although no evidence of two breeding by same pairs	two for some pairs	only one
date of departure	From August to late October	From August to early November	most late August, early September

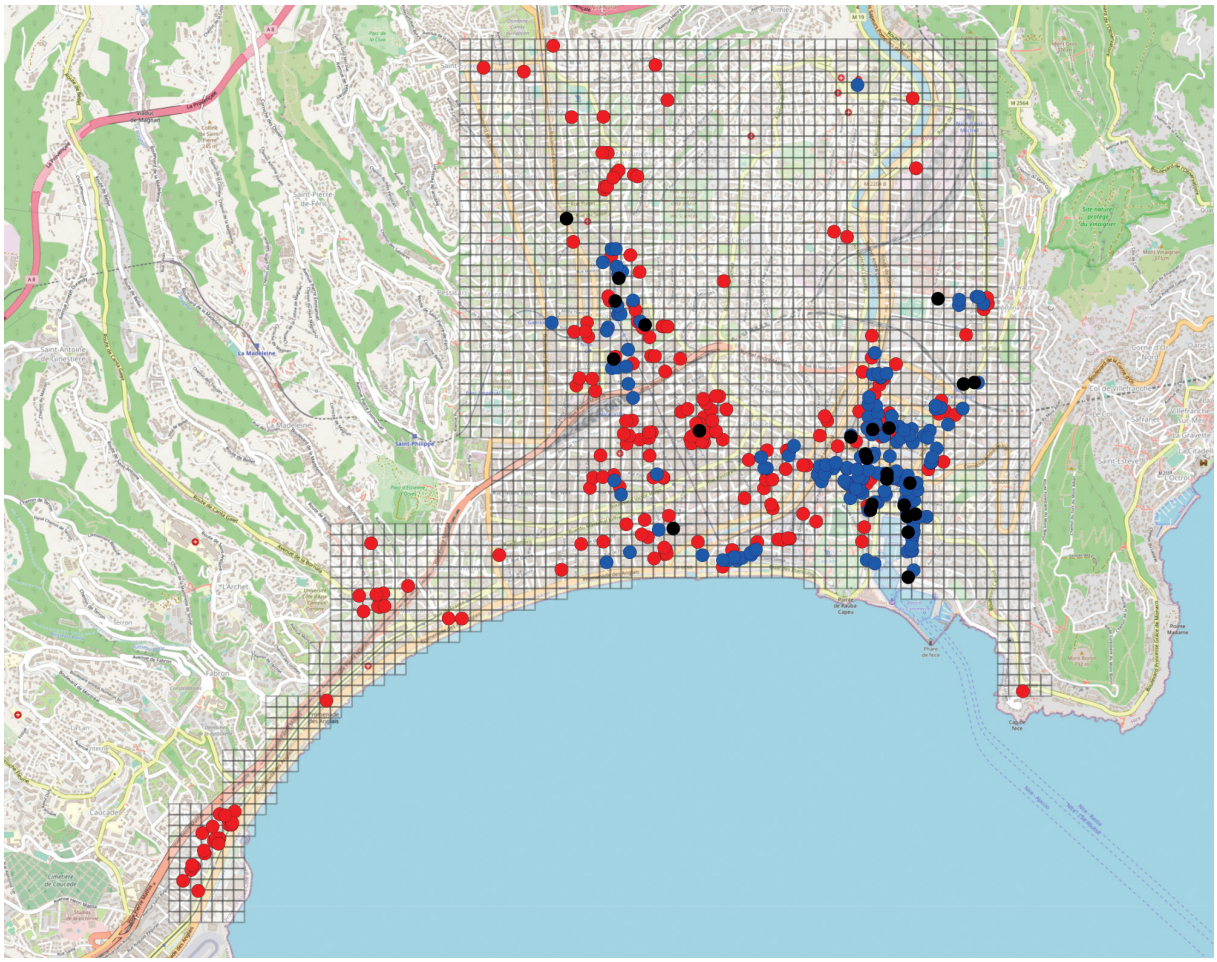

Fig. 2 - Distribution of Common Swifts (red dot), Pallid Swifts (blue dot), and mixed (black dot) nesting sites in Nice. / Distribuzione di rondoni comuni (punto rosso), rondoni pallidi (punto blu) e siti di riproduzione misti (punto nero) a Nizza.

Tab. 2 - Number of nesting sites counted in Nice (spread in the five districts) and Bastia. / Numero di siti di nidificazione censiti a Nizza (distribuiti nei cinque distretti) e Bastia.

Localities	Total number of nesting-sites	Common Swift	% Common Swift	Pallid Swift	% Pallid Swift	mixed	% mixed
Nice	394	206	52.3	163	41.4	25	6.3
Paillon-East	195	47	24.1	130	66.7	18	9.2
Paillon-West	90	76	84.5	12	13.3	2	0.2
Nice-North	77	51	66.2	21	27.3	5	6.5
Carras	20	20	100	0	0	0	0
Magnan	12	12	100	0	0	0	0
Bastia	156	85	55	57	36	14	9

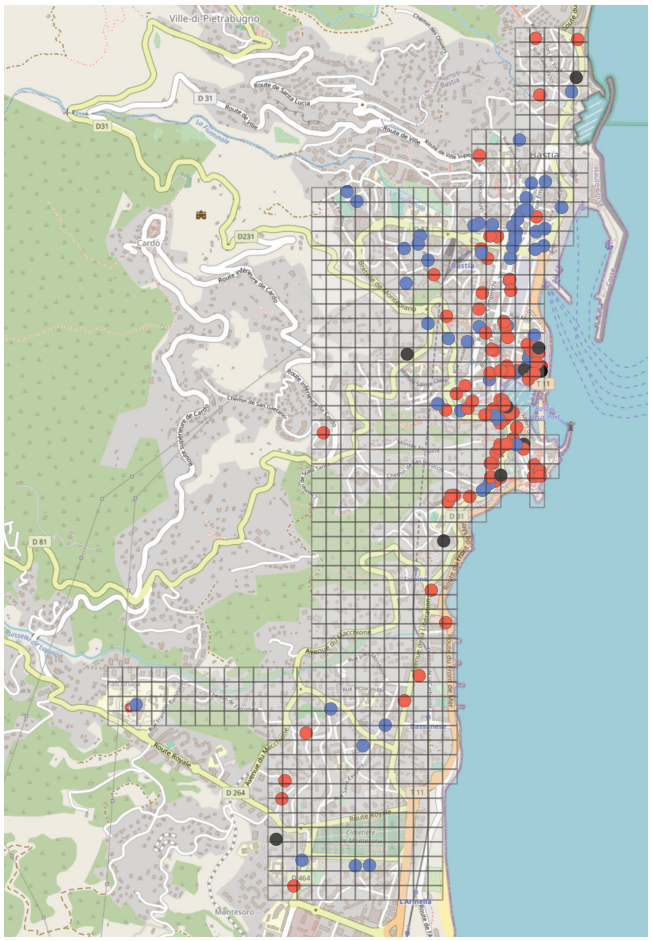

Fig. 3 - Distribution of Common Swifts (red dot), Pallid Swifts (blue dot), and mixed (black dot) nesting sites in Bastia. / Distribuzione di rondoni comuni (punto rosso), rondoni pallidi (punto blu) e siti di riproduzione misti (punto nero) a Bastia.

Tab. 3 - List of nesting-site supports (described in Fig. 1). / Elenco dei supporti del sito del nido (descritto in Fig. 1).

Nice	1=Common Swift	2=Pallid Swift	3=mixed
1=stone slate, tile	0	1	0
2=hole in wall	14	2	4
3=slot under balcony	20	19	2
4=vertical slot	7	4	2
5=window sill	6	11	1
6=mascaron	13	3	0
7=roller-shutter box	4	10	1
8=eaves or frame	118	97	13
9=gutters	38	40	9
Total	220	187	32
Bastia	1=Common Swift	2=Pallid Swift	3=mixed
1=stone slate, tile	26	0	6
2=hole in wall	51	12	9
3=slot under balcony	0	6	1
4=vertical slot	0	9	2
5=window sill	4	4	2
6=mascaron	0	0	0
7=roller-shutter box	3	22	1
8=eaves or frame	8	4	1
9=gutters	5	5	2
Total	97	62	24

DISCUSSION

In both towns, the total number of nesting sites is lower for Pallid than for Common Swifts, except in one district of Nice (Paillon-East) where the proportion of Pallid is clearly higher. Elsewhere in Europe, in the towns where the two swifts coexist, numbers of Common Swifts are higher: for instance in Sofia, Bulgaria (Antonov & Atanova, 2002), and in Marseille, France (F. Dhermain in Barthélemy, 2015). This situation contrasts with the southern part of the sympatric range, where Pallid Swifts are more numerous: in the town of Gibraltar (Finlayson, 1992), in Algeria (Laferrère, 1972) and in Morocco (Pineau & Giraud-Audine, 1979).

In Bastia, the two species shown marked differences on their choice of nesting sites: the Common Swift nests preferably under stone slates and in vertical holes, whereas the Pallid Swift prefers the roller shutter boxes. These differences are also associated with the age of the buildings, the slated roofs cover most of the buildings in the old center and roller shutter boxes equip more recent tenement.

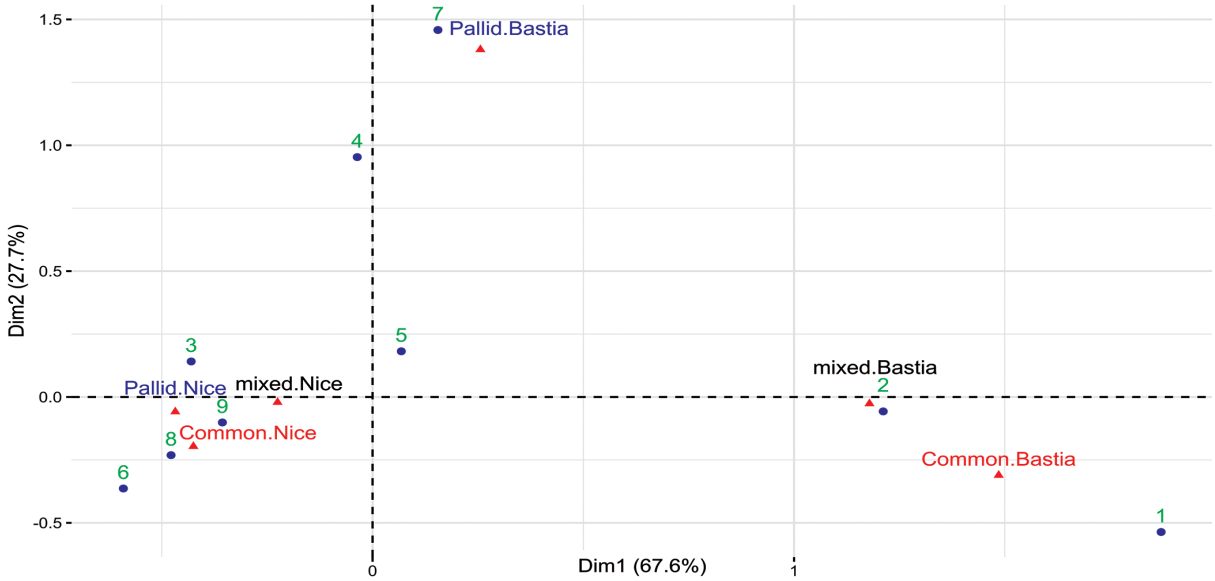

Fig. 4 - Correspondence analysis showing difference in the use of nesting-site supports in Bastia and in Nice. Numbers indicate the type of support (see Tab. 3); Pallid = Pallid Swift, Common = Common Swift, mixed = both swift species. / Analisi delle corrispondenze che mostra la differenza nell'uso dei supporti del sito di nidificazione a Bastia e a Nizza. I numeri indicano il tipo di supporto (vedi Tab. 3); Pallid = rondone pallido, Common = rondone comune, mixed = entrambe le specie di rondoni.

However, in other localities of Corsica the Common Swift occupies also the shutter boxes, like in Ajaccio where it is the only swift species. Such a marked difference between the two swifts was not found in Nice where they occupy in majority sites under-eaves or frames. These results should be analyzed at the light of the main architectural differences between the two towns. Stone slated roofs, which cover a large part of the building of the old center of Bastia, are replaced in Nice by sealed tiles that do not offer interstices favorable for the swifts. On the other hand, the wooden eaves are widespread in Nice and rare in Bastia. The holes in the walls, still frequent in the buildings of the old district of Bastia, are also rare in Nice, due to a wide renovation scheme that begun several decades ago.

The plasticity of nesting site use observed in the Nice and Bastia reinforces observations made within the sympatric range of the two species. In Gibraltar, both species nest in wall holes, eaves and gutters, but the Pallid Swift gives preference to modern buildings and Common Swifts to older habitat (Finlayson, 1992). In the towns of northern Morocco, the two swifts were noted in holes in walls, but the Pallid also used preferentially the roller shutter boxes in the modern buildings (Pineau & Giraud-Audine, 1979). In the Italian Piemonte and in the Swiss canton of Ticino, the two swifts can use holes on the same walls, with different species ratio depending on the locality: less Pallid than Common Swifts in Switzerland (Maumary *et al*., 2007), whereas the opposite was observed in Italy (Cucco & Malacarne, 1987). In Toulouse (France), the two species share the same walls, in which Common Swifts occupy holes with a narrower entrance than those of Pallid Swifts (Frémaux, 2002). In Bulgaria, both species use the eaves of buildings, although Pallid Swift used a wider range of heights and the whole range of recorded nest-cavity types (Antonov & Atanasova, 2002).

Social factors play a determinant role in swifts nest choice (Cucco & Malacarne, 1987). The social habits of a colonial bird group may differ from those of a neighboring colony (Danchin *et al*., 2005), explaining the variety of nest supports used by the same species at different places. For several centuries and perhaps more, the attractiveness of buildings and other artifacts has been very strong among the Apodidae, to become in Europe the main sites for Common and Pallid Swifts. When sympatric, differences in the spatial distribution of swifts in towns and in the use of nest supports seem to reflect mutual exclusion rather than specific ecological requirements. However, mix Common-Pallid pairs was observed in Morocco (Pineau & Giraud-Audine, 1979) and in the Swiss Jura (Oberli *et al*., 2013), and the Common-Pallid population of Bastia shows a rate of hybrid individuals reaching ca. 10% (Cibois *et al*., 2022), suggesting that this small-scale spatial isolation does not prevent hybridization. Interspecific competitive interactions in mixed sites with Pallid-Common, or Pallid-Alpine Swifts (*Tachymarptis melba*) remain to be studied: a study on natural nesting sites (cliffs) also revealed spatial segregation between Alpine and Pallid Swifts but did not provide direct evidences of interspecific interactions (Mazzotto *et al*., 1996). Within monospecific Common Swift colony, where competition for nest boxes is strong, antagonistic behaviors were commonly observed (Genton, 2010). In a competition context for nesting sites between the two swifts in Northern Italy, the superiority of the Pallid Swift was attributed to a chronological factor (Colombo & Galeotti, 1993), considering that the species reaches the breeding areas slightly earlier than the Common Swift. This cannot be however generalized over the sympatric range because arrival dates of the Pallid Swift on breeding grounds vary according to locality: slightly earlier than the Common Swift's arrival in Gibraltar, Northern Italy, and Bulgaria (Finlayson, 1992;

Boano & Cucco, 1989; Antonov & Atanasova, 2002), but after the Common Swift's arrival in Bastia and Nice (Tab. 1).

The recent decline of the Common Swift from the historical center of Bastia is linked to older building restoration and not by the colonization of their nesting sites by Pallid Swifts (Thibault *et al*., 2022). However, we also suspect that the numerical and spatial increase of the Pallid Swift in Bastia (and probably also in Sofia) could have been favored by demographic factors. Overall the breeding season is spread for the Pallid Swift and second clutches are regular in towns, whereas a single, contracted breeding season seems to be the rule for the Common Swift (Tab. 1). But again, generalization might be avoided across their entire breeding range, as Boano & Cucco (1989) found in Piemonte a low productivity for the Pallid Swift, the ratio of second clutch being low and highly variable among years and localities, and the late fledglings penalized by unfavorable autumn conditions.

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