scientific reports

Check for updates

OPEN

Opportunistic airport-collision samples from swifts reveal ant nuptial flight phenology

Odei Garcia-Garin[1,2,3]✉, Xavier Espadaler[4], Ferran Navàs[5], Oriol Castells-Morral[2,5], Marc Ruiz-Sagalés[2], Sílvia Abril[3], Crisanto Gómez[3] & Xavier Ferrer[2]

Ant nuptial flights are critical reproductive events, yet their environmental triggers and timing remain poorly characterised, particularly in Mediterranean ecosystems. Here we evaluate the potential of swifts (*Apus apus* and *Tachymarptis melba*) as biological samplers of alate ants using opportunistic carcasses collected after aircraft collisions at Josep Tarradellas Barcelona–El Prat Airport. By examining the oral cavities of 72 birds collected after bird strikes, ant remains were identified in 31 individuals, allowing us to assess the diversity and temporal distribution of ant flight events in the surrounding region. Sixteen ant species were detected, with *Tapinoma madeirense*, a species belonging to the *T. nigerrimum* complex, and *Tetramorium forte* being most abundant. Environmental variables (temperature, humidity, wind speed, rainfall) did not differ significantly between days with and without ant detections, suggesting that colony-level factors may influence flight timing. The inferred flight periods, with peaks in early morning and evening, align with heat-avoidance behaviour previously reported in several ant species but may also reflect swift foraging patterns. Most recovered alates were males, consistent with known sex ratios. This proof-of-concept study demonstrates that aerial insectivores can provide indirect information on insect reproductive phenology and highlights their potential as bioindicators for monitoring temporal dynamics of ant nuptial flights in Mediterranean landscapes.

Keywords Ant flight, *Tapinoma*, *Tetramorium*, Mediterranean basin, Swift predation, Opportunistic sampling

Ant reproductive strategies are strongly shaped by the timing and synchronisation of nuptial flights. In most species, sexual reproduction and dispersal occur via flight events during which males locate and inseminate females from other colonies, often relying on visual and pheromonal cues[1–5]. These mating flights are highly seasonal and typically synchronised at a population level, likely to maximise outbreeding opportunities and reduce predation pressure through a dilution effect[6–8]. However, the triggers and dynamics of nuptial flights remain poorly understood, particularly in regions with complex climatic conditions such as the Mediterranean basin.

Weather variables, including temperature, humidity, wind speed, barometric pressure, and rainfall, are known to influence the phenology of ant mating flights[9–13]. For instance, Gómez and Abril documented that *Messor barbarus* (Linnaeus, 1767) nuptial flights in the Iberian Peninsula occurred exclusively after rainfall events, highlighting the importance of rainfall as a trigger of reproductive activity[13]. Likewise, studies from temperate and tropical regions have consistently found that flight timing can vary widely between species and even within populations, often depending on microclimatic conditions such as temperature, humidity, and soil moisture[14,15]. One of the major challenges in studying ant nuptial flights lies in their brief duration, unpredictability, and the small size of alate individuals, which precludes traditional tracking methods such as radar or telemetry[7,16]. Until recently, our ability to measure key aspects such as dispersal distance, altitude, and synchrony among colonies was limited. However, recent advances using drone-mounted adhesive traps have provided new insights into the altitudinal preferences of flying ants, revealing that flight height may correlate with morphological traits like

[1]Institute of Aquatic Ecology (IEA), Universitat de Girona, Girona, Spain. [2]Institute of Biodiversity Research (IRBio), Department of Evolutionary Biology, Ecology and Environmental Sciences, Universitat de Barcelona, Barcelona, Spain. [3]Department of Environmental Sciences, Universitat de Girona, Girona, Spain. [4]CREAF, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain. [5]MINUARTIA, Sant Celoni, Barcelona, Spain. ✉email: odei.garcia@udg.edu

wing surface area, and that small-sized species can reach surprisingly high altitudes[17]. These methodological innovations offer promising new avenues for exploring the spatial dynamics of nuptial flights.

Predators such as birds, bats, and dragonflies opportunistically consume alate ants during flight[18–20]. Some aerial insectivorous birds, including swifts (Apodidae), have been proposed to exhibit a foraging specialisation on flying ants during mating swarms[21–23]. Swifts are obligate aerial insectivores that spend most of their active time in flight and forage on a wide range of airborne arthropods. Their diet therefore closely reflects the availability of insects in the aerial environment at a given time. During mass emergences such as ant nuptial flights, swifts can rapidly exploit these temporary but abundant prey resources. Because they forage over large areas and capture insects directly during flight events, their diet can provide indirect information on the timing and composition of aerial insect assemblages. As such, they represent a valuable yet underexplored bioindicator for investigating the phenology of ant flights.

In this study, we investigated the phenology of alate ant flights during spring in the northeastern Iberian Peninsula using the diet of Common Swift (*Apus apus* Linnaeus, 1758) and Alpine Swift (*Tachymarptis melba* Linnaeus, 1758) collected following bird strikes at Josep Tarradellas Barcelona-El Prat Airport. Swifts and other aerial insectivorous birds frequently forage in the open areas both within and surrounding the airport airfield, where ants and other flying insects are readily available. During the spring breeding season, collisions involving swifts occur repeatedly at the airport, providing a recurrent source of opportunistic specimens. In total, 72 swift carcasses were collected across three non-consecutive years (2015, 2018 and 2020). Because swifts are actively foraging at the time of impact, individuals often retain intact prey items in the oral cavity or crop, offering a time-resolved snapshot of recent aerial prey availability. Carcasses are retrieved under the airport's Foreign Object Debris (FOD) management protocol, typically within 15 min of the strike and never later than one hour, ensuring minimal post-mortem degradation of prey remains. Prey items were subsequently examined and identified through microscopic inspection of ant remains recovered from the oral cavity, and throat of the birds.

Bird strikes, although unfortunate, provide an independent biological sampling method of aerial insect availability. We used this opportunity to identify the presence and diversity of alate ants consumed by swifts, and to examine patterns in their flight activity. Specifically, our aims were: (i) to assess the relationship between environmental variables and the occurrence of ant flights, (ii) to determine the diel pattern of alate activity, (iii) to explore synchrony in the phenology of different ant species, and (iv) to examine sex ratios in the most abundant ant species.

Results

Diversity of ant species

A total of 72 swift individuals were collected between late March and early July across three non-consecutive years (2015, 2018, and 2020). A total of 16 species of alate ants were identified in the oral cavity of 31 swifts (Table 1). On the contrary, 41 swifts did not present alate ants in their oral cavities (Supplementary Tab. S1). The three most abundant species were *T. madeirense* (25%), the *T. nigerrimum* complex (34%), and *T. forte* (29%). A total of 15 swifts presented alate ants belonging to at least two different species in their oral cavities, and one swift had 8 species of alate ants (Fig. 1). *T. madeirense* and the *T. nigerrimum* complex were found together in 7 swift samples.

Species accumulation curves differed between months (Fig. 2). In May, taxonomic richness increased rapidly with the first analysed samples and then levelled off after approximately 15–20 swift samples. In contrast, the accumulation curve for June continued to increase across the range of analysed samples and did not reach a clear plateau.

Taxon	Detection (number of swifts)	Identification level
Aphaenogaster ichnusa	1	Species
Camponotus fallax	1	Species
Camponotus lateralis	1	Species
Formica (*Serviformica*) sp.	1	Genus
Lasius niger	2	Species
Pheidole pallidula	1	Species
Plagiolepis pygmaea	1	Species
Plagiolepis schmitzii	2	Species
Solenopsis sp.	2	Genus
Tapinoma sp.	3	Genus
Tapinoma madeirense	10	Species
Tapinoma nigerrimum complex	18	Species complex
Temnothorax specularis	1	Species
Temnothorax sp.	2	Genus
Tetramorium forte	9	Species
Tetramorium immigrans	6	Species

Table 1. Alate ant taxa detected in swift samples collected at Josep Tarradellas Barcelona–El Prat Airport.

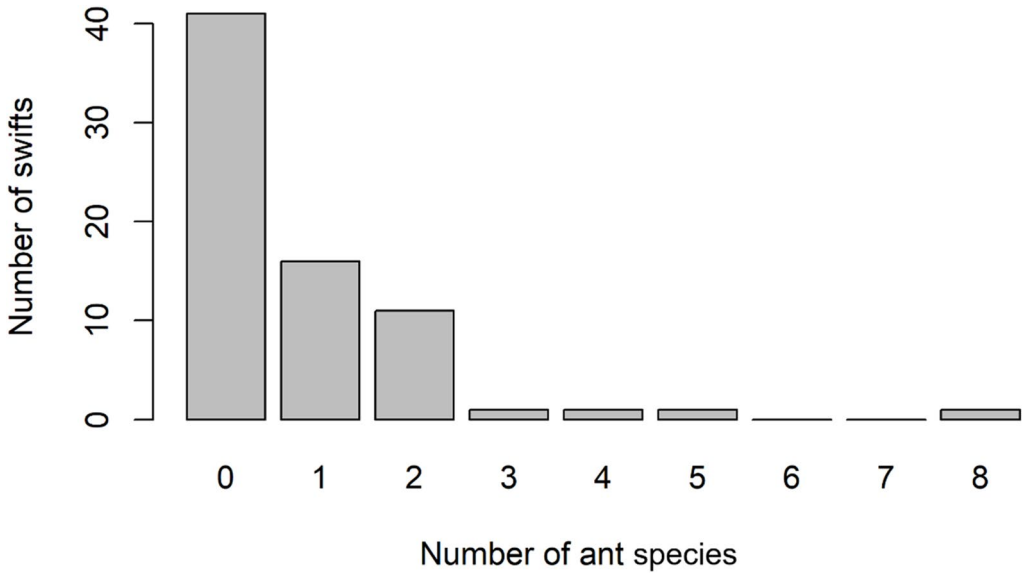

Fig. 1. Distribution of number of ant species per swift. Alate ants were collected from the oral cavity of dead swifts at Josep Tarradellas Barcelona-El Prat Airport.

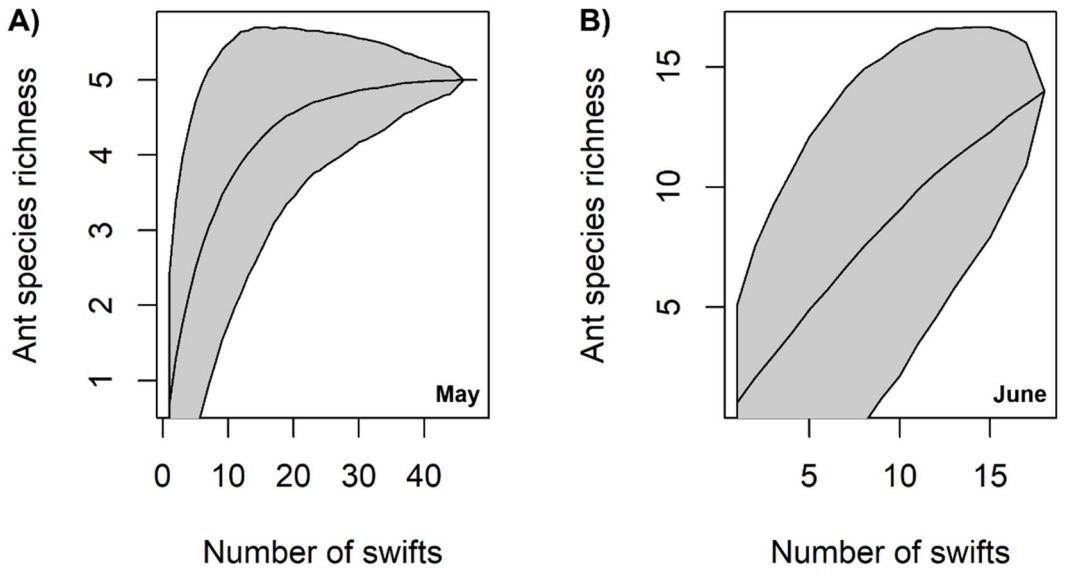

Fig. 2. Species accumulation curves for alate ant species detected in swift-derived samples during May (**A**) and June (**B**). Curves were generated using a randomised species accumulation approach (1000 permutations), where each point represents the expected cumulative number of ant taxa detected as a function of the number of analysed swift samples. Grey shaded areas represent 95% confidence intervals.

Method validation

The temporal dynamics of *T. forte* flights recorded at Barcelona–El Prat Airport closely mirrored those observed in the combined LaMarabunta and Antflight datasets (Fig. 3). Both sources indicated peak flight activity during May and June, with sporadic records in March, April, and July. A non-parametric correlation analysis revealed a positive but non-significant association between swift-derived detections and citizen science observations (Spearman's $\rho = 0.44$, p-value = 0.24), suggesting that both datasets captured similar temporal peaks of *T. forte* flight activity. In terms of daily flight timing (Supplementary Figure S2), the overall distribution of flight hours was also similar, with both datasets showing peaks in the morning and afternoon. A notable difference was observed in the diel distribution of flight records. Observations from LaMarabunta and AntFlights covered a broader range of hours, including numerous records between 12:00 and 18:00 h, whereas such midday events were largely absent from the swift-derived dataset (Supplementary Fig. S1).

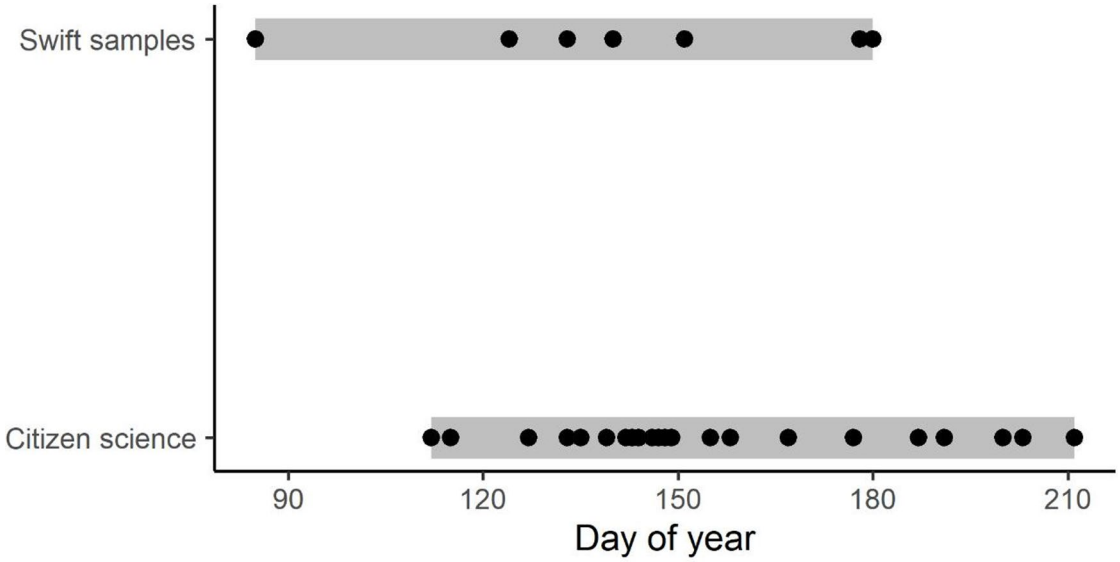

Fig. 3. Temporal occurrence of *Tetramorium forte* nuptial flight events detected using two independent approaches. Black points indicate days on which flight events were recorded from swift-derived samples (top) or citizen science observations from LaMarabunta and AntFlights (bottom). Grey bars represent the overall phenological window (minimum to maximum day of year) detected by each method. The figure combines records from three years of this study (2015, 2018, and 2020), observations from LaMarabunta (2007–2014), and records from AntFlights (2020–2025).

	Rain(mm)	Maximum wind(Km/h)	Humidity(%)	Minimumatmospheric pressure (hPa)	Temperature(°C)
Alate ants were captured by swifts	2.4 ± 6.0	34.1 ± 6.4	54.0 ± 9.7	1012.7 ± 3.9	19.9 ± 2.4
Alate ants were not captured by swifts	4.6 ± 6.2	31.6 ± 3.2	53.6 ± 9.9	1010.9 ± 3.8	19.0 ± 2.9

Table 2. Environmental variables (rain, wind, humidity, pressure, and temperature) recorded during the three days prior to a swift strike (mean ± SD) at Josep Tarradellas Barcelona-El Prat Airport.

Environmental variables and phenology

No relationship was found between environmental variables (i.e. rain, wind, humidity, pressure and temperature) and the day of flight of ants (Kruskal-Wallis rank sum test, p-value > 0.05; Table 2).

Both ant species richness and swift strike activity displayed marked temporal variability across the study period, with several notable peaks occurring between mid-May and late June (Fig. 4). Early in the season (March to early May), ant species richness and swift strikes were generally low (0–2 species per day), with an occasional peak on 26 March (5 species). From mid-May onwards, there was a marked increase in both ant species and swift strikes, with the highest richness and strike activity recorded in late May and early June. For instance, May 30th coincided with the maximum swift strike count (9 strikes) and a concurrent local increase in ant species. Conversely, late June showed peaks in ant species (8 species on 26th June and 4 species on 28th June), although these did not consistently align with increased swift strike counts. Overall, this pattern suggests that while swift strikes may reflect periods of heightened ant flight activity, their temporal overlap was inconsistent. A Spearman's rank correlation analysis confirmed the lack of a significant relationship between daily ant species richness and swift strike activity (rho = 0.31, p-value = 0.084), indicating that the timing of ant alate emergence and swift strike activity did not consistently coincide throughout the season (Fig. 4). Interestingly, three ant species (*Temnothorax sp*, *C. fallax*, *C. lateralis*) detected in late March, and seven species (*P. schmitzii*, *P. pygmaea*, *T. specularis*, *Solenopsis* sp, *A. ichnusa*, *Formica* (*Serviformica*) sp, *P. pallidula*) observed in late June were not recorded during the intervening period from April to mid-June. Moreover, two of the species identified in late March reappeared only in late June (Supplementary Tab. S1).

Hours of ant flights

Most alate ant individuals and ant species were active during specific hours of the day (Rayleigh test, Z = 261.89, p-value < 0.001, Median = 9:00 h, Fig. 5A; Rayleigh test, Z = 11.81, p-value < 0.001, Median = 9:00 h, Fig. 5B, respectively).

Most alate individuals of *T. madeirense* and the *T. nigerrimum* complex were active during specific hours of the day (Rayleigh test, Z = 144.59, p-value < 0.001, Median = 9:00 h, Fig. 6A; Rayleigh test, Z = 189.82, p-value < 0.001, Median = 10:00 h, Fig. 6B, respectively). Alate individuals of *T. forte* were also active during specific hours of the day, particularly following a bimodal distribution (Rayleigh test, Z = 8.44, p-value < 0.001, Modals = 6:00 and

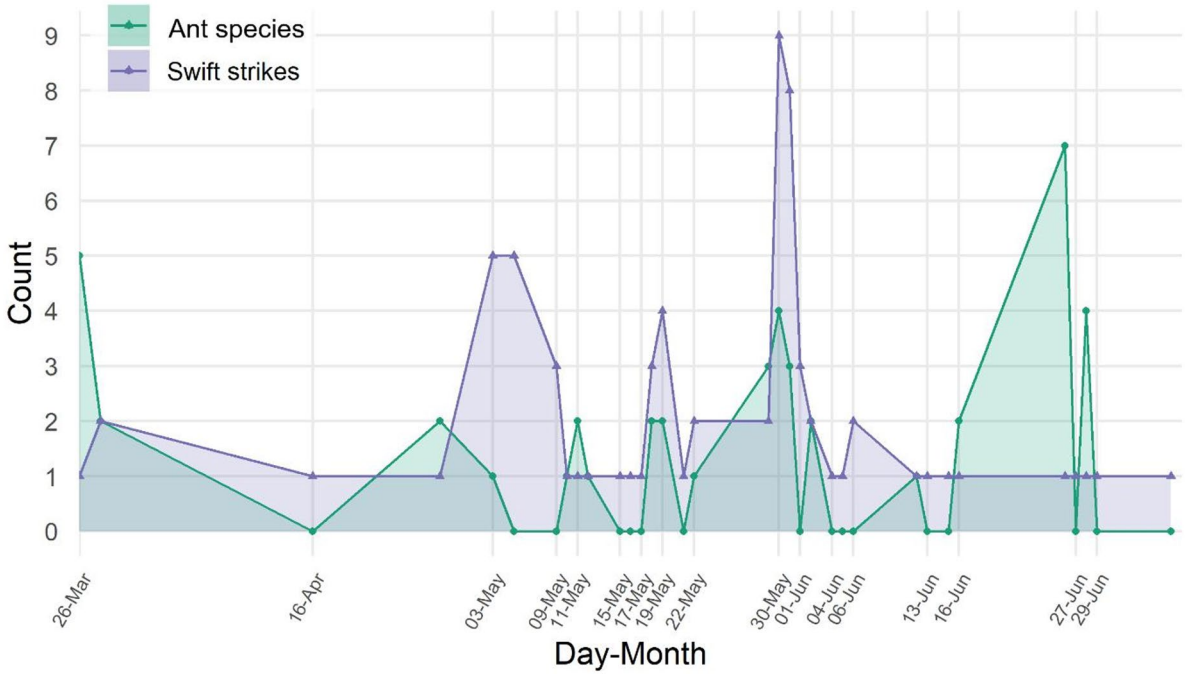

Fig. 4. Temporal dynamics of ant species richness and swift strike activity from March to July at Josep Tarradellas Barcelona-El Prat Airport. The line and points represent the daily count of ant species (green) and swift strikes (violet) recorded each day, with semi-transparent ribbons indicating the cumulative count from zero for each variable. The x-axis denotes the day and month of sampling (day–month) grouping the three years (2015, 2018 and 2020), while the y-axis shows the total count per day.

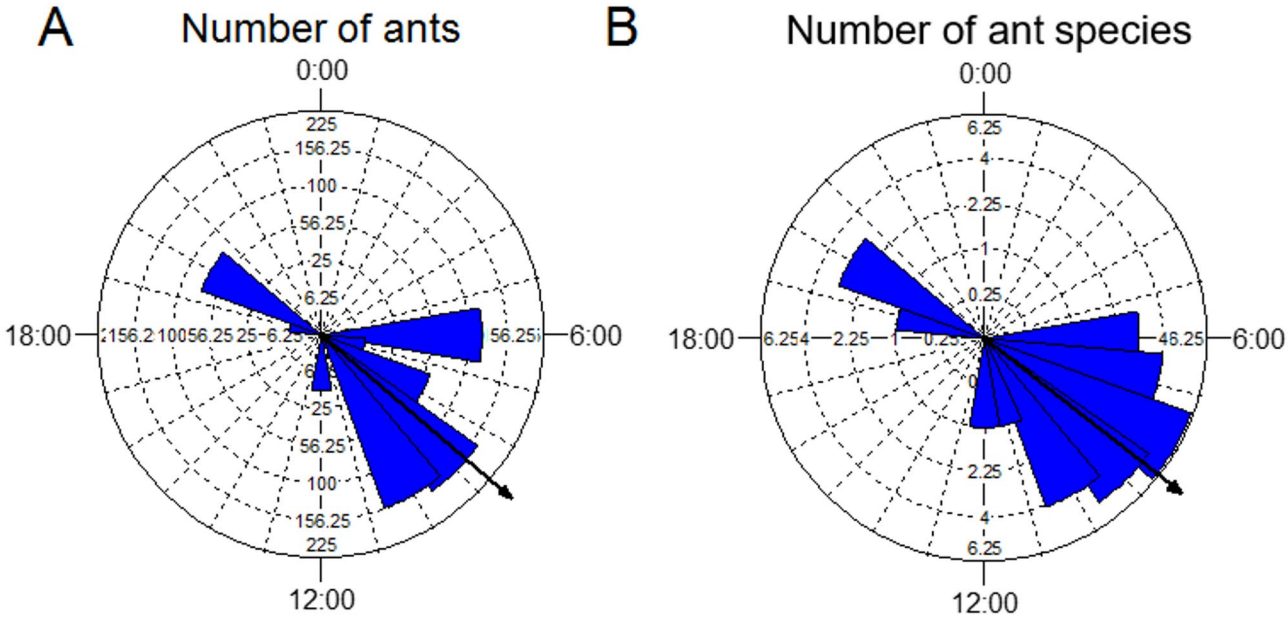

Fig. 5. Hours of ant flights by frequency of ants ($n = 595$) (**A**) and number of ant species ($n = 9$ species, and 28 observations) (**B**). Black arrows indicate the mean vector.

20:00 h, Fig. 6C). A strong correlation was found between the hourly activity patterns of alate *T. madeirense* and those of the *T. nigerrimum* complex (Spearman's rank test, $\rho = 0.74$, p-value < 0.001). Weaker but still significant correlations were also observed between *T. forte* and both *T. madeirense* ($\rho = 0.47$, p-value < 0.002) and the *T. nigerrimum* complex ($\rho = 0.51$, p-value < 0.009).

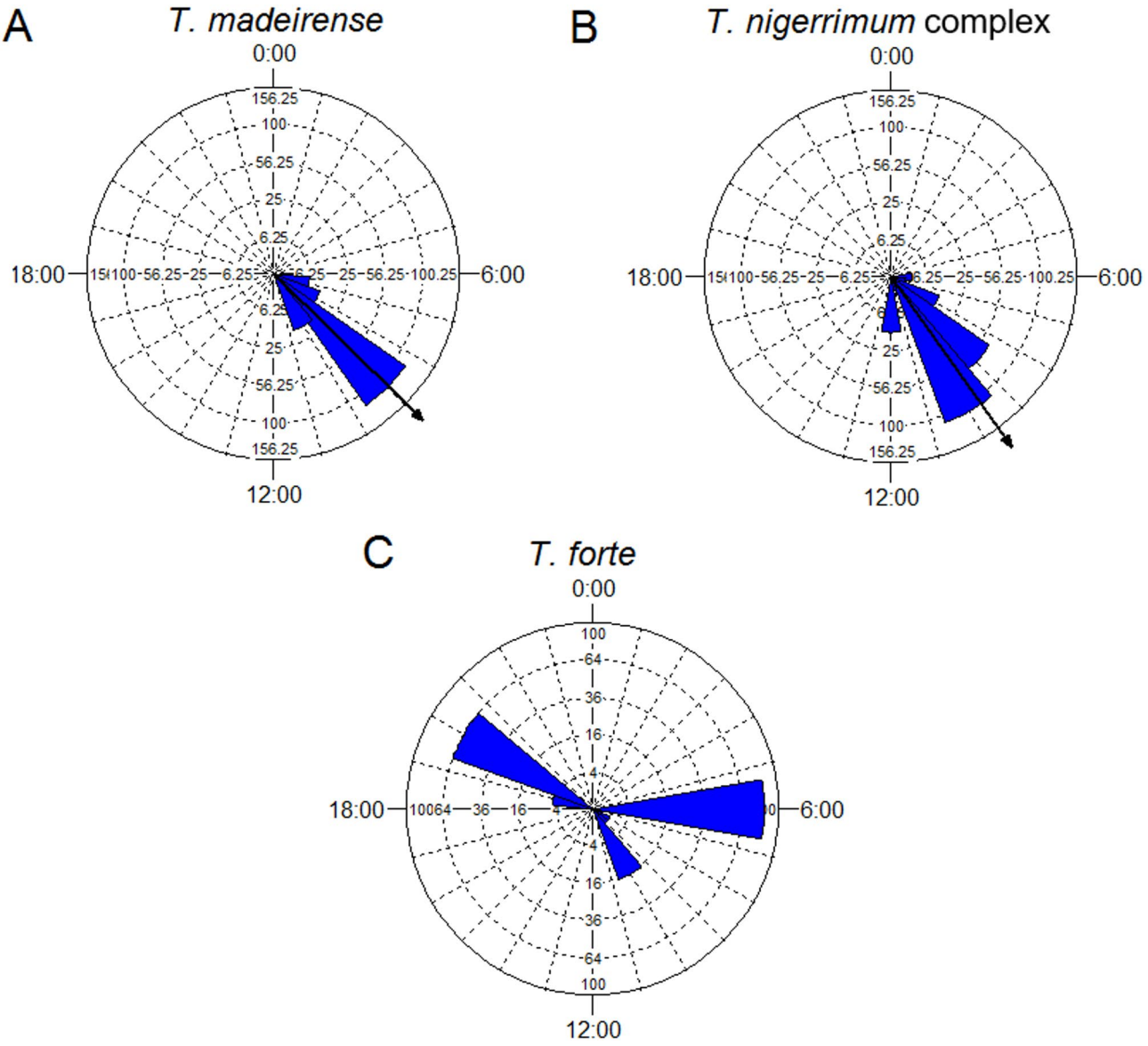

Fig. 6. Hours of ant flights for the three most abundant species (*Tapinoma madeirense* ($n = 148$) (**A**), the *Tapinoma nigerrimum* complex ($n = 202$) (**B**), and *Tetramorium forte* ($n = 171$) (**C**) in the study area of Josep Tarradellas Barcelona-El Prat Airport. Black arrows indicate the mean vector.

Ant flight by sex

No significant differences were found in the number of *T. madeirense* and *T. forte* by sexes (Wilcoxon signed rank test, V = 41.5, p-value = 0.17; Wilcoxon signed rank test, V = 10, p-value = 0.29, respectively). Conversely, the *T. nigerrimum* complex presented more alate males than alate queens (Wilcoxon signed rank test, V = 4.5, p-value < 0.001). Alate males of the *T. nigerrimum* complex were recorded from late March through late June, whereas queens were only detected from the end of May onwards.

Discussion

This study shows that swifts can act as effective biological samplers of alate ant flights. By analysing ant remains in swift carcasses collected after airport collisions, we detected 16 ant taxa and identified clear seasonal and diel patterns of flight activity. The phenology inferred for *T. forte* closely matched independent records from citizen science datasets, supporting the reliability of this predator-based sampling approach. Most detections occurred during late spring and concentrated in the early morning and evening hours, indicating that swift-derived samples can capture important aspects of ant nuptial flight timing.

The temporal dynamics of *T. forte* flights recorded at Barcelona Airport were highly consistent with those documented in the combined LaMarabunta and Antflight online community science datasets. This concordance in seasonal occurrence provided strong support for the validity of the protocol employed in the present study to detect ant flights. Nonetheless, the method used here did not capture *T. forte* during midday hours, unlike in

the aforementioned dataset. This divergence may be attributed to the diurnal activity patterns of swifts, which typically reduce foraging intensity during the hottest hours of the day, either to avoid thermal stress or to exploit more favourable aerodynamic conditions in the early morning and late afternoon[24,25]. As a result, ant flights occurring around midday may be underrepresented in swift-derived datasets, not necessarily because of their absence in the environment, but because detection depends on swift foraging behaviour. Importantly, aircraft movements at the airport remain high during midday hours, indicating that reduced air traffic is unlikely to explain the scarcity of midday detections.

A diverse assemblage of ant species was identified from the swift samples, with *T. madeirense*, the *T. nigerrimum* complex, and *T. forte* representing the most abundant species and accounting for the majority of remains identified. These species are common components of Mediterranean ant communities and opportunistic colonisers of disturbed habitats[26–28], and the genus *Tapinoma* is widely reported as a prevalent member of Mediterranean assemblages[27,28]. This aligned with the findings of Gómez et al.[28], who highlighted the prevalence of opportunistic ant species in Mediterranean landscapes affected by land-use change. Furthermore, the data suggested that swifts may facilitate the detection of exotic species such as *T. immigrans*, which was detected in several swift samples and is known to occur in human-altered environments[29]. The contrasting shapes of the accumulation curves suggest differences in sampling completeness between months. While the May curve approached saturation, indicating that most taxa present in the dataset were likely detected, the June curve did not reach an asymptote, suggesting that additional taxa may remain undetected. This pattern likely reflects differences in sampling effort and the temporal dynamics of ant nuptial flights.

Previous studies have shown that weather variables such as temperature, humidity, wind speed, and precipitation strongly influence the timing of ant nuptial flights across many species and regions[8,9,12,13,15]. In the present study, although environmental conditions were compared between days with and without ant flights, no significant differences were detected. Nevertheless, most flights occurred on days with moderate temperatures and medium–low wind speeds, broadly consistent with patterns reported elsewhere[8,9].

Notably, 16 out of 31 swifts contained individuals from at least two ant species simultaneously, and one individual contained up to eight different species, suggesting significant interspecific overlap of ant flight activity. This supports the notion that different ant species may exploit similar environmental cues, leading to coinciding reproductive flights[8]. Ant flights recorded in swift samples exhibited a distinct temporal pattern. Flight activity peaked notably in late May and early June. These periods broadly corresponded to the reproductive phenology of many Mediterranean and Iberian ant species, as documented in regional citizen-science datasets from the Iberian Peninsula[30–32] and consistent with previous studies highlighting timing linked to temperature and precipitation[9,33]. While certain peaks in ant species co-occurred with increased swift strike activity, suggesting swifts may opportunistically exploit ant mating flights as a food source, no statistically significant relationship was detected between daily ant species richness and swift strike frequency. This suggests that, although swift strikes occasionally aligned with ant flight periods, other factors, such as alternative prey availability, local weather conditions, and swift behaviour, also likely contributed to collision rates[34]. The observation that several ant species were detected exclusively in late March and again in late June, but not in the intervening period, suggests the existence of distinct flight windows for certain species. This temporal pattern may reflect species-specific reproductive strategies adapted to early or late-season conditions, potentially to reduce interspecific competition for mates or to exploit optimal microclimatic niches[9,16]. The reappearance of two species detected in both March and June could indicate either multiple, asynchronous flights within the same population or the presence of cryptic sympatric species with similar morphology but distinct phenologies. These findings underscore the importance of high-resolution temporal sampling to capture the full extent of nuptial flight phenology.

Analysis of swift strike timings suggested that most ant nuptial flights occurred in the morning (09:00–10:00 h) and, to a lesser extent, in the evening (20:00 h). This bimodal pattern aligns with reports that many ant species conduct mating flights during cooler hours of the day to avoid midday heat stress[9,35]. Larger-bodied ants generally require higher temperatures to initiate flight than smaller species[36]. For example, the large leafcutter ant *Atta vollenweideri* (Forel, 1893) performs mating flights in the evening when temperatures remain sufficiently high[35]. In contrast, smaller species such as *T. immigrans* typically initiate flights shortly after sunrise on calm, warm days but suspend activity if temperatures rise excessively[37]. Interestingly, *T. forte* exhibited a bimodal distribution in flight times (peaks at 06:00 h and 20:00 h), which may indicate a flexible mating strategy in response to microclimatic variations[15,36]. A similar bimodal distribution in a Neotropical assemblage has been reported[15]. *T. madeirense* and the *T. nigerrimum* complex co-occurred in seven swift individuals and a strong significant correlation was found between the active hours of both alate ants, which could suggest that these species share similar flight triggers or overlap in mating swarms; this hypothesis merits further testing using more extensive datasets or targeted field observations.

The majority of ant remains recovered from swift samples were males belonging to the *T. nigerrimum* complex, with queens being less frequent. This pattern is consistent with the reproductive biology of ant colonies, where males are generally produced in larger numbers than queens due to lower developmental costs and higher mating competition[9,15]. Furthermore, species of the *T. nigerrimum* complex is highly polygynous and forms extensive supercolonies in the Mediterranean region[38,39]. In such species, queens have fully developed wings but rarely disperse via long-range nuptial flights. Additionally, a temporal mismatch in the appearance of males and queens was observed within the *T. nigerrimum* complex. Male alates were recorded from late March to late June, while queens only appeared from the end of May onwards. This staggered emergence suggests a reproductive strategy in which males are released earlier, potentially allowing them to disperse and position themselves in advance of female emergence. Such timing may enhance outbreeding by promoting mating with queens from different colonies or reduce intraspecific competition during swarming events. Staggered emergence of sexes has been reported in other ant species and may represent an adaptive mechanism to maximise mating success

under variable environmental conditions[9,40]. In the case of *T. nigerrimum* complex, this pattern could also reflect its polygynous structure and limited queen dispersal, where early male release allows sufficient time to locate and inseminate the relatively scarce, philopatric queens. Conversely, the relatively balanced detection rates of queens and males in *T. madeirense* and *T. forte*, compared to the male-biased pattern observed in the *T. nigerrimum* complex, may reflect differences in queen dispersal behaviour and foraging selection by swifts. Queens are generally more nutritious than males and may be preferentially targeted by aerial insectivores during mass flights, as documented in other species[41]. However, since males are typically more abundant in ant mating flights due to their lower production costs[9], a selective preference for queens could result in a roughly equal number of queens and males consumed. In contrast, *T. nigerrimum* complex queens are known to be highly philopatric, often mating near the nest and dispersing only short distances by foot or limited flight[39]. This restricted aerial presence may explain their low detection in swift samples, as opposed to the more dispersive queens of *T. madeirense* and *T. forte*, which engage in longer flights and are more likely to be available as prey. Therefore, the observed sex ratios may result from a combination of reproductive strategies and prey selection rather than differences in visibility or body size alone, especially given that queens of *T. nigerrimum* complex and *T. madeirense* are morphologically similar in size.

Some limitations should be considered when interpreting these results. A clear constraint is the relatively small sample size: 72 swifts were collected across three years, of which 31 contained alate ants. Ant nuptial flights are naturally infrequent and highly synchronised events, typically occurring only on a few days each season for a given species[8,9,13]. Thus, even a limited number of detections can capture the key phenological windows of swarming, and in our case encompassed multiple species and independent flight events. However, this predator-based sampling approach may introduce biases related to swift foraging behaviour, spatial movement, and prey selection. For instance, swifts may preferentially forage during specific hours of the day or target particular prey sizes, potentially underrepresenting some flight events or species. In addition, the temporal resolution of bird strikes may not perfectly align with ant flight peaks, given the broad foraging range of swifts. Sampling effort remained relatively stable across the main period (May and June), but data from earlier months were less abundant, possibly underestimating early flights, and rare species may have gone undetected due to their scarcity or the fragmentary state of their remains.

Overall, this research demonstrates the utility of swift-strike samples as an alternative, cost-effective tool for studying ant flight phenology and community composition in hard-to-sample environments such as airports. Future studies combining direct field observations with swift dietary analyses would provide a more comprehensive understanding of the drivers of ant nuptial flights and their interactions with aerial insectivores in Mediterranean ecosystems. In addition, emerging molecular approaches such as DNA metabarcoding of gut contents could further improve taxonomic resolution and detect prey items that are difficult to identify morphologically, provided that reference barcode libraries for regional ant fauna continue to expand.

Methods

Study area and sampling

All samples were collected at Josep Tarradellas Barcelona-El Prat Airport, situated in the north-eastern Iberian Peninsula. Aircraft movements were used as a proxy for sampling effort (i.e., likelihood of sampling swift mortalities). During the spring sampling period, flight activity remained relatively stable, ranging from 630 to 700 aircraft movements per day. Movements were evenly distributed between 07:00 and 22:59 (representing 4.6–6.5% of daily activity per hour) and were considerably lower between 23:00 and 06:59.

During the study period, whenever a dead swift was recovered following a confirmed bird strike, it was individually bagged, labelled with the date, time, and location of the incident, and preserved at − 18 °C. The airport's FOD management protocol ensured the freshness of the specimens, preventing deterioration prior to analysis. Therefore, the recorded time of each collected swift was used as a proxy for the timing of ant flight activity. Because swifts capture prey while actively foraging and typically retain intact prey items in the oral cavity shortly after capture, the hour at which the carcass was retrieved following a bird strike was assumed to approximate the time at which the ants had been captured in flight.

Swifts (*A. apus* and *T. melba*) typically swallow prey items immediately after capture or aggregate them into boluses to feed nestlings several times per day[22,24]. The presence of intact ant alates in the buccal cavity of struck individuals therefore indicates that prey were captured shortly before collision and can be taken as evidence of recent feeding. Barcelona–El Prat Airport itself constitutes an important foraging area for swifts, as the large open airspace above the runways and surrounding habitats, including croplands and saline wetlands, provides suitable conditions for aerial hunting. Swifts are known to fly close to the ground when capturing prey, which makes them especially vulnerable to collisions with aircraft during take-off and landing, when planes are still flying at low altitude. For this study, only carcasses in good condition, with intact prey items in the mouth and throat, were analysed. It is therefore highly likely that the alates detected were consumed locally, during active foraging over the airport.

Swifts were collected between late March and early July across three non-consecutive years (2015, 2018, and 2020). A total of 72 swifts were collected: 11 individuals in 2015, 54 in 2018, and 7 in 2020. Of these, 31 individuals contained alate ants (7 in 2015, 22 in 2018, and 2 in 2020). Subsequently, they were examined for food balls located in the mouth and crop. Individuals were then dissected, and the contents of the gizzard were also examined. Ants were separated from other prey items and preserved in 70% ethanol for subsequent species identification and analysis.

Identification of ant species

Ant remains were examined under a binocular microscope at low magnification (10–15×) (Supplementary Fig. S2). Ant diversity is relatively low in the Mediterranean region where the swifts were foraging, and early-

season nuptial flights are typically limited in species richness. Identification was based on various preserved morphological structures. In some cases, ant specimens were well preserved; however, in most instances, corpses were fragmented, and identification relied on dismembered body parts. Whenever possible, specimens were identified to the species level. Each ant genus exhibited characteristic morphological features, and when identification was uncertain, comparisons were made with reference specimens (dry-preserved sexual castes associated with workers) from curated ant collections. Samples have been deposited with the Biodiversity Research Institute of the University of Barcelona (IRBio-UB). Details for each taxon are provided below:

A single male *Aphaenogaster ichnusa* (Santschi, 1925) was specifically identified using the recent revision by Schifani et al.[42].

Camponotus fallax (Nylander, 1856): Identification was based on a single queen head capsule, which was uniformly shiny black, with a characteristic anterior clypeal border. The specimen also included a partially preserved mesosoma and gaster. Comparison with preserved dry queens confirmed the identity.

Camponotus lateralis (Olivier, 1792): A queen head capsule with reddish lateral colouration and a pronounced clypeal incision, smaller than *C. fallax*, was attributed to this species.

Lasius niger (Linnaeus, 1758): Identification was achieved using head capsules, sometimes with intact antennae. Morphometric indices and biometric ratios were applied according to Seifert[43], and scape pilosity was short, consistent with *L. niger*.

Pheidole pallidula (Nylander, 1849): Identification was based on head capsules, with the presence, size, and number of hypostomal denticles used to confirm generic and specific identity. Reference specimens included queens associated with workers of all three *Pheidole* species reported from the region (*P. pallidula*, *P. indica*, *P. megacephala*).

Plagiolepis pygmaea (Latreille, 1798) and *P. schmitzii* (Forel, 1895). The combination of antennal morphology, specific relative size of males as compared with queens, and the different pubescence density at the antero-lateral scutum and scutellum in queens, were used to segregate between the three free-living *Plagiolepis* currently known from Spain (see a simple key in Espadaler et al.[44]).

Solenopsis sp.: Queens were identified to genus based on the distinctive mesosoma and petiole morphology.

Tapinoma madeirense (Forel, 1895) and the *T. nigerrimum* complex: These species exhibited a similar diagnostic profile. Identification was based on isolated head capsules and copulatory bulbs, with several whole specimens available. The genus was readily recognised by the characteristic anterior clypeal incision. Differences in mesosoma size and copulatory bulb structure were key to distinguishing the two species. The latter structure was notably distinct between species, and identities were cross-verified using preserved dry samples of sexuals linked to workers. Species-level identification within the *T. nigerrimum* complex was not possible due to the taxonomic complexity and cryptic diversity within this clade[39].

Temnothorax sp.: A queen of entirely dark coloration with a distinctive petiole profile allowed tentative identification at species level. Two additional yellowish queens were also assigned to this genus but could not be reliably identified beyond genus.

Tetramorium forte (Forel, 1904) and *T. immigrans* (Santschi, 1927): Generic identification was based on the distinctive vertical flange of the anterior clypeal border visible on the head capsule. Several queens and males were sufficiently well preserved to allow confident species-level identification. The copulatory bulb, a key taxonomic feature, was often intact and thus used for diagnosis. Species were distinguished based on petiole morphology and overall body size, with *T. immigrans* notably larger. Identification of *T. immigrans* was confirmed using the detailed illustrations of copulatory structures provided by Wagner et al.[29]. Male numbers were determined by inspecting the copulatory bulbs, while queens were identified based on mesosoma size, head width, and petiole morphology. Other *Tetramorium* species known from north-eastern Iberia (e.g., *T. bicarinatum*, *T. lanuginosum*, *T. meridionale*, *T. semilaeve*) were considered but excluded after comparison.

Method validation

To evaluate the reliability of the approach used in this study, temporal patterns of *T. forte* nuptial flights detected from swift-derived samples were compared with independent observations obtained from the citizen science platforms LaMarabunta[30] and AntFlights[31]. *T. forte* was selected for this validation because it was the most frequently recorded ant species in both external datasets and corresponded to the most detected species in the swift samples. Occurrence records from LaMarabunta (2007–2014) and AntFlights (2020–2025) were compiled and standardised by day of year (DOY) and hour of observation. The objective of this comparison was not to reproduce identical daily records between datasets, as the observations originate from different years and swift-derived detections represent opportunistic predator-based sampling. Instead, validation focused on whether both approaches captured comparable seasonal flight windows and temporal peaks of activity. To assess this, days were aggregated into 15-day temporal bins and the number of detections per bin was compared between datasets using a non-parametric correlation analysis (Spearman's rank correlation). In addition, diel flight activity was examined using circular plots based on the recorded hour of occurrence. Differences in the distribution of flight hours between datasets were expected because swift detections depend on predator foraging behaviour and may therefore underrepresent periods of reduced hunting activity, such as midday hours.

Statistical analysis

To evaluate whether sampling effort influenced the number of ant taxa detected through swift-derived samples, species accumulation curves were computed for the months with the highest number of records (May and June). Each swift carcass was treated as an independent sampling unit, and the presence of each ant taxon was recorded as a binary variable. Species accumulation curves were generated using the function specaccum in the R package vegan, applying a randomised accumulation procedure with 1000 permutations. Because the dataset spans three

non-consecutive years with a limited number of detections, analyses were conducted by pooling observations across years to characterise overall seasonal patterns rather than interannual variation.

Environmental variables (i.e., precipitation, wind speed, relative humidity, barometric pressure, and air temperature) were obtained from the open-access platform www.meteoclimatic.net to assess their potential influence on ant flight activity. For this purpose, meteorological conditions during the three days preceding ant-positive swift samples[13] were compared with those preceding swift strikes that yielded no alate ants in the oral cavity. Comparisons were conducted using a Kruskal–Wallis rank sum test.

A Spearman's rank correlation analysis was used to test for a relationship between daily ant species richness and swift strike activity.

To evaluate temporal patterns in alate activity, the Rayleigh test was employed to assess the significance of directional (circular) distributions in flight timing. This test was applied to (i) the total number of alate ants, (ii) the number of ant species detected per hour, and (iii) each of the three most abundant species: *T. madeirense*, the *T. nigerrimum* complex, and *T. forte*.

Correlations between flight hour and the frequency of occurrence for these three dominant species were examined using Spearman's rank correlation test. Additionally, the influence of sex on the frequency of alate individuals (males vs. queens) was assessed for each species using the Wilcoxon signed-rank test.

All statistical analyses were performed using Oriana® version 4.02[45] and R version 4.2.2[46].

Data availability

The datasets supporting the findings of this study are included in the supplementary material of this article.

Received: 12 November 2025; Accepted: 7 April 2026
Published online: 13 April 2026

References

1. Talbot, M. A comparison of flights of four species of ants. *Am. Midl. Nat.* **34**, 504–510 (1945).
2. Kannowski, P. B. The flight activities of formicine ants. *Symp. Genet. Biol. Ital.* **12**, 74102 (1963).
3. Hölldobler, B. & Haskins, C. P. Sexual calling behavior in primitive ants. *Science* **195**, 793–794 (1977).
4. Peeters, C. Morphologically primitive ants: comparative review of social characters, and the importance of queen-worker dimorphism. In: (eds Choe, J. & Crespi, B.) The Evolution of Social Behavior in Insects and Arachnids. (Cambridge Univ. Press, (1997).
5. Noordijk, J. et al. How ants find each other; temporal and spatial patterns in nuptial flights. *Insectes Soc.* **55**, 266–273 (2008).
6. Kaspari, M., Pickering, J. & Windsor, D. The reproductive flight phenology of a neotropical ant assemblage. *Ecol. Entomol.* **26**, 245–257 (2001).
7. Helms, J. A. The flight ecology of ants (Hymenoptera: Formicidae). *Myrmecol News*. **26**, 19–30 (2018).
8. Hart, A. G., Hesselberg, T., Nesbit, R. & Goodenough, A. E. The spatial distribution and environmental triggers of ant mating flights: using citizen-science data to reveal national patterns. *Ecography* **41**, 877–888 (2018).
9. Boomsma, J. J. & Leusink, A. Weather conditions during nuptial flights of four European ant species. *Oecologia* **50**, 236–241 (1981).
10. Depa, Ł. Weather conditions during nuptial flight of *Manica rubida* (Latreille, 1802) (Hymenoptera: Formicidae) in southern Poland. *Myrmecol Nachr.* **9**, 27–32 (2006).
11. Xu, Y. J., Huang, J., Lu, Y. Y., Zeng, L. & Liang, G. W. Observation of nuptial flights of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), in Mainland China. *Sociobiology* **54**, 831–840 (2009).
12. Kim, M., Lim, J. & Wang, S. Predicting mating flights through meteorological cues using multi-scale logistic regression. *Environmetrics* **20**, 275–282 (2009).
13. Gómez, C. & Abril, S. Nuptial flights of the seed-harvester ant *Messor barbarus* (LINNAEUS, 1767) (Hymenoptera: Formicidae) in the Iberian Peninsula: synchrony, spatial scale and weather conditions. *Myrmecol News*. **16**, 25–29 (2012).
14. Do Nascimento, I. C., Delabie, J. H. C. & Lucia, T. M. C. D. Phenology of mating flight in Ecitoninae (Hymenoptera: Formicidae) in a Brazilian Atlantic Forest location. *Ann. Soc. Entomol. Fr.* **47**, 112–118 (2011).
15. Feitosa, R. M., Silva, R. R. D. & Aguiar, A. P. Diurnal flight periodicity of a Neotropical ant assemblage (Hymenoptera, Formicidae) in the Atlantic Forest. *Rev. Bras. Entomol.* **60**, 241–247 (2016).
16. Diehl-Fleig, E. Sex ratio and nuptial flight pattern of the leaf-cutting ants *Acromyrmex heyeri* and *A. striatus* (Hymenoptera, Formicidae). *Insectes Soc.* **40**, 111–113 (1993).
17. Giannetti, D., Schifani, E. & Grasso, D. A. An adhesive drone trap to study the flight altitude preferences of winged ants. *Curr. Zool.* **71**, zoaf002 (2025).
18. Whitcomb, W. H., Bhatkar, A. & Nickerson, J. C. Predators of *Solenopsis invicta* queens prior to successful colony establishment. *Environ. Entomol.* **2**, 1101–1103 (1973).
19. Levin, E., Yom-Tov, Y. & Barnea, A. Frequent summer nuptial flights of ants provide a primary food source for bats. *Naturwissenschaften* **96**, 477–483 (2009).
20. Goffová, K. et al. Does breeding habitat affect the amount of ants in the diet of European bee-eater nestlings? *Biologia* **77**, 157–165 (2022).
21. von Glutz, U. N. & Bauer, K. M. *Handbuch der Vögel Mitteleuropas. Band 9 (Columbiformes–Piciformes)* (Akademische Verlagsgesellschaft, 1980).
22. Cramp, S. *The Birds of the Western Palearctic. Vol. IV* (Oxford Univ. Press, 1985).
23. Garcia-del-Rey, E., Collins, C. T. & Volpone, N. W. Food composition of the endemic Plain Swift *Apus unicolor* in the Canary Islands. *Ardea* **98**, 211–215 (2010).
24. Hedenström, A. et al. Annual 10-month aerial life phase in the common swift *Apus apus*. *Curr. Biol.* **26**, 3066–3070 (2016).
25. Petkliang, N., Gale, G. A., Brunton, D. H. & Bumrungsri, S. Wetland, forest and open paddy land are key foraging habitats for Germain's swiftlet (*Aerodramus inexpectatus germani*) in Southern Thailand. *Trop. Conserv. Sci.* **10**, 1940082917698467 (2017).
26. Arnan, X., Cerdá, X. & Retana, J. Distinctive life traits and distribution along environmental gradients of dominant and subordinate Mediterranean ants. *Oecologia* **170**, 489–500 (2012).
27. Retana, J. & Cerdá, X. Patterns of diversity and composition of Mediterranean ground ant communities tracking thermal variability. *Oecologia* **123**, 436–444 (2000).
28. Gómez, C., Casellas, D., Oliveras, J. & Bas, J. M. Structure of ground-foraging ant assemblages in relation to land-use change in the NW Mediterranean. *Biodivers. Conserv.* **12**, 2135–2146 (2003).
29. Wagner, H. C. et al. : Light at the end of the tunnel: Integrative taxonomy delimits cryptic species in the *Tetramorium caespitum* complex (Hymenoptera: Formicidae). *Myrmecol News*. **25**, 95–129 (2017).

30. LaMarabunta. Ant flight observations and community forum. (2025). Available at: https://lamarabunta.org/.
31. AntFlights. Worldwide ant nuptial flight data. (2025). Available at: https://antflights.com/.
32. Mirmecología. Vuelos nupciales o periodos reproductivos. (2025). Available at: https://mirmecologia.jimdofree.com/vuelos/.
33. Hölldobler, B. & Wilson, E. O. *The Ants* (Harvard Univ. Press, 1990).
34. Taylor, L. R. Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* **32**, 99–117 (1963).
35. Staab, M. & Kleineidam, C. J. Initiation of swarming behavior and synchronisation of mating flights in the leaf-cutting ant *Atta vollenweideri* FOREL, 1893 (Hymenoptera: Formicidae). *Myrmecol News*. **19**, 93–102 (2014).
36. Stukalyuk, S., Akhmedov, A., Stelia, V., Shymanskyi, A. & Netsvetov, M. Nuptial flight in ants (Hymenoptera: Formicidae). *Serangga* **27**, 152–179 (2022).
37. Moss, A. D., Swallow, J. G. & Greene, M. J. Always under foot: *Tetramorium immigrans* (Hymenoptera: Formicidae), a review. *Myrmecol News* **32** (2022).
38. Destour, G. et al. Genetic tracing reveals the role of ornamental plant trade in the spread of invasive ants in Western Europe. *HAL* hal-04617939v2 (2024).
39. Seifert, B. et al. Four species within the supercolonial ants of the *Tapinoma nigerrimum* complex revealed by integrative taxonomy (Hymenoptera: Formicidae). *Myrmecol News*. **24**, 123–144 (2017).
40. Peeters, C. & Ito, F. Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annu. Rev. Entomol.* **46**, 601–630 (2001).
41. Helms, I. V., Godfrey, J. A., Ames, A. P., Bridge, E. S. & T. & Are invasive fire ants kept in check by native aerial insectivores? *Biol. Lett.* **12**, 20160059 (2016).
42. Schifani, E. et al. Unrecognized for centuries: distribution and sexual caste descriptions of West European Aphaenogaster species of the subterranea group (Hymenoptera, Formicidae). *ZooKeys* **1153**, 141–156 (2023).
43. Seifert, B. A taxonomic revision of the Palaearctic members of the ant subgenus Lasius s. str. (Hymenoptera: Formicidae). *Abh Ber Naturkundemus Görlitz*. **66**, 1–66 (1992).
44. Espadaler, X., García, F., Roig, X., Vila, R. & Hormigas Hymenoptera, Formicidae) del Parc del Castell de Montesquiu (Osona, noreste de la península Ibérica). *Bol. Soc. entom arag.* **53**, 223–227 (2013).
45. Kovach Computing Services. *Oriana, version 4.02* (Kovach Computing Services, 2013).
46. R Core Team. R: A Language and Environment for Statistical Computing. (R Foundation for Statistical Computing. (2022). Available at: https://www.R-project.org/.

Acknowledgements

We thank the staff of Centro de Halcones BCN, S.L., contractor of the Wildlife Control Service at Josep Tarradellas Barcelona-El Prat Airport for their assistance in the collection, labelling, and storage of swift carcasses. We also acknowledge the invaluable collaboration from the Safety and Environmental Division of Josep Tarradellas Barcelona-El Prat Airport, led by Juan José Hita, and from Carme Rosell, and Albert Cama, from Minuartia. We are grateful to José Domingo Rodríguez-Teijeiro, Jessica Borrego, Jordi Serra-Cobo, and Joel Rodríguez-Segura for their help with field logistics, laboratory dissections, and valuable suggestions during the preparation of this work. We wish to thank all the members of the Foro LaMarabunta for compiling and sharing valuable data on nuptial flights of Iberian ant species, which were used in this study to validate our results. We are also grateful to the contributors of AntFlights for providing nuptial flight records, and in particular to Rubén Argüeso for kindly supplying the AntFlights dataset. Constructive feedback from two anonymous reviewers and the editor contributed to improve the manuscript. OG-G was supported by a Juan de la Cierva postdoctoral grant (JDC2023-050962-I), funded by MCIU/AEI/10.13039/501100011033 and the FSE+.

Author contributions

O. G-G. and X. F. conceptualized the study, X. E., F. N., O. C-M., M. R-S. and X. F. developed the methodology, F. N. conducted fieldwork, O. G-G. performed statistical analyses, O. G-G. wrote the manuscript and X. E., F. N., O. C-M., M. R-S., S. A., C. G. and X. F. revised the manuscript.

Funding

Partial funding was provided by Josep Tarradellas Barcelona-El Prat Airport.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-026-48191-1.

Correspondence and requests for materials should be addressed to O.G.-G.