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OPEN Sex-differences of survival and seasonal dispersal in a meta-population of greater horseshoe bats

Victor Ronget^{1,2✉}, Maxime Leuchtman^{3,4}, Mary Varoux¹ & Dominique Pontier¹

Demographic parameters such as survival and dispersal play a significant role in shaping population dynamics and genetic structure. However, dispersal remains difficult to estimate in natural populations, as it requires extensive individual sampling and monitoring in the landscape. We conducted a five-year capture-mark-recapture (CMR) study of *Rhinolophus ferrumequinum* in Nouvelle Aquitaine, France, monitoring 6673 individuals across 302 summer and winter roosts. For the first time in this species, we estimated seasonal survival and dispersal for both sexes using CMR models. We found high average adult survivals, with males displaying lower survival than females. Interestingly, both sexes showed high fidelity to summer or winter roosts with no strong marked differences between sexes. Strikingly, we found cues that females travelled on average longer distances than males to reach hibernation sites, challenging previous findings that dispersal is strongly male-biased in this species. Despite limited dispersal of both males and females, previous genetic studies have reported weak spatial genetic structure, suggesting that mating outside maternity colonies maintains gene flow. Our study highlights the importance of studying the full annual cycle monitoring in bats and supports conservation strategies that protect both maternity and hibernation roosts, as well as the landscape connectivity that enables seasonal movements.

Keywords Philopatry, Bats, Capture-recapture, Seasonal movement, Mortality, France, Greater horseshoe bat

Understanding how individuals of a species use space is one of the major questions in ecology. As terrestrial landscapes change rapidly due to anthropogenic activities, it is essential to identify environmental factors and individual characteristics that influence habitat use by individuals¹. Such knowledge is not only important for understanding spatial behavior but also for predicting how landscape structure affects population dynamic and for developing accurate conservation strategies².

In this context, the spatial structures of wild populations are largely shaped by key demographic processes, including survival, reproduction, and dispersal. Among these, dispersal—defined as the movement of young individuals from their natal site to a new breeding site (natal dispersal) or of adults between reproduction sites (breeding dispersal)—plays a central role in determining population connectivity and spatial structures in the landscape³. However, characterising dispersal patterns remains challenging, as it requires accurately tracking the movement of individuals. This is especially true for small, cryptic, highly mobile and nocturnal species such as temperate bats, whose seasonal movements and flight capabilities make them difficult to monitor directly. In particular, many species undertake seasonal movements in autumn to reach hibernation sites. This makes GPS tracking difficult to set up for those species due limitations in size, battery life and device recovery⁴. As a result, most studies on bat movement have so far relied on indirect methods to investigate individual movements and the spatial population structures^{5,6}.

One of the most commonly used indirect methods for quantifying dispersal is the use of genetic tools to describe the genetic structure of a population^{7,8}. As genetic structure reflects the cumulative effects of demographic processes over time, it can be used to formulate hypotheses about demographic rates such as dispersal⁹. Many studies of bat dispersal have relied on this approach^{10–12}. However, it can be challenging to

¹CNRS, Laboratoire de Biométrie et Biologie Évolutive, Unité Mixte de Recherche (UMR) 5558, Université de Lyon, Université Lyon 1, Villeurbanne, France. ²Institute for Organismic and Molecular Evolution, Johannes Gutenberg-University Mainz, Mainz, Germany. ³Nature Environnement, Surgères, France. ⁴France Nature Environnement Nouvelle-Aquitaine, Angoulême, France. ✉email: victor.ronget@gmail.com

formulate demographic hypotheses based on genetic structure alone, particularly for species with complex life cycles and seasonal habitat change⁵. Another method for studying dispersal is to use capture-mark-recapture (CMR) techniques across multiple sites³. This approach allows researchers to directly assess the movements of individuals between sites; however, such monitoring requires a significant investment of resources, as individuals from each site must be monitored every year to obtain accurate demographic parameter estimates using capture-mark-recapture (CMR) models¹³. Moreover, a sufficient number of monitoring sites is essential to adequately cover the entire spatial extent of the population and detect dispersal movements. However, determining which sites to include can be difficult in the absence of prior information on dispersal behaviour. For these reasons, few studies to date have attempted to study dispersal in bats using CMR methods (but see ^{14,15}).

The greater horseshoe bat (*Rhinolophus ferrumequinum*) is a wide-ranging¹⁶ and well-studied temperate insectivorous bat species, currently classified as Near Threatened in Europe¹⁷. It is considered relatively long-lived, with recorded longevity exceeding 30 years¹⁸. In early summer, females gather in maternity colonies, located in caves and various man-made structures, such as tunnels and house attics, where they give birth to a single offspring. Female greater horseshoe bats exhibit strong philopatry to these sites, returning to the same maternity colonies every summer¹⁹. This high site fidelity makes this species especially well-suited for CMR analysis. Until now, most studies on greater horseshoe bats have focused exclusively on maternity roosts²⁰, leaving key parts of the species' life cycle outside the summer largely unexplored. Adult males, for example, are rarely observed at maternity colonies during the breeding season and are generally more difficult to detect, contributing to a persistent knowledge gap regarding male movement and ecology. Both sexes migrate to winter hibernation sites, typically in cold, humid underground environments such as caves, mines, or tunnels. Males and females often share these hibernacula. However, the degree of site fidelity to winter roosts, the extent of seasonal movements, and the potential for sex-biased movement during this period remain poorly understood. Despite strong female philopatry, recent genetic studies of European and Asian populations^{21,22} have revealed unexpectedly high levels of genetic mixing over large geographical scales. It has been hypothesised that this pattern could result from higher male dispersal, consistent with the male-biased dispersal found across a majority of mammal species²³. However, there is currently no direct evidence supporting this hypothesis, as males are hard to observe and even more difficult to capture than females in this species. Additionally, the mating system of *R. ferrumequinum* adds further complexity. In this species, which is characterized by delayed embryo implantation²⁴, fertilization occurs months before pregnancy, suggesting that mating likely takes place at sites other than maternity roosts, generally from late August to October²⁵. Therefore, monitoring roosts outside the summer period is necessary to understand better the processes leading to reproduction and hence to the genetic structure observed in this population.

In this study, our objective was to quantify sex-differences in survival and dispersal in *Rhinolophus ferrumequinum* across the meta-population of Nouvelle Aquitaine in France. Over a five-year period, we conducted an extensive mark-recapture survey encompassing multiple roosting sites during both summer and winter. This monitoring effort allowed us, for the first time in this species, to estimate sex-specific demographic parameters across seasons using a CMR modelling approach. We demonstrated that, with rigorous and large-scale monitoring, it was possible to get reliable demographic information for both females and males in this species. In addition, we aimed to characterize both seasonal and inter-annual movements, in order to better understand the sex-specific spatial ecology of this species throughout its annual cycle. Based on patterns generally observed in most mammalian species²⁶, we predicted that male survival will be lower than that of females. Furthermore, in line with previous genetic studies²² suggesting male-biased gene flow, we expected to find a higher rate of reproductive dispersal in males. Importantly, the spatial extent of our previous genetic analysis²¹ is comparable to that of this CMR study. Both datasets originated from the same network of maternity colonies within the same regional landscape, and the genetic sampling was fully integrated into the long-term monitoring effort that also produced the CMR data. This spatial congruence ensured that any differences in findings would rather reflect the contrasting temporal scales and biological processes captured by each method. Taken together, our results helped clarify the demographic processes underlying the observed genetic structure and contributed to the development of more effective conservation strategies adapted to the complex life cycle and spatial ecology of *R. ferrumequinum*.

Results

Capture demographics

A total of 6673 greater horseshoe bats were PIT-tagged, with approximately 1112 bats tagged per year. The sex ratio of our total sample was biased towards females (5034 females vs 1639 males tagged during the entire study, Supplementary S1 for the number of captures per year and for the age-structure of tagged individuals). We were able to PIT-tag a large number of adult females ($n = 3845$) at summer sites, but only a small number of adult males ($n = 363$), most likely because males did not stay for extended periods in maternity roosts, unlike females. The sex ratio of tagged juveniles was almost balanced (1189 juvenile females vs 1276 juvenile males).

Capture-recapture analysis

In females, the probability of winter capture was influenced by both age class (juvenile, subadult and adult class) and calendar year of recapture, with the best-supported model including the additive effects of time, age and heterogeneity groups of capture (See supplementary S2, Tables S1–8 for model rankings). We identified two groups of individuals with heterogeneous capture probabilities. The probability of winter capture decreased with age, and a large majority of females belonged to the group characterized by low capture probabilities (Fig. 1A). In males, winter capture probability was also best explained by the model including the additive effects of time, age and heterogeneity groups of capture, but most individuals (76.4%) were assigned to the high capture probability group (Fig. 1B). In summer, the best-fitting model indicated that capture probabilities for both females and

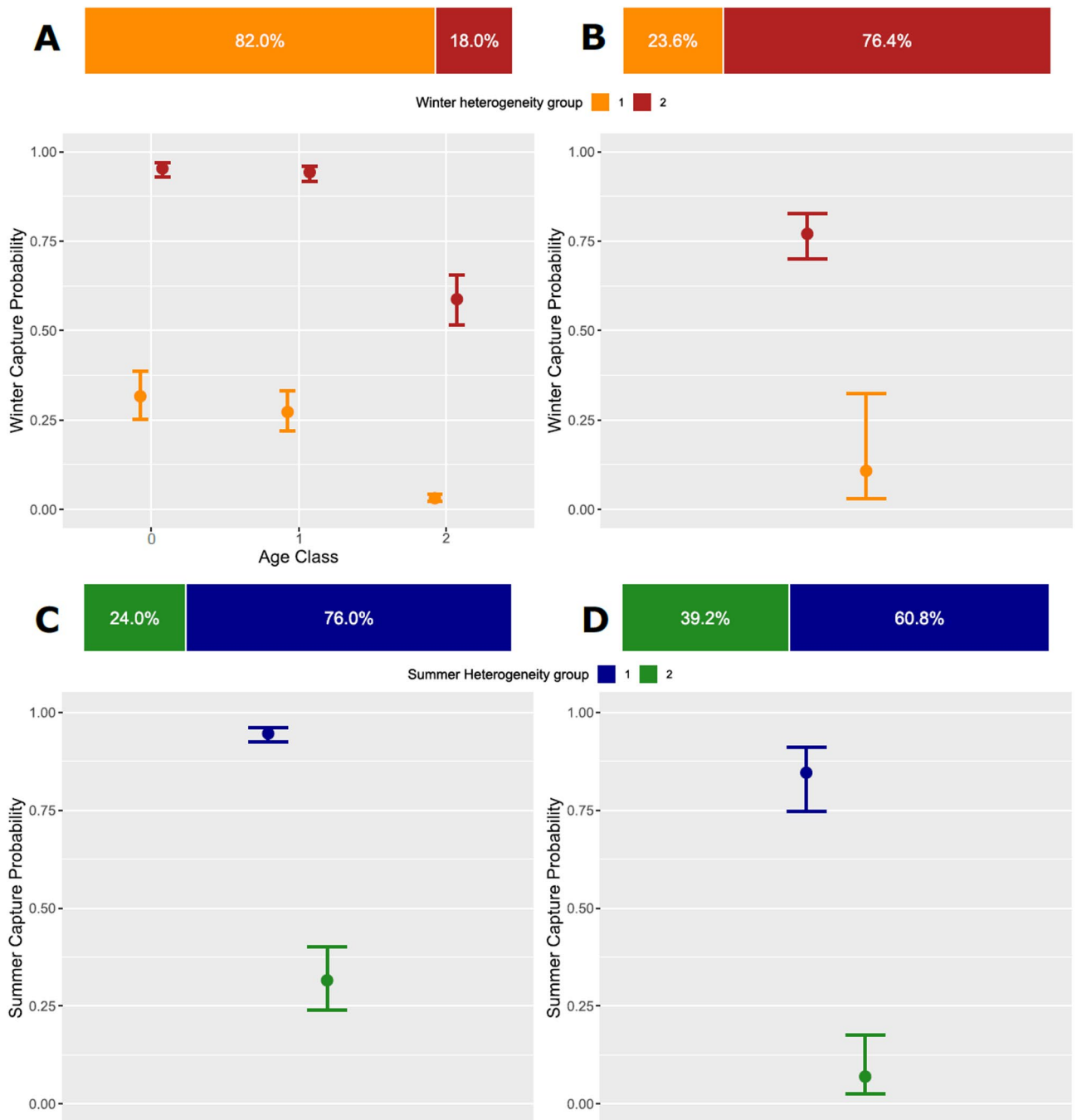


Fig. 1. Mean recapture probabilities during winter period for (A) females and (B) males or during summer period for (C) females and (D) males. Each colour bar represents the percentage of the two capture heterogeneity groups in males and in females. For the winter period, the group with low capture probability is shown in yellow and the group with high capture probability in red, and for the summer period the group with low capture probability is shown in green and the group with high capture probability in blue. Age classes correspond to 0 : juveniles (newborn individuals), 1 : subadults (first year individuals) and 2+ : adults (2 years old individuals or more). All mean parameters values are given with the 95% confidence interval associated.

males varied according to heterogeneity groups and year of recapture. Results were similar between males and females, with most individuals assigned to the high capture probability group (76.0% for females and 60.8% for males, Fig. 1C,D). However, male capture probabilities were lower than those of females during summer (0.946 [0.924;0.962] for females versus 0.846 [0.746;0.911] for males in the groups with high capture probabilities and 0.315 [0.240;0.401] versus 0.070 [0.025;0.175] for males in the groups with low capture probabilities).

For autumn survival probability, the best-fitting model included both age and year effects for males and females. Survival probability was lower for the juvenile age class compared to both subadults and adults

(Fig. 2A,B). On average autumn survival probability was lower for male juveniles compared to female juveniles (average across year for females: 0.711 [0.622;0.801] and for males: 0.568 [0.442;0.700]) but there were no strong differences between adult females and males (average across year for adult females: 0.896 [0.856;0.936] and for adult males: 0.888 [0.819;0.947], Fig. 2A,B). According to the best-fit model, the probability of spring survival depended on both age class and year for females, and on year only for males (Fig. 2C,D). For females, spring survival probability increased slightly with age, from juveniles to subadults and adults. Spring survival probability was on average slightly higher for females (average across year and age classes for females: 0.899 [0.790;0.975] and for males: 0.821 [0.711;0.937]). Interestingly, 2018 and 2020 were both associated with relatively lower spring survival probabilities for females and males.

Winter dispersal, defined as the probability of an individual changing winter roost between two consecutive years (*i.e.*, the complement of winter fidelity probability), was not influenced by age, as the constant model was selected as the best fit. Winter dispersal did not differ between males and females ($dw=0.173$ [0.136;0.217] for females; $dw=0.139$ [0.102;0.188] for males). Summer dispersal, defined as the probability of an individual changing summer roost between two consecutive years (*i.e.*, the complement of summer fidelity probability), was very low in females and was not related to any tested variables. In contrast, summer dispersal was higher in males than in females and decreased with age. The best model included an age effect for males, while a constant model was selected for females ($ds=0.009$ [0.007;0.012] for females; $ds=0.166$ [0.124;0.221] for juvenile males; $ds=0.073$ [0.040;0.130] for subadult males; $ds=0.040$ [0.018;0.086] for adult males).

Seasonal movements analysis

Autumn movement distance between summer and winter roosts varied with age and sex, with the best-fitting regression model including both main effects and their interaction, based on AIC ranking (Fig. 3, Table S9). For females, average autumn movement distance increased with age (37.5 [33.7;41.6] km for juveniles; 32.6

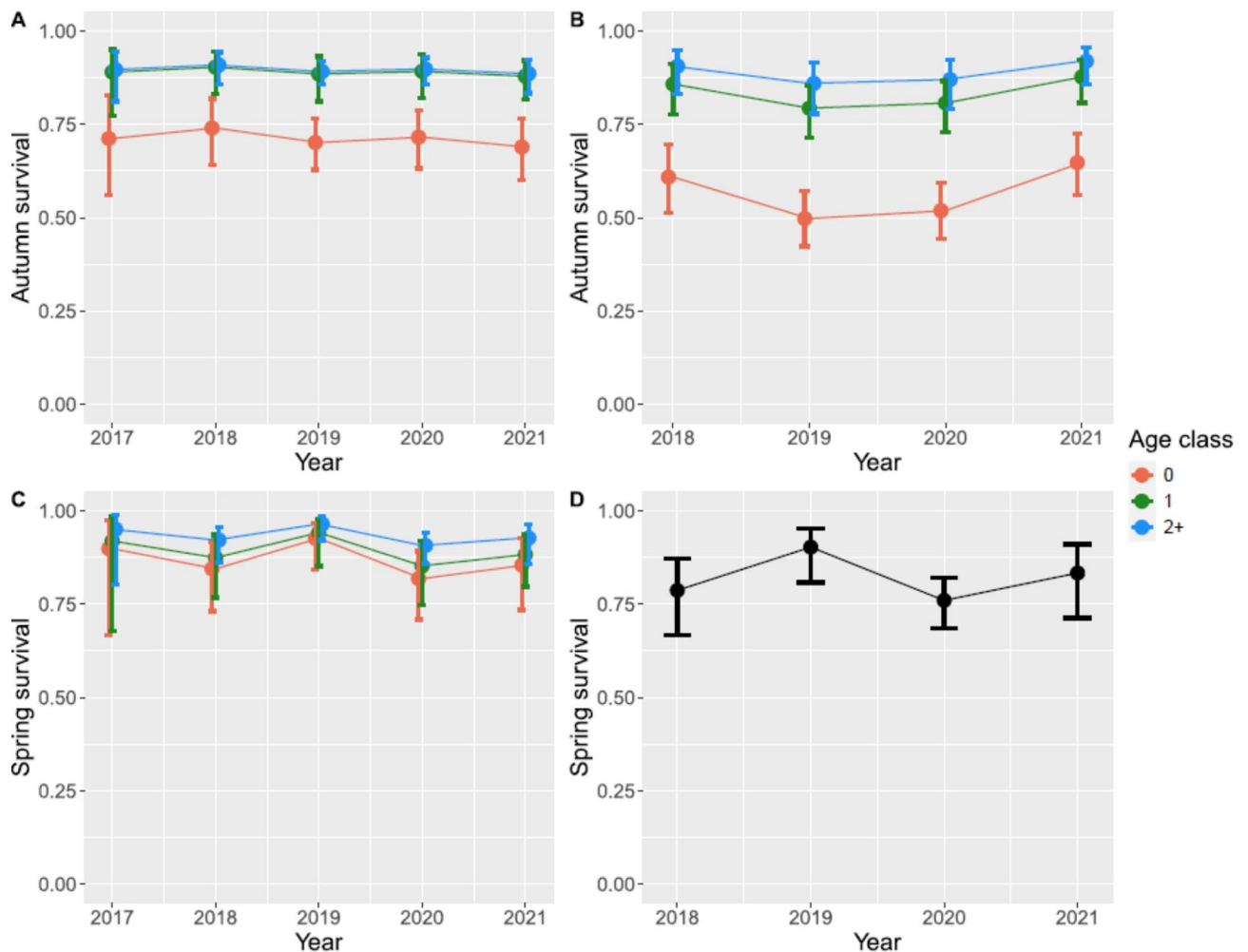


Fig. 2. Average survival probabilities during winter period for (A) females and (B) males or during summer period for (C) females and (D) males. All mean values are given with the 95% confidence interval associated. Age classes correspond to 0 : juveniles (newborn individuals), 1 : subadults (first year individuals) and 2+ : adults (2 years old individuals or more). Survival parameters associated with the best-fit model based on AIC ranking for females and males are presented.

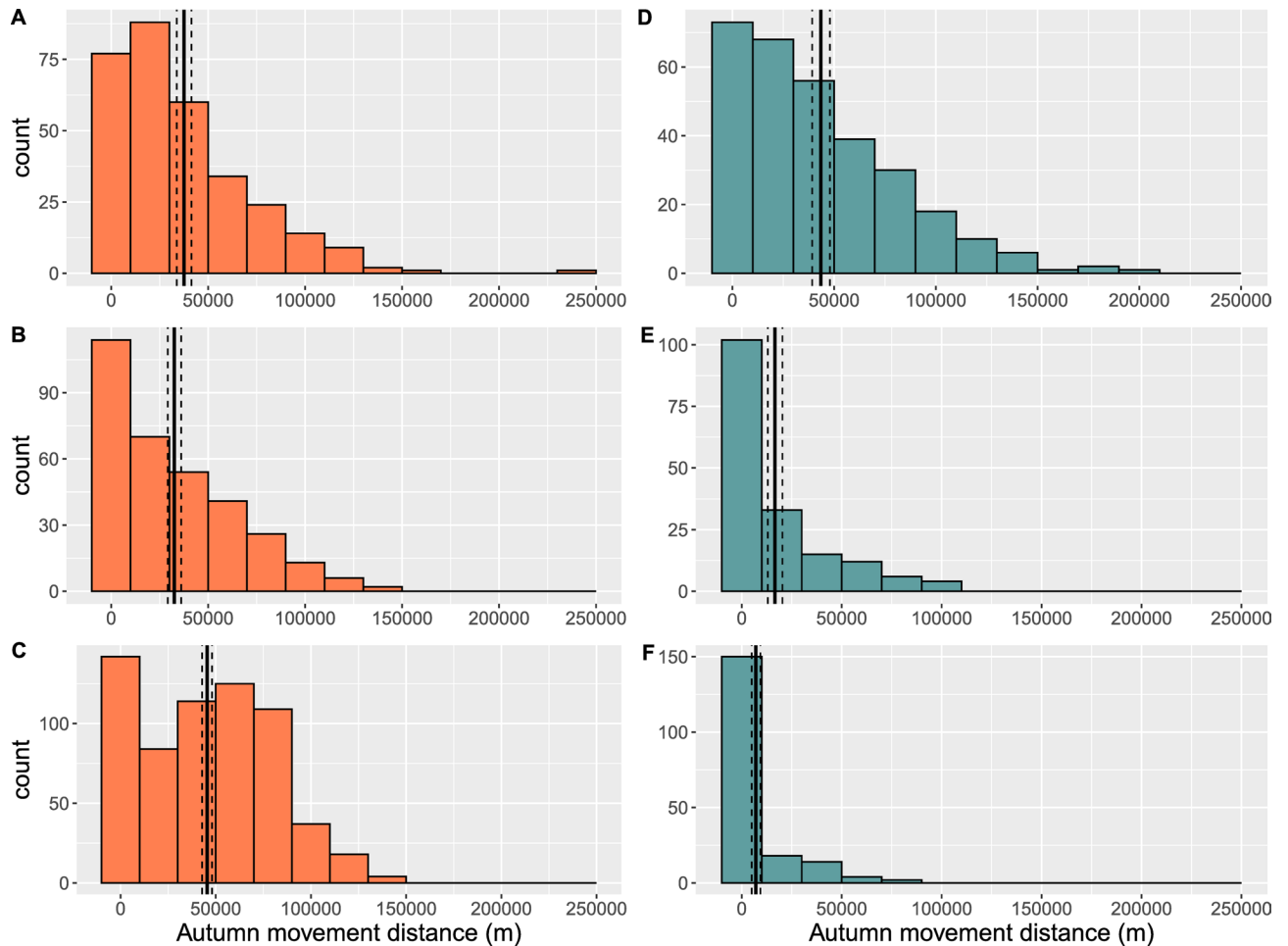


Fig. 3. Distribution of movement distance for females in autumn (A) Juveniles, (B) Subadults, (C) Adults, and for male (D) Juveniles, (E) Subadults, (F) Adults in kilometers. Black vertical lines represent the average of each distribution and dashed black lines represent the bootstrapped 95% confidence interval associated.

[29.1;35.9] km for subadults; 45.5 [42.9;48.1] km for adults), while for males, it decreased with age (43.4 [39.2;47.9] km for juveniles; 16.6 [13.1;20.4] km for subadults; 7.1 [5.0;9.3] km for adults). Juvenile males had a higher autumn movement distance than juvenile females. For subadult and adult males, autumn movement distance was much shorter than for females. Winter fragmentation, defined as the probability of two individuals from the same summer roost to end up in the same winter roost, differed strongly between the sexes, with males more likely to stay together and migrate to the same winter roost than females (winter fragmentation index for females: 0.788 [0.736;0.832]; winter fragmentation index for males: 0.587 [0.465;0.699], Fig. 4). The winter fragmentation indices did not depend on the sample size of the summer roost of departure ($t = -0.639$, $P = 0.525$) or on the number of winter roosts monitored in the vicinity of each summer site ($t = -1.483$, $P = 0.144$).

Discussion

Most studies in bats are carried out in maternity roosts, with the result that winter ecology and in particular dispersal patterns remain largely unknown for most temperate bat species^{5,27,28}. Our study sheds new lights on the demography of the greater horseshoe bat over its entire life cycle. Our large-scale longitudinal monitoring allowed us to obtain demographic records not only for females but also for males. Prior to this study, no information was available on the location of males outside the reproduction period in autumn¹⁹. Adult males were generally considered unobservable and difficult to capture during summer and winter. Our capture-mark-recapture analysis showed that males were in the vicinity of maternity roosts in summer, but it is still unclear whether they remain permanently in these roosts, as we only have information on their passage through the entrance to a roost. Using the high capture probabilities of males and females, we were able to highlight differences in survival and dispersal probabilities between the sexes.

Patterns of survival probabilities were in accordance with what was expected in other bats and mammals. The most critical period for survival was the autumn period associated to the first months of life for both sexes, in line with the common patterns observed in other bat species^{29–31}. Juveniles are likely frailer during that period compared to adults due to their lower size and lack of experience³². Adult survival probabilities were concordant with the long lifespan observed in previous records of individuals reaching over 30 years of age

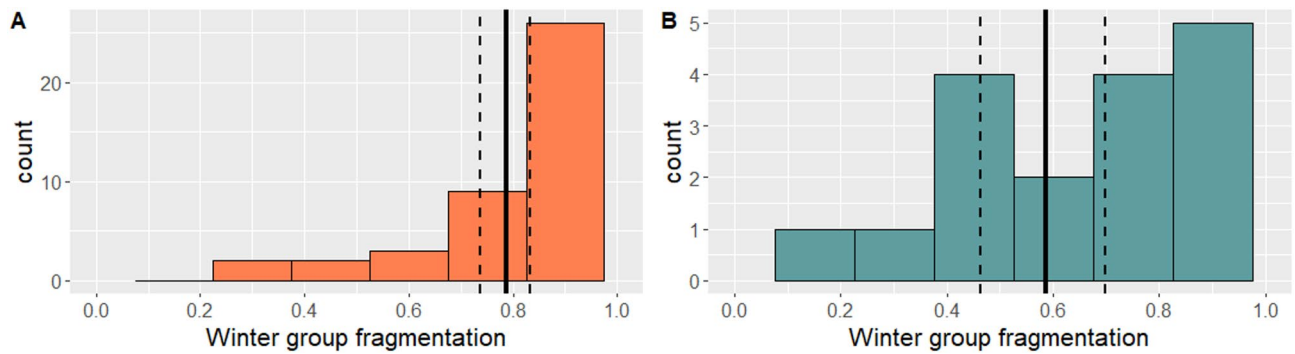


Fig. 4. Distribution of winter group fragmentation index for each summer roost/year for (A) females and (B) males. Black vertical lines represent the average of each distribution and dashed black lines represent the bootstrapped 95% confidence interval associated.

in this species^{18,33,34} but also in other closely related species^{35,36}. Overall, males had on average lower survival probabilities for most of ages. This pattern has also been found in most bats^{37,38} and other mammals²⁶. The female-biased survival was even more marked in juveniles (0.711 in juvenile females vs. 0.568 in juvenile males), whereas *R. ferrumequinum*, like most European bat species, shows a female-biased sexual dimorphism, with females being slightly larger than males^{39–41}. In mammals, high male-biased sexual size dimorphism has been associated to higher sexual competition between males leading to males experiencing higher costs⁴². Here the modest size difference between sexes is unlikely to fully explain the observed survival bias, it may interact with other factors. Another possible explanation for this difference in survival probability is that juvenile males may disperse beyond the monitored area or settle in non-monitored, independent roosts, resulting in an apparent lower survival rate due to permanent emigration. Although our monitoring covered a large number of known roosts, the possibility that some males use alternative or less detectable roosting sites cannot be excluded. Whether males tend to roost independently or outside the main monitored network remains uncertain and warrants further investigation, as it may significantly affect apparent survival probability estimates. A comparable sex-biased survival pattern has been found in another bat species (0.48 vs. 0.67 in juvenile males and females, respectively, of *Myotis nattereri*³⁰), and could be related to non-mutually exclusive mechanisms, such as a different foraging ecology, ‘incautious’ behaviour of juvenile males, or different strategies used by males to move to hibernation sites^{43–45}. We did not find any strong differences between autumn and spring survival probabilities in adults. We expected lower survival probabilities for adults after hibernation compared to before hibernation, possibly due to the depletion of fat reserves at the end of hibernation⁴⁶ or adverse environmental conditions, including reduced insect availability leading to food shortages^{47,48}. This absence of decrease after hibernation in adult survival probability did not match previously reported patterns in some bat species and in hibernating mammals in general^{31,49}, with adult summer survival probability being typically lower than autumn/winter survival probability, indicating that spring/summer is a critical season. Possible explanations for this discrepancy in our study could be linked to local climate conditions. Despite the absence of a critical survival period overall, there were between-year variations in spring survival probabilities with synchronous variations in males and females. The years 2018 and 2020 were characterized by lower spring survival probabilities. We were only able to associate 2018 and 2020 with higher spring precipitation levels compared to 2017, 2019 and 2021 (See Supplementary S2, Table S10 for precipitation levels and average temperatures close to the study sites), although more years are needed to robustly test this potential climatic effect using appropriate statistical methods. Climate may influence energy balance of bats in a number of ways both during hibernation and when they emerge from hibernation. For most bat species, it is known that colder hibernacula allow individuals to reduce their metabolic rate more efficiently^{50,51}. Furthermore, in some species a large amount of winter energy reserves is spent during arousals^{52,53} and arousals may be more frequent in warmer hibernacula^{54,55}. Last, low prey availability after the end of hibernation, due to poor weather conditions and especially high precipitation⁵⁶, may also be critical for individuals especially vulnerable at the end of hibernation. Investigating in the future environmental factors behind variations in spring survival is thus important for understanding the population dynamics of the greater horseshoe bats and for identifying their vulnerabilities. There is an urgent need to explore the patterns of physiological adaptation and survival of hibernating bat populations in the face of the rapid climate changes they are currently facing to guide effective conservation actions⁵⁷.

Females were extremely philopatric, as has been demonstrated in other greater horseshoe bat populations¹⁹. Even if we did not directly quantify natal dispersal in this study, the probability of dispersal occurrence for females from their breeding site each year was below 1% and was therefore considered very rare, hinting at a very high fidelity of females to the same summer site during their lives. Male summer dispersal probability was higher than that of females, yet most males remained at their previous summer site across years with a dispersal probability lower than 5% for adults. There were some occurrences of greater dispersal probabilities especially in juveniles, but the proportion remained low. Our results, therefore, indicate that males are also highly philopatric—an unusual and still poorly understood trait in mammals^{58,59}. Natal philopatry in males has been documented in two related bat species, *Rhynchonycteris naso*⁶⁰ and *Saccopteryx bilineata*⁶¹, both of which show a territory-based mating tactic in the roost. In *R. ferrumequinum*, for which females and males

from different maternity colonies meet in underground cavities in our study area⁶², remaining in the natal colony may offer advantages such as avoiding high costs associated with dispersal and better knowledge of local food resource distribution. Although males do not have the same constraints as females during the summer, especially regarding maternity^{5,63}, the birth site could still be a place with a sufficient amount of resources, and they might also have acquired experience from the previous year on how to navigate the landscape near that site. Prolonged female and male natal philopatry and little inter-colony female exchange suggest that genetic mixing at large geographic scale²¹ occurs mainly via extra-colony mating in hibernation sites⁶². Our preliminary results on fragmentation have confirmed this hypothesis, with a high proportion of individuals not remaining together when moving from summer sites to winter sites (21.2% for females and 41.4% for males). The observed sex differences in the spatial distribution between summer sites and hibernation sites could therefore reflect the reproductive strategies of males and females. To better understand the mechanisms underlying male philopatry, the fragmentation pattern of maternity colonies towards hibernation sites, and sex-specific selection of hibernation sites, new data will be needed. In particular, long-term individual tracking, detailed habitat characterization of transitional and winter roosts, and behavioral monitoring during the pre-hibernation and mating periods would be valuable. Additionally, studying the physiological state of individuals (e.g., fat reserves, stress markers) and integrating acoustic monitoring during the mating season could help clarify the roles of energetic constraints and reproductive tactics in shaping these movement patterns.

Capture probabilities during the winter were especially low, and some individuals were not even capturable at all during the winter. One plausible explanation for this result is that some individuals were not detected during winter because they either left the monitored area or used winter roosts that were not part of our survey. While we found that most individuals travelled on average less than 50 km—consistent with findings in other populations³⁴—some travelled more than 100 km. Moreover, we observed that individuals often moved to a wide range of smaller winter roosts across the landscape in autumn, many of which may not have been monitored. This high degree of fragmentation could explain the apparent absences and lower detection rates. We chose to focus our sampling effort on the winter sites with the highest number of individuals, under-sampling hibernation sites with few individuals. Despite our extensive sampling and monitoring effort, obtaining demographic data during the winter period remained challenging. Our conclusions could be affected by the fact that a small proportion of the population was recaptured in winter and that, consequently, we can only use the partial capture information as cues to predict the movement patterns of individuals in this meta-population during the winter migration. We found no sex-differences in winter site fidelity, dispersal between winters was higher than in summer, but a large majority of individuals chose to remain on the same roost for hibernation between winters. Similarly, a high fidelity of individuals to wintering sites was also found in other European bat species¹⁵. However, we found striking differences in autumn movements between the sexes. Wintering distances were higher for females compared to males with an excess of females moving around 50 km. In contrast, male adults did not move much and likely stayed in the same place in summer and winter. Similarly, females were moving to a much larger variety of wintering sites than males during the autumn. This result is consistent with the fact that most males stayed in the same site for winter. Why females are moving longer distances to reach their wintering sites while males do not is still unknown, as we might expect similar wintering requirements between the sexes. Interestingly, this pattern of higher movement rates for adult females was also found in the little brown bat⁶⁴. One possible explanation is that females may be selecting higher-quality wintering sites to compensate for the higher energetic cost of reproduction. Additionally, these broader movements may contribute to reducing the risk of inbreeding by increasing the likelihood of encountering unrelated mates. This could be particularly relevant if mating occurs not only in autumn but also at the end of winter²⁵.

In conclusion, and to answer the question whether males disperse more than females in the greater horseshoe bat, we found no evidence of such a pattern in our monitoring. Both males and females showed high fidelity to summer and winter sites. Although we found some evidence of a greater ability to move in females, low winter capture probabilities prevent us from generalizing this pattern to all individuals in the population. This study is a first step towards a better understanding of the life cycle of temperate bats outside the maternity period. Our findings have highlighted that wintering movement might be more complex than initially assumed on the basis of previous genetic studies¹⁵. Notably, although our demographic results reveal strong philopatry and limited dispersal in both sexes, previous genetic studies have shown a surprisingly low level of genetic structure over large geographic scales²². This apparent contradiction can be reconciled by the occurrence of mating outside the maternity colony during autumn, when individuals from several maternity colonies congregate at shared transit and/or hibernation sites⁶¹. Mating outside the natal colony—rather than permanent dispersal—could therefore be sufficient to ensure genetic connectivity in *R. ferrumequinum*. Our results also have important conservation implications. While many conservation efforts currently focus on protecting key hibernation sites (Natura 2000, Arrêtés Préfectoraux de Protection de Biotope, etc. in France), our study highlights that females and most males are highly dependent on their maternity colonies. Protecting these summer roosts is therefore just as crucial. For a long-lived species such as the greater horseshoe bat, measures to protect maternity colonies and hibernation sites, as well as the landscapes that link them⁶⁵, is of particular importance in times of global climate change with an expected increase in temperatures⁶⁶.

Methods

Ethics statement

All experimental protocols with bats described in this study were authorized by the Ministry of Ecology, Environment and Sustainable development and approved by the Museum National d'Histoire Naturelle over the period 2015–2020 (approval no. C692660703 from the Departmental Direction of Population Protection, Rhône, France) and over the period 2021–2025 (approval no. D692660703 from the Ministère de l'Enseignement

supérieur de la recherche et de l'innovation). Capture and handling protocols were carried out in accordance with followed published guidelines for treatment of animals in research and teaching.

Study Site

The *R. ferrumequinum* maternity colonies included in our monitoring program are distributed across a wide range of landscape types, reflecting the environmental diversity of the Nouvelle-Aquitaine region. Some colonies are located in traditional bocage landscapes, characterized by a dense network of hedgerows, permanent meadows, and small woodlots, providing highly suitable foraging habitats for insectivorous bats. Others are situated in more forested areas dominated by deciduous, coniferous, or mixed forests, offering extensive woodland cover. Several colonies are also found in agricultural settings, with landscapes dominated by temporary meadows, vineyards, or poplar plantations, which tend to be more open and fragmented. Finally, some colonies are located in orchard-rich zones or areas of woody moorland, contributing further to the diversity of the landscape matrix. This broad environmental variation ensures that our dataset captures a representative range of habitat compositions likely to influence both survival and movement patterns. Hibernation sites used by *R. ferrumequinum* were equally diverse, encompassing both natural and anthropogenic underground structures. These included natural caves and karstic cavities, as well as disused mushroom cellars, tunnels (e.g., former railway or mining galleries), underground quarries, and, more occasionally, large, vaulted basements or cellars. These sites typically provide stable microclimatic conditions (temperature and humidity), favorable for hibernation. Their diversity reflects both the ecological flexibility of the species and the historical availability of such structures in the region. The study site comprised 27 maternity (summer), 33 mixed, and 231 hibernation (winter) roosts across the Nouvelle Aquitaine Region in France (Fig. 5). Summer and winter roosts were initially identified based on previous surveys and observations documented by naturalists prior to the start of this study. Mixed roosts serve as both hibernation and maternity sites. Maternity colonies correspond to the roosts where female bats gather from May to August, give birth, and rear their young⁶⁷. In August, individuals leave their summer roosts and disperse to hibernation roosts where they hibernate from around October–November to April.

Field data collection

Each summer from 1st of June to 1st of September, harp traps (Faunatech, Mount Taylor) were set up to capture individuals at the entrance of summer roosts. We removed the individuals from the harp trap and placed them in individual cotton bags before handling them. Upon first capture individuals were sexed and aged using

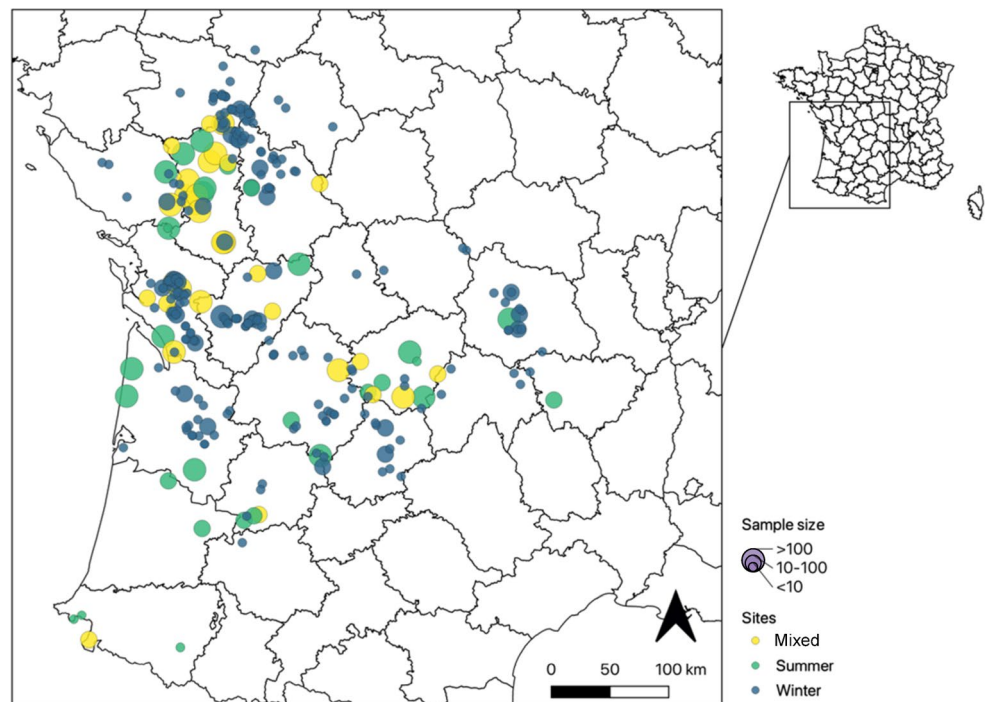


Fig. 5. Location of each study site across Nouvelle Aquitaine. Sample size is defined as the number of capture and recapture event combined for each site. Summer sites correspond to sites when individuals were only captured during summer period (1st June to 1st September), winter sites correspond to sites when individuals were only captured during winter period (1st November to 1st March) and individuals were captured during both periods in mixed sites.

morphological cues to classify the individual as juvenile (absence of a cartilaginous core at the metacarpal-phalangeal joints and colour coat). Juveniles are born with a grey coat, and the coat colour will change over time until they moult. According to what we have observed with the greater horseshoe bat (Leuchtman *et al.*, personal observations), juveniles born in summer do not begin their first moult until after winter. Juveniles therefore remain grey until the following spring. We used the following codes age 0 (juvenile), age 1 (sub-adult), age 2+ (adult) to classify the age of the individuals. Individuals were marked using Passive Integrated Transponder (PIT) tags (Biomark APT 12 FDX-B) inserted under the skin using a sterilised 12-gauge needle, with the injection site sealed with surgical adhesive to minimise tag loss. All PIT-tags were checked for correct function using a hand-held PIT-tag scanner (Biomark® GPR Plus) both before and after insertion. Summer capture ran from early June to end of August. After the first capture, tagged individuals were monitored using continuous automatic antennas connected with the Biomark® HPR Plus or the IS1001 reader, in summer and in some winter roosts. Automatic antennas were placed at the entrance of the roosts so we could monitor the specific date each tagged individual enters the roost. In most of winter roosts no automatic antenna was installed because individuals were much more dispatched in the landscape resulting in less populated winter roost. During winter individuals are entering a hibernation phase and are typically not moving anymore. Hand antennas were used to check tagged individuals in those winter roosts. Data were collected from the automatic antennas approximately monthly in all equipped sites. Individuals were monitored from summer 2016 to summer 2021. In total, 5,034 females and 1,639 males were monitored during that period.

Capture-mark-recapture model

We used a capture-recapture multievent model⁶⁸ to estimate the three different types of transition we were interested in for this study, namely survival probability, site dispersal probability (defined as an individual changing site between two consecutive years), and capture probability. One of the main assumptions of these CMR models is that the population is considered as closed from outside of the study area, meaning that no individuals leave or enter the study area. It is likely that this assumption is not respected in this study, leading to an underestimation of survival (apparent survival probability is calculated, rather than true survival), as individuals leaving the study area are erroneously considered as very likely to be dead in CMR models. In this model, we chose to focus solely on assessing site dispersal (change of site between years) and did not assess natal dispersal (change of site in relation to the natal site). The model was implemented using the E-SURGE⁶⁹ software. We used a modelling approach close to that described in⁷⁰, due to the high number of study sites we chose not to directly use the identity of the site for dispersal modelling but rather to monitor whether individuals were seen in the same site or not in relation to the last season of the previous year. We thus defined dispersal here as the complementary event to site fidelity between two consecutive years. For this analysis, we considered two specific periods for recapture events, June 1st to September 1st for the summer roost and November 1st to March 1st for the winter roost. We classified a recapture event as successful during a period if the individual was seen once or more during that period. Our goal was to estimate the different types of transition occurring during the winter and summer periods.

Individuals can be defined on the basis of their state depending on their survival, dispersal and capture history. We coded information associated to the winter period as *W* and information associated to the summer period as *S*. Any information associated with the previous year's capture history was displayed before the letter *W* and *S* and, respectively, information associated with the current year's capture history was displayed after the letter *W* and *S* in our notation. Information on the previous year's history was required to estimate the dispersal rate. In our study, it was only possible to model dispersal for a specific period if individuals were captured in the previous year. Survival was coded as *a* being alive or *d* being dead in a specific period. Capture was coded as *+* being captured or *o* being not captured in a specific season. Dispersal was coded as *R* for residents (or non-dispersed) and as *D* for dispersed. For example, an individual state coded as *+ WaD + oSao* corresponds to an individual captured during the previous winter that survived, dispersed and was captured in a new location in winter but was not captured during the previous summer, survived until the current summer but was not captured during that summer period. A total of six transition stages were considered in this CMR model (see Fig. 6 for a summary of the transitions included).

- Step 1 Autumn survival Individuals can survive from summer period to the winter period with probability ϕ_w . Either they stay alive with transition probability ϕ_w to state *Wa*, or they die with transition probability $1 - \phi_w$ to state *Wd*.

- Step 2 Winter dispersal Individuals can disperse to a new wintering site compared to the previous year with a *dw* probability. We were only able to assess dispersal if the individuals were captured during the previous winter and survived until this transition. An individual can either disperse to a new wintering site with a transition probability *dw* to the *+ WaD* state, or remain in the same wintering site with a transition probability $1 - dw$ to the *+ WaR* state. Some individuals were captured in different geographically close locations during the same winter period. In this case, we defined a dispersal event only if there was no overlap between the locations of the previous year and current year's winter periods. Individuals that were not captured in the previous season or that died were not affected by this step.

- Step 3 Winter capture An individual could be captured with probability *pw* if it was still alive during the winter. An individual could be captured with a transition probability *pw* to the *Wa +* state (independent of dispersal state) or not captured with a transition probability $1 - pw$ to the *Wao* state (independent of dispersal state). Individuals already dead were not affected by this step.

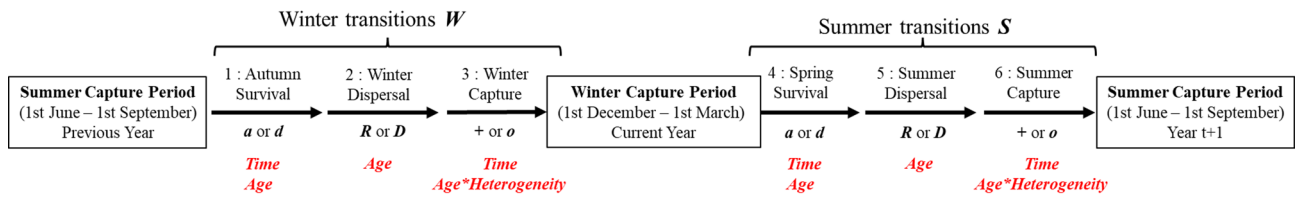


Fig. 6. Diagram representing the different transitions included in the CMR model. Each arrow represents a transition step, with the corresponding outcome nomenclature indicated below. For each transition, a transition probability was estimated using our model. Autumn survival and spring survival are the probabilities to survive from the summer to the winter period and from the winter period to the summer period, respectively. Winter dispersal refers to the probability of changing winter sites between two consecutive winters, while summer dispersal refers to the probability of changing summer sites between two consecutive summers. Winter capture and summer capture represent the probabilities of recapture during the respective periods. A detailed explanation of each transition is given in the Methods section. Factors tested for their effect on each transition probability are shown in red. Only the full model is presented here. “Time” refers to the effect of calendar year of recapture, “Age” to the effect of age class (juveniles vs subadults vs adults) and “Heterogeneity” to the effect of considering heterogeneity in capture probabilities between two groups. “*” correspond to interactions tested in the full model.

- **Step 4 Spring survival** Individuals can survive from winter period to summer period with probability φ_s . Individuals that died during the previous autumn’s survival transition were not affected by this step. They can either stay alive with a transition probability φ_s to the $Wa Sa$ state, or die with a transition probability $1 - \varphi_w$ to the $Wa Sd$ state.

- **Step 5 Summer dispersal** Individuals can disperse to a new summer location relative to the previous year with probability d_s . We were only able to assess dispersal if individuals were captured during the previous year’s summer and survived until this transition. An individual can either disperse to a new summer site with a transition probability d_s to the $Wa + SaD$ state, or remain in the same summer site with a transition probability $1 - d_s$ to the $Wa + SaR$ state. As in the case of winter dispersal, some individuals were captured in different geographically close locations during the same summer period. In this case, we defined a dispersal event if all the locations were different between the previous and current summer periods. Individuals that were not captured during the previous season or that died during the autumn or spring transition were not affected by this step.

- **Step 6 Summer capture** An individual still alive until summer can be captured with probability p_s . It can be captured with a transition probability p_s to the $Wa Sa +$ state (independent of dispersal state in winter and summer and of capture state in winter), or not captured with a transition probability $1 - p_s$ to the $Wa Sao$ state. Individuals already dead in winter or summer were not affected by this step.

Due to the large number of steps and resulting states, computing the full model was especially slow. To improve computational efficiency, we split the model into two sub-models, each with five steps. The first model, called the ‘winter dispersal model’, included steps 1,2,3,4 and 6, while the second, the ‘summer dispersal model’, included steps 1,3,4,5 and 6. Both models estimated capture and survival probabilities for winter and summer, but one focused exclusively on winter dispersal and the other on summer dispersal. We presented results from the summer dispersal model for survival and capture probabilities. Since survival and recapture transitions were defined identically in both models, we verified that survival and recapture estimates were the same for both sub-models.

Due to the large number of study sites included in this study, heterogeneity in individual capture probabilities was likely. For example, capture probabilities may vary significantly depending on whether sites are monitored continuously using automatic antennas or checked periodically with a handheld antenna. To account for this potential heterogeneity, we modelled a mixture of two discrete groups, each with distinct capture probabilities for each period²¹. In the CMR model, the likelihood of an individual to be assigned from birth to a specific capture heterogeneity group is estimated based on the maximum likelihood optimisation procedure which allows to calculate the average proportion of individuals in the studied population belonging to each group. Capture heterogeneity groups were assigned independently for winter and summer captures and coded in our state variable as 1 or 2. For example, $W1S2$ indicates individuals assigned to the first heterogeneity group for winter captures and to the second heterogeneity group for summer captures. We defined hw and hs as the probabilities of being assigned to the first heterogeneity group in winter and summer, respectively. To evaluate the impact of accounting for capture heterogeneity, several models were run both with and without accounting for this effect, and their results were compared.

The winter dispersal model included 37 states and 8 observable events related to capture histories from previous winter, current winter, and current summer. Similarly, the summer dispersal model included 35 states and 8 observable events based on capture history from previous summer, current winter, and current summer. All matrices associated with the assignment of initial states, the transition between states, and the link between states and events are given in supplementary S3 and S4 for each sub-model, while the capture history dataset associated to each sub-model is given in supplementary S5.

All models were implemented using the software E-SURGE⁶⁹. Given the expected strong sex differences due to different life cycles and to limit the number of models run, male and female models were run independently to assess sex-specific differences in transition probabilities. We also tested whether factors such as time (calendar year of monitoring) or age class influenced transition probabilities. Because running all possible combinations of model parameters from the full model was computationally prohibitive, we used a stepwise approach running a selected set of 88 models to identify the best model explaining our data. Models were ranked using the corrected AIC criterion (AICc) for small sample sizes⁷². The model with the lowest AICc was selected as the best, and only results from this model were presented here. We first ran all combinations of models for autumn survival probability and winter capture probability together. Then, after selecting the best model for autumn survival probability and winter capture probability, we ran all combinations for spring survival probability and summer capture probability together. Finally, with the best survival and capture model fixed, we tested all combinations for winter and summer dispersal probabilities. For each survival transition probability, the full model included additive effects of age and time. For each capture transition probability, the full model included the effect of time as well as the interaction between age and capture heterogeneity groups. For dispersal probability, only age was included in the full model due to insufficient sample size per year (See Fig. 6 for a presentation of the full model tested on each transition probability). In total, 88 different CMR models were run for model comparison. All AIC ranking results are presented in supplementary S2. Only the results and coefficients with 95% confidence intervals from the best model are presented here.

Seasonal movement analysis

In addition to estimating between-year dispersal probabilities, we aimed to characterize seasonal movements within the meta-population. Greater horseshoe bats typically leave their maternity sites after giving birth to move to wintering sites. However, the extent of these seasonal movements remains poorly documented. For each individual captured in both summer and winter of the same year, we computed the Euclidian distance between the last site where we encountered the individual during the summer period and the first site where we encountered the individual during the winter period. To assess the effects of age class and sex on these seasonal movements, we used Tobit regression models implemented in the R package ‘censReg’⁷³, which is well-suited for censored dependent variables such as distances, which cannot be negative. Starting from a full model including the effects of age class, sex and their interaction, we calculated the Akaike information Criterion (AIC)⁷² for all models that are derived from the full model. Models were ranked based on AIC, and the model with the lowest AIC was selected as the best-fitting model to describe the observed data (See Table S9 for AIC ranking). We then calculated the mean of seasonal movement distance for each sex and age group and estimated the 95% confidence interval associated with the mean of each group using a bootstrapping procedure.

Greater horseshoe bats often live in large groups, sometimes comprising several hundred individuals. However, it is still unknown whether individuals roosting in the same summer roost migrate together to the same winter roost or whether the group breaks up and disperses across multiple sites. For this analysis, we included only summer roosts in which more than 20 individuals were captured during a given summer season. When males and females shared the same summer group, we analyzed each sex separately. Each individual from a summer group was assigned a corresponding winter roost based on its observed location during the next wintering period. To quantify the degree of the summer group fragmentation across winter roosts, we used a Simpson index. While this index is typically used for diversity measurement ranging from 0 to 1⁷⁴, here it was used to measure the diversity of wintering destinations. A high Simpson index value (approaching 1) indicates a high level of fragmentation, meaning individuals from the same summer roost migrated to a wide variety of winter roosts. Conversely, if all individuals from a summer roost migrated to the same roost, the diversity in destination sites would be null, corresponding to a Simpson index of 0. Simpson indices were calculated using the ‘abdiv’ package in R⁷⁵. Due to the uneven spatial distribution of study sites, variations in group fragmentation indices could potentially be influenced by the number of available winter sites sampled around each summer site. To account for this, we counted the number of winter roosts located within a 70 km radius of each summer roost—this distance corresponding to the 80% quantile of observed winter travel distances. We then used a linear regression model to test the effects of three factors on winter group fragmentation (dependent variable): the number of possible winter roosts within 70 km, the number of individuals from each summer roost, and the sex of individuals. All analysis related to seasonal movements were performed using R version 4.2.1.

Data availability

Data is provided within the manuscript or supplementary information files.

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Author contributions

D.P. and V.R. designed the study. M.L. and M.V. collected the data. V.R. analyzed the data. V.R. and D.P. wrote a first version of the manuscript which was then discussed and revised by all authors.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to V.R.

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