A multi-scale approach unveils the ecology of the Critically Endangered Sardinian long-eared bat

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Abstract Human-induced pressures such as climate and land-use changes in the Anthropocene disproportionately threaten island ecosystems and the endemic species they host. Shedding light on the ecological needs of island species is key to the conservation of these fragile ecosystems and their unique species. Here we present the ecological needs of a bat species endemic to Sardinia, the long-eared bat *Plecotus sardus*, and analyse the relationship between this Critically Endangered species and the insular environment at different spatial scales to inform action for its conservation. We show that besides displaying a unique phenology and roost use, the species is closely associated with the dry broadleaf forests of native oaks *Quercus ilex* and *Quercus suber* at all scales and, in contrast, is negatively affected by coniferous stands, open pastures and urban environments. Our results not only provide key information for the conservation of *P. sardus* but also provide insights into the unique adaptations of insular endemic species to the fragile island ecosystems, highlighting the importance of ecological studies to informing conservation in biodiversity hotspots. We also demonstrate that protection and restoration of key habitats, particularly within 2 km of roosts, are key to protecting the few known reproductive colonies.

Keywords Chiroptera, Critically Endangered, endemism, Mediterranean, *Plecotus sardus*, Sardinia, Sardinian long-eared bat

Introduction

Understanding the processes that shape and affect biodiversity is a key asset in ecology and conservation biology. Pressures such as habitat deterioration and fragmentation have become increasingly important as potential drivers of biodiversity loss in terrestrial ecosystems (Gonçalves-Souza et al., 2020). Island ecosystems are in great need of conservation in the Anthropocene as many islands are biodiversity hotspots that host unique habitats and wildlife assemblages, including endemic taxa that are disproportionately affected by anthropogenic alterations (Graham et al., 2017; Russell & Kueffer, 2019). Yet a large proportion of island biodiversity is threatened globally by a growing human footprint that has caused significant habitat losses (Fordham & Brook, 2010). This is particularly evident in islands with a long history of human occupancy, such as most of those in the Mediterranean basin (Blondel, 2010; Vogiatzakis et al., 2016). This area is known both as a global biodiversity hotspot and as one of the cradles of human civilization in Western Europe and beyond (Medail & Quezel, 1999). Consequently, the Mediterranean basin is also amongst the four most altered biodiversity hotspots in the world (Lozano et al., 2013). Terrestrial vertebrates on Mediterranean islands are threatened by a set of anthropogenic stressors such as the increased frequency of extreme climatic events (e.g. droughts and associated wildfires) and by land-cover changes, which can have short- and long-term impacts on wildlife within the limited areas afforded by islands (Diffenbaugh et al., 2007; Ruffault et al., 2020). Shedding light on the ecological needs of species on islands is therefore fundamental to properly assessing habitat quality and availability, and thus to aiding conservation efforts in the long term.

More than 60% of extant bat species occur on islands, with almost 25% being island endemics (Jones et al., 2009). Despite the acknowledged key ecosystem roles played by these mammals (Ghanem & Voigt, 2012), insular bats remain poorly studied and, in comparison to continental species, more threatened (Conenna et al., 2017). The few documented cases of bat extinctions to date (all a result of anthropogenic factors) have involved island endemic species (Jones et al., 2003).

Located in the west of the Mediterranean Sea, the Italian island of Sardinia is a key area of endemism within the Mediterranean basin hotspot, both because of its spatial extent (being one of the largest islands in the area) and the number of endemic species and subspecies present there (Grill et al., 2006). Sardinia is home to 21 bat species (Loy et al., 2019), including the endemic Sardinian long-eared bat *Plecotus sardus* (Mucedda et al., 2002). This species is one of the most recently described European bats (Kiefer et al., 2023), and has been little studied to date. Despite its uniqueness and its inclusion in Annex IV of the EU

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Habitats Directive (92/43/EU), *P. sardus* has suffered a dramatic decline in population size over the last 2 decades: from c. 1,000 individuals at the time of its description in 2002 to c. 300 individuals in 2020 (Ancillotto et al., 2021) and c. 150 individuals in 2023 (MM, pers. obs., 2023). This rapid decline led to a recent reassessment from Vulnerable to Critically Endangered on the global and Italian Red Lists (Rondinini et al., 2022; Russo & Cistrone, 2023). However, no specific action is currently being undertaken to conserve the species, partly because its ecological needs are poorly known.

To effectively conserve bats, it is vital to understand their environmental needs at different spatial scales, as bats are highly mobile and their relationships with environmental factors are subtle (e.g. from fine-scale roost microhabitats to landscape-scale habitats; Kalda et al., 2015). Evidence suggests that *P. sardus* uses both buildings and caves for roosting, but no systematic information (e.g. on roost occupancy patterns) is yet available (Kiefer et al., 2023). Similarly, nothing is known about the habitats used by the species for foraging, which in turn may affect its occurrence on a larger spatial scale.

We focus here on the ecological needs of *P. sardus* as a poorly known, highly threatened island-endemic species and assess its habitat requirements at two spatial scales, focusing on the effects of land use on the range-wide probability of occurrence and on individual spatial behaviour, to identify key habitats and inform conservation actions. Most long-eared bats of the genus *Plecotus* are forest specialists (Spitzenberger et al., 2006; Ancillotto et al., 2022) that forage in relatively close proximity of their roosts (Entwistle et al., 1996; Ancillotto et al., 2022); thus, we hypothesize that *P. sardus* does not use habitats according to their availability in the landscape, and predict that forests are positively selected against other habitat types at different spatial scales.

We describe the species' roosting ecology in terms of roost types and phenology, and also examine potential differences in roosting ecology between the sexes. Most temperate bats use different roosts and roost types during the different phenological phases of their annual cycles (e.g. between nurseries and hibernacula or swarming sites) or according to sex, rarely using the same roost all year round, mostly because of varying thermoregulatory needs in different seasons (Kunz, 1982). As such, we predict that *P. sardus* will also have different roosting preferences during the year and between sexes. As documented in other European bats, male and female *P. sardus* may show ecological and/or spatial segregation (Senior et al., 2005). This may provide females, which expend greater amounts of energy than males in the summer, a fitness advantage at lower elevations. We therefore predict that females are more likely to be found at lower elevations than males during the breeding season, and that individuals at lower elevations will be in better body condition.

Study area

We studied *P. sardus* on the c. 24,100 km² island of Sardinia (Fig. 1a,b), which has an elevation range of 0–1,834 m; the area occupied by *P. sardus* is restricted to the centre of the island, from the eastern coast to the interior, extending west to Omodeo Lake (Fig. 1c). The species occurs in two spatially distinct subpopulations (eastern and western) separated by a narrow strip of apparently unsuitable area (Bosso et al., 2016; Ancillotto et al., 2021). Sardinia features typical Mediterranean habitat types, comprising a wide extent of anthropogenic (secondary), dry grasslands (pastures) derived from millennia of agropastoralism, as well as sclerophyllous scrublands and rocky areas (Pungetti et al., 2008). Nonetheless, forest habitats are also relatively well represented on the island, and are considered valuable because of their ecological uniqueness and conservation relevance. As an example, Sardinia hosts the largest and most ancient forest standings of holm oak *Quercus ilex* L., as well as some of the most valuable cork oak *Quercus suber* L. forests in Europe (Medail & Quezel, 1999); other forest types on the island are both natural and artificial conifer stands (*Pinus* spp.) and sweet chestnut *Castanea sativa* Mill. groves.

Methods

Roosting ecology

To assess roosting preferences, we compiled a comprehensive list of roosts used by *P. sardus*, as found during monitoring activities by authors MM and EP during 2000–2023. We described phenology by assessing numbers of individuals, sex and reproductive status of *P. sardus* at each roosting site, as assessed by systematic year-round monthly observations at three focal sites during 2015–2016 and opportunistic visits to all 20 known roosts during 2000–2023. Each roost was classified according to type (building, underground or tree), subpopulation (western or eastern; Bosso et al., 2016; Ancillotto et al., 2021) and use (hibernaculum, nursery or temporary roost). We used a χ^2 test to examine differences in the proportions of roost types used by male and female bats and according to season.

Sexual segregation

We compiled a database of all *P. sardus* individuals captured during 2003–2023, recording capture date, site location and elevation, the animal's forearm length and body weight following Dietz et al. (2009), and sex and age class following Racey (1988); we then calculated the Scaled Mass Index (Peig & Green, 2010) as a proxy of body condition. To assess differences in spatial ecology, size and body condition between the sexes, we used generalized linear models with

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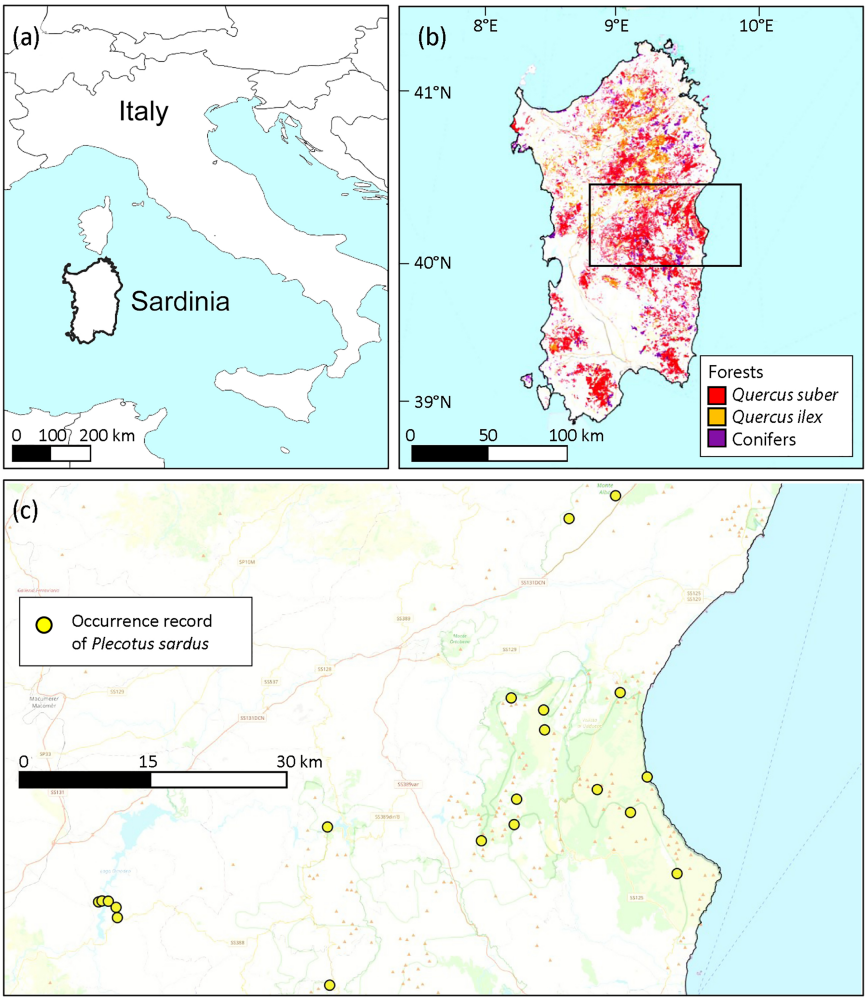

FIG. 1 Map of the study area, showing: (a) the location of Sardinia in Europe, (b) the distribution of Mediterranean broad-leaved dry forests and conifer stands on the island, and (c) the known occurrence locations of the Sardinian long-eared bat *Plecotus sardus*. Base maps from OpenStreetMap (2023). (Readers of the print journal are referred to the online article for a colour version of this figure.)

Gaussian error distributions and log-link functions, using forearm length and Scaled Mass Index as response variables, and sex, elevation and subpopulation as potential explanatory factors. We also assigned each record to elevation class (low elevation: 0–500 m; high elevation: > 500 m) and assessed differences in the distribution of the sexes, using χ^2 tests. We considered results with $P < 0.05$ as significant.

Habitat selection and ranging behaviour

We conducted a radiotracking campaign during July–September 2015, focusing on the largest known roost of *P. sardus*, in the western part of the species' range, counting c. 90 adult bats at that time. We captured *P. sardus* by mist-netting individuals emerging from the roost at dusk, and identified each captured individual to species following Mucedda et al. (2002). We then fitted captured bats with VHF radio transmitters (V3 Telemetrie-Service Dessau, Germany) secured between the shoulder blades by skin adhesives (SAUER-Hautkleber-Original, Manfred Sauer, Germany). Transmitter weight never exceeded c. 5% of body mass. Using a receiver and antenna, we tracked bats continuously on foot and by car from sunset to dawn (Bontadina et al., 2002), recording an individual location every c. 15 min. We established individual fixes either by homing in on the tracked individuals or by triangulating from different bearing positions. During triangulation, operators recorded their position with a GPS to 5-m accuracy, and measured the direction of the signal with a compass. During radiotracking we also assessed bat activity. We later classified this activity as either foraging or commuting, following Ancillotto et al. (2021). In the habitat selection analysis (see below) we only included fixes assigned to foraging behaviour. We classified fixes assigned to individuals in fast and directional flight (assessed by rapid changes in signal direction and intensity) as commuting, and those that remained in relatively delimited areas as foraging (Ancilloto et al., 2022). Individuals that were not moving were interpreted as non-flying (i.e. night-roosting).

We generated a land-use map of the study area by using the Corine Land Cover classification (Copernicus, 2018) and confirmed land class assignment by direct observation in the field. We quantified available habitats by calculating the proportion of each habitat type within the area

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encompassing all fixes of all tracked individuals. We calculated proportions of each habitat used by counting the number of fixes per individual bat falling within each habitat type. We then calculated individual home ranges as 100% minimum convex polygons encompassing all fixes for each bat (Bontadina et al., 2002). We defined the study area a posteriori as the 100% minimum convex polygon encompassing fixes of all tracked individuals.

We then assessed individual-based habitat selection, comparing the per cent of habitat used by each individual bat with the available proportion of the same habitat at the scale of the study site (second-order habitat selection) and the individual home range (third-order habitat selection; Johnson, 1980). To conduct this assessment, we used the non-parametric methodology proposed by Fattorini et al. (2014) based on a permutation of the sign test. We obtained an overall statistical value for the simultaneous assessment of habitat selection in all of the habitat types by combining P-values from each test through a permutation procedure (Fattorini et al., 2014). We considered four habitat types: pasture, coniferous woodland, broad-leaved woodland and urban. We applied sign tests to the original data to determine whether a habitat was used proportionally according to its local availability, or whether it was avoided or preferentially selected (Fattorini et al., 2014). We performed the non-parametric testing of habitat selection using the package *phuassess* (Fattorini et al., 2017) in *R 4.3.0* (R Core Team, 2021).

Habitat associations at the regional scale

We modelled the probability of occurrence of *P. sardus* across the entire island as a function of land-use composition, to assess the range-wide environmental preferences of the species and to identify important habitat types for its conservation. Firstly, we overlapped the map of Sardinia with a grid of 3.16×3.16 km cells (10 km^2). We then selected the 20 grid cells with at least one occurrence record of *P. sardus* (derived from our own data collected during 2000–2023 and comprising all types of data; i.e. roosts and direct observations) and 60 control cells with occurrences of at least five other bat species (based on the Habitats Directive IV reporting maps) but no *P. sardus* records. Within each grid cell we extracted land-use composition as per cent cover per class, reclassifying the 2018 Corine Land Cover into five classes: (1) Mediterranean broad-leaved forests, comprising stands of holm and cork oaks; (2) conifer stands, comprising mostly plantations of *Pinus halepensis* Mill. and *Pinus pinea* L.; (3) pastures, mainly comprising dry, natural and semi-natural herbaceous vegetation with scattered shrubs or isolated trees; (4) water, comprising open water habitats, mainly artificial lakes and natural rivers; (5) urban areas, dominated by impervious surfaces associated with buildings and infrastructure.

We then built a generalized additive model with a binomial error distribution and a logit link function using the occurrence of *P. sardus* (presence = 1, absence = 0) as the response variable and land-use composition at the grid-cell scale as potential explanatory variables. We first checked for autocorrelation by running a Pearson correlation test, which resulted in significant correlation between urban and water surface values ($|r| > 0.5$, $P < 0.05$); we therefore excluded water habitats from our analyses. We assessed model fit by inspecting conditional R^2 values, considering as significant those variables whose effect size resulted in $P < 0.05$ and confidence intervals of the estimates not encompassing zero. We built the model using the package *lme4* (Bates et al., 2009) and evaluated the model using the package *DHARMa* (Hartig & Hartig, 2017) in *R*.

Results

Roosting ecology

Of the 20 roosting sites, nine (45%) were in buildings or infrastructure (bridges and viaducts), six in natural and five in anthropogenic underground sites (i.e. karstic caves and tunnels, respectively). The western population only used buildings and infrastructure for roosting. No difference was evident in the frequency of roost types according to either season of observation or sex (all $P > 0.05$). The five known nurseries are in three attics, two of which are in abandoned buildings and one in a building that is still in use, and in two natural caves. We identified no clear hibernacula comprising large aggregations (i.e. we found only isolated individuals or small groups of 2–3 bats in the winter months). At least two roosts were used year-round by *P. sardus*, hosting nurseries in spring and smaller groups/isolated bats in winter. All other roosts in artificial tunnels, old buildings, underground air-raid shelters and bridges comprised 1–3 individuals across all seasons. At focal sites reproductive females began to form nurseries in late March, and we recorded maximum numbers of adults in early May. Females gave birth to single pups in mid May. Adult and young bats remained in the same roost until as late as mid September, when the numbers of individuals started to decrease.

Sexual segregation and dimorphism

We measured 100 adult bats (41 males, 59 females), captured at 18 locations in both the eastern (n = 27) and western (n = 73) parts of the species' range. Male and female *P. sardus* showed significantly biased frequencies of occurrence at increasing elevations ($R^2 = 12.02$, $P < 0.001$). Although the overall altitudinal range was the same for males and females (0–1,030 m), males were disproportionately more frequent at high-elevation sites.

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Plecotus sardus shows sexual size dimorphism, with females being significantly larger than males (model estimate: −0.74 ± SE 0.24, $P < 0.01$; 41.88 ± SE 1.09 vs 40.94 ± SE 0.85 mm forearm length, respectively) but not heavier (model estimate: -0.21 ± SE 0.11, $P > 0.05$; 8.73 ± SE 0.89 vs 8.46 ± SE 1.14 g, respectively). Body condition differed significantly only between bats from the two subpopulations (model estimate: -0.03 ± SE 0.01, $P < 0.01$), with individuals from the western part of the range having a lower mass index (0.20 ± SE 0.02) than those from the eastern part (0.22 ± SE 0.03).

Habitat selection and ranging behaviour

We captured and tagged six bats, but three transmitters failed within the first 24 h, resulting in only three individuals (all post-lactating females) providing data suitable for spatial analyses. We followed tracked bats individually for 3 nights each on average, obtaining 40.0 ± SD 1.5 activity fixes per bat and totalling 119 foraging activity fixes. Throughout the study period, all tracked individuals used the same roost at which they were captured (i.e. we recorded no roost switching). Individual home ranges covered on average 285.7 ± SE 22.3 ha (100% minimum convex polygon, also encompassing roost location), with the maximum distance between roost and foraging fixes being 2.3 ± SE 1.1 km. Mean distance between a fix and roost was 1.52 ± SE 0.75 km, but 50% of all fixes fell within a distance of < 0.8 km. *Plecotus sardus* selected specific land-use classes at both the study site (second order) and individual home range (third order) spatial scales (Fig. 2). At both scales, tracked bats positively selected broad-leaved Mediterranean dry forests of *Q. ilex* and *Q. suber* (both $P < 0.001$) and strongly avoided pastures (second order: $P < 0.01$; third order: $P < 0.001$). Conifer stands were avoided at the study site scale ($P < 0.001$), but were used proportional to their availability within an individual's home range. Urban areas were used proportional to their availability at both spatial scales (Fig. 2).

Habitat associations at the regional scale

Our model performed well in explaining the probability of occurrence of *P. sardus* across the region ($R^2 = 0.65$), with all four land-use classes exerting a significant effect on species presence (Fig. 3). Effect sizes and variance partitioning analysis revealed that the strongest effect was a positive association with broad-leaved Mediterranean forest cover (sign test T: 0.72 ± SD 0.11, $P < 0.01$; partial $R^2 = 0.53$), followed by negative effects of conifer stands (-0.04 ± SD 0.01; $P < 0.05$, partial $R^2 = 0.11$) and urban areas (-0.02 ± SE 0.01; $P < 0.01$, partial $R^2 = 0.09$). Pastures also showed a significantly negative effect on probability of species occurrence, but with high uncertainty (-0.01 ± SE 0.01; $P < 0.05$, partial $R^2 = 0.05$).

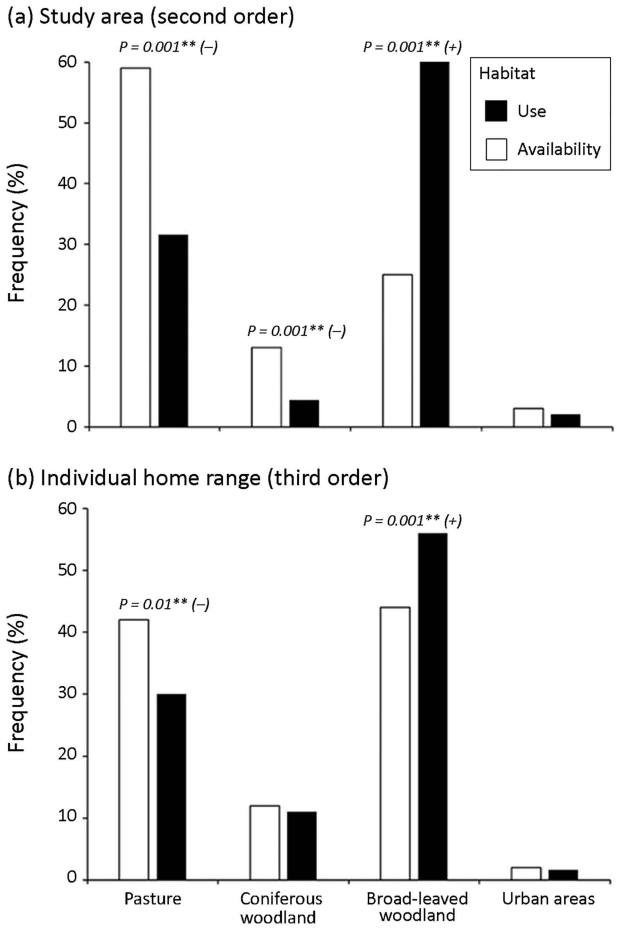

FIG. 2 Patterns of habitat selection by the Sardinian long-eared bat in Sardinia, Italy, as assessed by radiotracking of post-lactating females (n = 3) within (a) the study area (second order), and (b) individual home ranges (third order). Bars indicate mean values of the frequency of fixes across the three tracked individuals.

Discussion

We provide first insights into the ecological needs of the Critically Endangered Sardinian long-eared bat. As predicted, the species seems to be strongly associated with the Mediterranean broad-leaved dry forests that characterize the island, comprising mature stands of *Q. ilex* and *Q. suber*, at both of the spatial scales examined. This type of forest was the main driver of the species' occurrence at the island scale, as well as being the only land-use class positively selected by radiotracked individuals at both the study site and individual home range scales. Conversely, conifer stands had a negative effect on the large-scale probability of occurrence of *P. sardus* and were negatively selected at the study site scale. This pattern is similar to that of the congeneric brown long-eared bat *Plecotus auritus* on the Italian mainland (Ancillotto et al., 2021) and in other areas across Europe (Entwistle et al., 1996). *Plecotus auritus* can be found in mixed or even coniferous forest stands, but these seem to

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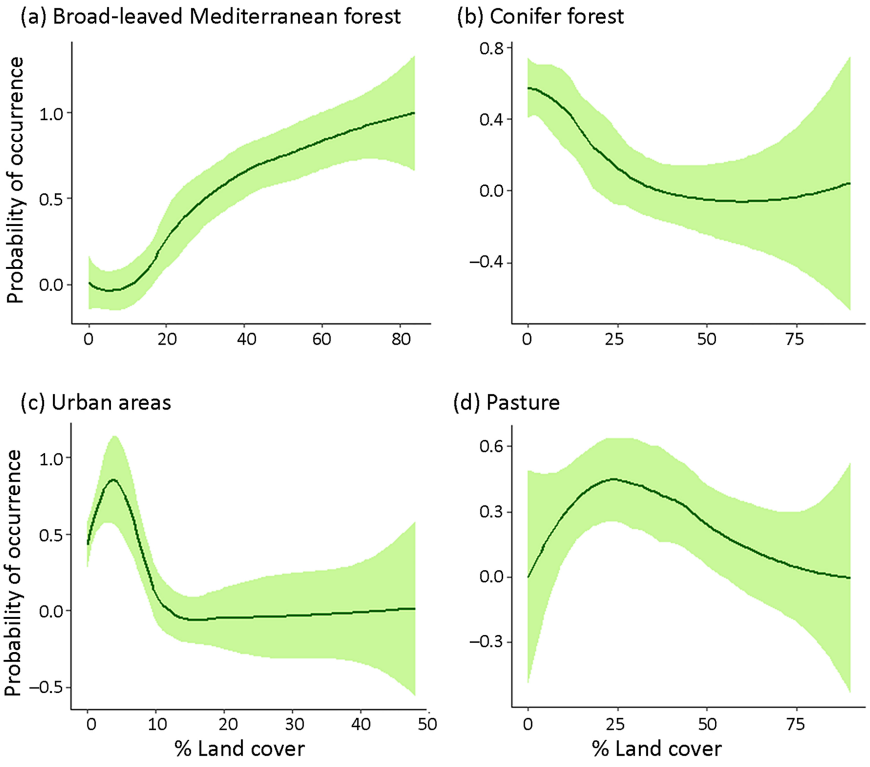

FIG. 3 Probability of occurrence of the Sardinian long-eared bat as a function of land-use composition (as percentage of land cover within 10 km² grid cells) across its distribution in Sardinia, Italy. Shaded areas indicate 95% confidence intervals.

provide relatively little prey and roost opportunities for this forest specialist. Conversely, brown long-eared bats are considered to be highly susceptible to dehydration as they are usually associated with relatively humid conditions (Webb et al., 1993), and even congeneric species that are better adapted to drier conditions (e.g. *Plecotus kolombatovici* and *Plecotus gaisleri*; Razgour, 2023) are highly dependent on the availability of water (e.g. ponds) in dry Mediterranean habitats (Lison & Calvo, 2014; Ancillotto et al., 2020). In our study we did not detect any tracked *P. sardus* individuals over Lake Omodeo (or in its immediate proximity), suggesting the species uses other water sources for drinking. *Plecotus sardus* thus appears to prefer the semi-arid habitats of Sardinia and its dry forests, being absent from the more humid *C. sativa* woodlands in the south (Bacchetta et al., 2004). Both *P. auritus* and *Plecotus austriacus* occur in Sardinia, but their habitat preferences differ from those of *P. sardus*; they are associated with high-altitude forests and Mediterranean scrublands, respectively (MM, pers. comm., 2024). Such divergence in the habitat preferences of closely related species further highlights the uniqueness of *P. sardus* and may suggest that the occurrence of the congeneric *P. auritus* and *P. austriacus* in Sardinia (Mucedda & Pidinchedda, 2010) may have played a role in shaping the current niche of *P. sardus* (as seen for other species on the continent; Ashrafi et al., 2013).

Our findings only partially support our prediction on the roosting ecology of the species: *P. sardus* showed no sex or seasonal biases in the use of different roost types, with males and females utilizing buildings and natural and artificial underground sites throughout the year. In addition, and different to the closely related *P. auritus* (Spitzenberger et al., 2006; Dietz et al., 2009), we did not document *P. sardus* using trees as roosts (Ancillotto et al., 2021; this study). Conversely, and confirming our hypothesis, male and female *P. sardus* showed size dimorphism and altitudinal segregation. As predicted, *P. sardus* males occur throughout the altitudinal range of the species but are disproportionately more frequent at higher elevations than females (in this specific case $>$ 500 m). Such altitudinal segregation is well documented in several temperate bat species (Senior et al., 2005; Angell et al., 2013) and is explained by the energetic benefit for females when roosting at lower elevation, securing faster growth of their young. Males, however, exploit higher-altitude sites and thus lower temperatures, which enables more efficient torpor and reduces energy expenditure (Kunz, 1982). The differences we found in body condition between the two subpopulations cannot be easily explained, but the western population only roost in buildings, which can expose bats to greater thermal stress, particularly during heatwaves (Czenze et al., 2022), potentially affecting individual health. Notably, the species shows an earlier phenology in comparison to other European bats (Dietz et al., 2009), with births occurring in mid spring. The early phenology we report here may also be explained by the relatively mild conditions typical of Sardinian winters, potentially leading to shallow or short hibernation, although this is not observed in other bat species occurring on the island

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and may thus be an adaptation of *P. sardus* to the semi-arid environment of Sardinia. Both reproductive timing and the year-round use of the same roosts by *P. sardus* are key information for planning of conservation actions, such as the timing of renovation of buildings that host colonies, particularly as all the nurseries in this type of structure have shown a gradual decrease in colony size and two have now disappeared, possibly because of mortality and disturbance (Ancillotto et al., 2021).

Several important aspects of the ecology of the Critically Endangered *P. sardus* are still unknown. No information is available on seasonal movements, dispersal distances, diet composition or year-round patterns of habitat selection (Kiefer et al., 2023). Our results (particularly those related to patterns of habitat selection of individuals) are based on a small sample size; this is often the case for highly threatened species that are rare and difficult to detect, but even data from a limited number of individuals may provide useful insights for conservation planning (Benstead et al., 2001; Lovari et al., 2017; Monadjem et al., 2018). In our case, the species is rare, with an estimated total population size of c. 150 adults in 2023 (MM, pers. obs., 2023), making *P. sardus* the rarest and most threatened bat species in Europe (Ancillotto et al., 2021). Sudden declines in island bats have been previously documented, highlighting that fast action is needed to conserve these rare species, and that a slow response by policymakers could lead to extinction, as with the Christmas Island pipistrelle *Pipistrellus murrayi* (Martin et al., 2012). As such, knowledge of habitat selection and ranging behaviour, even from a few individuals, may be key to the conservation of *P. sardus*, particularly in designing and managing protected areas for its conservation.

Our results indicate the strong affiliation of *P. sardus* with Mediterranean dry broad-leaved forests of *Quercus* spp., highlighting the uniqueness of this insular endemic species and suggesting it may be heavily affected by anthropogenic changes occurring in these fragile habitats. As an example, greater wildfire surveillance and avoidance of the application of pesticides to control defoliating insects in *Quercus* forests could be important actions to preserve *P. sardus* (Ancillotto et al., 2021), particularly in the immediate surroundings (c. 1–3 km based on our results) of key roosting sites, as has also been seen for the congeneric *P. austriacus* in Mediterranean contexts (López-Baucells et al., 2021). Any species recovery plan for *P. sardus* should also focus on conserving mature Mediterranean dry broad-leaved forests and the unique diversity they host (Seddaiu et al., 2020). The extent of broad-leaved dry forests in Sardinia (covering areas within the range of *P. sardus*) changed markedly in the 20th century, decreasing significantly during 1935–1990 (Puddu et al., 2012) but increasing again more recently (but see Seddaiu et al., 2020). Such changes in suitable habitat suggest that the observed decline of *P. sardus* could also be the result of past deforestation (i.e. the species may be suffering from an extinction debt; Kuussaari et al., 2009). The ongoing recovery of Mediterranean forests in Sardinia (Puddu et al., 2012) may thus be insufficient to support the recovery of *P. sardus* without additional habitat restoration.

Our findings indicate that Mediterranean oak forests are key habitats for the conservation and potential restoration of the Sardinian long-eared bat, particularly in the immediate surroundings of nursery sites. A species distribution modelling approach that includes intersexual differences and patterns of habitat selection could guide the identification of additional roosts. Because of the negative population trend of *P. sardus* and the high risk of extinction, we recommend that known roosts are secured, key habitats and sites are included in protected areas, and long-term surveillance and monitoring are implemented as soon as possible to ensure the persistence of this Critically Endangered species.

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Conflicts of interest None.

Ethical standards Field activities including capture, handling and tagging of bats were approved by the Ministry of Environment, together with regional authorities, as reported in permits released during 2004–2023: DPN/2D/2004/7489 of 15/03/2004, DPN-2007-0003938 of 13/2/2007, DPN-2010-0009609 of 07/05/2010, Prot. 0035017–03/05/2013 – PNM-II, Prot. 0007134/PNM of 08/04/2016 Div II, Prot. PNM.U.0012867 of 05/06/2019, Reg. Uff. 0045901 of 14/04/2022. This research otherwise abided by the *Oryx* guidelines on ethical standards.

Data availability Data are available from the corresponding author upon reasonable request.

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