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Artificial permanent ponds are valuable for bats: a comparison with temporary ponds in a Mediterranean region

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Abstract

Ponds are crucial habitats for bats in Mediterranean regions, providing significant sources of food and drinking water. However, the intensification of land use and the increase in arid landscapes are threatening these ecosystems, leading to a significant decline in water availability. Our aim is to assess the influence of biotic and abiotic pond features on bat communities, with a focus on the hydrological regime (artificial permanent or natural Mediterranean temporary ponds), and including prey-availability, wind speed and surrounding land use type. We surveyed bat and feeding activity and species richness in 32 ponds – 16 permanent and 16 Mediterranean temporary — along the southwestern coast of Portugal during two consecutive spring seasons. In total, we recorded 3802 bat passes in permanent ponds and 984 in temporary ponds. Both bat activity and species richness were significantly higher in permanent ponds, which also hosted a greater number of species of conservation concern: *Myotis myotis/M. blythii*, *M. escalerai,* and *Nyctalus lasiopterus/N. noctula*. Our results revealed that pond hydrological regime influenced species richness, whereas variation in bat activity was mainly explained by other factors. We found a strong and positive effect of the availability of Diptera insects and the proportion of urban areas on bat overall and feeding activity and species richness. In contrast, wind speed, even low, exhibited a clear negative influence on bat overall and feeding activity, with weaker influence on species richness. This study highlights the key role of permanent ponds in the Mediterranean region for bat conservation, but also demonstrates the importance of maintaining ponds with different flooding periods, as these increase water availability, landscape heterogeneity and connectivity.

Keywords Drier landscape, Habitat use, Prey-availability, Urban areas, Wetlands

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Introduction

Ponds are a freshwater resource recognized for their significant contribution to biodiversity conservation [46], being particularly important in the Mediterranean region [15]. These habitats are shallow waterbodies that can be categorized according to the period they hold water, the hydrological regime: permanent ponds present water levels and depths relatively stable throughout the year, while temporary ponds show alternating phases of flooding and drying. This is the key factor influencing the biological communities in these habitats [11].

Permanent ponds in the Mediterranean region have been artificially created to support agriculture and livestock, effectively transforming them into artificial wetlands [65]. In many cases, this was done by deepening temporary ponds. Indeed, the intensification of agricultural practices and anthropogenic pressures have significantly contributed to the degradation of natural ponds [10, 61]. In addition, the effects of climate change add additional pressure on these habitats due to the decreasing rainfall levels which reduce water availability in the landscape [28, 64]. Such rapid environmental changes are particularly concerning for species with slow reproduction rates, as their evolutionary responses to emerging threats tend to be lengthy [12].

Bats are very sensitive species that highly depend on ponds [29, 54]. These ecosystems provide them with significant resources, including drinking water and insect-prey essential for their survival [29, 34, 62]. Due to the high energy demands of flight, bats face a great risk of dehydration, intensifying their use of ponds during the summer months for a successful reproduction [1, 51, 57]. Lactating females visit them significantly more often when compared to non-lactating [1]. Thus, ensuring the preservation of ponds within the landscape matrix is therefore essential for bat populations.

There are several factors that may influence the use of ponds by bats, which include water surface area [63, 65], wetland type [17, 33], pre- and post-restored water bodies [43], surrounding landscape features [67]. Moreover, bat activity and diversity in ponds can also be comparable to other aquatic environments, such as rivers [17, 45]. More recently, several review paper have further highlighted the importance of aquatic habitats for bats, including in Mediterranean and arid regions, but also emphasize that studies addressing the role of pond hydrological regime remain scarce and often inconclusive [36, 41, 59]. Razgour et al. [54] found no significant differences in bat activity or species richness between permanent, semi-permanent and temporary ponds, while Razgour et al. [55] observed variations in bat community structure and activity patterns in response to interspecific competition in the ponds. Williams and Dickman [71] compared several habitat types, revealing a preference of most bat species for temporary waters, followed by permanent waters, without significant differences.

Given the diversity of factors influencing bat habitat preferences, our study aims to compare bat overall activity, feeding activity, and species richness between artificial permanent and natural Mediterranean temporary ponds, while accounting for the influence of biotic and abiotic features and surrounding land use. We hypothesize that the hydrological regime influences the use by bat communities, whereas other environmental variables, such as prey availability, positively contribute to pond use by bats.

Methods

Study area

The study area is in the Southwest Coast of Portugal (Fig. 1), within the Mesomediterranean biogeographic region [56]. The climate is predominantly dry, with average temperatures ranging from 12°C (in winter) to 20°C (in summer), and an average rainfall of 467 mm, concentrated mainly between October and March [66]. The average annual wind intensity is 5.5 m/s [66]. The study area extends over ca. 118,267 ha and is partly included in the Natural Park of Southwest Alentejo and Vicentina Coast. Most of the land is used for extensive agriculture, livestock raising and forestry, excluding the Irrigation Perimeter of Mira, dedicated to irrigated intensive agriculture. The region features a mosaic landscape, hosting numerous ponds that vary in origin (natural or artificial), hydrological regime (permanent or temporary) and conservation status.

The surveyed temporary ponds were selected from Mediterranean temporary ponds (Habitat 3170*) inventoried and monitored by the LIFE Charcos Project (LIFE12/NAT/PT/997). These ponds are considered priority habitats, supporting high biodiversity, including rare and endemic species [26, 48, 72], and will hereafter be referred to as temporary ponds. Meanwhile, artificial permanent ponds were selected through aerial photos available on Google Earth 7.1.7 (https://earth.google.com/web/), with field visits to assess their suitability. These ponds were built by farmers for livestock drinking or crop irrigation, often involving the excavation of natural ponds and are, in most cases, deeper than temporary ponds. Hence forward, they will be termed permanent ponds.

Bat acoustic sampling and identification

Acoustic surveys were conducted over a single night in 32 ponds: 16 permanent and 16 temporary, between April and May 2015, and in May 2016. This period encompasses the flooded phase of temporary ponds and the early bat breeding season. To minimize the effect of weather conditions and spatial variation on bat

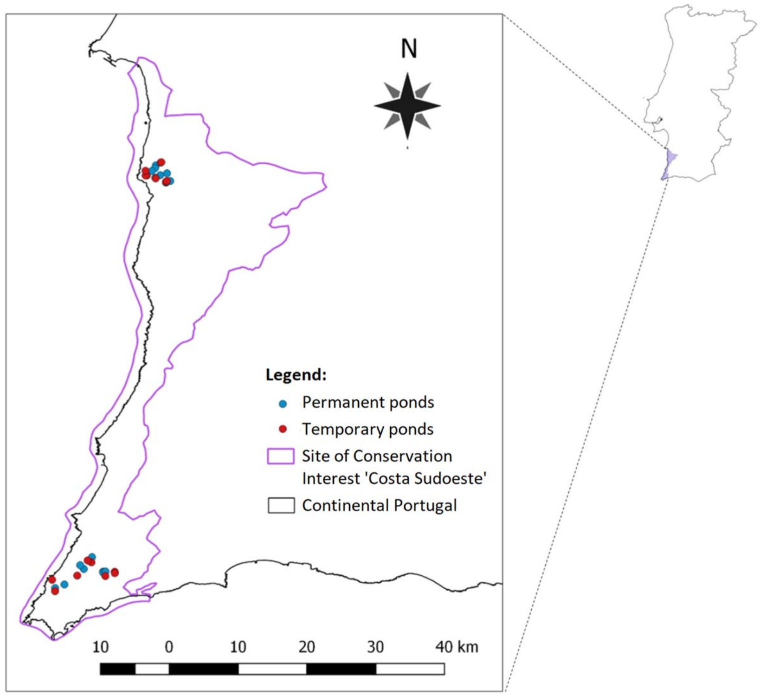

Fig. 1 Study area (purple line) in Continental Portugal (black line), with the locations of permanent (blue points) and temporary (red points) ponds

assemblages, we simultaneously sampled one to three sets of paired permanent and temporary ponds located less than 3 km apart. We used bat acoustic detectors (Petterson D500x, Petterson Eletronik AB) to passively detect, record and store full-spectrum bat echolocation sequences. The recordings lasted 3 s without pre-trigger and were digitized at 300 kHz with 16 bits resolution, covering a frequency range of 5–190 kHz. Bat detectors were set up on tripods approximately 1.5 m above ground, facing the pond. Surveys started 10 min before sunset, to allow for varying emergence times of different bat species, and ended 240 min after sunset, thus encompassing the peak period of nightly bat activity [51]. Surveys were only performed on dry and low wind-speed nights [8]. For acoustic analysis and species identification, a bat pass was considered as a sequence of three or more echolocation pulses in the microphone sampling cone [20]. Faint pulses were accounted in activity analyses but classified as unidentified to reduce identification error. Recordings were screened for pulse shape and were measured for parameters such as frequency of maximum energy, pulse duration and inter-pulse interval, using Audacity 2.1.0 (https://sourceforge.net/projects/audacity/). Bat calls were identified to the species level or assigned to species acoustic complexes following dichotomous keys for Portugal [53]. Acoustic complexes were established to group bat calls with great overlap of echolocation pulses characteristics, either within the same genus or from different genus [53]. These included *Pipistrellus* spp.; *Plecotus* spp.; *Nyctalus* spp.; *Myotis* spp.; *N. lasiopterus/N. noctula*; *Eptesicus serotinus/E. isabellinus*; *E. serotinus/E. isabellinus/N. leisleri*; and *M. myotis/M. blythii*. We also recorded the feeding activity by counting the number of feeding buzzes, a distinctive sound pattern indicative of a prey capture attempt.

Arthropod sampling and identification

We measured the arthropod prey availability at the ponds using custom made light traps. Each trap consisted of a frame holding a UV light tube connected to a 12 V battery mounted on a white bucket, which funneled the arthropods inside. At the bottom of the bucket, we placed a sponge sprayed with insecticide. These traps where positioned at the edge of each pond, approximately 0.5 m from the ground. We set up the traps at the greatest possible distance from the bat detectors to avoid any potential interference with the acoustic sampling. To coincide arthropod sampling with bat acoustic sampling, each trap was turned on immediately before the recordings started and turned off when they ended, ensuring correspondence between measurements. The collected arthropods were preserved and later identified to the order level using a stereo microscope, in accordance with the field guide Insects of Britain and Northern Europe [16]. Then, they were dried at 60º C for 48 h and weighted using a precision scale Mettler AE 100 with a resolution of 0.1 mg. For each order and for the total arthopod sample, we recorded the number of individuals and their biomass (g).

Abiotic pond features and land use type

We recorded the abiotic features for each pond. We measured the water physicochemical parameters in situ, including conductivity, pH, temperature and dissolved oxygen, using a multi-parameter probe (Multi 340i, WTW). We also measured the water surface area using a GPS. Wind speed was recorded near the ponds with a digital anemometer. Pond hydrological regime was evaluated as a categorical variable encoding the pond as permanent or temporary. Additionally, we analyzed the proportion of land use type within a 1000 m buffer surrounding each pond. Land use data was extracted from level two of COS2007 [19]. Portuguese land cover map, and re-classified into 10 land use types: urban areas (Urban); industry, trade and transports (Industry); quarries and construction sites (Quarries); temporary crops of wheat, rice and irrigation (Temp. crops); permanent crops of vineyards, orchards or olive groves (Perm. crops); permanent pastures (Pasture); mosaic of vineyards, orchards or olive groves, with natural and semi-natural areas (Agriculture mosaic); softwood, hardwood or mixed forests (Forests); open forests with shrub or herbaceous vegetation (Open forests); and open areas or areas with low vegetation (Open natural areas) (Table 1). These analyses were performed using QGIS 2.14.7 [49].

Statistical analysis

We investigated the influence of pond characteristics and their surroundings on bat activity, feeding activity and species richness, using Generalized Linear Models (GLMs). The 35 explanatory variables were divided into three subsets: pond abiotic features, prey-availability and land use type (Table 1). Logarithmic transformations were applied to bat activity and feeding activity values to approach normal distribution and mitigate the effects of outliers [73]. Explanatory variables with skewed distributions were also transformed for normality and reduce the influence of extreme values (Table 1).

We paired sets of permanent and temporary ponds within a 3 km radius and compared bat activity, feeding activity and species richness between them. One temporary pond exhibited substantially higher total bat-passes than all others combined, being excluded from the overall analysis, along with its paired permanent pond. Consequently, 31 ponds were included in the exploratory analysis, and 30 in the comparative ones.

Then, we compared all explanatory variables differentiating by pond hydrological regime. These paired comparisons were carried out using the "Wilcoxon signed rank test", with significance set at 0.05, using R statistical package "PairedData".

Prior to modeling, we conducted pairwise correlation tests to investigate collinearity among the explanatory variables. When variable pairs showed correlation values exceeding 0.7, we excluded the variable less ecologically meaningful [68]. The base category of pond hydrological regime used in our models was permanent.

We used the Gaussian distribution to model bat activity and feeding activity, and the Poisson distribution to model species richness.

For each response variable, we generated 30 models with the highest explanatory power. Model selection was based on the Akaike Information Criterion adjusted for small sample sizes (AICc) and corresponding Akaike weights (wi) for ranking [14]. For the best models of bat activity and feeding activity (ΔAICc < 2), we assessed the goodness of fit using the explained variance (adjusted R^2). For species richness models – Poisson distribution – we evaluated the goodness of fit using the pseudo-R^2, derived from CoxSnell, Nagelkerke, MsFadden and Pearson^2 formulae, applying the R package "modEVA" [5]. For the Poisson model we also calculated the dispersion parameter to assess its adjustment [74].

Since no single model was convincingly the most plausible, we performed a model averaging approach for each group of models with ΔAICc < 2, using the R package "MuMIn" [13]. We conducted all analyses using the R 3.3.2 version [50] and used the R package "glmulti" for model selection analyses.

Results

Comparison between permanent and temporary ponds

In total, we recorded 4786 bat-passes, of which 3294 (69%) were identified to the species or acoustic complex level (Table 2). The most common recorded species was *P. pipistrellus* (n = 1619 passes), followed by the complex *E. serotinus/E. isabellinus/N. leisleri* (n = 510), and *P. kuhlii* (n = 342).

The total bat-passes were distributed by 27 ponds: 3802 in permanent ponds (mean = 237.6, min = 0, max = 996) and 984 in temporary ponds (mean = 65.6, min = 0, max = 598). No activity was detected at three temporary and one permanent pond. Similarly, feeding activity (buzzes) was higher in permanent ponds: 222 feeding buzzes in permanent ponds (mean = 13.9, min = 0, max = 74) and 141 feeding buzzes in temporary ponds (mean = 9.4, min = 0, max = 104). There were significant differences between pond hydrological regimes in bat activity (V = 22, p-value = 0.03), but not in feeding activity (V = 19.5, p-value = 0.25). Species richness was also higher in permanent ponds (mean = 4.1, min = 0, max = 8) than in temporary ponds (mean = 2.2, min = 0, max = 6), showing significant differences (V = 17.5, p-value = 0.03). Among species or acoustic complexes, *E. serotinus/E. isabellinus/N. leisleri* and *P. kuhlii* presented significant differences with greater activity in permanent ponds (V = 22, p = 0.007 and V = 2.5, p = 0.018, respectively) (Table 2). Rare species or species of high conservation

Table 1 Description and summary statistics of the 35 explanatory variables included in pond abiotic features, prey-availability and land use type (calculated in a 1000 m buffer from the ponds)

Abiotic pond features	Description	Transformation	Temporary ponds		Permanent ponds	
			Mean ± S.D	Range	Mean ± S.D	Range
Water area	Water surface area (m2)	Log(x)	5131 ± 7915,2	142—29,174	2938 ± 4910,6	31—19,930
Conductivity (µS)	Water conductivity	-	687 ± 446,3	102—1568	621 ± 270,8	156—1085
pH	Water pH	-	7 ± 0,7	5,72—8,15	8 ± 0,9	5,78—9,4
Temperature (C°)	Water temperature, measured with pH probe	-	22 ± 4,4	16,3—30,5	22 ± 2,9	18—28,4
O_2 (ml/l)	Oxygen content of water	-	3 ± 2,6	0,56—8,09	7 ± 2,3	0,54—9,39
Wind speed (m/s)	Wind speed, measured close to the pond	-	2 ± 2	0—6	1 ± 1,2	0—3,5
Pond Type	Temporary or permanent, according to the hydrological regime. The base category used on our models was permanent	-	-	-	-	-
Prey availability						
n Arthropoda		Arcsin	49,1 ± 74,7	1—249	92 ± 138,8	1—556
Arthropoda biomass (g)		Arcsin	0,06 ± 0,07	0,0003—0,3	0,062 ± 0,064	0,001—0,224
n Diptera		Log(x + 0,00001)	20,1 ± 29,3	0—107	69,8 ± 121,7	1—484
Diptera biomass (g)		Log(x + 0,00001)	0,008 ± 0,011	0—0,0339	0,03 ± 0,05	0,0002—0,2
n Hemiptera		Log(x + 0,00001)	11,8 ± 25,1	0—83	9,8 ± 19,2	0—79
Hemiptera biomass (g)		Log(x + 0,00001)	0,005 ± 0,009	0—0,0291	0,003 ± 0,006	0—0,03
n Coleoptera		Log(x + 0,00001)	10,9 ± 16,6	0—52	5 ± 10,07	0—39
Coleoptera biomass (g)		Log(x + 0,00001)	0,02 ± 0,04	0—0,15	0,02 ± 0,03	0—0,08
n Lepidoptera		Log(x + 0,00001)	3 ± 3	0—9	4,9 ± 7,8	0—27
Lepidoptera biomass (g)		Log(x + 0,00001)	0,01 ± 0,01	0—0,05	0,01 ± 0,02	0—0,06
n Hymenoptera		Log(x + 0,00001)	2,6 ± 8,2	0—34	1,7 ± 3	0—11
Hymenoptera biomass (g)		Log(x + 0,00001)	0,0005 ± 0,0013	0—0,006	0,001 ± 0,004	0—0,02
n Orthoptera		Log(x + 0,00001)	0,06 ± 0,24	0—1	0,1 ± 0,3	0—1
Orthoptera biomass (g)		Log(x + 0,00001)	0,0007 ± 0,0027	0—0,01	0,0007 ± 0,002	0—0,007
n Dermaptera		Log(x + 0,00001)	0 ± 0	0—0	0,06 ± 0,24	0—1
Dermaptera biomass (g)		Log(x + 0,00001)	0 ± 0	0—0	0,0002 ± 0,0007	0—0,003
n Arachnida		Log(x + 0,00001)	0,5 ± 1	0—4	0,6 ± 0,8	0—2
Arachnida biomass (g)		Log(x + 0,00001)	0,0006 ± 0,001	0—0,005	0,001 ± 0,002	0—0,0061
Land use type						
Urban	Proportion of urban areas	Sqrt(Arcsin(x))	0,01 ± 0,02	0—0,07	0,02 ± 0,03	0—0,11
Industry	Proportion of industry, trade and transports	Sqrt(Arcsin(x))	0,001 ± 0,003	0—0,01	0,0009 ± 0,003	0—0,01
Quarries	Proportion of quarries and construction sites	Sqrt(Arcsin(x))	0,0007 ± 0,003	0—0,01	0,002 ± 0,004	0—0,01
Temp. crops	Proportion of temporary crops of wheat, rice and irrigation	Sqrt(Arcsin(x))	0,25 ± 0,19	0,02—0,74	0,4 ± 0,1	0,12 –0,54
Perm. crops	Proportion of permanent crops of vineyards, orchards or olive groves	Sqrt(Arcsin(x))	0,002 ± 0,004	0—0,02	0,007 ± 0,01	0—0,04
Pasture	Proportion of permanent pasture	Sqrt(Arcsin(x))	0,1 ± 0,2	0—0,5	0,1 ± 0,1	0—0,27
Agriculture mosaic	Proportion of mosaic of vineyards, orchards or olive groves, with natural and semi-natural areas	Sqrt(Arcsin(x))	0,04 ± 0,06	0—0,2	0,08 ± 0,09	0—0,23
Forests	Proportion of softwood, hardwood or mixed forests	Sqrt(Arcsin(x))	0,1 ± 0,09	0—0,3	0,1 ± 0,08	0—0,3
Open forests	Proportion of open forests with shrub or herbaceous vegetation	Sqrt(Arcsin(x))	0,3 ± 0,3	0—0,7	0,3 ± 0,3	0—0,8
Open areas	Proportion of and open areas or areas with low vegetation	Sqrt(Arcsin(x))	0,2 ± 0,3	0—0,9	0,04 ± 0,1	0—0,4

concern were recorded with low activity, occurring in both pond hydrological regimes but more frequently in permanent ponds: *M. myotis/M. blythii* (permanent: $n = 24$; temporary: $n = 1$), *M. escalerai* (permanent: n = 6; temporary: n = 3), *Plecotus spp.* (permanent: n = 1; temporary: n = 2 passes). However, *N. lasiopterus/N. noctula* were only present in permanent ponds: ($n = 8$).

Regarding prey availability, we recorded eight orders of arthropods associated with the ponds: Diptera,

Table 2 Summary statistics of the bat species detected in the temporary ponds and permanent ponds

Species	Temporary ponds			Permanent ponds			Frequency detected (%)		p
	Median	Mean ± S.D	Range	Median	Mean ± S.D	Range	Tem	Perm	
Pipistrellus spp.	0	0.9 ± 2.3	0—8	1	14.1 ± 28	0—106	1.42	5.94	0.116
P. kuhlii	2	1.8 ± 2.2	0—8	3	19.7 ± 39.6	0—142	2.74	8.29	**0.018**
P. pipistrellus	0	42.4 ± 138.1	0—557	1	61.4 ± 109.4	0—398	64.63	25.85	0.363
P. pygmaeus	0	1.1 ± 3.2	0—13	0	3.9 ± 8	0—25	1.63	1.63	0.231
Plecotus spp.	0	0.1 ± 0.3	0—1	0	0.06 ± 0.2	0—1	0.20	0.03	0.772
Nyctalus spp.	0	0.7 ± 2.2	0—9	0	1.9 ± 3.2	0—15	1.02	0.82	0.090
N. lasiopterus/noctula	0	0 ± 0	0—0	0	0.5 ± 1.9	0—8	0.00	0.21	-
N. leisleri	0	1.2 ± 2.7	0—9	0	7.1 ± 15.1	0—58	1.83	3.00	0.106
Eptesicus serotinus/isabellinus	0	0.9 ± 2.2	0—8	0.5	15.4 ± 22.7	0—76	1.32	6.47	0.059
E. serotinus/isabellinus/N. leisleri	0	7.7 ± 24.7	0—99	1.5	24.6 ± 40.3	0—132	11.79	10.36	**0.007**
Myotis spp.	0	0.3 ± 0.9	0—3	0	0.6 ± 1.9	0—8	0.26	0.51	1.00
M. myotis/blythii	0	0.07 ± 0.2	0—1	0	1.5 ± 3.5	0—13	0.10	0.63	0.100
M. escalerai	0	0.1 ± 0.5	0—2	0	0.4 ± 0.8	0—3	0.02	0.16	0.345
M. daubentonii	0	0 ± 0	0—0	0	0.5 ± 0.9	0—3	0.00	0.21	-
Barbastella barbastellus	0	0 ± 0	0—0	0	0.1 ± 0.5	0—2	0.00	0.05	-
Tadarida teniotis	0	0 ± 0	0—0	0	0.2 ± 0.7	0—3	0.00	0.08	-
Rhinolophus ferrumequinum	0	0 ± 0	0—0	0	0,06 ± 0.2	0—1	0.00	0.03	-
Not identified	0	8.3 ± 22.4	0—88	9	85.5 ± 127.7	0—403	12.66	35.98	**0.008**

Significant *p*-values related to the frequency detected (%) are indicated in bold

Hemiptera, Coleoptera, Lepidoptera, Hymenoptera, Orthoptera, Dermaptera and Arachnida (Table 1).

When comparing the 35 explanatory variables subdivided into pond abiotic features, prey-availability and land use type between ponds (Table 1), we observed significant differences in pH ($p = 0.03$), oxygen content ($p = 0.03$), proportion of temporary crops ($p = 0.05$) and biomass of Diptera ($p = 0.02$), which exhibited higher values in permanent ponds. In contrast, wind speed was higher in temporary ponds ($p = 0.02$).

Effect of pond features and land use type

Five best models with Δ AICc < 2 explain bat activity at the ponds with similar support (see all 30 models in Online Resource 1). The variance explained by each model is similar and above 66% for all resulting models. These models identify six variables influencing bat activity, listed in order of relevance: biomass of Diptera, proportion of urban areas, wind speed, proportion of open forests, biomass of Arachnida and total biomass of arthropods (Tables 3, 4). The average model, summarizing the five best models, reveals a positive relationship of bat activity with biomass of Diptera, proportion of urban areas, biomass of Arachnida and total biomass of arthropods (Table 4) (Fig. 2 A-D). Conversely, wind speed and proportion of open forests are negatively related with bat activity (Fig. 2 E, F).

Feeding activity in ponds follows a similar pattern to overall bat activity (see all 30 models in Online Resource 2), showing a correlation between them. Four models, with Δ AICc < 2, demonstrate robust statistical support for explaining feeding activity which include six variables, listed in order of relevance: proportion of urban areas, wind speed, biomass of Diptera, proportion of open forests, total biomass of arthropods and proportion of pastures (Tables 3, 4). The explained variance of each model is higher than 55%. The average model of the feeding activity (Table 4) exhibits a positive influence of the proportion of urban areas, biomass of Diptera and biomass of arthropods (Fig. 3 A, B, E), while wind speed, proportion of open forests and proportion of pasture show a negative relationship on feeding activity (Fig. 3 C, D, F).

Three models with strong support (Δ AICc < 2) explain bat species richness on ponds (see all 30 models in Online Resource 3). They comprise four variables, listed by order of relevance: biomass of Diptera, proportion of urban areas, pond hydrological regime (permanent or temporary) and wind speed (Tables 3, 4). We confirmed that the goodness of fit values are consistent across all pseudo-R^2 formulas (CoxSnell, Nagelkerke, MsFadden and Pearson^2). The dispersion value calculated for the best fitting model—Diptera biomass and Urban area—is 1.15, indicating that the Poisson model is suitable for our species richness analysis. The averaged model (Table 4) indicates that, like the models for bat overall and feeding activity, species richness increases with higher biomass of Diptera and proportion of urban areas (Fig. 4 A, B), and decreases with higher wind speed (Fig. 4 C). The hydrological regime of the ponds is included in the model as a factor influencing species richness, with permanent ponds (the base category) having a positive effect.

Table 3 Summary of the models with higher explanatory power of bat activity, feeding activity and species richness in the ponds. These models have ΔAICc < 2 and show the respective values of AICc, weights (Wi) and explained variance (R^2—adjusted). The species richness models show the explained variance (pseudo-R^2) calculated according to CoxSnell method. Type is a categorical variable corresponding to permanent ponds

	Bat activity models	AICc	Wi	R^2-adjusted
1	Wind speed + Diptera biomass + Urban	111.80	0.143	0.67
2	Wind speed + Diptera biomass + Urban + Open forests	111.94	0.133	0.69
3	Wind speed + Diptera biomass + Arachnida biomass + Urban + Open forests	113.00	0.078	0.70
4	Wind speed + Diptera biomass + Arachnida biomass + Urban	113.50	0.061	0.68
5	Wind speed + Arthropoda biomass + Diptera biomass + Urban	113.75	0.054	0.67
	Feeding activity models	**AICc**	**Wi**	**R^2-adjusted**
1	Wind speed + Diptera biomass + Urban + Open forests	98.07	0.165	0.58
2	Wind speed + Diptera biomass + Urban + Pasture + Open forests	99.37	0.086	0.59
3	Wind speed + Diptera biomass + Urban	99.85	0.068	0.53
4	Wind speed + Arthropoda biomass + Urban + Open forests	99.96	0.064	0.56
	Species richness models	**AICc**	**Wi**	**Pseudo—R^2**
1	Diptera biomass + Urban	123,62	0,198	0,56
2	Type + Diptera biomass + Urban	125,06	0,096	0,58
3	Wind speed + Diptera biomass + Urban	125,25	0,087	0,57

Discussion

Comparison between permanent and temporary ponds

This study assesses the bat use of permanent vs temporary ponds by measuring bat overall and feeding activity, species richness, and considering biotic and abiotic features and surrounding land use type.

Permanent ponds supported significantly higher bat activity and richness species compared to temporary ponds. Furthermore, some common phonic groups/species (*E. serotinus/E. isabellinus/N. leisleri* and *P. kuhlii)* showed higher activity in permanent ponds, also with significant differences. In addition, *M. myotis/M. blythii*, *M. escalerai* and *N. lasiopterus/N. noctula*, which are phonic groups of high conservation concern [42], had greater activity or were only found in permanent ponds. These results indicate a clear preference of bats for permanent ponds, contrasting with Razgour et al. [54] and Williams and Dickman [71] who reported equivalent levels of bat activity and species richness in permanent and temporary ponds in drier regions. However, our results support previous inventories in the Southwest Portugal where very few species were recorded in temporary ponds: only *P. kuhlii* and *E. serotinus* [22]. While our study shows a great increase in the number of species detected in temporary ponds in the study area (a total of 12 species), species richness remains lower compared to permanent ponds.

Comparisons of pond features and surrounding land use revealed significant differences in pH, oxygen content, the proportion of temporary crops and biomass of Diptera, all of which were higher in permanent ponds. Although we did not measure water depth, the deeper water columns, observed in most cases in these ponds, likely contribute to the elevated pH and oxygen content levels [9]. The higher Diptera biomass in permanent ponds is consistent with other results comparing densities of Diptera in permanent and temporary ponds [9, 18]. In contrast, wind speed was significantly higher in temporary ponds, indicating greater exposure of these ponds, likely due to fewer surrounding trees and buildings that provide shelter. The more favorable conditions

Table 4 Model averaging standardized coefficients of bat activity, feeding activity and species richness. Full – average of the coefficient values considering the value zero in the models that does not include the variable. Subset – average of the coefficient values considering just the models that include the variable. Type is a categorical variable corresponding to permanent ponds

Bat activity							
	(Intercept)	**Diptera biomass**	**Urban**	**Arachnida biomass**	**Arthropoda biomass**	**Open forests**	**Wind speed**
Full	0	1.097	0.717	0.091	0.028	−0.184	−0.706
Subset	0	1.097	0.717	0.307	0.246	−0.408	−0.706
Feeding activity							
	(Intercept)	**Urban**	**Diptera biomass**	**Arthropoda biomass**	**Pasture**	**Open forests**	**Wind speed**
Full	0	0.534	0.434	0.075	−0.057	−0.340	−0.513
Subset	0	0.534	0.521	0.450	−0.254	−0.413	−0.513
Species richness							
	(Intercept)	**Diptera biomass**	**Urban**	**Wind speed**	**Type**		
Full	0	0.494	0.220	−0.027	−0.031		
Subset	0	0.494	0.220	−0.116	−0.122		

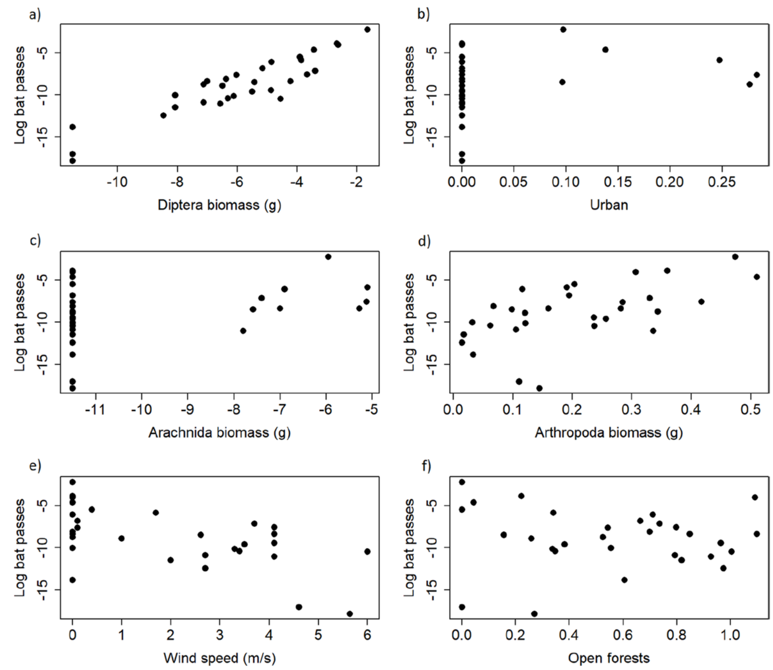

Fig. 2 Relationship between estimated bat activity and: (**a**) biomass of Diptera (logarithm), (**b**) proportion of urban areas (angular transformation), (**c**) biomass of Arachnida (logarithm), (**d**) biomass of Arthropoda (angular transformation), (**e**) wind speed and (**f**) proportion of open forests (angular transformation)

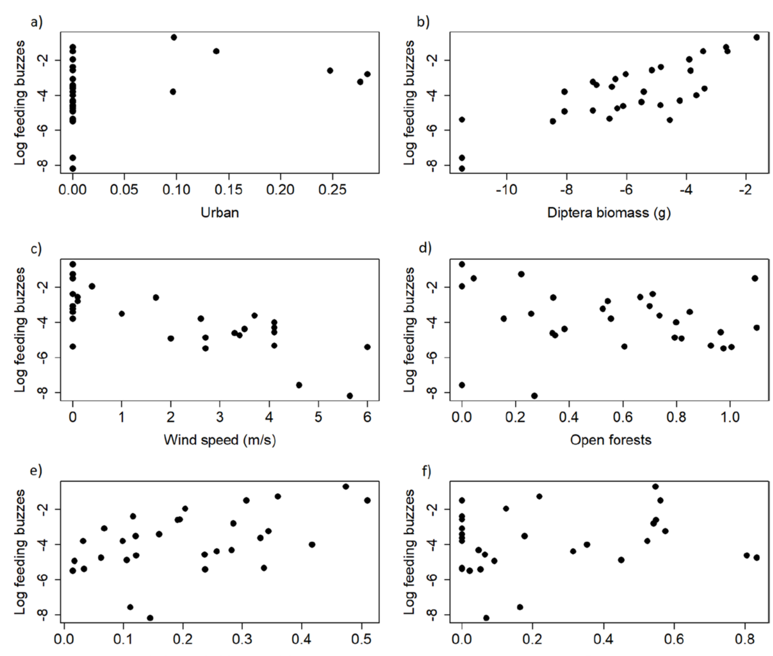

Fig. 3 Relationship between estimated feeding activity (logarithm) and: (**a**) proportion of urban (angular transformation), (**b**) biomass of Diptera (logarithm), (**c**) wind speed, (**d**) proportion of open forests (angular transformation), (**e**) biomass of Arthropoda (angular transformation), (**f**) proportion of pasture

in permanent ponds, resulting from higher Diptera biomass and lower wind speed, may have contributed to the higher bat activity and species richness observed in these habitats compared to temporary ponds.

Effect of pond hydrological regime

Our findings from GLM models indicate that pond hydrological regime only influences species richness, leading to an increase in the number of species in

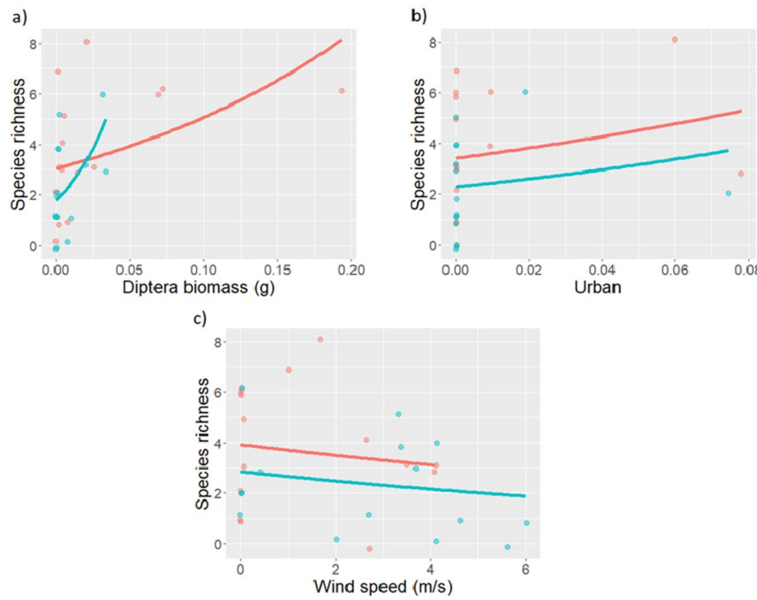

Fig. 4 Relationship between species richness and: (**a**) biomass of Diptera (logarithm), (**b**) proportion of urban (angular transformation), (**c**) wind speed, showing the difference between permanent (red) and temporary (blue) ponds

permanent ponds. These results contrast with studies conducted in arid regions, where pond hydroperiod had no significant impact on bat activity or species richness. Razgour et al. [54] reported that pond hydroperiod only influenced bat community composition when associated with pond size, while Razgour et al. [55] observed that interspecific competition shaped bat communities and activity patterns, with species partitioning pond use either spatially or temporally.

However, in the Mediterranean region, the development of artificial wetlands has become a common management practice [21, 47], and bat species can indeed benefit from them [69]. New-built permanent ponds have the potential to increase opportunities for drinking and preying, reduce competition among individuals and increase connectivity between foraging habitats [29, 37, 65]. Amorim et al. [3] observed that bats showed weak associations with specific habitat features in spring during pregnancy, but, as the season advances, bat activity and species richness consistently increase on permanent waters over the breeding season. This suggests that bats may track spatial variations in water availability, particularly in regions like the Mediterranean, where temporary water sources decline from spring to summer [3, 24, 39, 69].

Although our study emphasizes the importance of permanent ponds, temporary ponds also remain highly valuable throughout the year. Salvarina et al. [60] showed that Mediterranean temporary ponds in Greece sustain high levels of bat activity and species richness year-round, influenced by distance from water, presence of water and air temperature. Together, these findings highlight the complementary role of permanent and temporary water bodies. While permanent ponds provide a stable habitat with consistent drinking water and insect populations, becoming crucial during critical periods of drought both for common and threatened species [3, 69], temporary ponds hold moist conditions that may be highly suitable for bats or their prey, even when dry, thus sustaining bat activity and diversity across seasons.

Effect of pond features and land use type

The increase in Diptera biomass and the surrounding proportion of urban areas, and the decrease in wind speed were the main factors influencing bats in our study. These variables were included in the models for overall bat activity, feeding activity, and species richness.

Diptera insects are the favorite prey for various bat species, including *P. pipistrellus* [6], *P. kuhlii* [25], *P. pymaeus* [7], *N. leisleri, N. noctula* and *Myotis daubentonii* [70]. Other species, such as *E. serotinus* and *E. isabellinus,* also consume substantial amounts of Diptera [35, 70]. Moreover, *Rhinolophus ferrumequinum* frequently preys on Diptera, representing about 35% of its diet [2]. Diptera are found in high densities in the permanent ponds [18] but are also abundant in temporary ponds [11], representing a dominant prey for bats. The arthropods biomass, which influenced bat overall and feeding activity, is directly associated with Diptera biomass. This influence is well-documented in the literature supporting the positive relationship between bats and the availability of arthropods [23, 30, 54]. The Arachnids biomass affected bat activity, as they are also consumed by insectivorous bats, although in smaller quantities (*P. pipistrellus*—[6],*P.*

kuhlii—[25]). In addition, this importance is likely associated with the presence of Dipterans, as they are commonly preyed upon by Arachnids.

The proportion of urban areas is positively affecting the bat community likely due to the high availability of roosts in nearby buildings and other constructions. Roost-generalist species, such as *Pipistrellus* spp. and *E. serotinus,* thrive in urban areas and often roost in these environments, as they tolerate high light intensity and traffic noise [4, 52]. In particular, *P. pipistrellus,* the most common species observed in our study, is broadly described as an 'urban adapter' [27]. Our results are consistent with [44], who found greater species richness in urban areas and parks than in other habitat types, when excluding waterbodies. However, despite the overall increase in bat activity and species richness near urban areas, some species that are relatively common and urban-tolerant may still respond negatively to urbanization at a local scale [32]. In our study, *Tadarida teniotis*, *Plecotus* spp. and *R. ferrumequinum* were absent from ponds near urban areas, indicating that these species avoid or limit the use of urban settings in Mediterranean regions [40, 51]. While urban areas seem to support common species, improving shelter near ponds may attract rarer species and those of conservation concern. Thus, increasing tree cover or installing shelter boxes around the ponds should increase their overall value for bats, particularly for threatened species, provided the boxes are appropriately designed to minimize exposure to excessive heat and oriented towards the southeast. Further considering land use type, we also found that an increasing proportion of open forests, shrub and herbaceous vegetation surrounding the ponds negatively affect bat activity and feeding activity. In addition, the proportion of pasture had a negative but weak impact on feeding activity. While open forests with gaps between trees may sometimes benefit less maneuverable species [17], bats usually prefer to use ponds situated within dense tree cover, which enhances habitat suitability and shelter [27, 67]. Native and unimproved pastures seems to benefit bat communities, however, our pastures are intensively managed and there is no evidence of promoting feeding activity [31].

Furthermore, weather conditions had a significant impact on bats, despite our sampling has been restricted to nights with low wind speed ($<6\ ms^{-1}$). This effect is commonly reported and may result from reduced prey activity and disturbances caused by ripples on the water surface, which interfere with the prey-target detection [17, 29, 58, 71].

This study contributes to an in-depth understanding of the importance of both permanent and temporary ponds for bat conservation in Mediterranean regions. Permanent ponds hosted higher bat activity and species richness, including more rare and high conservation concern species, which emphasize the ecological value of these habitats and the need to integrate them into bat conservation plans. Temporary ponds, despite being associated with lesser bat activity and a lower species richness, are still highly used by bats, which shows the important role they have in supporting local communities, even when dry [60]. In addition, they are an interesting ecosystem for several animal groups in the Mediterranean region, encompassing unique and endemic species [38].

Future research should focus on these ecosystems to explore potential variations in bat activity and species richness across different regions. Additionally, assessing the detailed vegetation structure surrounding the ponds, particularly along their edges, would provide valuable insights into habitat suitability for bats. A comprehensive approach that incorporates these factors could further inform conservation strategies and habitat management for bats in these environments.

Conclusions and conservation implications

In Mediterranean regions, ponds of different types are known to attract bats due to the availability of drinking water and abundance of insects. Our study shows that artificial permanent ponds, often built for irrigation in agricultural landscapes, support higher bat activity and species richness than temporary natural ponds. This can be driven by their stability in water availability and insect populations throughout the year. However, it can also be a result from the higher levels of Diptera biomass and lower wind speed, which we found as factors that greatly influenced bat overall and feeding activity and species richness. These findings emphasize the conservation value of permanent ponds in the Mediterranean region, while also underlining the importance of maintaining ponds with different flooding regimes, which increase water availability, contribute to greater landscape heterogeneity and serve as rich feeding areas for bat communities. Thus, we argue that conservation efforts should focus on the protection of both pond hydrological regimes.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12862-025-02449-w.

Supplementary Material 1.

Supplementary Material 2.

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Authors' contributions

Conceptualization: Joana Ribeiro-Silva, Carla Pinto-Cruz, António Mira, Tiago Marques; Formal analysis: Joana Ribeiro-Silva, Tiago Marques; Funding acquisition: Carla Pinto-Cruz , António Mira, Tiago Marques; Investigation: Joana Ribeiro-Silva, Carla Pinto-Cruz, Tiago Marques; Methodology: Joana Ribeiro-Silva, Tiago Marques; Project administration: Carla Pinto-Cruz, António Mira, Tiago Marques; Resources: Carla Pinto-Cruz, António Mira, Tiago Marques; Supervision: Tiago Marques; Writing – original draft: Joana Ribeiro-Silva; Writing – review & editing: Joana Ribeiro-Silva, Carla Pinto-Cruz , António Mira, Tiago Marques.

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Data availability

Data is provided within the supplementary information files.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing Interests

The authors declare no competing interests.

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