Ecology of a threatened nomadic duck species in Morocco, the Marbled Duck (Marmaronetta angustirostris) : implications for conservation

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Chapter 1: General introduction

1. Biodiversity crisis and wetlands degradation

Biodiversity is declining at an alarming rate as a result of multiple anthropogenic pressures. These can be grouped into direct drivers, such as habitat loss and degradation, conversion of natural landscape into agricultural land, infrastructure development, overexploitation of natural resources, and invasive alien species; and indirect drivers primarily linked to climate change through chemical atmospheric perturbations, rising temperatures and sea level rise (IPBES, 2019). These pressures have intensified throughout the 20th and 21st centuries, especially in recent decades, in concordance with human expansion and the growing intensity of industrial and agricultural activities (Hersperger & Bürgi, 2009). Their impacts occur across different spatial and temporal scales, threatening ecosystem structure, function, and resilience with cascading consequences for public health and human livelihoods (Isbell *et al.*, 2017; Newbold *et al.*, 2018). Recent global assessments indicate that a substantial proportion of species and ecosystems are now at risk of collapse, with particularly severe consequences in regions where climatic stressors and human demands for natural resources converge (IPBES, 2019). For example, over the last century, thousands of species' populations size have been reduced, with vertebrate populations declining by 68% on average, and populations in tropical regions of the Americas reaching declines up to 94% as measured by the Living Planet Index (Barnosky *et al.*, 2011; Ceballos *et al.*, 2015; Ceballos, Ehrlich, & Raven, 2020; WWF, 2020). Many of these declines have already resulted in species extinctions. The present extinction rate is thousands of times higher than the natural background rate, and projections indicate that future rates could be 10,000 times higher (Pimm et al., 2014; De Vos et al., 2015).

Among the major underlying drivers of the biodiversity crisis are habitat loss, degradation, and fragmentation (Convention on Biological Diversity, 2020). Global assessments have estimated that approximately 75% of ice-free land has now been substantially altered by human activities (IPBES, 2019). The consequences are especially evident in certain ecosystems such as tropical rainforests, which have suffered extensive losses in recent decades. For example, the Amazon rainforest has experienced serious deforestation over the past decades, and is now approaching a tipping point beyond which vast parts of the forest are expected to dry out and to be transformed into degraded savannahs (Lovejoy & Nobre, 2019).

Wetlands are another group of ecosystems of critical concern. They are among the most important and diverse ecosystems on the planet, providing vital services for both humans (supporting cultural values, economic activities, and livelihoods of billions of people worldwide) and various species, including many threatened and endangered plants and animals (Gardner & Finlayson, 2018; Lynch et al., 2023). For example, despite covering less than 1% of the Earth's surface, freshwater habitats are vital ecosystems supporting over 10% of all known species, including about one-third of vertebrates and half of fish (Strayer & Dudgeon, 2010). Wetlands have suffered significant losses over the last century. About 85% of the wetland area that existed in the 1700s is now gone, and 65% of the remaining wetlands today face moderate to high pressures from human activities (IPBES, 2019). Over the past century, a large proportion of natural wetlands has been drained, converted, or severely modified, primarily for agriculture, urban development, and water extraction (Davidson, 2014). Regardless of their importance for humans and species, wetlands have received less conservation effort in comparison to terrestrial and marine species and ecosystems (Abell & Harrison, 2020).

Climate change constitutes an additional pressure on wetlands by intensifying hydrological variability through altered precipitation regimes, increased evapotranspiration, and more frequent droughts, further accelerating wetland degradation, especially in mid-latitude regions such as the Mediterranean basin (Collins *et al.*, 2013). The Mediterranean basin is recognized as one of the most important biodiversity hotspots in the world, and the third richest in plant diversity and endemism (Mittermeier *et al.*, 2004). Within this context, wetlands cover only a small proportion of the region, but they support over a third of its species richness (CEPF, 2024). Characterized by a semi-arid to arid climate, strong interannual variability in rainfall, and a long history of human land and water use, Mediterranean wetlands are highly sensitive to both climatic fluctuations and increasing water demand (Cramer *et al.*, 2018; Lionello & Scarascia, 2018).

Recent assessments indicate the area of natural Mediterranean wetlands has declined by almost half since the 1970s, while artificial wetlands have expanded markedly over the same period due to the construction of numerous hydraulic infrastructures, including dams, reservoirs, and agricultural ponds (MWO3, 2025). While this transformation is widespread across the Mediterranean basin, the Maghreb still exhibits an exceptionally high level of wetland naturalness (approximately 95%), with most wetlands being temporary and precipitation-dependent (MWO3, 2025). However, in Morocco, artificial wetlands account for a much larger share, approaching 38% of the total, reflecting extensive dam construction and water management development. This profound reconfiguration of hydrological regimes and wetland types shapes the landscape used by waterbirds and other taxa (MWO3, 2025; Fig 1.A). Combined with water pollution and urban expansion (Fig 1.B), the conversion of natural wetlands lead to the degradation and loss of habitats essential for the life cycles of numerous plant and animal species, thereby negatively affecting their conservation status (Fig 1.C), with more than 40% of these species currently threatened with extinction (MWO3, 2025).

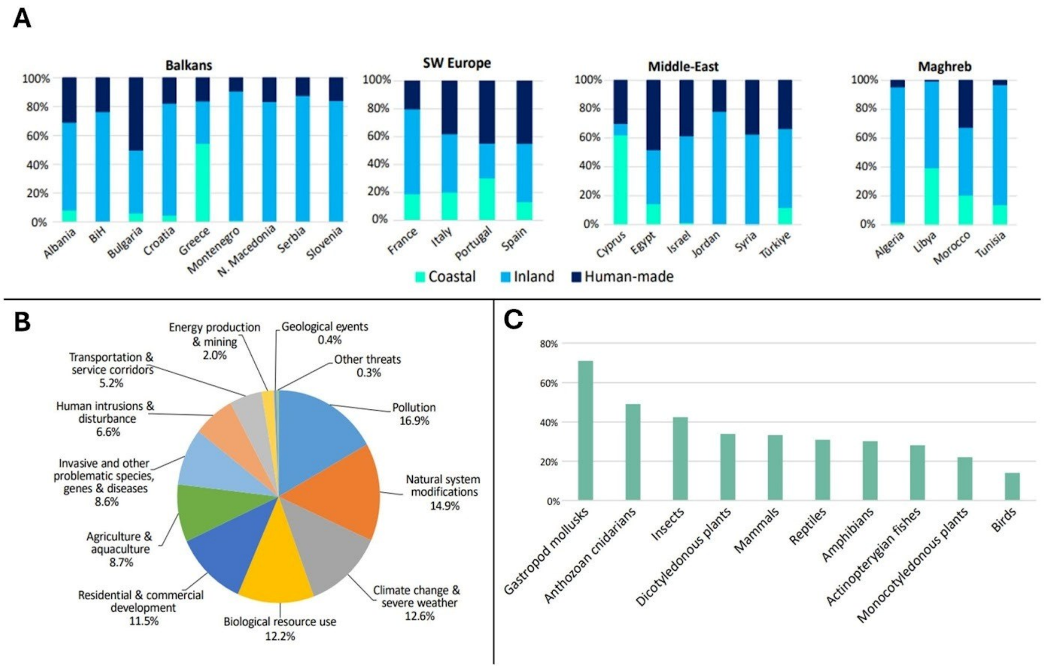

Figure 1. *A: Wetland types distribution according to Ramsar reporting classes for each Mediterranean country where data is available. B: Frequency of threats affecting species in Mediterranean wetlands based on IUCN Red List data. C: Percentage of species that are threatened, near threatened, or data deficient by taxonomic class. Only species occurring in wetlands in at least one Mediterranean country are included. Both figures were taken from MWO (2025), with permission from the authors.*

Waterbirds are among the animal groups most affected by the loss and degradation of Mediterranean wetlands, as many species depend on these habitats for key phases of their annual cycle, including breeding, wintering, and migration stopovers (Knudsen et al., 2011). However, their responses to environmental change are highly variable and often shaped by the dynamic nature of wetland ecosystems. In many regions of the world, waterbirds exhibit flexible and sometimes nomadic or mixed movement strategies that allow them to track spatially and temporally unpredictable resources (Teitelbaum & Mueller, 2019). In arid and semi-arid landscapes, highly variable rainfall and evaporation create mosaics of ephemeral wetlands and rapid shifts in local conditions, favoring irregular, nomadic long-distance movements that are not fixed in timing or direction (Gibson *et al.*, 2022; Nicol, Lloyd-Jones, & McGinness, 2024). For example, flamingos in South America move over large distances in response to fluctuating water levels and salinity conditions, while Straw-necked ibis (*Threskiornis spinicollis*) and Royal spoonbills (*Platalea regia*) in inland Australia show variable combinations of residency, migration and nomadism, shifting between wetlands over continental scales in response to episodic rainfall and wetland filling (McGinness *et al.*, 2024*a*, 2024*b*). Similarly, several duck species inhabiting wetlands in arid regions, such as the Pacific Black duck (*Anas superciliosa*) and Grey teal (*Anas gracilis*), undertake opportunistic long-distance flights of up to ~1000 –1200 km, sometimes triggered by heavy rainfall, but also including exploratory movements into regions with little surface water (Roshier, Asmus, & Klaassen, 2008; Kingsford, Roshier, & Porter, 2010). These strategies highlight the importance of understanding how individuals respond to environmental variability, particularly in arid and semi-arid systems where habitat availability is unpredictable, temporary and degrading (Donnelly *et al.*, 2022).

Such ecological flexibility complicates population monitoring and conservation assessment. Beyond their value as ecological indicators (Newton, 1998; Gregory *et al.*, 2005; Green & Elmberg, 2014), many of these species are conservation priorities in their own right, facing significant and often concurrent threats from habitat loss, hydrological alteration, and climate change. Threatened species such as the White-headed duck (*Oxyura leucocephala*, Endangered), Ferruginous duck (*Aythya nyroca*, Near Threatened), Common Pochard (*Aythya ferina*, Vulnerable), Crested coot (*Fulica cristata*, Critically Endangered) and the Marbled duck (*Marmaronetta angustirostris*) are threatened by the combined effects of habitat loss, hydrological alteration, anthropogenic pressures, and climate change (Ramírez *et al.*, 2018; Khelifa, Mahdjoub, & Samways, 2022). Species associated with temporary and highly variable wetlands are particularly vulnerable, as they depend on habitats that are inherently unpredictable in space and time. These species often exhibit low breeding densities, high mobility, and nomadic movement strategies, making their populations difficult to monitor and their responses to environmental change complex to interpret (Nicol, Lloyd-Jones, & McGinness, 2024). As a result, key aspects of their ecology, including population size, spatial organization, and behavioural responses to environmental variability, remain poorly understood in many regions. Addressing these knowledge gaps is essential for understanding the processes driving population dynamics and for designing effective conservation strategies (Bolam *et al.*, 2021).

The Marbled duck is a near-threatened species that exemplifies these challenges. Like other waterbirds in semi-arid and arid regions, it occupies a spatially and temporally variable mosaic of ephemeral wetlands whose presence depends on irregular rainfall events, leading to highly unpredictable local conditions (Salvador, Amat, & Green, 2023). The species is characterised by flexible and opportunistic movement strategies, including long-distance movements and marked inter-individual variation in daily distances travelled, consistent with nomadic behaviour in response to changing wetland availability (Pacheco-Guardiola *et al.*, 2025). The western Mediterranean population is estimated to have declined by approximately 46% between 2008 and 2018, primarily due to wetland loss and degradation, as well as anthropogenic pressures such as illegal killing (Wetlands International, 2018). Morocco is considered a stronghold for the species, supporting a substantial proportion of the western Mediterranean wintering population (Ouassou *et al.*, 2021). Key aspects of its ecology, including reliable estimates of population size, movement strategies, and habitat use under varying climatic conditions, remain insufficiently understood. These knowledge gaps largely stem from the species' nomadic behaviour, and the high spatiotemporal variability of the wetlands it occupies.

Addressing these challenges requires the integration of complementary monitoring and analytical approaches. In particular, robust estimates of abundance and population trends must explicitly account for imperfect detection, especially in systems where individuals are sparsely distributed and unevenly observable. At the same time, advances in biologging technologies provide new opportunities to investigate how individuals use space, move between wetlands, and respond to environmental variability at fine temporal and spatial scales. Combining these approaches with environmental and habitat data is essential for linking individual behaviour to broader ecological processes, and for identifying the key drivers shaping population dynamics. Together, such tools provide a quantitative framework for improving our understanding of the Marbled duck' ecology and for informing conservation strategies in highly dynamic and data-poor systems such as North African wetlands. These tools, and the frameworks that underpin them, are introduced in the following section.

2. Tools for conservation

2.1. Abundance, monitoring, and imperfect detection

One of the most widely used metrics in wildlife conservation is the estimate of population size (Stephens *et al.*, 2015). This tool is considered one of the most influential metrics in conservation ecology, and the development of such metrics is crucial for designing effective management plans and conservation measures for species and their habitats (Stephens *et al.*, 2015; López-Bao *et al.*, 2018). Many key conservation and policy tools rely directly on population size metrics. These include, for example, IUCN Red List of Threatened Species Assessments (IUCN, 2022) and the designation of Ramsar sites (Wetlands of International Importance,Popoff *et al.*, 2021), which rely on quantitative population thresholds. Such information is essential for determining whether populations are large or small, increasing, stable, or declining. It therefore supports the assessment and updating of species' conservation status (e.g. IUCN Red Lists), as well as the identification of sites holding significant portions of a species' global population (Ashe *et al.*, 2013; Camaclang *et al.*, 2015; Baker *et al.*, 2019). However, acquiring such metrics can be challenging, especially when the species of interest is rare and occurs at low densities, and this challenge can be further exacerbated by limited logistics for surveying wildlife, highlighting the need for cost-efficient sampling methods (Skalski, 1994; Parker *et al.*, 2011).

A variety of methods have been developed to estimate wildlife abundance and trends, each with specific assumptions and data requirements, consequently leading to the development of a variety of corresponding statistical frameworks (Royle, 2004*a*, 2004*b*; Sutherland, 2006). These methods span a continuum from simple count-based indices to fully-model-based estimators that explicitly account for detection probability and demographic processes. On one hand, raw count indices are typically defined as the number of individuals seen/heard per visit; they often serve as indices of relative abundance, and are considered to be easy and cheap to collect and many long-term bird monitoring programs use these methods (wintering waterbird counts, breeding bird surveys). However, these methods are affected by imperfect detection and therefore do not provide unbiased estimates of true population size (Kéry & Schmidt, 2008). To deal with this issue, researchers have developed several methods that account for imperfect detection, such as capture-mark-recapture (CMR) methods, distance sampling, removal sampling, double observer and N-mixture models (Nichols *et al.*, 2000; Farnsworth *et al.*, 2002; Williams, Nichols, & Conroy, 2002; Royle, 2004*a*; Abadi *et al.*, 2010; Buckland *et* *al.*, 2015). However, some of these methods can be expensive and require substantial efforts; for example, CMR methods require the capture of birds and individually marking them, while distance sampling can be impractical or even unsuitable in complex habitats (Costa *et al.*, 2021). On the other hand, methods that do not rely on marked individuals, such as the acoustic surveys and point counts, can be coupled with N-mixture models to estimate abundance, which have proven to be useful and easily applicable (Royle, 2004*a*).

Hierarchical N-mixture models appear particularly relevant for this thesis. These models have been widely applied across a range of taxa from insects to large mammals due to their ability to simultaneously estimate species abundance and detection probabilities from repeated count data (Royle, 2004*a*; Kéry & Royle, 2015; Kidwai *et al.*, 2019; Manica *et al.*, 2019). Additionally, their capacity to model variation in abundance and detectability using relevant covariates enhances the ecological validity of resulting inferences compared to conventional index-based approaches (Gilbert *et al.*, 2021). Another key feature of these models is the hierarchical separation between the latent state process and the observation process. This framework allows estimation of population abundance by explicitly modelling both ecological variation in true abundance and imperfect detection during surveys. To obtain unbiased inferences of population abundance, it is therefore necessary to explicitly model the measurement error processes underlying observed data. Survey-based ecological studies are typically confronted with two sequential inferential steps, as illustrated in Figure 2. The first concerns the state process (λ), which describes variation in true abundance among sites, whereby species are expected to occur at higher abundance in habitats that match their needs. The second concerns the observation process p (measurement process), which models imperfect detection by accounting for individuals present but not observed during surveys, as not all individuals present are available for detection or detected during a survey (Royle & Dorazio, 2008; Zipkin et al., 2014; Denes, Silveira & Beissinger, 2015; Kéry & Royle, 2020).

When embedded within a probabilistic sampling design, this hierarchical framework further enables extrapolation of abundance to unsampled areas, providing national-scale population estimates. This is especially relevant for nomadic species such as the Marbled duck, whose local distribution shifts in response to fluctuating wetland availability. This forms the statistical basis of Chapter 1, which addresses the breeding population size of the Marbled duck in Morocco and the habitat predictors of its breeding occurrence.

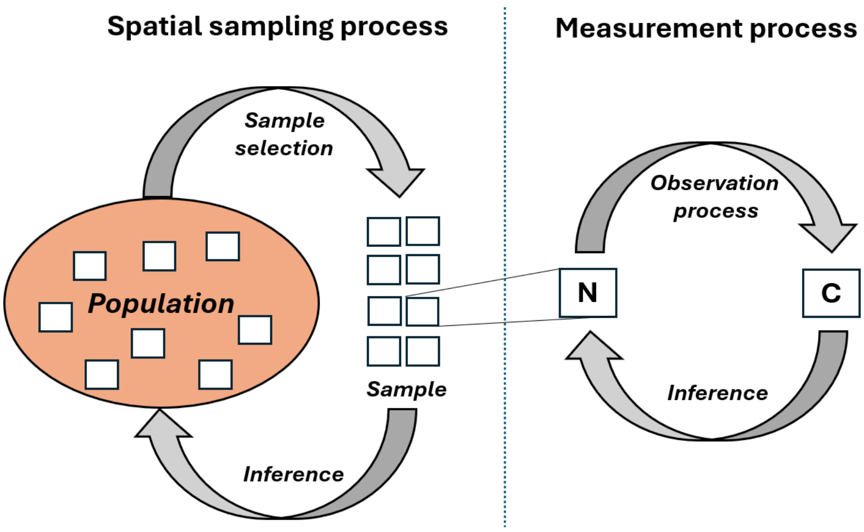

Figure 2. *A: Representation of the two underlying processes involved in abundance estimation. Spatial sampling is used to estimate the number of individuals (N), which in turn conditions the number of individuals detected (C) during a count. Adapted from Figure 1.4 in Kéry & Royle, 2015*

2.2. From behaviour to space use: biologging for conservation

Effective conservation and management require a thorough understanding of animal behaviour and habitat use. This knowledge links environmental change to population-level responses, such as survival, reproductive behaviour, and dispersal (Caro, 2007; Gaillard *et al.*, 2010; Berger-Tal *et al.*, 2011). Behavioural decisions about where and when to forage, rest, breed, or migrate determine how individuals encounter resources and threats, including predation, disturbance, pollutants, and harvest (Sutherland, 1998; Berger-Tal *et al.*, 2011). For wetland-dependent birds, the timing of movements between roosts and feeding areas, their selection of particular wetland types and their tolerance of human activity directly influence exposure to habitat loss, water-level fluctuations and disturbance, making behaviour and space use key targets for conservation planning (West & Caldow, 2006; Navedo & Herrera, 2012; Kays *et al.*, 2015; Navedo *et al.*, 2019).

Historically, animal behaviour and habitat use were primarily inferred from direct field observation, typically combining scan sampling of groups with focal follows of individuals to describe activity budgets and habitat associations (Altmann, 1974; Sutherland, 2006). These approaches provided valuable qualitative and quantitative descriptions of behaviour but are constrained in both space and time, often limited to daylight hours and accessible locations (Sillett, Holmes, & Sherry, 2000; Wilmers et al., 2015). Separately, capture-recapture methods allowed inferences on survival, movements between sites, and broad-scale migratory connectivity by tracking marked individuals across observation periods (Cam *et al.*, 2002). However, these approaches are logistically demanding and provide little information on daily movements or events occurring between capture locations, making transient use of remote habitats, such as stopover sites, easily missed (Webster *et al.*, 2002; Kays *et al.*, 2015). In parallel, early studies of habitat use relied on comparing observed locations or counts of animals with habitat availability derived from maps or land-cover data, often assuming that all used sites were known and that individual detection was uniform across habitats (Manly *et al.*, 2004; Beyer *et al.*, 2010). While these traditional approaches laid the foundations of movement and habitat-selection theory, they rarely captured fine-scale temporal dynamics or the full range of habitats used by cryptic or wide-ranging species, and they provided limited insight into how individuals respond to rapidly changing, human-dominated landscapes (Cagnacci *et al.*, 2010; Kays *et al.*, 2015).

The development of animal-borne telemetry (bio-logging) revolutionized the study of behaviour, movement, and habitat use by allowing the tracking of individuals in their environment in the absence of human observers (Cooke *et al.*, 2004; Kooyman, 2004; Cooke, 2008; Bograd *et al.*, 2010). Early very high frequency (VHF) radio-tracking enabled researchers to locate animals repeatedly and document home ranges and habitat associations, but required intensive field effort and often provided relatively coarse spatial and temporal resolution (Kenward, 2001; Mech & Barber, 2002). Subsequent technological advances from the early 1980s onward, progressively transformed bio-logging, with reductions in device size, improved battery technology and the introduction of microprocessors and solid-state memory enabling smaller loggers to record multiple variables simultaneously at higher temporal resolution (Kooyman, 2004; Evans, Lea, & Patterson, 2013). From the early 2000s, bio-logging systems became increasingly sophisticated, capable of collecting high-frequency, multi-sensor data while also recording environmental conditions associated with animal behaviour (Ropert-Coudert & Wilson, 2005). In parallel, advances in GPS and satellite telemetry dramatically improved the precision, frequency, and duration of positional data, making it possible to quantify movement paths, home-range dynamics, dispersal and exploratory movements, and habitat selection at fine spatial and temporal scales, including across migration routes and remote regions (Ponchon *et al.*, 2013; Kays *et al.*, 2015; Silvy, 2020).

More recently, multi-sensor biologging, especially the combination of high-resolution accelerometers with GPS, has extended bio-logging beyond "where" animals go to "what they do" in space and time, offering detailed insights into animal behaviours and energy expenditure (Wilmers *et al.*, 2015). Accelerometers have been applied across various taxa, and are used to study a wide range of topics. These applications include informing daily activity patterns, detecting specific events like predation, and monitoring important aspects of breeding and parental care (Shepard *et al.*, 2008; Whitney *et al.*, 2010; Shuert, Pomeroy, & Twiss, 2018). Accelerometer data can be used to classify behavioural states such as flying, resting, preening, and foraging using either unsupervised or supervised machine-learning methods trained on annotated reference data (Shepard *et al.*, 2008; Shamoun-Baranes *et al.*, 2012). When these classified behaviours are linked to GPS positions, researchers can construct behaviour-specific utilisation distributions, identify core roosting and foraging areas, and detect temporal routines in activity patterns and their responses to environmental and anthropogenic variables (Shepard *et al.*, 2011; Mosser *et al.*, 2014; Katzner & Arlettaz, 2020). This behaviour-informed tracking approach is particularly valuable for cryptic species in complex landscapes, where different behaviours may be associated with varying types of habitats and disturbances (Cullen *et al.*, 2023; VonBank *et al.*, 2023). In addition, the same data streams can be used to quantify individual variation and consistency in behaviour and space use, which has implications for vulnerability to habitat change and for the design of site-based protection measures (Mitchell *et al.*, 2020).

These developments are particularly relevant for studying species in semi-arid wetland systems, such as parts of the Mediterranean region where water availability varies strongly in space and time and where artificial wetlands are increasingly replacing natural ones (MWO3, 2025). In such dynamic landscapes, behaviour-informed telemetry provides a powerful tool to study nomadic species such as the Marbled duck, whose high mobility and dependence on ephemeral wetlands make it difficult to study using conventional methods. This forms the methodological basis of Chapters 2 and 3, which address how Marbled ducks organise their behaviour and space use across functional units during the wintering period, and how they allocate habitat use among natural, artificial, and accidental wetlands under varying climatic conditions.

3. Study system:

This section introduces the model species and the study areas where data were collected. Methodological details are described separately in each chapter.

3.1. Model species: Marbled Duck

The Marbled duck *(Marmaronetta angustirostris)* is a Near Threatened, small and slender duck, characterized by a distinctive dark eye-patch (Fig. 3). It is known for exhibiting nomadic and partially migratory behaviour, resulting in pronounced spatial and temporal variability in wetland use across its range (Salvador, Amat, & Green, 2023). Depending on hydrological conditions and wetland availability, individuals display a wide range of movement strategies, from local residency to long-distance seasonal movements, (Pacheco-Guardiola *et al.*, 2025).

Figure 3. *Marbled duck couple. © Saint Louis Zoo.*

Foraging ecology and diet

The Marbled duck is an omnivorous dabbling duck whose diet is dominated by aquatic plant seeds, complemented by invertebrates and green plant material (Green & Sánchez, 2003; Fuentes *et al.*, 2004). Across Mediterranean and Palearctic wetlands, seeds of submerged and emergent macrophytes, particularly Cyperaceae and Potamogeton, constitute the bulk of the diet, while animal prey represents a smaller but nutritionally important component, especially for ducklings (Fuentes *et al.*, 2004). Foraging occurs mainly in shallow water and relies on feeding modes typical of dabbling ducks, including surface picking and head-dipping, with less frequent use of gleaning, neck-dipping, and upending (Salvador, Amat, & Green, 2023).

Individuals generally forage at shallow depths (range: 1-49cm), often close to emergent vegetation, and frequently move between feeding patches (Green, 1998*b*). The Marbled duck contributes to ecological connectivity by dispersing aquatic plant seeds and invertebrate propagules between wetlands (Green, Figuerola, & Sánchez, 2002; Figuerola & Green, 2005). Experimental studies show that a substantial proportion of seeds remain viable after gut passage (Figuerola *et al.*, 2010).

Breeding biology

The Marbled duck is a relatively late-breeding duck, particularly at higher latitudes, with breeding phenology strongly influenced by climatic conditions and wetland availability and extending from April to September (Perrins, 1978; Green, 1998*c*). The species produces a single brood per breeding season, and there is no evidence of regular replacement clutches (Salvador, Amat, & Green, 2023). Nests are constructed by the female alone and usually placed on the ground, close to water, under low shrubs or dense herbaceous cover, although nesting on lake shores, over water in temporary wetlands, or occasionally near human structures has been reported (Perrins, 1978; Navarro Medina *et al.*, 1995; Salvador, Amat, & Green, 2023). The incubation period in the wild is from 25 to 27 days (Isakov, 1952). Clutch size generally ranges from 9 to 14 eggs, with larger clutches sometimes resulting from intraspecific brood parasitism (Perrins, 1978; Salvador, Amat, & Green, 2023).

Hatchlings are precocial and nidifugous, capable of feeding independently shortly after hatching (Perrins, 1978). Ducklings fledge approximately 50-54 days after hatching, and brood amalgamation may occur (Salvador, Amat, & Green, 2023). Most males abandon females after hatching, although biparental attendance has been documented in some populations, with both adults occasionally remaining with broods until or even after fledging (Navarro Medina *et al.*, 1995; Green, 1997).

Movement and migration

The Marbled duck is a partially migratory and highly mobile species, adapted to spatiotemporal fluctuations in wetland availability, and exhibits nomadic movements both before and after the breeding season (Salvador, Amat, & Green, 2023). In autumn, individuals typically move southwards, while spring movements are generally northward; however, a substantial proportion of the population may remain in breeding areas year-round when wetlands remain flooded (Salvador, Amat, & Green, 2023). Available evidence suggests limited dispersal during early life stages and a degree of short-term site fidelity (Green *et al.*, 2004). Marked and GPS-tracked juveniles released in south-east Spain remained at their natal site during their first year, and most ringed individuals showed little dispersal (Botella *et al.*, 2020). In contrast, adults often undertake nomadic movements at the end of the breeding season, as indicated by ringing recoveries and telemetry data (Navarro Medina *et al.*, 1995).

Recent GPS-tracking studies have begun to clarify migration patterns in the western Mediterranean. Individuals tagged in Spain have been recorded moving between Spain, Morocco, and Algeria during both autumn and spring, with some completing full migratory cycles and others exhibiting flexible, multi-directional movements between regions (Pacheco-Guardiola *et al.*, 2025). Census data further suggest an interannual redistribution of birds between Spain and North Africa, likely driven by regional differences in rainfall and wetland availability (Gilissen, 2002).

Distribution and habitat

The Marbled duck has a highly fragmented distribution across the western and central Palearctic, extending from the Iberian Peninsula and north-west Africa in the west to the Middle East and western central Asia in the east (Salvador, Amat, & Green, 2023). Its breeding range (Fig. 4) varies strongly according to wetland availability and climatic conditions, and currently includes southern Europe (Spain, and Sicily in Italy), northwest Africa, the Middle East, and parts of western and central Asia (Salvador, Amat, & Green, 2023). Several former breeding populations in southern Europe, the eastern Mediterranean, and the Balkans have disappeared during the twentieth century, and the species is now considered extinct as a breeder in Turkey (Perrins, 1978; Green, 1993; Salvador, Amat, & Green, 2023*a*). In North Africa, the species breeds in Morocco, Algeria, Tunisia, and Libya (Isenmann, 2005; Aourir, Bergier, & Qninba, 2016), while in west Africa the species can be found breeding in Senegal, and most recently an important population was found breeding in the Ounianga lakes in Chad (300–400 breeding pairs estimated, Hering, Hering, & Winter, 2025). The Marbled duck occupies a broad wintering range spanning Spain, North Africa, the Sahel, the Middle East, and South Asia (Fig. 4). Within this range, four distinct population units are recognised: the western Mediterranean, eastern Mediterranean, southwestern Asia, and South Asia populations (Fig. 4).

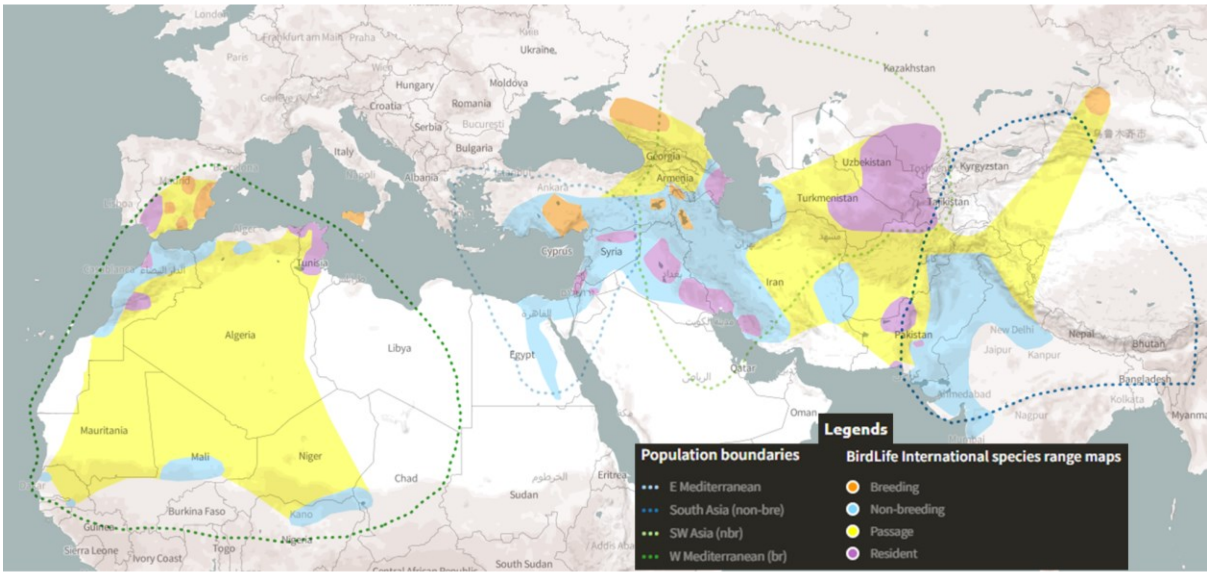

Figure 4. *Global range and population structure of the Marbled duck. Coloured areas indicate breeding (orange), non-breeding (blue), passage (yellow), and resident (purple) ranges according to BirdLife International. Dotted lines delineate the four recognised population units: western Mediterranean (green), eastern Mediterranean (light blue), southwestern Asia (light green, non-breeding), and South Asia (blue, non-breeding). Adapted from Wetlands International, BirdLife International. Critical Site Network Tool. Available at: https://criticalsites.wetlands.org*

Across its range, the Marbled duck can be found in both temporary and semi-permanent wetlands. It is typically associated with shallow wetlands, typically with mean water depths below 1 m, and shows a preference for brackish or moderately saline systems over purely freshwater or hypersaline habitats (Green, 1993, 1998*a*; Navarro Medina *et al.*, 1995). It occupies a wide variety of wetland types, including natural wetlands such as marshes, lagoons, estuaries, lakes, deltas, and artificial wetlands like reservoirs, saltworks, rice fields, and fish ponds, provided that extensive emergent and submerged vegetation is present (Green, 1998*a*; Green & Hamzaoui, 2000; Fuentes *et al.*, 2004). Emergent vegetation such as Phragmites, Typha, Scirpus, and Juncus appears particularly important for nesting, brood concealment, and protection from predators and extreme temperatures, especially in arid and semi-arid environments (Salvador, Amat, & Green, 2023). Differences in habitat use between breeding and non-breeding seasons are generally limited, although breeding sites tend to be characterised by higher vegetation cover and diversity (Green, 1993; Green *et al.*, 2002).

Population status and threats

The global population size of the Marbled duck has been estimated to range widely between approximately 15,000 and 61,250 individuals, reflecting substantial uncertainty and uneven monitoring across its range (BirdLife International, 2022). Regional estimates suggest that the largest populations occur in southwest Asia (Fig. 4), with figures ranging from 7,000 to 50,000 individuals, while the western Mediterranean (Fig. 4) are estimated to support around 7,500-10,000 individuals, with the largest wintering population believed to be in Morocco (Ouassou *et al.*, 2021; BirdLife International, 2022). Much smaller populations persist in the eastern Mediterranean and South Asia (Fig. 4), where estimates range from a few hundred to approximately 1,000 individuals (BirdLife International, 2022). Recent winter counts in the western Mediterranean and North Africa are broadly consistent with these figures, with totals of 6,087 and 7,435 individuals recorded in 2013 and 2017, respectively (Sayoud *et al.*, 2017; Nagy & Langendoen, 2020). In contrast, winter counts in southern Iraq have revealed exceptionally high numbers in some years, including up to 44,000 individuals in 2010, underscoring strong spatial and temporal variability (BirdLife International, 2022).

Despite these uncertainties, the overall population trend of the Marbled duck is considered to be declining (Nagy & Langendoen, 2020). Historically abundant across much of its range during the nineteenth century, the species experienced pronounced declines throughout the twentieth century in Central Asia, the Middle East, and the Mediterranean basin, largely driven by wetland loss, hydrological alteration, and increasing human pressure (Green, 1993). In several regions, including southern Spain and Turkey, breeding populations have undergone severe contractions or local extirpations over recent decades (Perrins, 1978; Salvador, Amat, & Green, 2023*b*). The western Mediterranean population has declined by 46% in 11 years (over the period 2008-2018) (Wetlands International, 2025), and is classified under the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) categories 1a and 1c, with numbers fewer than 10,000 individuals, and in which Morocco constitute a major part of its range (AEWA, 2026). At the broader species level, the Marbled duck is listed in Appendix I of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), which obliges range countries to conserve its habitats, minimize obstacles to its migration, and generally prohibits the taking of specimens (CMS, 2020).

A notable exception to this trajectory of decline is found in Spain, where conservation intervention has resulted in the recovery of the species at the national scale. As part of the Spanish National Strategy for the conservation of the species, a population reinforcement programme was initiated in 2001 based on the release of captive-bred individuals at key wetlands in south-eastern and south-western Spain. More than 2350 individuals were released from the captive breeding centre at Cañada de los Pájaros alone between 2007 and 2022, in addition to 1267 individuals released in the Valencian region during the 2009–2022 period (Salvador, Amat, & Green, 2023). This sustained effort, combined with habitat restoration and legal protection measures under the LIFE Cerceta Pardilla project, has contributed to a notable demographic recovery: 172 breeding pairs were recorded in 2025, up from just 20 pairs in 2009 (LIFE Marbled Teal project, 2024). However, this recovery is at least partly dependent on the continued release of captive-bred individuals, and the long-term viability of the wild population without ongoing reinforcement remains uncertain (Pérez-García *et al.*, 2024). The Spanish case thus represents the most documented example of active population management for the species in the Western Mediterranean, and its outcomes, both successes and limitations, carry important implications for conservation planning across the region, including in Morocco.

The decline of the Marbled duck is considered to be primarily driven by habitat loss and degradation resulting from wetland drainage, hydrological alteration, water extraction, and pollution, particularly in arid and semi-arid regions (Green *et al.*, 2002). In Morocco, for example, approximately 25% of the country's wetland area was destroyed between 1978 and 1999, mainly low-salinity systems, resulting in the loss of 98% of seasonal mesohaline wetlands and 33% of seasonal Phragmites/Schoenoplectus lacustris marshes (Green *et al.*, 2002). As a late breeder reliant on temporary wetlands, the species is highly vulnerable to shortened hydroperiods caused by drought and climate change, which can prevent successful breeding in dry years (Green, 2000; Salvador, Amat, & Green, 2023*b*). Additional pressures include illegal killing and trapping, bycatch in fishing gear, contamination by pesticides and heavy metals, lead poisoning from spent ammunition, and mortality from collisions with power lines (Salvador, Amat, & Green, 2023).

Knowledge gaps

Substantial knowledge gaps remain regarding the ecology and population dynamics of the Marbled duck. Population size and trends are still poorly quantified across much of the species' range, particularly in North Africa, the Middle East and Central Asia, where systematic monitoring is limited (Salvador, Amat, & Green, 2023). Although recent GPS-tracking studies in Spain have provided initial insights into Marbled duck movements (Pacheco-Guardiola *et al.*, 2025), crucial aspects such as habitat use, seasonal movements, key stopover sites, and connectivity among populations remain poorly documented across most of the species' range (Salvador, Amat, & Green, 2023). In addition, key demographic parameters such as adult and juvenile survival, reproductive output, and sex ratios are poorly known, constraining demographic inference and the development of population viability models. As a result, it remains unclear to what extent the recent declines documented in parts of the range are driven by reduced survival, low productivity, or declines in habitat carrying capacity, or by interactions between these processes. Other gaps include limited understanding of spatial and temporal variation in diet, moulting ecology, and the long-term effectiveness of captive-breeding programmes, as well as uncertainty regarding future distribution under climate change (Salvador, Amat, & Green, 2023).

This thesis addresses several of these gaps, with a focus on the Moroccan population. Chapter 1 addresses the absence of robust, nationally representative estimates of breeding population size and the habitat predictors of breeding occurrence. Chapter 2 addresses the limited understanding of how individuals organise their movements, behaviour, and space use at fine spatial and temporal scales during the wintering period. Chapter 3 addresses the lack of knowledge on how Marbled ducks allocate habitat use among wetland types of different origins under varying climatic and hydrological conditions. Together, these three chapters provide an integrated assessment of the population status, spatial behaviour, and habitat ecology of the Marbled duck in Morocco, contributing to improved conservation knowledge for the species across its western Mediterranean range.

4. Thesis overview and structure

The overarching aim of this thesis is to improve understanding of the population status, movement ecology, and habitat use of the Marbled duck in Moroccan and North African wetland systems, by combining probabilistic population surveys with behaviour-informed biologging. Data used in this thesis is based on two complementary sources: brood surveys used to estimate the breeding population size, and GPS-accelerometer data used to investigate movement, behaviour, and habitat use. Data were collected across different spatial and ecological contexts. Methodological details specific to each dataset are presented separately in the corresponding chapters.

Breeding population size and habitat predictors (Chapter 1)

Chapter 1 addresses the lack of reliable breeding population estimates by providing the first national-scale estimate of Marbled duck breeding population size in Morocco, while explicitly accounting for imperfect detection. It specifically aims to (i) quantify breeding population size and associated uncertainty, (ii) identify key habitat predictors of breeding occurrence, and (iii) establish a transferable sampling protocol suitable for other waterbird species and North African contexts.

Study area and data:

Data were collected during national surveys conducted in 2023 and 2024, spanning a wide latitudinal gradient from the Moulouya River in the north to Saharan wadis in the south. A two-stage random sampling design was implemented, with 35 primary sampling units (PSU) (100 km²) and 187 secondary sampling units (SSU) (0.25 km²) surveyed across the national wetland network.

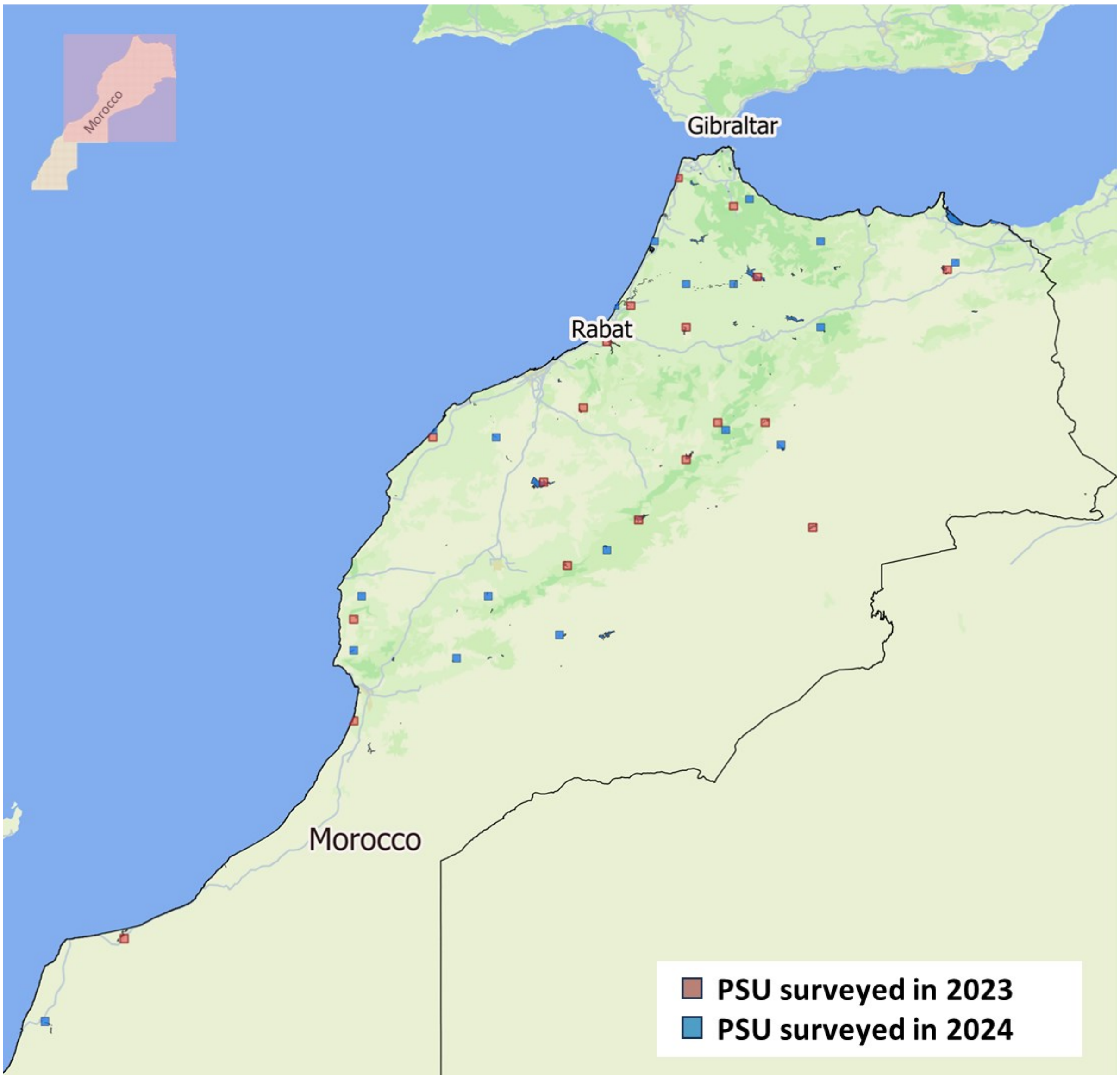

Figure 5. *Distribution of primary sampling units (PSUs) surveyed during the national breeding survey of the Marbled duck in Morocco in 2023 (red) and 2024 (blue)*

Behaviour and spatiale organisation (Chapters 2)

Chapter 2 investigates fine-scale movement and behavioural organisation during the wintering period using GPS-accelerometer data. It examines whether individuals exhibit consistent spatial routines, characterised by stable roosting areas linked to distinct foraging sites, and evaluates the environmental and anthropogenic drivers of roosting and foraging site selection.

Study area and data:

Between 2023 and 2025, a total of 11 adult individuals (2 females and 9 males) were equipped with tracking devices at two key wetland complexes: Sidi Moussa-Oualidia on the Atlantic coast and Saqia El Hamra in southern Morocco (Fig. 1, Chapter 2). These sites represent contrasting hydrological and ecological contexts within the Moroccan wetland network and are regularly used by Marbled duck during both wintering and breeding seasons.

Habitat use across wetland types under climatic variability (Chapters 3)

Chapter 3 examines how Marbled ducks allocate space among natural, artificial, and accidental wetlands across a transboundary network spanning Morocco and Algeria. It aims to (i) quantify habitat use across wetland categories, (ii) identify climatic, hydrological, and anthropogenic drivers of wetland use, and (iii) assess the role of human-derived wetlands under increasing water scarcity.

Study area and data:

GPS data from individuals tracked in Morocco (Chapter 2) were complemented with data from Marbled ducks captured in Spain that undertook long-distance movements and used wetlands in Morocco and Algeria.

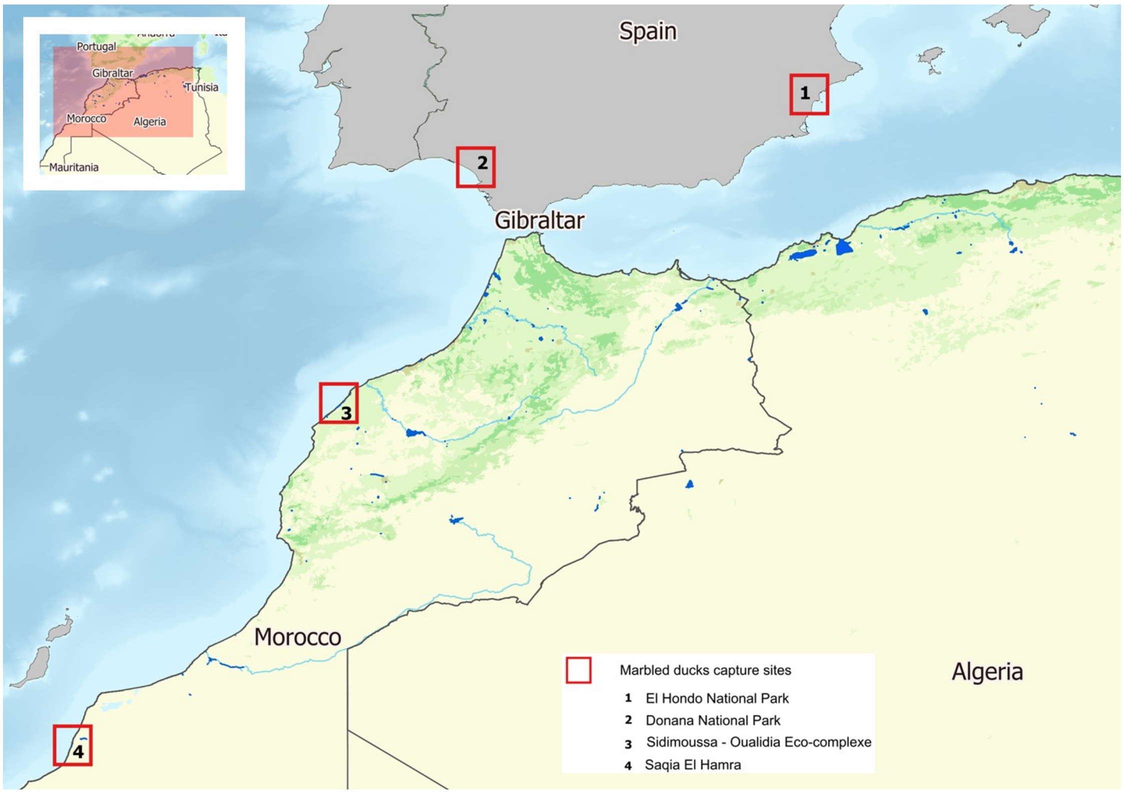

Figure 6. *Location of Marbled duck capture sites. Individuals captured at sites 3 (Sidi Moussa-Oualidia Eco-complexe) and 4 (Saqia El Hamra) in Morocco were used in Chapter 2. Individuals from all four capture sites were used in Chapter 3.*

Together, these chapters provide a multi-scale, integrative framework linking population estimation, behaviour, and habitat use, and demonstrate how combining survey data with biologging can strengthen conservation strategies for waterbirds in rapidly changing wetland landscapes. In the general discussion, we build on these findings to discuss their implications for the conservation of the Marbled duck in North Africa. We examine how the results can inform habitat restoration and protection strategies and evaluate the role of anthropogenic wetlands in supporting the species under increasing water scarcity, while considering the risks of over-reliance on these systems at the expense of natural habitat conservation. We conclude by identifying future research and monitoring directions needed to further improve conservation planning for the species across its western Mediterranean range.

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Chapter 2: Using two-stage random sampling and N-mixture models to estimate the breeding population size of a threatened nomadic species in Morocco

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Abstract

Robust estimates of animal population size are critical for effective conservation planning, yet such studies remain scarce in the North African region, making it difficult to assess the population status of various species. Here, we present the results of a national-scale census of the rare and elusive Marbled duck (*Marmaronetta angustirostris*) conducted over two years in Morocco. Using a two-stage random sampling design, we surveyed 187 secondary units of 0.25 km² nested within 35 primary sampling units of 100 km², spanning from the Moulouya River to the Saharan wadis. We applied hierarchical binomial N-mixture models to estimate the population size of the species and identify key breeding habitat features. At the scale of sampled sites that covers 46.75 km² of wetlands, our best-supported model estimated a total of 24 broods, with an average detection probability of 0.71 (95% BCI: 0.30–0.95), highlighting the need to account for imperfect detection in field surveys. When extrapolated to all Moroccan wetlands (748 km²), this translated into a national breeding population size estimate of 382 broods (95% BCI: 280–484). Emergent vegetation was found to be the strongest predictor of brood abundance. Among wetland types, ponds showed positive associations with brood abundance relative to dams, while rivers were associated with lower abundance. These findings represent the first robust national-scale estimate of Marbled duck breeding population size in Morocco. The analysis highlights emergent vegetation and wetland types as predictors of brood abundance, offering direction for habitat-focused conservation efforts. The scalable survey and modelling framework used here can be adapted elsewhere to improve monitoring and conservation efforts of vulnerable waterbird species.

Keywords

ecological modelling, spatial ecology, Marmaronetta angustirostris, waterbird monitoring, wetland conservation

Introduction

Reliable estimation of the population size of animals is essential for developing effective management plans and conservation measures for both species and their habitats. Population size is considered to be among the most impactful metrics in conservation ecology (Stephens et al., 2015; López-Bao et al., 2018). This metric is comparable across populations and species and is useful for assessing threat classifications, evaluating whether a species qualifies for a conservation status update, and identifying areas that hold significant portions of a species' global population (Moilanen et al., 2005; Arcos et al., 2012; Ashe et al., 2013; Camaclang et al., 2015; Baker et al., 2019). However, estimating population size is often challenging, due to imperfect detection. These difficulties are amplified for highly mobile and cryptic species, particularly those occurring at low densities over large areas, which makes monitoring efforts complex and costly (Skalski, 1994). These challenges are often further exacerbated by limited human resources to monitor wildlife, highlighting the importance of developing robust, cost-efficient, and effective sampling methodology (Parker et al., 2011). Methods that do not account for detection probability can lead to poor assessments of conservation status (Vallecillo et al., 2021), hindering the ability of managers to set appropriate conservation objectives and to evaluate the impact of management actions (Wiest et al., 2018).

In the Mediterranean region, the protection and conservation of wetlands is of utmost importance as these ecosystems play a critical role in hosting a wide variety of waterbird species (Sayoud et al., 2017; Verniest et al., 2023). More than half of the wetlands in this region have been lost (Sayoud et al., 2017; Verniest et al., 2023). In the southern part of the Mediterranean region, North African wetlands are of critical importance to the African-Eurasian flyway, hosting approximately 2 million wintering waterbirds from more than 150 species (Sayoud et al., 2017; Verniest et al., 2023; Wetlands International, 2025). However, these wetlands and their bird populations face numerous threats, primarily due to habitat loss and degradation caused by drainage and conversion for agricultural and urban development (Verniest et al., 2023). Over the last few decades, climate change has intensified these challenges, altering hydrological regimes and leading to droughts and irregular flooding patterns that disrupt the balance of these ecosystems (Verniest et al., 2023).

Morocco hosts several threatened species of Anatidae and Rallidae, yet information regarding their breeding distribution and abundances remains poorly known and the lack of population size estimates hinders conservation status assessments. The Marbled duck (Marmaronetta angustirostris) is one of those threatened species, with its Western Mediterranean breeding population size still largely unknown. In 2025, the species was classified as "Near-threatened" by the IUCN Red List of Threatened Species ('Birdlife International', 2022), and facing various threats such as habitat loss and degradation, illegal hunting, and reduced rainfall in the Mediterranean basin due to climate change (Salvador, Amat, & Green, 2023). Between 2008 and 2018, the West Mediterranean population of the species has been estimated to have declined by 46% (Wetlands International, 2018) and the largest wintering population (47%) in this region is believed to be in Morocco (Wetlands International, 2018; Ouassou et al., 2021). However, population size estimates of the species are lacking across much of the region and those that do exist do not account for imperfect detection, leading to a risk of underestimation of the true population size. The only available estimate is derived from the national mid-winter counts for a total of around 6000 - 7500 individuals wintering in the West Mediterranean population, and an average of 3071 in Morocco alone (Wetlands International, 2018; Ouassou et al., 2021). Taken together, these knowledge gaps and ongoing threats highlight the urgent need for robust monitoring to accurately assess the status of the Marbled duck in Morocco.

These monitoring challenges are particularly pronounced in nomadic duck species inhabiting arid environments. Such species exploit different habitats throughout their annual cycle and often move opportunistically in response to unpredictable rainfall and the ephemeral nature of wetlands in desert regions, leading to variations in habitat use across seasons (Henry, Ament, & Cumming, 2016). The Marbled duck is no exception. It is considered to be nomadic, with an ecology adapted to cope with the spatiotemporal fluctuations in habitat availability, making it a cryptic and challenging species to study (Green, 1993; Salvador, Amat, & Green, 2023). As a result, its movements and local distribution are strongly influenced by rainfall patterns and wetland dynamics (Green, 1993; Salvador, Amat, & Green, 2023). This complicates assessments of its breeding population, which hence cannot be directly inferred from wintering population size. As such, breeding population assessments must be designed to account for the species' nomadic behavior and the spatially dynamic use of breeding sites. Consequently, the monitoring approach must be capable of capturing the spatial and temporal variability in breeding activity, while also accounting for imperfect detection.

In response to the scarcity of reliable breeding population data for the Marbled duck, we implemented a two-stage random sampling approach and adapted it to align with the Moroccan wetland inventory, thereby establishing a sampling design suitable for conducting brood surveys nationwide. Data collected were analyzed using hierarchical binomial N-mixture models to estimate the species breeding population size while accounting for imperfect detection and yielding associated uncertainty intervals. The objectives of our study were: i) to develop a standardized sampling design to estimate the breeding population size of the Marbled duck, while ensuring reproducibility of the method for other waterbird species across other North African countries; ii) to estimate breeding population size of the Marbled duck; and iii) to identify the relevant variables affecting the breeding of the species and its detection probability.

Methods and materials

Species

The Marbled duck is a relatively small (450-520 g in adult males), globally threatened duck species with a distribution spanning from Central Asia to Northwest Africa and the Iberian Peninsula. It is well adapted to spatiotemporal fluctuations in wetland availability and exhibits nomadic movements before and after the breeding season, which typically extends from April to September (Salvador, Amat, & Green, 2023). The species is monogamous and a relatively late summer breeder. Females construct nests on the ground close to water, typically under low shrub or herbaceous cover, and lay clutches that can produce large broods, sometimes reaching up to 14 ducklings (Salvador, Amat, & Green, 2023). Males generally abandon the nest after hatching. The chicks fledge at approximately seven weeks (Green, 1998*b*).

Two-stage random sampling design

The national survey was performed in 2023 and 2024 using a sampling design consisting of a two-stage random sampling (Thompson, 2012). In the first stage, primary sampling units (PSUs) of 100 km² were randomly selected. In the second stage, within each PSU we randomly selected a number of secondary sampling units (SSUs; 0.25 km² each) to cover approximately 30% of that PSU's wetland surface area. The choice of PSU 100 km² dimension ensures a wide spatial sampling coverage while capturing diverse wetland habitats within Morocco at a large scale. The SSUs 0.25 km² dimension was determined in order to provide a manageable scale for accurate brood detection and collection of habitat-specific variables. The 30% SSU allocation was determined based on the number of available observers and the need to cover the largest area possible, thereby generating a dataset that would incorporate the greatest possible diversity of habitats across the entire Moroccan territory. No prior information about the Marbled duck's breeding sites was thus used for the sampling design to avoid bias and ensure randomness, enabling us to extrapolate the results from the sampling sites to the rest of Morocco.

To identify the PSUs available for random sampling, we first used a raster file of all potential wetlands in Morocco (Guelmami, 2023) and extracted a layer containing only permanently flooded wetlands, as Marbled ducks breed in summer when most temporary wetlands are dry. We then overlaid this layer with Morocco's 100 km² grid and retained only the grid cells intersecting the wetland polygons, which defined the PSU sampling frame. This procedure identified a total of 241 primary sampling units (PSUs) available for sampling. Due to logistical constraints, including limited personnel and field capacity, we randomly selected a subset of 35 PSUs for field surveys (Fig. 1A). We followed a similar procedure for SSUs: the selected wetlands polygons from the first stage were overlaid with Morocco's 0.25 km² grid layer. Only the grid cells intersecting with the wetlands polygons were retained, creating the second-stage layer of SSUs available for sampling (Fig. 1B). This process resulted in the selection and monitoring of 187 SSUs nested within 35 PSUs across Morocco, from the mouth of the Moulouya River in the Northwest (35.1844° N, 2.4257° W) to the Saharan wadis in the South (26.6801° N, 13.0956° W).

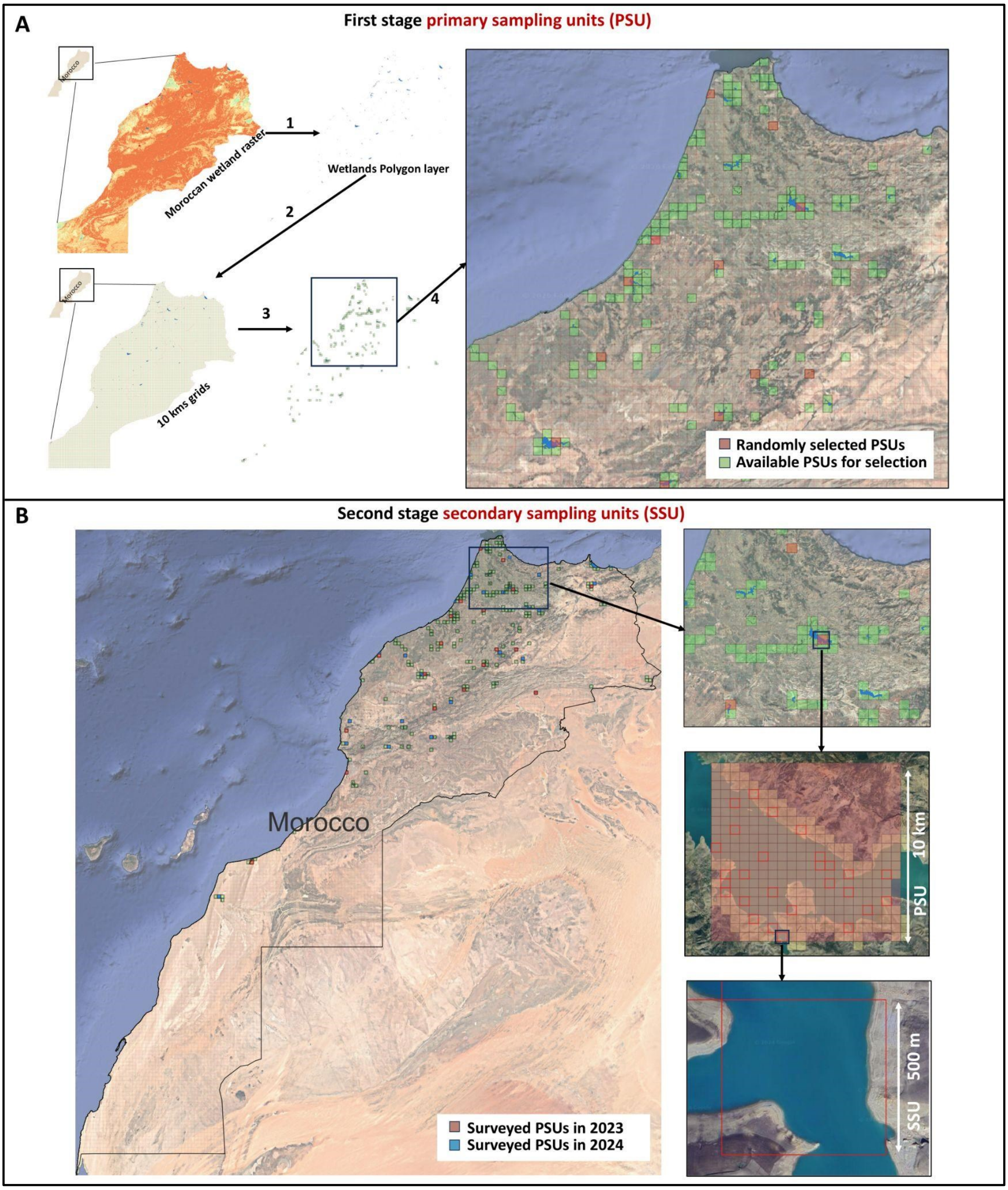

Figure 1. *Two-stage random sampling design for estimating Marbled duck broods in Morocco. (A) primary sampling units PSUs (100 km²) intersecting permanently flooded wetlands that were identified and randomly selected. (B) Within each PSU, 30% of secondary sampling units SSUs (0.25 km²) were randomly chosen. PSUs surveyed in 2023 are in red, while the ones surveyed in 2024 are in blue.*

Data collection

Data collection was carried out to coincide with the peak of the brood-rearing season and was completed before the chicks were able to fly (Salvador, Amat, & Green, 2023). The SSUs were surveyed from one to three visits, separated by three weeks apart, between the 3rd of June and the 12th of August in 2023 and the 7th of June and the 14th of August in 2024. The different SSUs were surveyed by 19 experienced birdwatchers, members of the national Moroccan ornithologist association, GREPOM/Birdlife Morocco. They used binoculars, telescopes, and cameras in order to detect, identify, and count all the Marbled duck broods encountered. Each observer determined the best strategy for covering the entire sampling unit (observation point, transect, or both). Each SSU was surveyed for a duration of 30 minutes to 1.5 hours, depending on the complexity of the habitats. During each visit, the observers surveyed the entire SSU, making sure to walk through shoreline areas obscured by vegetation or other visual barriers. Observers counted Marbled duck adults and recorded the brood size and the age of the chicks. Estimation of chick age was based on plumage development, which allowed for determining laying dates and identifying any multiple broods in the same wetland, and avoiding double counting (Link *et al.*, 2018; The Marbled Teal Life Project, 2025). Observers also recorded the percentage of emergent vegetation that covered the wetland within each SSU using a standardized visual reference guide (Appendix 2 in Oldham, Keeble, & Jeffcote, 2000), following prior training to ensure consistency among observers. Wetland type was recorded as well (dam, river, lagoon, pond, saltpan, lake, or marsh).

Statistical analyses

We applied a hierarchical model-based approach to estimate the breeding abundance of the Marbled duck in Morocco and to assess the environmental factors influencing both abundance and detection probability. The analysis was carried out using N-mixture models (Royle, 2004), which explicitly account for imperfect detection by modelling the detection process separately from the state process (abundance). A key assumption of N-mixture models is that the population is demographically and geographically closed during the repeated surveys at each site (Royle, 2004). For the Marbled duck, fledging occurs around 54 days after hatching (Green, 1998b), while a study by Gereg (2012) suggests it may extend up to 10 weeks. In our study, the mean interval between the first and last visit was 6.4 weeks, with a maximum of 9.1 weeks. Given the relatively sedentary nature of broods before fledging, the closure assumption was therefore assumed to be met. The response variable is the count of broods. For site SSU and visit, the state and detection parameter can be expressed as follow:

State parameter: N_i ~ Poisson or Negative binomial (λ_i)

Detection parameter: y_{ij} ~ Binomial (N_i, p_{ij})

where:

N_i is the latent abundance defined as the true number of broods at site i

λ_i is the expected abundance defined as the mean number of broods at site i.

y_{ij} is the observed count which is the count recorded at site i, survey j

p_{ij} is the probability of detecting each brood at site i, survey j

To meet the dual objectives of estimating abundance and identifying influencing factors of abundance, we structured the analysis in two complementary steps. To accomplish our first objective, abundance was estimated by including covariates only in the detection component, while keeping the state process (abundance) constant, as expressed in the R code syntax below (1). This structure enabled extrapolation to unsampled areas (outside SSUs) across Morocco, assuming constant abundance given that habitat-specific variables were unavailable for unsampled SSUs. Primary Sampling Units (PSUs) were included as random effects in the state process (abundance) to account for the two-stage sampling design, while year was added as a fixed effect to capture interannual variation. Detection covariates were incorporated to model heterogeneity in detection probability. To accomplish our second objective, we kept the best detection covariate from the previous step in the detection process and included all the habitat covariates hypothesized to explain the abundance, as expressed in the R code syntax below (2). This allowed us to determine environmental factors influencing local abundance patterns and to contrast those findings with patterns in detection probability. The specific detection and abundance covariates are detailed in the section below.

(1) Abundance submodel: log (λ) ~ year + (1|PSU); Detection submodel: logit (p)~ detection covariates

(2) Abundance submodel: log (λ) ~ year + (1|PSU) + Abundance covariates ; Detection submodel: logit (p)~ detection covariate retained in the first analysis

National breeding population size estimates

The detection process included the following covariates: sampling effort, time of the day, and date (expressed as day of the year). Sampling effort (time spent inside SSUs in minutes): We hypothesize that detection probability increases with greater sampling effort, following a positive linear relationship. Time of day (hour): We expected broods to be more detectable during sunrise and sunset hours (Pagano & Arnold, 2009), reflecting a non-linear (quadratic) relationship between detection and time of day. Accordingly, both linear and quadratic terms were included in the detection model. Day of the year: we anticipated that detection would be highest in June, coinciding with the hatching of brood (Salvador, Amat, & Green, 2023), and would decline progressively as the season advanced. Observer identity was not included as a detection covariate due to highly inconsistent observer effort across PSUs (Figure S1): most observers surveyed only one PSU, only a few observers visited more than two PSUs, and a single observer visited many PSUs. Under this sampling design, observer identity is confounded with site identity.

In order to estimate total population size at the national level, a proportional scaling approach was adopted, simulating a new set of abundance estimates for Morocco based on the posterior samples from our sampled sites. We used an extrapolation metric, defined as the total water surface area of Morocco divided by the sum of the water surface area of the sampled sites. To account for uncertainty, Monte Carlo simulations (10,000 iterations) were applied by drawing brood abundance values from the posterior samples of the best model. These values were then scaled by the extrapolation metric to generate a national population estimate along with corresponding credible intervals.

Identification of variables explaining abundance

We used a similar approach to estimate the effect of variables influencing abundance and the detection process. The abundance of broods likely results from a complex interplay of factors, including breeding pair abundance, nesting chronology, nest survival, brood survival, and the selection of wetlands by breeding females (Walker *et al.*, 2013). To assess the influence of these factors, we tested several covariates in the state process (abundance). Emergent Vegetation: Higher brood abundance was expected with higher emergent vegetation cover, as they use it as a shelter from predators, and they are rich in food resources (Carrlson *et al.*, 2018). Wetland Surface Area: Based on a study which showed that the probability a wetland is occupied by broods increases with wetland area, we hypothesize that brood abundance will increase with wetland surface area (Walker *et al.*, 2013). Year: Similar brood abundance was expected between years, assuming stable environmental conditions during the study period. Wetland Type: Natural wetlands were hypothesized to host more broods than artificial wetlands, as they provide more diverse foraging and refuge habitats. Wetland types represented by a single PSU (lagoon, marsh, saltpan; each n = 1) were grouped into a single 'Other' category to avoid confounding between wetland-type fixed effects and the PSU random effect.

All statistical analyses were performed using R version 4.1.1 (R Core Team, 2021). To estimate the abundance of the Marbled duck, we constructed single-species N-mixture models using the SpAbundance package version 0.2.1 (Doser *et al.*, 2024) which employs a Bayesian approach to fit models. We assessed whether abundance was best fitted by a Poisson or a Negative Binomial (NB) distribution. The latter is known to allow for over-dispersion, a common feature of population count data (Knape *et al.*, 2018). Models were fitted using Markov Chain Monte Carlo (MCMC) with 3 chains each containing 155,000 samples and 10,000 burn-in. Samples were then thinned to retain only 1 out of every 10 samples. We estimated model parameters by setting default vague prior hyperparameter values, with hypermeans set to 0 and hypervariances set to 2.72 for detection coefficients and to 100 for abundance coefficients (Doser *et al.*, 2024). Same default priors were used for both poisson and negative binomial models, and we used a default uniform prior (lower bound to 0 and the upper bound to 100) for the negative binomial overdispersion parameter. Additionally, other alternative prior specifications were tested, including more informative priors for the PSU random effect, to reduce the variability observed with non-informative priors.
Posterior convergence was assessed using visual inspection of trace plots and the Gelman-Rubin scale reduction factors (Rhat), which were required to be smaller than 1.1 (Brooks & Gelman, 1998). All predictors were standardized prior to model fitting by centering and scaling, resulting in standardized coefficients with comparable effect magnitudes. We reported posterior means as point estimates for parameters and used the (0.025, 0.975) quantiles of the posterior distribution to compute the 95% Bayesian Credible Intervals (BCI) for these estimates. We assessed strength and uncertainty of the predictors by reporting the proportion of posterior samples (p+ or p-) supporting the positive or negative direction of the estimate. Effects whose direction is supported by more than 95% of the posterior distribution are considered well supported, and those with direction support of more than 90% are considered weakly supported (McElreath, 2018; McShane *et al.*, 2019; Martin *et al.*, 2020).

We performed model selection separately for both analyses. For each analysis, we fitted a set of candidate models with different additive combinations of covariates that we hypothesized to be important for site abundance and brood detection. For every candidate structure, we considered both Poisson and negative binomial distributions, and model comparison was conducted across all candidate models irrespective of their distributional assumption. Models were compared using the Widely Applicable Information Criterion (WAIC) (Watanabe, 2010) and all models with ΔWAIC < 2 were examined based on their structure and parameter estimates significance. For the second analysis, we carried forward the best-supported detection submodel identified in the first analysis. After determining the best model, we performed a Posterior Predictive Check (hereafter PPC) for both analysis, to assess models' fit, where models with a good fit to the data had Bayesian p-values greater than 0.05 and smaller than 0.95 (Gelman, Meng, & Stern, 1996). The abundance estimation was then retrieved from the posterior samples of the best identified model. Subsequently, Bayesian Credible intervals and total abundance over the sampled sites were computed.

Results

A total of 21 Marbled duck broods were detected during the study period (see data availability statement). The earliest brood detection occurred on the 6th of July, and the latest on the 14th of August. Several visits could not be completed due to logistical constraints, resulting in 5% of SSUs (n=9) being missed during the first survey round, 11% (n=17) during the second, and 42% (n=66) during the final round. Observers surveyed seven different wetland types (Table 1).

Table 1. *Summary of wetland types surveyed for Marbled Duck broods across Morocco at the Primary Sampling Unit (PSU) level, including the number of PSUs and their surface-area range (in hectares). Other category includes lagoons, marshes and saltpans.*

Wetland Type	Number of PSUs	Min Surface Area (ha)	Max Surface Area (ha)	Mean Surface Area (ha)
Dam	19	13.6	3948.0	1649.2
Lake	3	21.8	273.2	174.0
River	8	64.4	1072.2	420.7
Pond	2	45.6	80.2	71.6
Other	3	31.1	768.3	323.2

Marbled duck breeding population size estimation

We fitted a total of 12 Bayesian N-mixture models to estimate the Marbled duck brood abundance, covering all additive combinations of detection covariates under both Poisson and Negative Binomial distributional assumptions (Table 2). Six models had delta WAIC < 2, including two null models and four models incorporating time of day (with and without a quadratic term) under both distributional assumptions. However, examination of parameter estimates from models including time of day revealed no directional support for this covariate, and its inclusion did not meaningfully improve model fit. The two null models, Poisson and

Negative Binomial, showed negligible differences in WAIC, with posterior predictive checks indicating an adequate fit to the observed data for both models. The estimated brood abundance at the sampled-site level was consistent between the two models (Table 2), and the detection probability was relatively high at 0.71 (95% BCI [0.49-0.86]), indicating good detectability during surveys. Given their negligible differences, we based inference on Model null 1 but note that conclusions are robust to using either model.

Models incorporating day of the year as a detection covariate were initially considered but discarded due to convergence issues. Its exclusion, therefore, reflects a methodological limitation rather than a lack of ecological relevance. Using the model null 1 estimation for brood abundance in the sampled sites, we extrapolated this estimate to all Moroccan wetlands, obtaining a national breeding population size of 386 broods (95% BCI: 283–487).

Table 2. *Summary of N-mixture models used to estimate Marbled duck brood abundance in Morocco. Models vary by distribution assumption (Poisson or Negative Binomial) and detection covariates, and are ranked by the difference in Widely Applicable Information Criterion (ΔWAIC). Reported metrics include WAIC, the effective number of parameters (pD), and posterior predictive check (PPC) p-values. Mean brood abundance estimates and their 95% Bayesian Credible intervals (BCI) are also provided. Model selected for inference is highlighted in grey.*

Model	Distribution	Detection Covariates	WAIC	Delta WAIC	pD	PPC p-value	Abundance Estimate	Abundance 95% Crl
Model Null 1	**Poisson (P)**	—	**128.0**	**0.00**	**11.4**	**0.51**	**24.7**	**21-34**
Model Null 2	**Negative Binomial (NB)**	—	128.2	0.15	11.2	0.54	24.7	21-34
Model 1	**P**	hour	129.6	1.56	12.4	0.51	24.5	21-34
Model 2	**NB**	hour	129.8	1.76	12.2	0.53	24.6	21-34
Model 7	**P**	hour + hour²	129.8	1.76	14.8	0.47	24.6	21-34
Model 8	**NB**	hour + hour²	130.0	1.96	14.8	0.48	24.6	21-34
Model 5	**P**	effort	132.6	4.56	13.8	0.47	29.0	21-52
Model 6	**NB**	effort	132.8	4.76	13.7	0.48	29.0	21-53
Model 3	**P**	hour + effort	135.0	6.96	12.4	0.51	30.0	21-57
Model 4	**NB**	hour + effort	135.5	7.46	12.2	0.53	30.0	21-57
Model 9	**P**	effort + hour + hour²	135.5	7.46	14.9	0.46	30.0	21-57
Model 10	**NB**	effort + hour + hour²	135.6	7.56	14.8	0.49	30.0	21-59

Variables explaining abundance

We fitted a total of 15 Bayesian N-mixture models to assess the influence of habitat covariates on Marbled duck brood abundance, using both Poisson and Negative Binomial assumption (Table S1). Four models had ΔWAIC values below 2, indicating similar explanatory power. These models were structurally similar, differing only in the inclusion of the surface area covariate and distributional assumption. We examined their parameter estimates and found that effect directions and Bayesian Credible intervals were consistent across them, with wetland surface area showing no directional support. We therefore selected the model with the lowest WAIC (Model 7 in Table S1) as a representative model for inference, noting that inferences about habitat effects are robust across these four models (Table S1).

Based on the selected model, emergent vegetation had a positive association with Marbled duck brood abundance, (p+= 0.95; Fig. 2), supporting its role as a key habitat feature. Several wetland types showed a positive association with brood abundance. Compared to dams, ponds (p+= 0.97; Fig. 2), and Other (p+= 0.97; Fig. 2), were associated with higher brood abundance, whereas rivers were associated with lower brood abundance (p- = 0.97; Fig. 2) relative to dams. Lakes were associated with higher brood abundance relative to dams but directional support was weak (p+ = 0.88; Fig. 2). Surface area (p+ = 0.30; Fig. 2) and year (p+= 0.62; Fig. 2) showed no directional support. The random effect variance was large, indicating a strong heterogeneity among PSUs (Table S2).

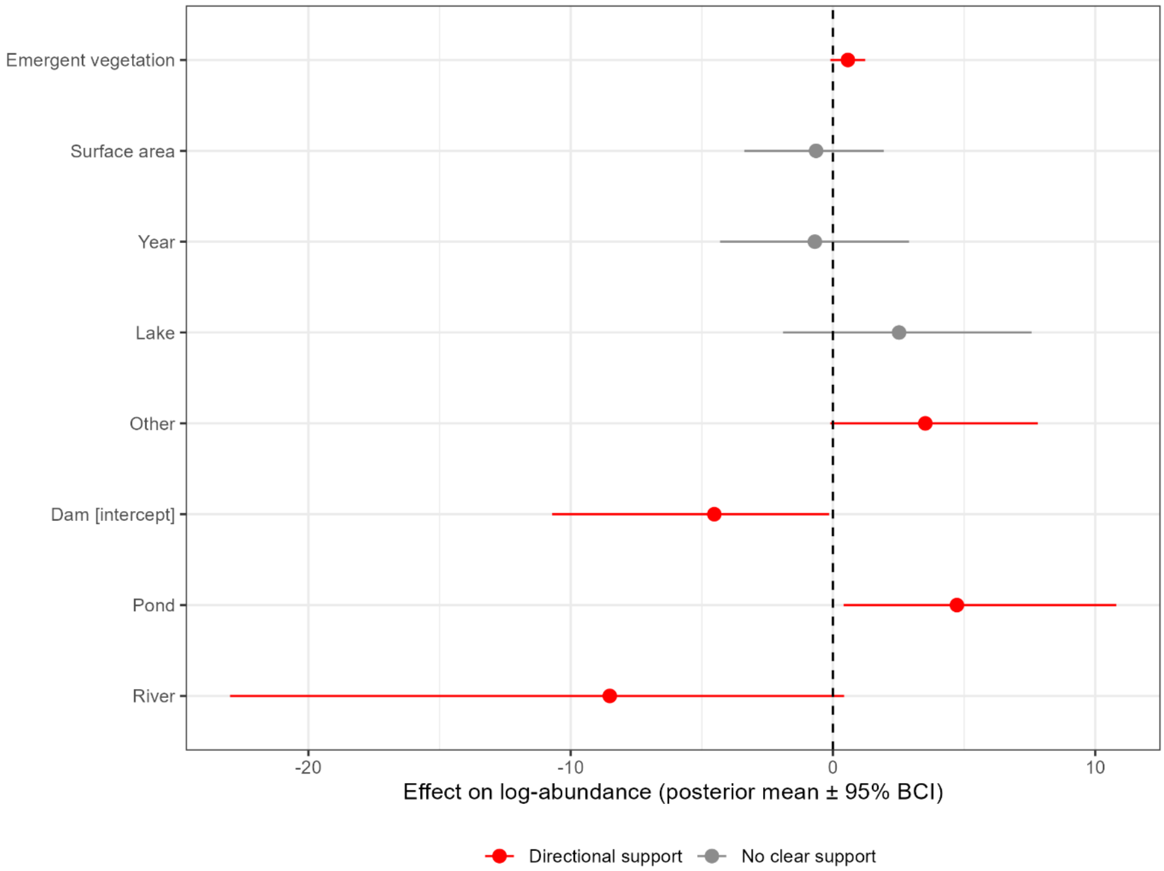

Figure 2. *Posterior estimates (mean and 95% Bayesian Credible intervals) of habitat covariate effects on Marbled duck brood abundance from the top-ranked Bayesian N-mixture model (Model 7 in Table S1). Estimates are presented on the log-abundance scale. Points shown in red indicate predictors with strong directional support (posterior probability of direction, p-dir ≥ 0.95), whereas grey points indicate*

no clear directional support. Wetland type is treated as a categorical variable, with Dam as the reference level.

Discussion

This study represents the first application of a statistically robust method to estimate the breeding population size of the Marbled duck, a scarce and threatened duck species, at the scale of an entire Mediterranean country. We estimated a national breeding population size of 386 breeding pairs (95% Bayesian Credible Interval: 283-487) for Marbled duck in Morocco.

Breeding population size estimation

Direct comparisons with previous national or regional estimates remain challenging due to the absence of studies using comparable methods. Most existing data on Marbled duck breeding populations in Morocco have been derived from opportunistic or localized surveys based on raw counts, often lacking standardization or statistical correction for underdetection. For instance, past assessments reported numbers ranging from 50 to 250 breeding pairs (El Agbani & Qninba, 2011; Aourir, Bergier, & Qninba, 2016). A recent census conducted under the Spanish Marbled duck LIFE project counted 60 broods in Morocco (Zerrouk et al., 2025), which is substantially lower than our estimate of 386 broods. This discrepancy likely stems from differences in survey design. The Spanish survey focused exclusively on wetlands already known as breeding sites for the Marbled duck, whereas our estimate was based on a randomized, design-based sampling approach that included a broader and more representative set of permanently flooded wetlands across the country, not limited to historically known breeding sites. Given the Marbled duck's high mobility and use of a wide range of wetland habitats, restricting monitoring to historically known breeding sites likely overlooks a substantial part of the population. For example, using our method, a new site was discovered as a new breeding site for the species (dam Sidi Mhamed Ben Slimane El Jazouli). Our results underscore the importance of large-scale, probabilistic sampling to account for spatial shifts in habitat use and to produce more reliable national estimates.

Our findings improve current understanding of the western Mediterranean population, indicating that Morocco, in addition to Spain, supports an important breeding population. For instance, conducting exhaustive and synchronized data collection, a total of 130 breeding pairs was reported in Spain in 2024 (The Marbled Teal Life Project, 2025), 115 breeding pairs in 2021 (Botella, F., & Pérez-García, J. M, 2021) while between 1992 and 2002, numbers fluctuated between 30 and 200 breeding pairs (Green et al., 2005). Hence, our results suggest that Morocco may now support a larger part of the West Mediterranean population, reinforcing its role as a stronghold for the population in the Mediterranean. In other countries, such as Tunisia, Algeria, Chad and Senegal, several breeding sites have been documented (Hering, Hering, & Winter, 2025; Wetlands International, 2025), though comprehensive national estimates of breeding numbers are still lacking. While comparisons with raw count data from neighboring countries provide regional context, these figures likely underestimate true population size due to imperfect detection and therefore warrant cautious interpretation relative to our estimates. Nevertheless, they emphasize the regional importance of the Moroccan breeding population and its potential to sustain the Western Mediterranean population.

Direct count methods remain widely used in wildlife monitoring, particularly under resource-limited conditions (Johnson, 2008; Gerber & Kendall, 2017). However, they have critical limitations, most notably their failure to account for imperfect detection. As a result, raw count data can underestimate true population size, potentially misrepresenting population trends and obscuring the actual conservation status of a species. Our best-supported model estimated an average detection probability of 0.71 (95% BCI: 0.49 - 0.86), indicating moderate overall detectability and underscoring the importance of accounting for imperfect detection in field surveys, as a substantial proportion of Marbled duck broods remain undetected even under standardized survey conditions. It further indicates that none of the tested covariates, including time of day and sampling effort, improved detection estimates, suggesting that other factors, such as habitat structure or observer variability, may have a stronger influence on detection. Accordingly, detection uncertainty likely reflects variation in observer skill, local habitat conditions, and weather-related visibility. Incorporating tools like camera traps at brood-use wetlands, could help standardize detection and reduce false negatives by providing continuous time-lapse (e.g. images every 10 minutes) of broods across days and times of day when ground observers are absent, thereby extending temporal coverage and minimizing observer bias (Pidwerbesky et al., 2025).

To further assess the plausibility of our breeding population size estimate, we evaluated whether the number of Marbled duck broods estimated here is coherent with the observed wintering population size in Morocco of 3,071 individuals (Wetlands International, 2018; Ouassou et al., 2021). Assuming an equal sex ratio (Pérez-García et al., 2024), this corresponds to ~1,535 wintering females. Using an adult annual survival rate of 0.46 (Pérez-García et al., 2024), and an average of 3.12 fledglings (mean brood size observed during our final survey in late August when ducklings are close to fledging) per brood reaching winter, adjusted to 1.56 females per brood assuming a 1:1 sex ratio, a simple equation predicts that ~ 1308 wintering females would result from the estimated 386 broods in Morocco. This winter estimate is slightly lower than the observed 1,535 wintering females. This small discrepancy might arise from several non-exclusive factors. First, winter counts in Morocco may include migrants from neighboring countries like Algeria and Spain, meaning that January counts reflect both local breeders and incoming winter migrants (Pacheco-Guardiola et al., 2025). However, the opposite pattern has also been observed, as one ringed Marbled duck in winter was later observed breeding in Spain (H.B, pers. obs). Second, fledging success and post-fledging survival may vary among years (Guillemain et al., 2013), meaning that fledging success estimated in our study may underestimate productivity. Finally, the wintering counts itself may underestimate true population size as they do not take into account imperfect detection (Nagy et al., 2022). This highlights the importance of integrating movement ecology, post-fledging survival, and region-wide monitoring to improve the coherence of demographic parameters estimated across the annual cycle. Our results suggest that Morocco serves not only as a major wintering site but also as a critical breeding area. This suggests Morocco is an important region for the long-term conservation and viability of the Marbled duck in the West Mediterranean.

Habitat drivers of abundance

Understanding habitat drivers of Marbled duck is crucial for informing targeted conservation actions. Emergent vegetation cover and wetland type were found to be the strongest predictors of Marbled duck brood abundance, whereas there was no evidence of wetland surface area effect on brood abundance. Abundance increased strongly with greater emergent vegetation cover (Figure S2), which is consistent with previous studies showing that dense emergent vegetation, particularly reedbeds, provide nesting habitat, shelter from predators, and abundant food resources (Green, 1998a; Fuentes et al., 2004, 2005; Atiénzar et al., 2012; Sebastián-González et al., 2013; Cherkaoui, Magri, & Hanane, 2016; Cherkaoui, Selmi, & Hanane, 2017). The positive association of ponds with brood abundance aligns with previous studies emphasizing the importance of shallow temporary wetlands rich in seeds and invertebrates, which provide both food and cover essential for Marbled duck broods (Green & Sánchez, 2003; Fuentes et al., 2004; Sebastián-González et al., 2013). By contrast, dams appeared less attractive possibly due to unsuitable depth profiles, reduced food availability, or greater exposure to disturbance, while the negative association with rivers may reflect greater flow variability, or reduced availability of sheltered shallow margins preferred by broods. The 'Other' category grouped lagoon, marsh, and saltpan because they were each poorly represented in the random sampling. In the sampled lagoon, no broods were detected across five SSUs, whereas marsh supported seven broods across three SSUs, and saltpan supported three broods in a single SSU. These contrasts suggest that brood abundance may differ among these wetland types, with marshes and saltpans likely supporting higher brood presence than lagoons in our dataset, as they can share key features with ponds, such as shallow waters and dense emergent vegetation. However, due to low sample size, this interpretation should be considered with caution.

Overall, our findings underline the importance of shallow, vegetated wetlands particularly smaller coastal wetlands for sustaining Marbled duck breeding populations in Morocco. This aligns with the results of Cherkaoui, Selmi & Hanane (2017) who emphasized the species' preference for coastal, low-altitude wetlands providing shallow water and dense vegetation. These preferences mirror broader patterns in waterbird species, where vegetation cover, diversity and habitat heterogeneity promote higher richness and abundance of threatened species (Sebastián-González et al., 2013; Cherkaoui et al., 2015; Cherkaoui, Magri, & Hanane, 2016). Conservation efforts should therefore prioritize, maintaining and restoring wetlands with abundant emergent vegetation, diverse microhabitats, and extensive shallow water areas.

Limitations, and future directions

In the context of our results, we recommend periodic monitoring of the Marbled duck and other waterbirds based on a standardized, two-stage probabilistic sampling design. This sampling framework, combined with hierarchical abundance models that correct for imperfect detection, allows for consistent and repeatable assessments of population size across time and space. In addition, it may allow robust comparisons of the contribution of every country to the population size. Similar model-based frameworks have been effectively adopted in waterbird monitoring programs elsewhere (Conway, 2011; Stanton et al., 2015; Aubry et al., 2023; Guillemain et al., 2025), and their application at the scale of the West Mediterranean population and specifically to North Africa could support coordinated conservation efforts across political borders. Evidence suggests that Morocco likely hosts individuals originating from other parts of North Africa, not only during winter but possibly also during the breeding season (Pacheco-Guardiola et al., 2025). This highlights the need to complement monitoring with satellite tracking programs across Algeria and Tunisia, in addition to Morocco, to better understand population connectivity, migratory pathways, and regional dynamics. While this study represents a significant advancement in monitoring the Marbled duck, estimates may not capture full interannual variability or rare events. Future research should prioritize multi-year monitoring to assess temporal trends and incorporate demographic parameters such as nest success and fledgling survival.

A major limitation of our study was the lack of fine-grained spatial habitat layers (e.g., fine-grained land cover, wetland typology, or emergent vegetation cover). In the absence of such predictors of brood abundance, the extrapolation step was constrained to total wetland area alone. Under this framework, the estimated breeding population size represents the most robust and reliable approach currently possible. However, any difference of habitat heterogeneity between sampled and unsampled wetlands could introduce bias into the final estimate (under- or overestimation), yet in the absence of such layers, the direction of bias cannot be quantified. Developing comprehensive habitat layers for Moroccan wetlands should therefore be set high in the research agenda on wetland ecology in Morocco, as these would enable fine-scale mapping of suitable breeding habitats and more precise habitat-based extrapolation of population size of waterbirds, and other wetland-dependent taxa (Tuia et al., 2022). A further limitation concerns wetland type replication. Because certain wetland types were represented by only one PSU, their estimated effects reflect site specific conditions rather than general habitat-type associations. Additional sampling across multiple wetlands per type is necessary to support generalizable inference.

In conclusion, our study provides the first statistically robust estimate of the breeding population of the Marbled duck in Morocco and demonstrates the utility of integrating probabilistic sampling with hierarchical models for estimating population size of elusive species. Our findings confirm the ecological importance and vulnerability of the Moroccan population, identify key habitat drivers of abundance, and are consistent with demographic expectations based on wintering counts. By establishing a scalable, repeatable monitoring framework, this work lays the foundation for a long-term population survey, a key asset for an adaptive management approach to the conservation of this species. Given the country’s importance to the West Mediterranean population, these actions are not only a national priority but a regional conservation imperative.

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Author Contributions

H.B., A.B. and J.C. conceived the ideas and designed the methodology. H.B. led the writing of the manuscript. H.B. conducted the analyses. H.B., R.E. contributed to data acquisition. All authors revised the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability statement

The R scripts and datasets used in this study are publicly available on Zenodo at: https://doi.org/10.5281/zenodo.15367140

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Conflict of interest statement

The authors declare no conflicts of interest.

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Supplementary Material

Table S1. *Summary of N-mixture models used to explore the effect of habitat covariates on brood abundance in Morocco. Models vary by distribution assumption (Poisson or Negative Binomial) and detection covariates, and are ranked by the difference in Widely Applicable Information Criterion (ΔWAIC). Reported metrics include WAIC, the effective number of parameters (pD), and posterior predictive check (PPC) p-values. Model selected for inference is highlighted in grey. All models share the same detection submodel structure retained from Stage 1 (intercept only).*

Model	Distribution	Abundance Submodel	WAIC	ΔWAIC	pD	Bayesian p-value
Model 7	**Poisson (P)**	Year + Wetland type + Surface area + Emergent vegetation	123.3	0.0	11.47	0.41
Model 14	**Negative Binomial (NB**	Year + Wetland type + Surface area + Emergent vegetation	123.6	0.3	11.33	0.43
Model 4	**P**	year + wetland type + emergent vegetation	123.9	0.6	11.51	0.44
Model 11	**NB**	year + wetland type + emergent vegetation	124.3	1.0	11.44	0.45
Model 1	**P**	year + emergent vegetation	126.1	2.8	11.45	0.44
Model 6	**P**	year + surface area + wetland type	126.4	3.1	11.63	0.44
Model 5	**P**	year + emergent vegetation + surface area	126.5	3.2	11.36	0.42
Model 13	**NB**	year + surface area + wetland type	126.5	3.2	11.45	0.46
Model 8	**NB**	year + emergent vegetation	126.5	3.2	11.34	0.46
Model 12	**NB**	year + emergent vegetation + surface area	126.6	3.3	11.27	0.43
Model 2	**P**	year + wetland type	126.9	3.6	11.61	0.45
Model 9	**NB**	year + wetland type	127.1	3.8	11.37	0.48
Model 3	**P**	year + surface area	127.7	4.4	11.32	0.48
Model 10	**NB**	year + surface area	127.9	4.6	11.25	0.49
Model null 1	**P**	year	128.0	4.7	11.44	0.51

Table S2. *Posterior summaries for the best-supported N-mixture model estimating the effects of habitat and environmental predictors on Marbled Duck brood abundance across Moroccan wetlands. Shown are posterior means, standard deviations (SD), 2.5% and 97.5% Bayesian credible interval limits, Gelman-Rubin convergence diagnostic (Rhat), posterior probability of a positive effect (P-dir), and inferred effect direction for each parameter. Fixed effect estimates supported by more than 95% of the posterior are highlighted in bold. The random effect for primary sampling unit (primunite) is reported as its posterior mean and 95% credible interval. Others category groups saltpans, marshes, and lagoons.*

Parameter	Mean	SD	2.5%	97.5%	Rhat	P-dir	Direction
Dam (Intercept)	-4.52	2.66	-10.71	-0.15	1.08	0.98	negative
Lake	2.51	2.34	-1.90	7.57	1.00	0.88	positive
Pond	**4.72**	**2.62**	**0.40**	**10.8**	**1.00**	**0.97**	**positive**
River	**-8.51**	**6.15**	**-22.98**	**0.42**	**1.00**	**0.97**	**negative**
Other	**3.52**	**1.97**	**-0.1**	**7.80**	**1.00**	**0.97**	**positive**
Year	-0.69	1.79	-4.30	2.9	1.05	0.62	negative
Surface area	-0.64	1.31	-3.38	1.94	1.00	0.30	negative
Emergent vegetation	**0.56**	**0.33**	**-0.1**	**1.23**	**1.00**	**0.95**	**positive**
Random effect- Primary unit:	2.88	1.94	0.82	7.92	1.00		

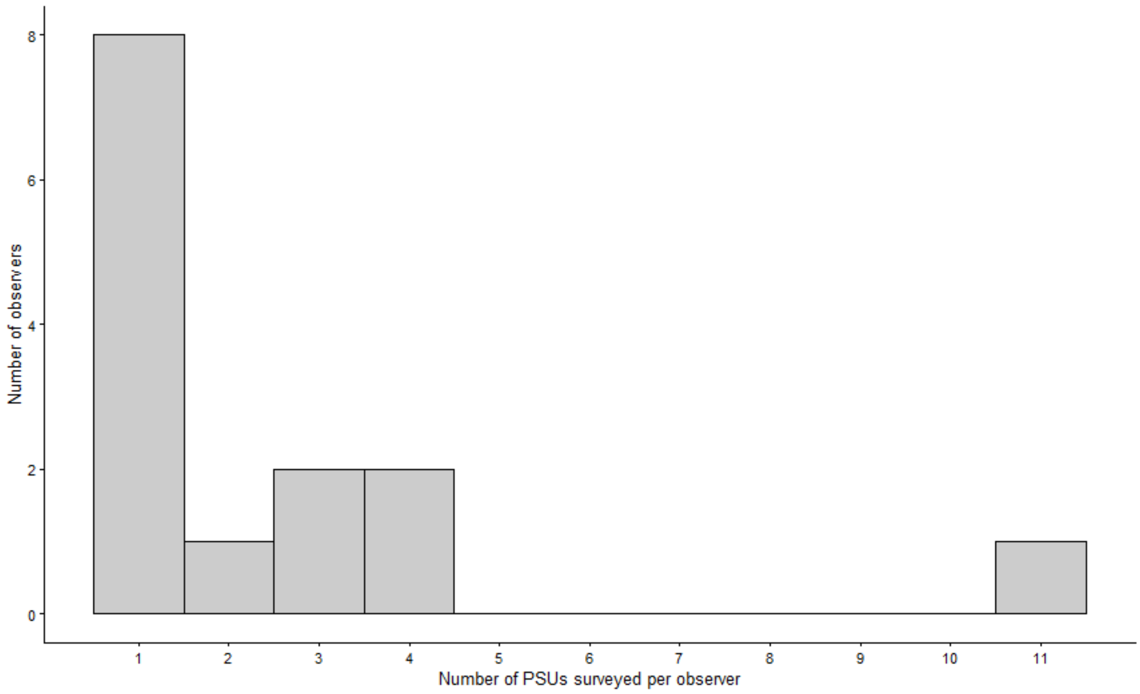

Figure S1. *Distribution of observer effort amongst primary sampling units.*

Regarding the observer effect, the distribution of observers across primary sampling units (PSUs) was highly unbalanced: most (8) observers surveyed only one PSU, only five observers visited more than two PSUs. Under this sampling design, observer identity is almost perfectly confounded with site identity. Consequently, including observer as a detection covariate would not be estimable in a meaningful way and would likely absorb site-level, rather than capturing genuine observer-related differences in detectability.

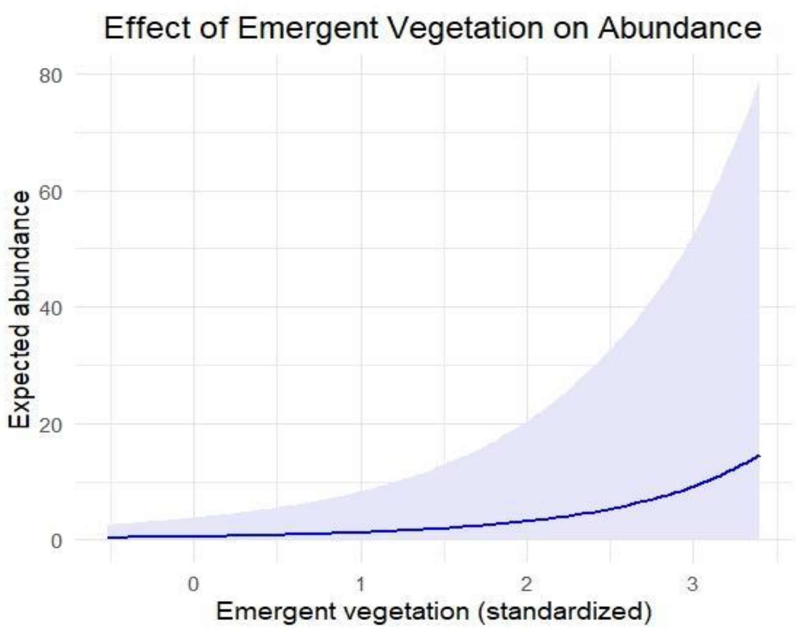

Figure S2. *Predicted abundance as a function of emergent vegetation percentage*

Chapter 3: Combining accelerometry and GPS tracking reveals functional units in the Marbled duck

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Abstract

Background: Understanding when and where animals forage, where they roost and how they move between these locations is central to movement ecology and conservation. For highly mobile species, such patterns remain difficult to quantify using traditional observation methods, particularly when activity occurs at night. Advances in bio-logging, especially the integration of GPS and tri-axial accelerometry, now allows fine-scale investigation of how animals organize their space use. In waterbirds, this approach offers the framework to examine ecological concepts such as that of functional units-defined as spatially consistent associations between roosting and foraging areas. This concept is particularly important for waterbird species, in which part of their functional units can be overlooked in conservation planning

Methods: We combined tri-axial accelerometer and GPS data from 6 wild Marbled duck tracked in Morocco to investigate functional units during the wintering period. Multiple supervised machine-learning models trained on annotated reference dataset from 3 captive birds were tested to classify accelerometry data into 5 behaviour classes: flying, foraging, active, preening and resting. The best performing model was applied to data of wild birds, to predict their behaviours, and map them to explore functional units. Environmental and anthropogenic covariates were then evaluated to characterize used roosting and foraging sites.

Results: Using the best model, behaviours of captive birds were reliably classified achieving an overall performance of 89%. Spatial analyses revealed strong inter-individual variation in functional units. Some Marbled ducks displayed spatially distinct roosting and foraging sites, whereas others relied on multifunctional wetlands where both behaviours occurred within the same area, indicating that Marbled ducks use several space-use strategies. In addition, foraging sites were characterized by specific environmental and anthropogenic conditions, with temperature, vegetation density (NDVI), and distance to roads emerging as important predictors.

Conclusion: The joint use of accelerometers and GPS allowed us to better understand the spatial organization of the marbled duck, and highlight the need to conserve spatially connected roosting and foraging sites, rather than focusing on isolated wetlands.

Keywords: Activity budget, Biologging, Accelerometer, behavioural classification, Supervised machine learning, Waterbird, Functional units, Marmaronetta angustirostris

Background

A better knowledge of where animals forage, where they roost, and how they move between these locations is often key information to set up sound conservation actions [1–3]. These spatio-temporal behavioural patterns reflect how individuals allocate time and energy to essential activities such as feeding, resting, and avoiding predators, thereby influencing fitness and population dynamics. Quantifying the energetic costs of movement and the efficiency of foraging-roosting routines is thus critical for understanding time-energy allocation strategies and for informing conservation and management of sites used [4]. However, acquiring such data remains particularly challenging for elusive, highly mobile species such as many waterbirds that are difficult to observe directly or are active when visual observation is not feasible [5].

To overcome these limitations, researchers have developed advanced tracking technologies that capture both spatial and behavioural information [5]. Among these, the use of GPS with tri-axial accelerometers has greatly expanded our ability to study the fine-scale behaviours of free-ranging animals across diverse taxa [6–11]. Accelerometers have been used to study animal behaviour since the late 1990s. They allow continuous, high-frequency recording of animal motion in three dimensions, typically referred to as heave (dorso-ventral movement, up-down z-axis), surge (anterior-posterior movement, forward-back x-axis), and sway (lateral, side-to-side movement, y-axis). This information is acquired without the need for visual contact, making it possible to detect subtle behaviours that would otherwise remain unnoticed [12,13]. Beyond identifying behaviours, accelerometers also provide powerful proxies for energy expenditure (e.g., Overall Dynamic Body Acceleration, ODBA), allowing researchers to compare activity-related effort across behaviours or habitat contexts [14]. This enables the study of trade-offs between foraging effort and safety or between commuting distance and energetic efficiency, central to understanding how animals optimize their daily routines in variable environments [15,16].

Movement is both a driver and a consequence of ecological processes, often reflecting behavioural responses to changing environmental conditions (Ullmann et al., 2020). While spatial metrics like home range size or travel distance are commonly used to infer movement responses (Bonte et al., 2006; Schai-Braun & Hackländer, 2014), these approaches often overlook the behavioural mechanisms that underlie changes in space use, such as shifts in foraging effort, roost fidelity, or predator avoidance strategies [17]. Accelerometry provides a way to bridge this gap by inferring specific behaviours such as flying, resting, or foraging from body motion data. These behaviours can be classified using either supervised or unsupervised machine learning approaches [7]. Supervised models rely on direct behavioural observations from tagged animals to match distinctive acceleration signatures with known behaviour, whereas unsupervised methods involve clustering similar signals and assigning behaviour categories post hoc based on expert knowledge [7,18,19]. After this step, part of the validated acceleration data is used to train the machine learning algorithm, while another part is reserved to evaluate its performance. The final model is then applied to the remaining unlabelled accelerometer data to assign behavioural categories. [7,13,20].

Among birds, waterbirds have long served as model systems for exploring spatial behaviour in seasonal and dynamic habitats. A particularly influential concept in waterbirds is that of functional units first described in wintering Eurasian Teal (Anas crecca) in the Camargue region of southern France (Tamisier 1974, Guillemain *et al.*, 2010). In this system, distinct groups of individuals consistently used specific roosting sites during the day and returned at night to the same foraging areas, forming stable and spatially cohesive units (Tamisier & Tamisier, 1981). These patterns were interpreted as adaptive responses to the trade-offs between safety, energy expenditure, and food acquisition, with day/night behavioural cycles structured around predictable movement between core resting and feeding locations. Similar patterns of behaviour and site fidelity have since been reported in other duck species, often linked to commuting distances, social structure, and landscape configuration [22–24].

The concept of functional units was first formalized in waterfowl, yet spatial organization has been described in other bird taxa. For instance, shorebirds such as the Dunlin Calidris alpina show stable associations between roosting and foraging sites during winter, forming spatially cohesive functional units that persist over time [25]. Likewise, studies of migratory shorebirds in intertidal ecosystems have shown that individuals commute daily between high-tide roosts and low-tide feeding grounds [26,27]. These recurrent spatial and temporal patterns reflect a general principle of movement ecology that animals organize their space use to minimize energetic costs and maximize safety and resource intake [28].

Here, we use high-resolution accelerometer and GPS data collected from the rare and elusive Marbled duck Marmaronetta angustirostris to infer the spatio-temporal dynamics of foraging and roosting behaviours and the environmental factors influencing it. Our goal is to explore whether in the wild, individuals display consistent spatial routines that would correspond to the concept of functional units, i.e., fixed roosting areas linked to distinct foraging sites.

Using a supervised machine learning framework trained on an annotated reference dataset from captive birds, we classify behavioural bursts into three categories: (1) Flying, (2) Roosting, which includes the sleeping/resting and preening classes, and (3) Foraging, which includes the active and feeding classes. We then analyze the spatial distribution of these behaviours during the wintering period in wild Marbled ducks captured and fitted with tracking devices in Morocco. Finally, we identify the ecological and anthropogenic drivers of roosting and foraging site selection. Specifically we evaluated the hypothesis that site use is driven by both environmental and anthropogenic variables, such that roosting and foraging sites differing systematically in vegetation cover density (indicator of concealment sites important of roosting) as approximated by the Normalized Difference Vegetation Index (NDVI), distance to roads (as a proxy for anthropogenic disturbance), local weather conditions (hourly temperature, wind speed), and moon fraction (potentially influencing nocturnal foraging activity during full-moon nights). In addition, we hypothesized a consistent daily activity pattern, with roosting occurring primarily during daylight hours and foraging predominantly at night.

Methods

Wild Marbled duck capture and tracking

Between 2023 and 2025 during the months of January and February, 11 adult wild Marbled ducks (2 females and 9 males) were captured at two wintering sites in Morocco: the Sidi Moussa-Oualidia wetland complex and Oued Assaquia Al Hamra wetland (Figure 1). Birds were captured by trained bird ringers using whoosh nets and manually operated drop nets, both of which are non-lethal trapping techniques suitable for waterfowl. Each individual was fitted with a solar-powered GPS/accelerometer tag (Ornitela OT-10 3G, Lithuania; https://www.ornitela.com/) and marked with both a standard metal ring and a yellow PVC alphanumeric leg ring for visual identification. Morphometric measurements (e.g., wing length, tarsus length, weight) were recorded. Birds were sexed in the field based on bill coloration and head shape, following Green (2000).

Tags were mounted on the birds' backs using backpack-style harnesses made of ribbon Teflon (4 mm), a widely used and minimally invasive material for avian telemetry [30]. The combined weight of the tag and harness was 11 g, well below the commonly accepted threshold of 3% of body mass for migratory birds (mean: 484g; min: 450g; max: 520g) ensuring minimal impact on behaviour and flight performance [31]. The Ornitela tags allows remote programming of both GPS and tri-axial accelerometer sampling settings via GSM/GPRS network. Devices were configured to record a GPS fix and a 7-second burst of acceleration data at 10Hz sensor burst frequency, every 30 to 60 minutes, depending on battery charge.

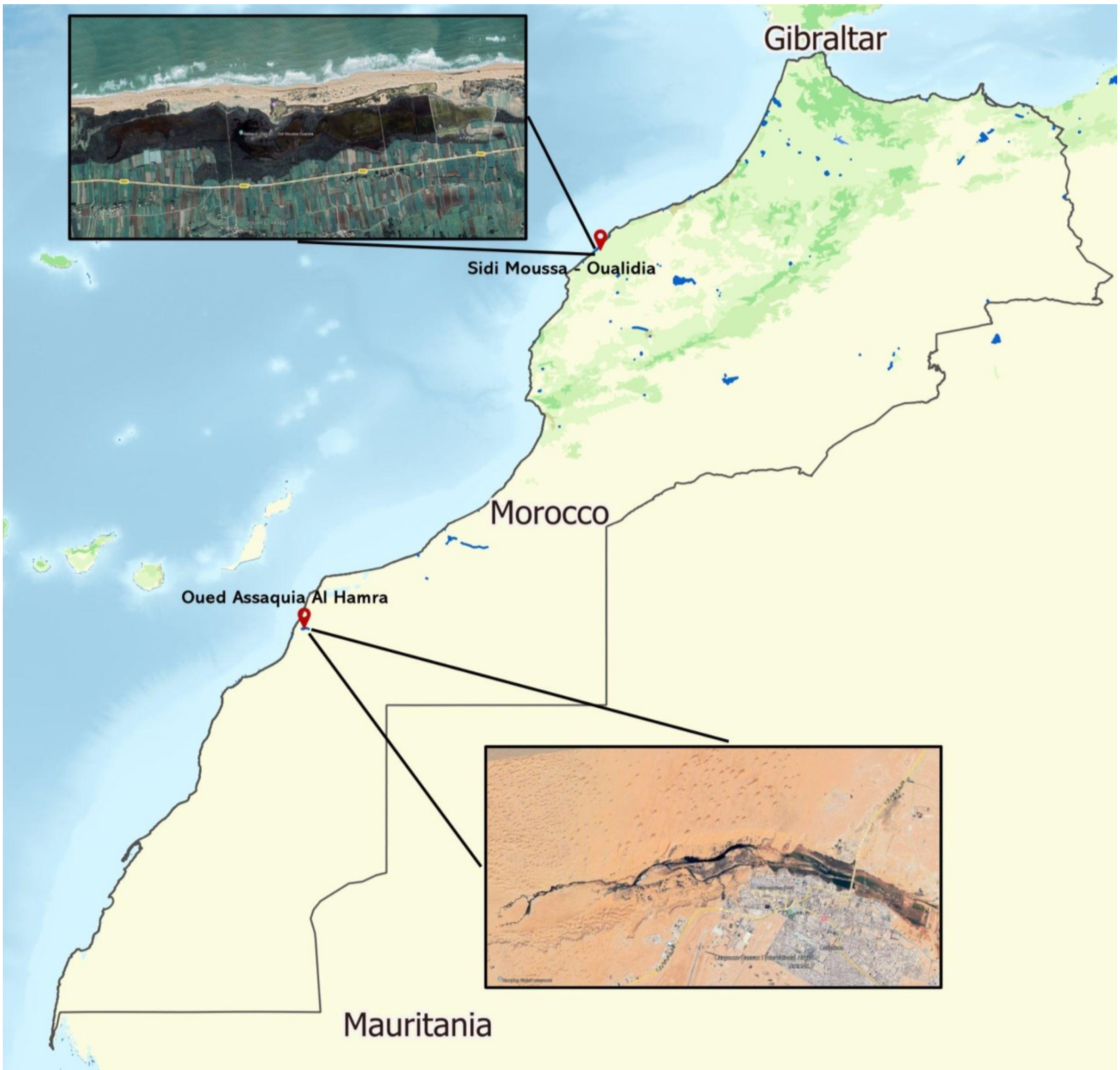

Figure 1. *Study area and capture sites in Morocco.*

Data Collection and Preprocessing

We used behavioural observations on three captive Marbled duck equipped with the same GPS-GSM-accelerometer tags described above at the Parc animalier de Branféré (Le Guerno, France) between 7 and 11 May 2024 to annotate a range of behavioural states. Birds were housed in a pond environment that allowed free movement and were filmed over two consecutive days while the accelerometers continuously recorded acceleration data. In total, we collected 161 minutes of video from the captive birds. After that behavioural events observed in the videos were annotated using BORIS software (version 7.9.7, Friard & Gamba, 2016). The observed behaviours (Figure 2) included: feeding, preening, resting/sleeping, and active (swimming and walking combined under this category). Annotations were then temporally aligned with corresponding acceleration bursts using timestamp synchronization, producing a labeled dataset suitable for supervised behavioural classification. Time synchronization between video recordings and accelerometer data was achieved using a universal time clock application. Due to flight restrictions in the captive setting, flight behaviour could not be recorded directly. As an alternative, we manually annotated flight behaviour by identifying stereotypical acceleration patterns associated with flight from 3 wild tagged individuals, as previously done in other studies [32]. Of the recorded footage, 2128 seconds (~35.5 minutes) of video could be precisely synchronised with accelerometer data and were retained for analysis. The total duration of video annotated data for each behaviour can be found in Table S1.

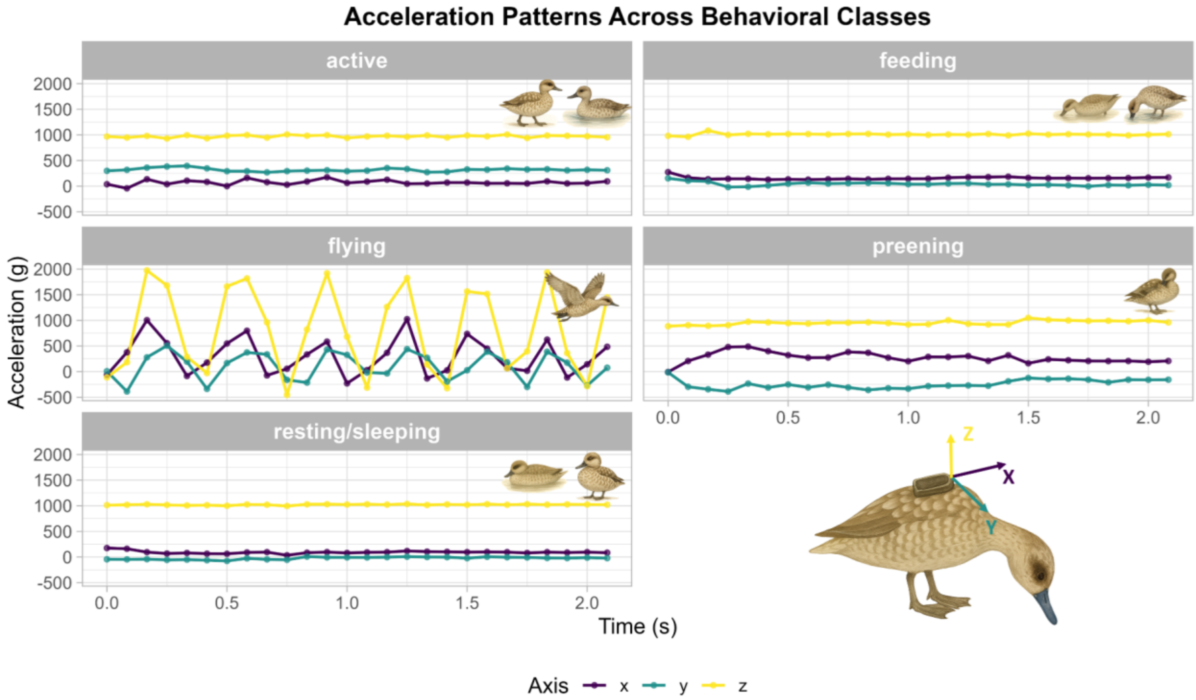

Figure 2. *Mean acceleration patterns across behavioural classes in Marbled duck. Lines represent smoothed tri-axial acceleration over 2-s bursts of annotated behaviour recorded during calibration trials. Distinct signatures are visible across behaviours. Bird illustrations were generated with the assistance of ChatGPT (OpenAI, 2025).*

Segmentation and feature extraction

To identify the behavioural states of Marbled duck, we first segmented the tri-axial acceleration data and then extracted metrics from each segment to serve as predictor variables for machine learning. We compared two segmentation approaches: (1) fixed segmentation approach, which divides the acceleration time series into uniform windows (0.4, 0.8, and 1.2 seconds were tested in our case), and (2) flexible segmentation approach, which applies a change point detection algorithm to dynamically create segments based on abrupt acceleration changes. The flexible segmentation was implemented using the processStream function of the R package cpm version 2.3 [33] with a Generalized Likelihood Ratio (GLR) test to detect changes in both the mean and variance of the signal using the ARL_0 (Average Run Length) parameter to control sensitivity to change points [34]. The latter was shown to result in a better accuracy of behaviour classification, as it cuts segments at the point of change in the acceleration data, which generates one segment for each behaviour [34].

From each segment, we computed a set of metrics describing the acceleration signal. Metrics were derived from the two principal components of acceleration: static acceleration, which reflects gravitational pull and informs about body posture, but is sensitive to tag orientation, and dynamic acceleration, which reflects body movement and is more robust to changes in orientation.

Models feature selection

Based on the previous metrics, we defined two feature sets to test two different models.
The full model included both static and dynamic acceleration-based metrics computed separately for each axis, like the mean, minimum, maximum, skewness, kurtosis, power spectral density (PSD), dominant frequency, linear trend, residual noise, and dynamic body acceleration metrics like ODBA (Overall Dynamic Body Acceleration) (Wilmers *et al.*, 2015). The orientation-invariant model was designed to be robust against tag misalignment and loose-fitting devices. It used only orientation-invariant metrics, derived from combined axes. These included: vectorial dynamic body acceleration (VeDBA) and ODBA; magnitude-based metrics (mean, standard deviation, range, skewness, kurtosis); frequency domain features (maximum PSD, dominant frequency), and zero crossing rate (ZCR) of the acceleration magnitude. This dual model approach enabled us to compare the classification performance of all available metrics with a subset specifically designed to be robust to sensor orientation.

Machine learning modelling

behavioural classification was performed using Random Forest models [35], implemented with the randomForest package version 4.7.1.2 in R [36]. Random Forests were chosen due to their strong performance in behaviour classification in previous studies [37,38]. The dataset was split into 70% training and 30% testing.

We assessed model performance per behaviour by computing precision, sensitivity, and F-measure. Each predicted behaviour was labelled as either true positive (TP), when correctly classified as this behaviour; false positive (FP), when incorrectly classified; true negative (TN), when correctly classified as a different behaviour; and false negative (FN), when incorrectly classified as a different behaviour. These statistics were then used to derive: precision (equation 1), which shows the percentage of correct positive classifications; sensitivity (equation 2), denoting the probability of correct behavioural classification, and F-measure (equation 3) which is the harmonic mean of precision and sensitivity [20].

(1) Precision = $\frac{\boldsymbol{TP}}{\boldsymbol{TP+FP}}$; (2) Sensitivity = $\frac{TP}{TP+FN}$; (3) F-measure = $\frac{2\,TP}{2\,TP+FP+FN}$

After identifying the best-performing model, we assessed the effect of class imbalance correction by comparing down-sampling and up-sampling strategies. We subsequently compared the performance of the full model with that of an orientation-invariant model. After identifying the best model, we used the mean decrease gini (Figure S1) to identify the importance of each feature in the model, with higher features values indicating higher importance.

Functional units in wild Marbled ducks

After identifying the best model, we used it to generate daily activity patterns of eight wild Marbled ducks from both capture sites. We restricted the analysis to the wintering-pre-breeding period months (15 January - 15 April, just before nesting, [39]) adjusted by the date of capture in January or February and the tag failure or mortality if occurring before mid-April. Three individuals were excluded due to early mortality or tag failure.

Mapping behavioural space use to explore functional units

To explore the spatial organization of functional units in wild Marbled ducks, we generated a behaviour-based spatial map combining GPS positions and accelerometer data derived from behavioural classifications. We focused on two key behavioural states: roosting (resting/sleeping and preening) and foraging (active behaviours including feeding, walking, and swimming), grouped under their respective functional labels.

For each individual, GPS points with known behaviours were grouped into day and night periods based on the solar elevation, using the Suncalc package version 0.5.1 in R [40]. Daytime was defined as the period when the solar elevation was $\geq 0°$ (from sunrise to sunset), while nighttime was restricted to astronomical night, when the solar elevation was $\leq -18°$ (from night to night end). We then spatially aggregated the behaviour of classified GPS points by rounding latitude and longitude coordinates to 3 decimal places (~ 100 x 100 m resolution), creating a grid of pixels across the study areas.

We first quantified the intensity of space use for each behaviour and time period by counting the number of behaviour-specific data per pixel. These maps illustrate how intensively each location was used for roosting or foraging during day and night, highlighting the spatial concentration and overlap of behavioural activity. Secondly, for each pixel, we computed the number of roosting and foraging observations, and calculated the behavioural balance index as the difference between the number of foraging and roosting data.

This exploratory visualization allowed us to spatially detect potential functional units, defined as spatially distinct but regularly used pairs of roosting and foraging sites. By identifying areas with strongly contrasting day/night behaviour patterns, we could delineate zones used consistently for roosting vs. foraging across days.

Modeling the drivers of functional unit use

After developing individual-level daily activity patterns and mapping spatial behaviour to identify functional units, we used these patterns to formally test the ecological and anthropogenic drivers of roosting and foraging site use. To do this, we focused on the Oued Assaquia Al Hamra wetland (26.8161° N, –12.8083° W), where consistent patterns of functional space use were detected. The site comprises 9500 ha of wetland adjacent to Laayoûne city (~250.000 inhabitants), predominantly fed by sewage waters from the city [41,42]. Ducks hunting is prohibited, though illegal killing may occur. Since 2019 the wetland hosts each winter on average 600 Marbled ducks [43] distributed in a few scattered groups. We selected six Marbled ducks that used this wetland extensively and restricted the analysis to the wintering-pre-breeding season months, excluding two individuals that were in other wetlands at that moment of the year.

To investigate the ecological and anthropogenic drivers of roosting and foraging site use and whether daily activity patterns were behaviourally consistent across individuals and between day and night, we fitted a generalized linear mixed model GLMM (1) with behaviour (0 = foraging, 1 = roosting) as the response variable with a binomial error distribution and a logit link. Fixed effects included, time period (day or night), normalised values of NDVI, distance to road, hourly temperature, wind speed, and the fraction of moon illumination using the suncalc package in R [40]. Sex was also included as a fixed categorical covariate, while bird identity (Individual ID) as a random intercept and slope. This allowed us to model baseline differences among individuals in their probability of foraging. In addition, we included random intercepts and random time period slopes by individual, thereby allowing the strength of the day-night contrast in foraging to vary among birds. This tested whether the diel roosting pattern was consistent across individuals and between day and night. We also included an interaction between time period and distance to road as we expected the foraging propensity close to road to be lower during the day than during the night (see Appendix S1 for the model mathematical annotation).

All statistical analyses were performed using R version 4.4.1 [44]. All continuous predictors were standardized to facilitate model convergence and comparison of effect sizes. Collinearity among explanatory variables was assessed using variance inflation factors (VIF) and pairwise Pearson correlations. We used cutoffs of $|r| \geq 0.7$ and VIF ≥ 3 to to indicate high collinearity among the predictors [45,46]. The modelling approach was done in a Bayesian framework using the R package brms version 2.23.0 [47], which allowed us to obtain posterior distributions of effect sizes and credible intervals, and to assess variation among individuals in intercepts and slopes. Four Markov chain Monte Carlo chains were run for each model, with 3000 iterations each (with 1000 warm-up). Convergence was assessed using visual inspection of trace plots and the Gelman-Rubin scale reduction factors (Rhat), which were required to be smaller than 1.1 [48]. We performed a Posterior Predictive Check (here after PPC) to assess model fit, where a model with a good fit to the data had Bayesian p-values superior to 0.05 and smaller than 0.95 [49]. We reported posterior means as point estimates for parameters and used the (0.025, 0.975) quantiles of the posterior distribution to compute the 95% Credible Intervals (CrI) for these estimates. We assessed effect strength using standardized coefficient magnitudes, while statistical support was assessed by examining if the 95% CrI excluded zero (indicating high directional certainty) versus overlapping zero (indicating directional uncertainty). We distinguished between well-supported effects (CrI excludes zero), marginally supported effects (CrI narrowly overlaps zero with posterior mean notably displaced from zero), and unsupported effects (CrI substantially overlaps zero with posterior mean near zero).

Results

Classification performance

The comparison between the full statistical feature set and the orientation-invariant feature (here after, OIF) set revealed notable differences in classification performance (Table 1). Both models achieved high classification performance, with the full model reaching 88.4% and the OIF model 88.8%. While the full model performed better for dominant behaviours such as active and resting/sleeping, the OIF model showed superior detection of less frequent but ecologically relevant behaviours like feeding. Given that OIF explicitly accounts for potential tag misalignment and improves recognition of key foraging behaviours, we retained this approach for subsequent analyses.

Table 1. *Comparison of classification performance metrics for each behaviour between model with all statistical features (Full) and model with only orientation invariant features (OIF). Values represent sensitivity (proportion of correctly classified segments for a given behaviour), Precision (the proportion of correct positive classifications), and F-measure (harmonic mean of precision and sensitivity), all computed per behaviour on the test dataset.*

behaviour	Sensitivity (OIF)	Sensitivity (Full)	Precision (OIF)	Precision (Full)	F-measure (OIF)	F-measure (Full)
Active	0.74	0.90	0.84	0.86	0.79	0.88
Feeding	0.89	0.71	0.83	0.80	0.86	0.76
Flying	1.00	1.00	1.00	1.00	1.00	1.00
Preening	0.94	0.83	0.85	0.81	0.89	0.82
Resting/sleeping	0.87	0.95	0.93	0.96	0.9	0.96

Among fixed window lengths, 0.4 s produced the best balance (F-measure: Active = 0.82, Feeding = 0.86, Preening = 0.89, Resting = 0.90, Table S2), whereas longer windows (0.8–1.2 s) reduced sensitivity for minority behaviours such as feeding and preening. Flexible segmentation with ARL values of 100-5000 yielded consistently good results, with particularly high sensitivity for feeding (0.9 at ARL 500, Table S2) and balanced performance across all behaviours. Given its robustness to variable burst lengths and its improved detection of key foraging behaviours, we retained the fixed segmentation approach for subsequent analyses.

Application of the best model to classify wild Marbled duck behaviours

We used the best model (OIF with fixed segmentation approach) to map wild marbled duck behaviour of the 8 marbled duck tracked in winter in Morocco. Daily activity patterns revealed clear diel variation in Marbled duck behaviour (Figure 5). Birds spent most of the day resting or sleeping, particularly during midday hours, while active behaviours peaked in the early morning and late afternoon. Preening occurred throughout the day at lower levels, while feeding showed increases around dawn and dusk and at night. Flying was rare but occurred mainly around dawn and dusk. These patterns were consistent across individuals, with some variability highlighting a strong diurnal rhythm characterized by daytime roosting and nighttime increase in foraging activity.

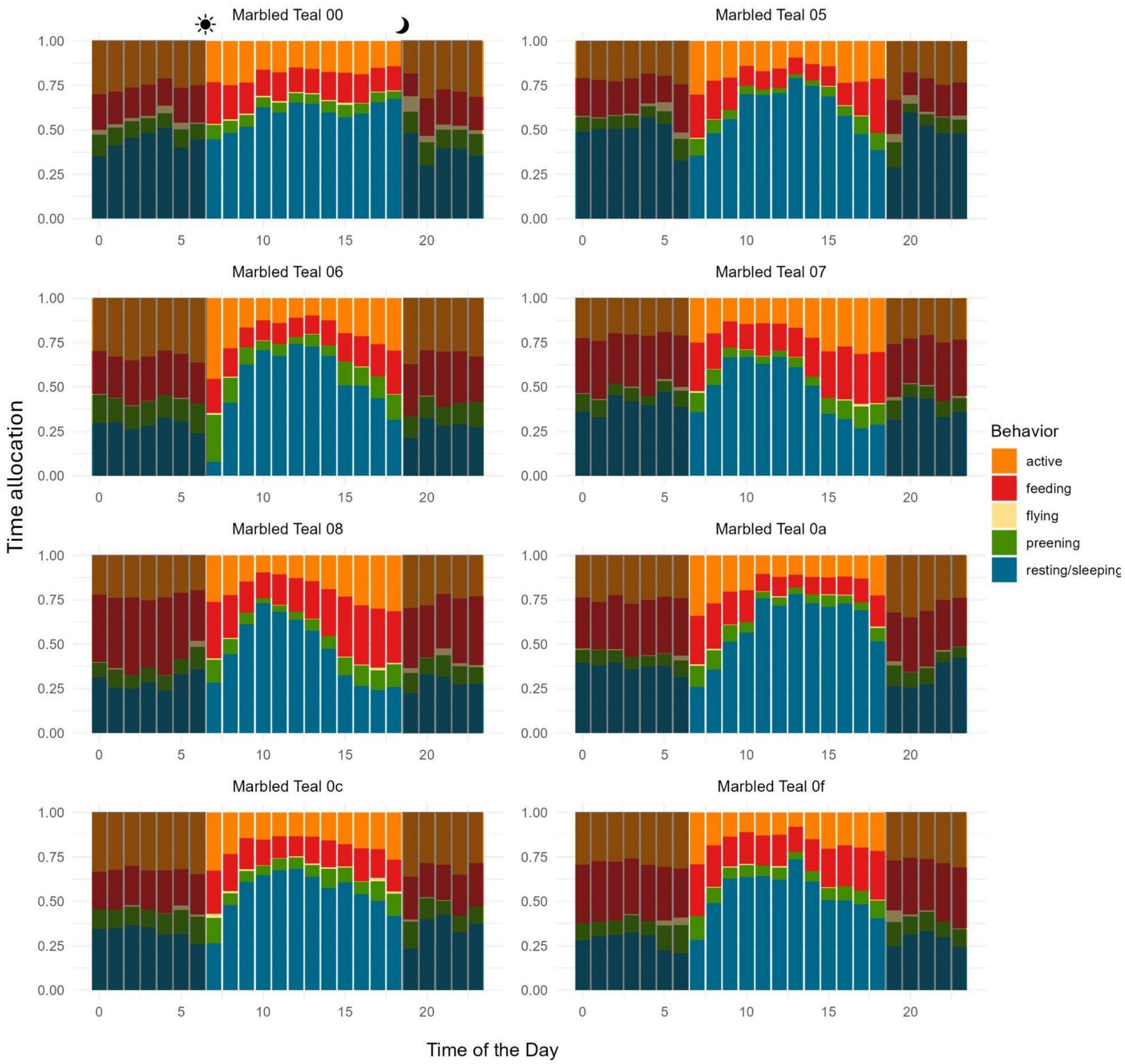

Figure 5. *Proportional predicted daily activity patterns of Marbled duck using the best behaviour classification model. Each panel represents an individual bird, with behaviours (resting/sleeping, active (swimming or walking), feeding, preening, and flying) shown as stacked proportions across 24 hours. Dark shaded polygons indicate the nocturnal period (from sunset to sunrise).*

Functional units

Spatio-temporal distribution of roosting versus foraging behaviours of wild Marbled duck

The spatial distribution of behaviour-specific activity is shown in Figure 6 for Marbled duck 0F and Figure S2 for the other individuals . Separate intensity maps (Figure 6, A) for roosting and foraging revealed distinct spatial patterns of space use across Oued Assaquia Al Hamra wetland. Roosting activity (blue pixels) was concentrated in a few core zones closer to the city, whereas foraging activity (red pixels) extended over a broader area, including peripheral zones near the city during the day and far away feeding sites at night. The distribution of the behavioural balance map (Figure 6, B) revealed a general pattern of separation between roosting and foraging sites, especially for individuals 0F, 0A and 0C (Figure S2). In most cases, foraging areas were located both closer and farther from human infrastructure (depending on time period). However, individual variability was apparent. While several birds consistently utilized distinct areas for day roosting and night foraging, others, such as individuals 06, 07, and 08 (Figure S3), exhibited minimal spatial separation between these behaviours. These individuals displayed overlapping areas where both roosting and foraging took place, suggesting that certain sites simultaneously supported multiple behavioural functions.

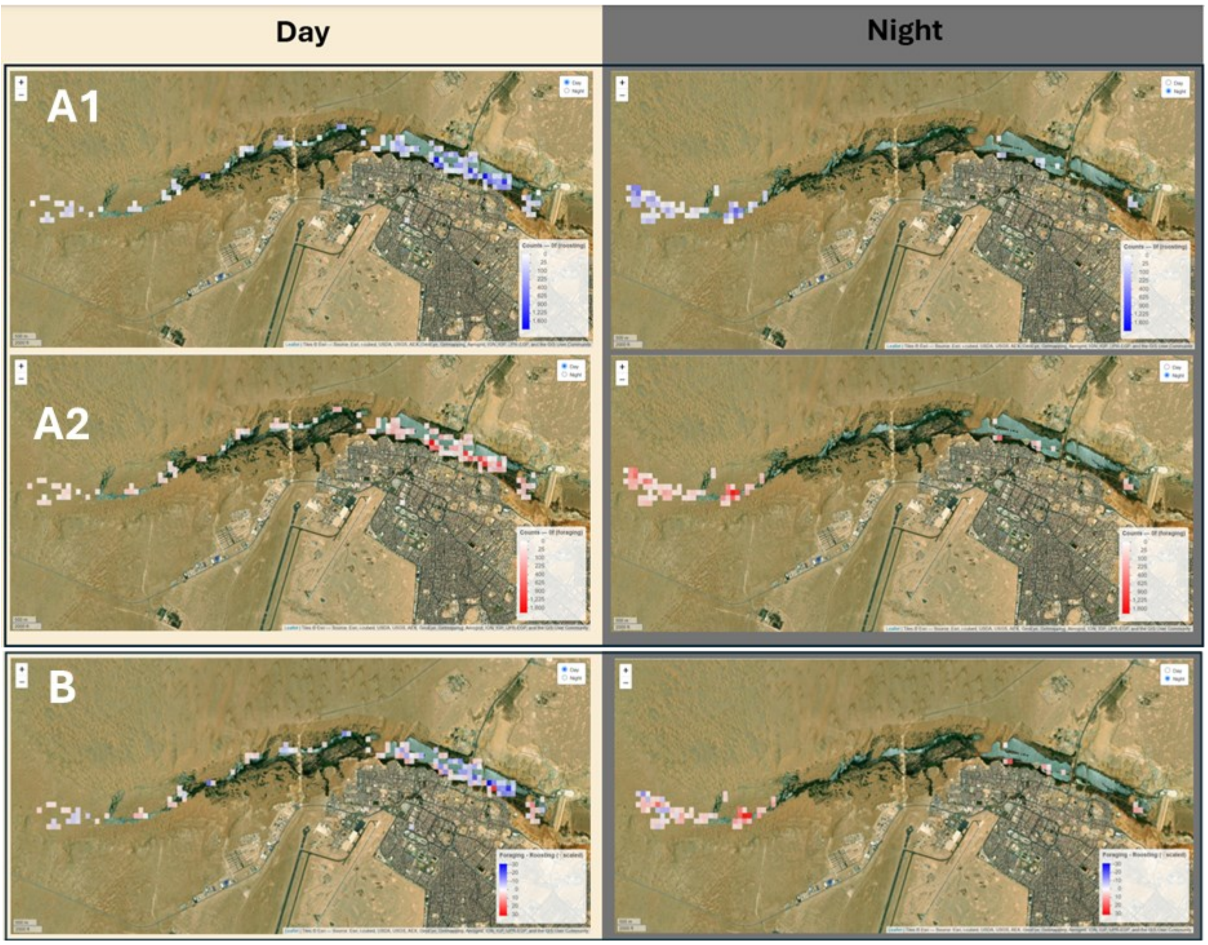

Figure 6. *Spatial distribution of Marbled duck 0F behavioural activity in Oued Assaquia Al Hamra wetland.* behavioural intensity maps showing the number of roosting (blue pixels, A1) and foraging (red pixels, A2) observations per 100 × 100 m pixel during day and night. (B) behavioural balance map showing the difference between foraging and roosting observations per pixel (red = foraging dominated, blue = roosting dominated) during day and night.

Factors explaining spatio-temporal functional units use

No strong correlations were detected among continuous predictors (all $|r| < 0.35$). Variance inflation factors VIF were below 7 for all fixed effects, indicating no problematic multicollinearity (Tables S3–S4). Modelling identified clear diel, ecological, and anthropogenic drivers of foraging probability in Marbled duck (table 3). Foraging was substantially higher at night than during the day (β = 0.70, 95% CrI: 0.24–1.14), indicating a strong nocturnal activity pattern. Foraging decreased with greener vegetation (NDVI; β = −0.12, 95% CrI: −0.13 to −0.11; Figure. 7A) and with higher hourly air temperature (β = −0.09, 95% CrI: −0.11 to −0.08; Figure. 7C), but slightly increased under stronger wind speeds (β = 0.07, 95% CrI: 0.05–0.08). The effect of moon illumination was weak and its credible interval overlapped zero (β = 0.00, 95% CrI: −0.01 to 0.01). We found no evidence for sex differences in foraging probability (β = −0.18, 95% CrI: −0.78 to 0.41). The interaction between diel period and distance to roads revealed a clear spatial pattern: while distance to roads had little effect during the day, at night foraging probability was higher than during the day close to the road but did not differ to day pattern with increasing distance from roads (β = −0.17, 95% CrI: −0.22 to −0.13; Fig. 8A).

Table 3. *Posterior estimates from Bayesian generalized linear mixed model explaining Marbled duck foraging probability as a function of time period, environmental, and anthropogenic predictors, including a Night x Distance to road interaction. Values are posterior means with 95 % Bayesian credible intervals (CrI), posterior standard errors, odds ratios (OR), and convergence diagnostics ($\hat{R}$).*

Term	Estimate [95% CrI]	Est.Error	Rhat	OR [95% CrI]
Intercept	−0.23 [−0.76, 0.28]	0.26	1.00	0.79 [0.47, 1.32]
Time period	0.70 [0.24, 1.14]	0.22	1.00	2.01 [1.27, 3.13]
NDVI	−0.12 [−0.13, −0.11]	0.01	1.00	0.89 [0.88, 0.90]
Distance to road	0.02 [−0.02, 0.06]	0.02	1.00	1.02 [0.98, 1.06]
Moon phase	0.00 [−0.01, 0.01]	0.01	1.00	1.00 [0.99, 1.01]
Hourly temperature	−0.09 [−0.11, −0.08]	0.01	1.00	0.91 [0.90, 0.92]
Wind speed	0.07 [0.05, 0.08]	0.01	1.00	1.07 [1.05, 1.08]
Sex	−0.18 [−0.78, 0.41]	0.29	1.00	0.84 [0.46, 1.51]
Night × Distance to road	−0.17 [−0.22, −0.13]	0.02	1.00	0.84 [0.80, 0.88]

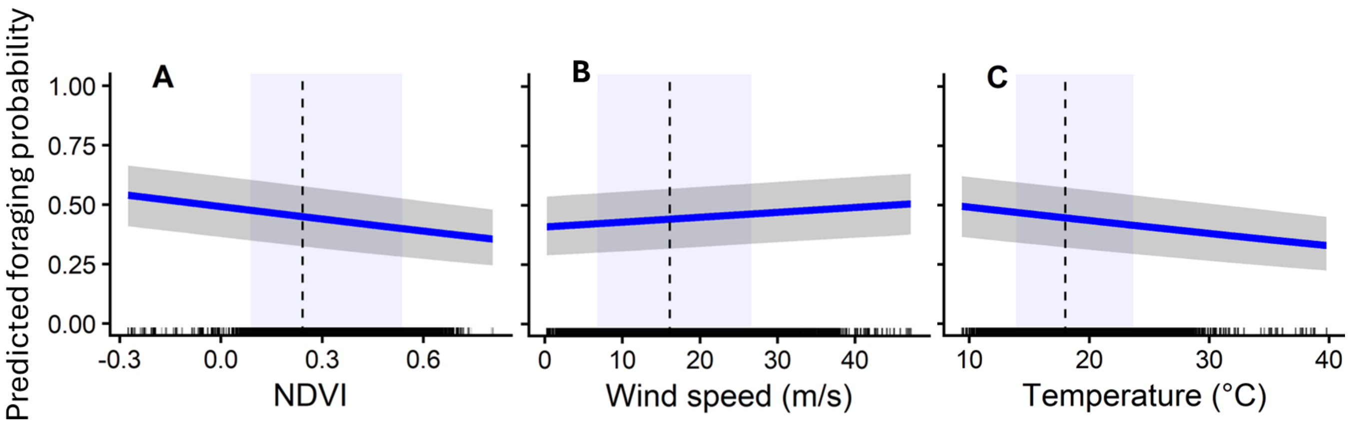

Figure 7. *Posterior relationships between environmental and anthropogenic predictors and the probability of roosting in Marbled duck. Solid blue lines show posterior means and shaded bands 95% Bayesian credible interval. The dashed vertical line shows the median, and the lightly shaded vertical band corresponds to the interquartile range (10th–90th percentiles). Rug marks along the x-axes indicate the distribution of observed covariate values. Panels: (A) vegetation greenness (NDVI); (B) wind speed; (C) air temperature.*

Predicted probabilities revealed a consistent diel pattern across individuals (Figure. 8, B). Foraging probability increased markedly at night for some birds more than others, supporting the species' primarily nocturnal foraging activity. However, the magnitude of the night/day contrast differed among individuals: some (e.g., individuals 0C and 0A) showed an increase in foraging activity at night, whereas others (e.g., 07) exhibited a weaker diel shift.

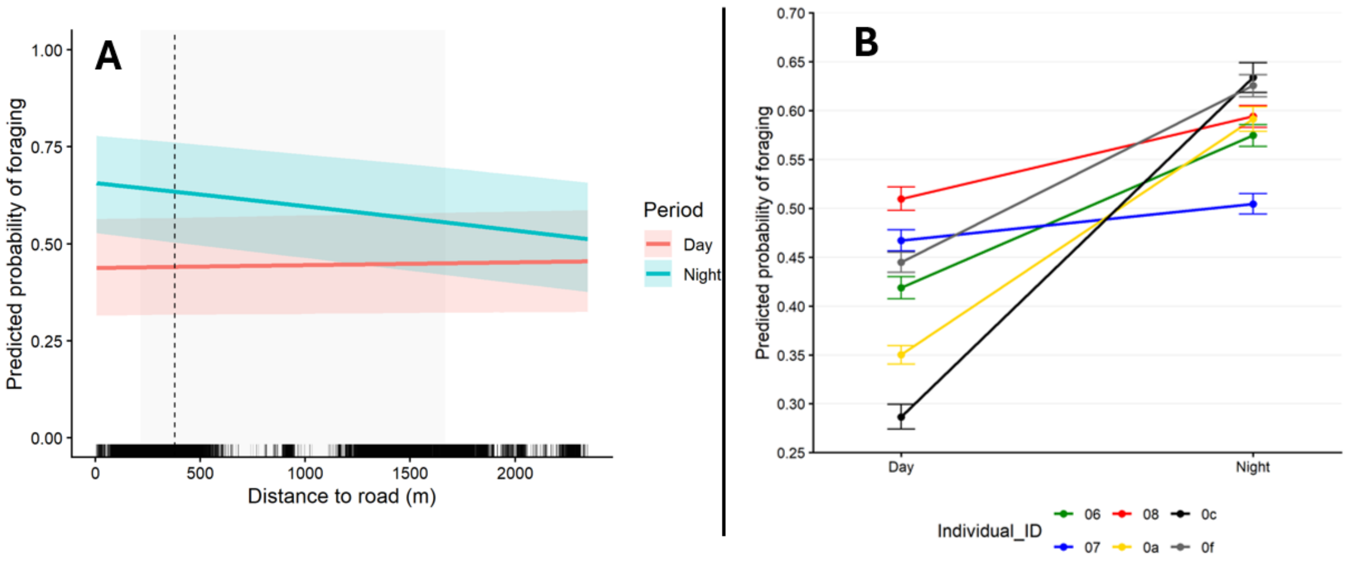

Figure 8. *(A) Predicted probability of foraging as a function of distance to roads for day (red) and night (blue) periods. Shaded bands represent 95 % credible intervals. (B) Predicted probability of foraging during the day and night for each Marbled duck individual. Points show posterior means and error bars represent 95 % credible intervals.*

Discussion

This study aimed to develop a supervised model for classifying behaviours from accelerometer data collected on captive Marbled duck, and applied it to wild individuals in Morocco to understand their spatial ecology. We show that behaviours could be reliably identified from acceleration data using a Random Forest classifier trained on a reduced number of annotated videos, with an overall accuracy of 89%. Application of the trained model to wild Marbled ducks revealed clear diel differences in activity patterns. Mapping of predicted behaviours showed that three individuals relied on spatially distinct roosting and foraging sites, while the other three used multifunctional wetlands where roosting and foraging areas overlapped. To our knowledge, this is the first accelerometer-based behavioural classification for Marbled duck, and more broadly, the first study to explore functional units in a waterbird species in North Africa, a region where information on movement ecology of waterbirds remains scarce.

Both the full and OIF models yielded high performance in predicting Marbled duck behaviour, though their sensitivity varied across behaviours. Analysis of the confusion matrix showed that flying was classified with perfect accuracy, and resting/sleeping and preening also had high F1-scores (0.90 and 0.89, respectively). Misclassifications were primarily observed between feeding and preening, likely due to their overlapping acceleration signatures and similar head and neck movements in these behaviours. Across segmentation strategies, both fixed and flexible approaches produced comparable accuracies, yet the flexible segmentation proved more robust to variable burst lengths and better captured short, dynamic events. The performance of the Random Forest model is consistent with results reported in other accelerometer-based behavioural studies across various taxa. For instance, high overall accuracy has been observed in several avian species, including pacific black ducks (92% accuracy) [50], black cockatoos (86% accuracy for flight and foraging) [51], and woodpigeons [52]. Eurasian spoonbills showed F-measures ranging from 0.73 to 0.94 depending on the behaviour type [38]. Comparable high performance has also been demonstrated in mammals, with F-scores between 0.80 and 0.96 across most behaviours for pangolins [53], arctic foxes [54], dingoes [20], and ibex [55].

The application of the behavioural classifier to wild accelerometer data confirmed expected diel patterns in Marbled duck activity, aligning with both species-specific and broader dabbling duck diel patterns. Notably, resting and sleeping behaviours were dominant during the day, while feeding and other active behaviours remarkably increased around dusk and night, and flying around crepuscular time. This clear diel pattern is consistent with previous research showing that Marbled ducks are primarily active between sunset and sunrise and remain mostly inactive during daylight hours [56]. Similarly, in a study on non-breeding birds in Doñana (Spain), and Sidi boughaba (Morocco) they reported that Marbled duck were mainly nocturnal foragers with almost no diurnal feeding during midwinter, and feeding restricted to crepuscular periods when nights were short [57]. Similar patterns have been documented at Garaet Timerganine in Algeria [58], where Marbled duck showed time activity budgets consistent with predominantly nocturnal foraging, with diurnal feeding increasing only when food resources were scarce. By contrast, in some other Algerian wetlands (Guerbes-Sahhadja), unusually high diurnal feeding (34.9%), suggest that local resource availability and predation pressure can modulate diel rhythms [59].

Marbled duck diel rhythm is similar to the one found in other duck species. Ferruginous ducks devote most of the day to resting (30-40%) and feed predominantly at night [60], while wintering ducks show diurnal budgets dominated by resting (40%) and only modest daytime feeding [61]. These similarities indicate that a daytime resting/nighttime foraging strategy is a widespread energy-saving pattern among small and medium-sized ducks, often interpreted as a strategy to reduce predation risk and human disturbance [1,62,63]. Flight activity occurred primarily during crepuscular periods consistent with commuting movements between roosting and feeding areas. Marbled ducks are known to perform short daytime flights in response to predator disturbance towards open water or vegetated refuges [57,59,64]. However, these disturbance-driven flights were rare and too brief to be captured reliably in our predicted activity patterns. Instead, the main flight signal detected by accelerometers corresponded to regular, crepuscular commuting flights, which were repeatedly recorded over time and showed consistent temporal patterns across individuals. Commuting flights at dawn and dusk are a well-established feature of duck movement ecology and have been documented across Anatidae [62,63,65].

Our spatial exploratory analysis revealed that Marbled ducks do not rely on a single spatial strategy. Instead, individuals differed in whether they structured their movements around distinct roosting and foraging sites or used multifunctional wetlands where both behaviours occurred in the same location. Three of six birds (individuals 0F, 0A, and 0C) showed a clear separation between daytime resting zones and night time foraging areas, with predictable crepuscular flights linking these sites. This pattern corresponds to the functional unit framework originally described for dabling ducks [1,21,24,66,67]. In contrast, the three other individuals (06, 07 and 08) showed little spatial segregation between behaviours. In these cases, roosting and foraging occurred within the same wetland units, suggesting that some sites simultaneously satisfied energetic and safety requirements. This flexibility was also documented among dabbling ducks [67]. One explanation is that remaining in day roost sites at night may be energetically or ecologically advantageous when the site provides high-quality foraging habitats; consequently, reducing energetic costs by avoiding long flights, and lower predation or disturbance risks [67]. Conversely, individuals that undertake regular commuting flights may be those experiencing lower foraging efficiency, greater competition, or suboptimal food conditions near the roost [67]. Competitive interactions and dominance hierarchies can exclude subdominant ducks from high-quality areas at night, forcing them to forage in riskier peripheral habitats [68]. Such a mechanism has been described in oystercatchers: some individuals remain on mussel beds around the clock, while others shift to cultivated fields at high tide; habitats that are riskier but sometimes necessary for birds with lower feeding efficiency or inferior competitive status [69,70]. These examples underline how individual differences in efficiency, dominance, or access to resources can generate divergent spatial strategies within the same population. Unfortunately, our study did not allow for assessing characteristics explaining the two strategies observed. More data may test for social rank hypothesis considering a strategy varying among sexes, years (with lower competition when resources are more abundant), or age.

We found that functional units were affected by a combination of environmental conditions and anthropogenic context. The probability of foraging decreased as NDVI increased, consistent with Marbled duck feeding strategy where birds fly from daytime roosts to exposed shallow feeding sites at dusk [39]. This suggests that the Marbled duck exhibited a tendency to forage in open areas with low vegetation density. In contrast, roosting probability increased with NDVI, indicating an association with vegetated sites that likely provides concealment from predators and thermal insulation [67,71]. The negative effect of air temperature on foraging probability is consistent with general patterns of waterfowl energetics. Specifically, feeding effort increases to meet elevated metabolic demands during cooler conditions, whereas foraging activity tends to decline during warmer periods when thermoregulatory costs are reduced [63,72]. Wind speed showed a small positive effect on foraging probability, contrasting with previous studies that reported negative effects of wind speed due to the altered water surface dynamics, limiting access to food resources [73]. One explanation is that moderate winds may concentrate food resources without altering water surface dynamics. By contrast, the effect of moon illumination on nocturnal activity appears to be weak. While some studies report increased activity under brighter lunar conditions, others have found inconsistent or negligible effects across species and habitats [21,74]. Interestingly, the interaction between diel period and distance to roads revealed that, at night, Marbled duck were more likely to forage closer to roads. While roads represent a disturbance source during the day, reduced human activity at night may relax this constraint. Moreover, in highly modified landscapes, road-adjacent wetlands may receive nutrient inputs through runoff, potentially increasing local productivity and prey availability [75]. Finally, individual variation in the strength of nocturnal foraging suggests that different strategies coexist within the population, likely reflecting differences in energetic needs, habitat quality, or functional unit organization.

The behavioural flexibility of the Marbled duck, expressed through two distinct space-use strategies, highlights the importance of conserving interconnected wetland networks rather than isolated sites [67,76]. Effective management should ensure the availability of secure roosting and nocturnal foraging habitats, that are often overlooked by traditional monitoring approaches, and maintain safe movement corridors to commute between them. At the same time, multifunctional wetlands that support both roosting and foraging represent particularly high-value habitats in arid landscapes and deserve strong protection. Our results also indicate that anthropogenic features such as roads may have context-dependent effects, with some road-adjacent areas being used for nocturnal foraging in the absence of disturbance [77]. This emphasises the need for time-specific management, including limiting nocturnal disturbance and preserving key buffer zones around wetlands [78].

While our model successfully transferred from annotated videos to wild individuals, this study was based on a limited number of birds in the training dataset. Despite this, behavioural sequences were coherent and ecologically plausible, confirming the robustness of the approach when feature extraction and scaling are carefully standardised. Seasonal and year variation could not be fully explored and deserves attention across both breeding and wintering periods. Future studies should expand sample size, integrate dietary and habitat-quality assessments, and test how management actions (e.g. disturbance reduction, water-level control) influence functional-unit use. Testing the drivers of functional units could be extended to other bird species allowing further comparative analyses to deepen our understanding and importance of functional units within Aves class. In addition, it will strengthen evidence-based conservation planning at broader spatial scales.

Conclusion

The integration of accelerometer and GPS data represents a major advance for studying cryptic species such as the Marbled duck. Unlike traditional scan sampling, this approach enables continuous monitoring, capturing short behavioural events and nocturnal activity that remain otherwise inaccessible. Our study provides a proof of concept that functional units in Marbled duck can be identified through behavioural information derived from accelerometers. By linking classified behaviours to spatial data, we showed that Marbled duck can adopt two distinct strategies within a single landscape: (1) a functional-unit strategy, characterised by spatial separation between roosting and foraging areas connected by crepuscular commuting, and (2) an integrated-site strategy, in which both behaviours occur within the same wetland. More broadly, this framework offers a scalable tool for identifying critical functional areas for threatened waterfowl and can directly inform spatial planning and wetland restoration efforts in North Africa and beyond.

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Author Contributions

H.B., A.B., J.C. and R.M. conceived the ideas and designed the methodology. H.B. led the writing of the manuscript. H.B. conducted the analyses. H.B., R.M., A.P., contributed to data acquisition. All authors revised the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request

Ethics approval and consent to participate

All capture and handling procedures were conducted in accordance with national regulations and authorized by the Agence Nationale des Eaux et Forêts (Morocco) under the following permits: N°34/2022 DLCDPN/DPRN/CFF (2023), N°01/2024 DLCDPN/DPRN/CFF (2024), and N°50/24 DLCDPN/DPRN/CFF (2025).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Additional files

Analysis of feature importance revealed that variables related to signal magnitude and dynamic body acceleration were the most influential for behavioural classification (Figure S1). In particular, mean, minimum, maximum, and range of the acceleration magnitude, together with dynamic body acceleration metrics (ODBA, VeDBA), consistently ranked highest across both importance measures.

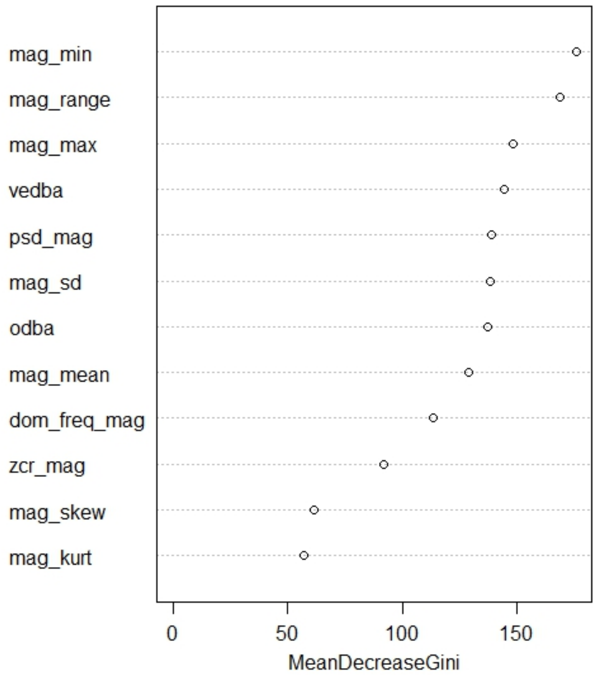

Figure S1. *Mean decrease GINI of the predictor variables included in the Random Forest classifier ordered by importance to the best model.*

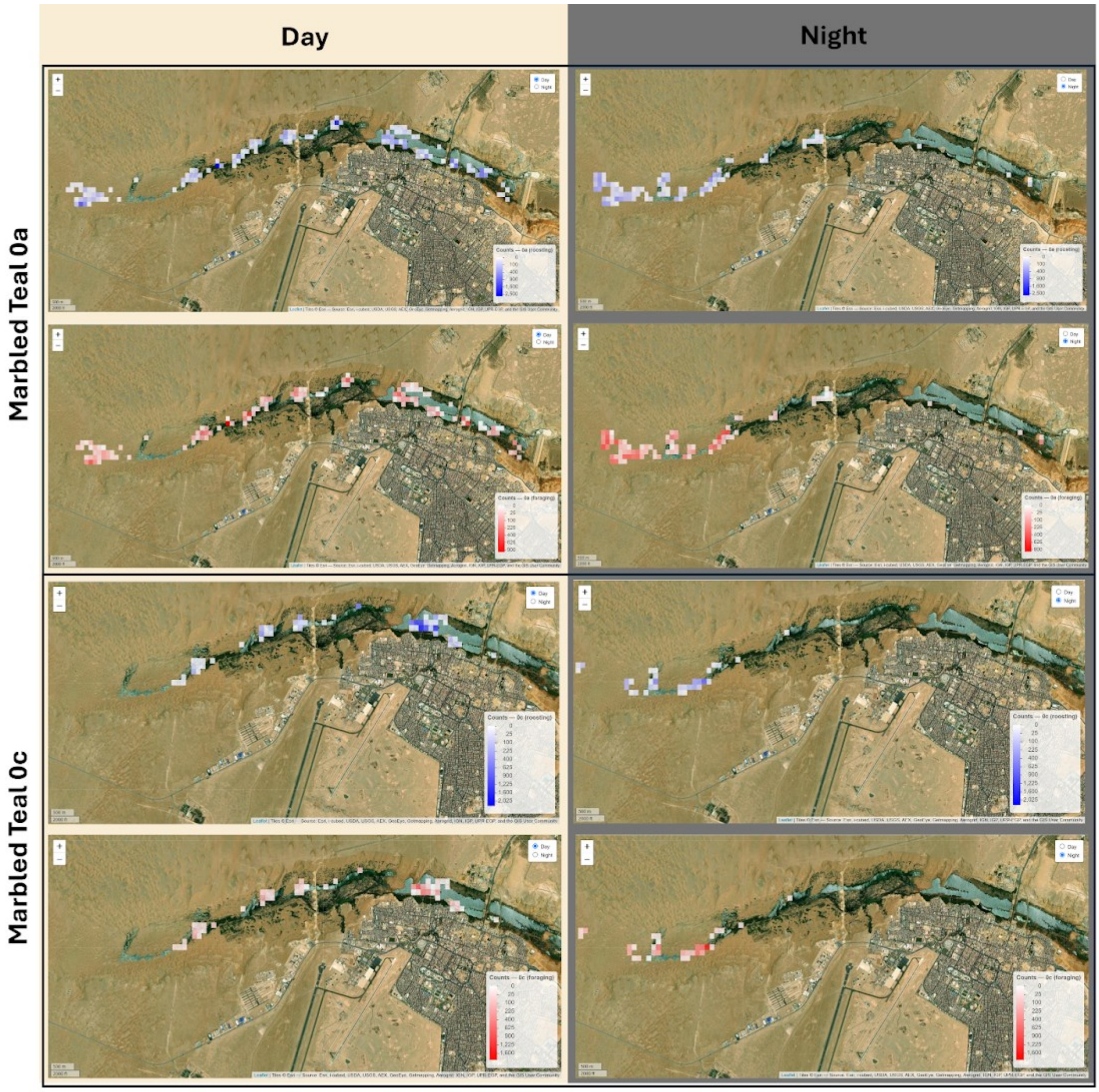

Figure S2. *Behavioural intensity maps showing the number of roosting (blue scale) and foraging (red scale) observations per 100 × 100 m pixel during day and night in Oued Assaquia Al Hamra wetland. Each row corresponds to a tracked Marbled duck individual (ID shown on the left). Daytime maps are displayed on the left and nighttime maps on the right.*

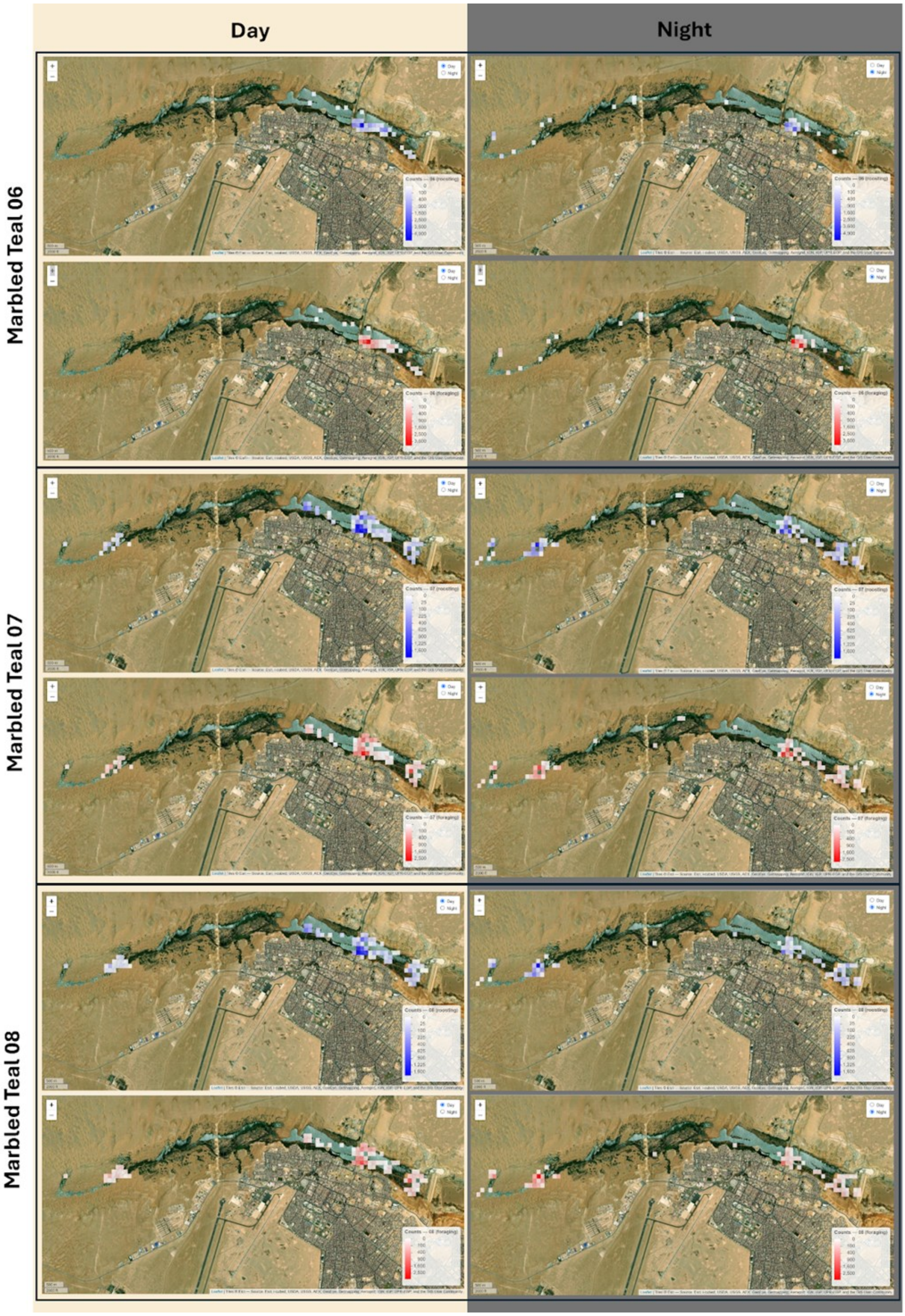

Figure S2 (continuation). *Behavioural intensity maps showing the number of roosting (blue scale) and foraging (red scale) observations per 100 × 100 m pixel during day and night in Oued Assaquia Al Hamra wetland. Each row corresponds to a tracked Marbled duck individual (ID shown on the left). Daytime maps are displayed on the left and nighttime maps on the right.*

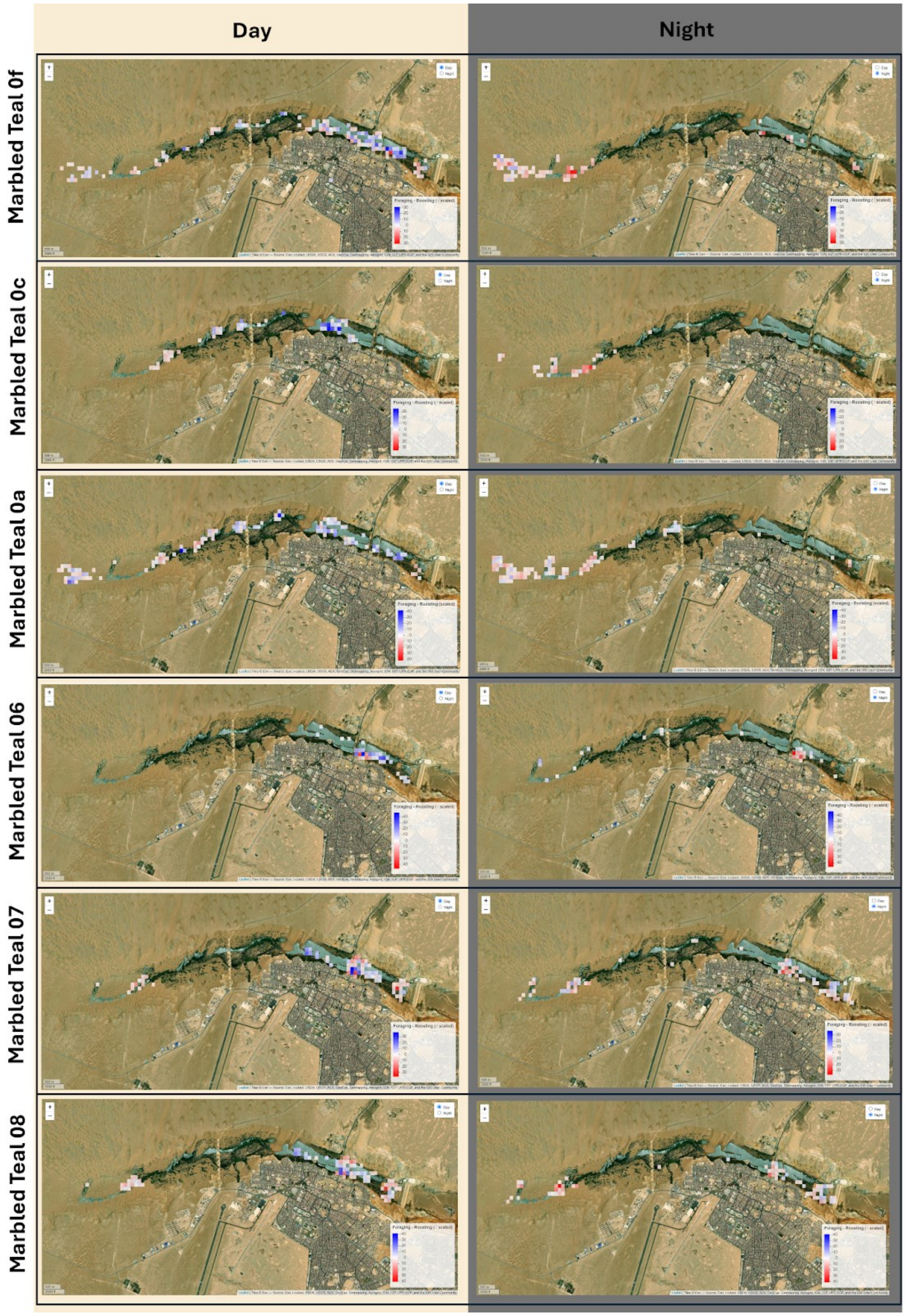

Figure S3. *(B) Behavioural balance map showing the difference between foraging and roosting observations per pixel (red = foraging dominated, blue = roosting dominated) during day and night in Oued Assaquia Al Hamra wetland. Each row corresponds to a tracked Marbled duck individual (ID shown on the left). Daytime maps are displayed on the left and nighttime maps on the right.*

Table S1. *Total duration (seconds) and proportion of synchronised annotated data used for training the behavioural classification model. Swimming and walking were pooled under the "active" category.*

Behaviour	Total duration (s)	% of annotated time
resting/sleeping	901.92	40.2%
active	648.25	28.9%
feeding	324.58	14.5%
preening	240.67	10.7%
flying	128.33	5.7%

Table S2. *Comparison of classification performance across behaviours using fixed segmentation with different window lengths (0.4–1.2 s) and flexible segmentation with varying ARL thresholds*

Segmentation approach	Segments length and ARL values	Active	Feeding	Flying	Preening	Resting/sleeping
		Sensitivity				
Fixed	0.4s	0.79	0.89	1.00	0.94	0.87
	0.8s	0.70	0.45	1.00	0.48	0.92
	1.2s	0.78	0.32	1.00	0.46	0.95
Flexible	ARL_0 100	0.86	0.88	1.00	0.86	0.89
	ARL_0 500	0.80	0.90	1.00	0.94	0.83
	ARL_0 5000	0.84	0.90	1.00	0.90	0.83
		Precision				
Fixed	0.4s	0.84	0.83	1.00	0.85	0.93
	0.8s	0.63	0.58	0.98	0.5	0.92
	1.2s	0.64	0.52	1.00	0.58	0.91
Flexible	ARL_0 100	0.83	0.87	1.00	0.85	0.94
	ARL_0 500	0.9	0.85	1.00	0.83	0.96
	ARL_0 5000	0.88	0.84	0.99	0.84	0.93
		F-measure				
Fixed	0.4s	0.82	0.86	1.00	0.89	0.90
	0.8s	0.66	0.51	0.99	0.49	0.92
	1.2s	0.71	0.39	1.00	0.51	0.93
Flexible	ARL_0 100	0.84	0.87	1.00	0.85	0.91
	ARL_0 500	0.85	0.87	1.00	0.87	0.89
	ARL_0 5000	0.86	0.87	1.00	0.87	0.88

Table S3. *Pairwise Pearson correlation coefficients among continuous predictors included in the model. All predictors were standardized (z-transformed).*

	NDVI_z	DistRoad_z	MoonFrac_z	temp_z	wind_z
NDVI_z	1.00				
DistRoad_z	-0.05	1.00			
MoonFrac_z	-0.08	0.02	1.00		
temp_z	0.16	-0.26	-0.01	1.00	
wind_z	0.05	-0.12	-0.08	0.34	1.00

Table S4. *Variance inflation factors (VIF) for fixed effects included in the model.*

Term	VIF
time_period	2.05
NDVI	2.31
Moon Fraction	2.16
temperature	2.13
wind speed	1.96
Sex	1.22
time_period × NDVI	2.33
time_period × Moon Fraction	2.19
time_period × temperature	2.31
time_period × wind speed	1.98
Distance to Road	6.92
time_period × Distance to Road	5.74

Appendix S1. Mathematical formulation of the generalized linear mixed model (GLMM) used to analyse the probability of roosting versus foraging, including fixed effects, interaction terms, and random intercepts and slopes for individual identity.

$$\text{behaviour}_{ij} \sim \text{Bernoulli}(\pi_{ij})$$

$$\text{logit}(\pi_{ij}) = \beta_0 + \beta_1\,\text{TimePeriod}_{ij} + \beta_2\,\text{NDVI}_{ij} + \beta_3\,\text{DistRoad}_{ij}$$

$$+\beta_4\,\text{MoonFrac}_{ij} + \beta_5\,\text{Temp}_{ij} + \beta_6\,\text{Wind}_{ij} + \beta_7\,\text{Sex}_i$$

$$+\beta_8\,(\text{TimePeriod}_{ij} \times \text{DistRoad}_{ij}) + u_{0i} + u_{1i}\,\text{TimePeriod}_{ij}$$

$$\begin{pmatrix} u_{0i} \\ u_{1i} \end{pmatrix} \sim \mathcal{N}\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \boldsymbol{\Sigma} = \begin{pmatrix} \sigma^2_{u_0} & \sigma_{u_0 u_1} \\ \sigma_{u_0 u_1} & \sigma^2_{u_1} \end{pmatrix}\right)$$

where:

i = individual, j = observation, u_{0i} = random intercept, u_{1i} = random slope of time period for individual i, and $\boldsymbol{\Sigma}$ is the variance–covariance matrix of the random effects.

Chapter 4: From natural wetlands to wetlands fed by wastewater: habitat use of the Marbled Duck in a semi-arid context

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Abstract

Mediterranean wetlands are increasingly shaped by hydrological modification and water scarcity, yet the contribution of anthropogenic wetlands to waterbird spatial ecology remains poorly quantified. In this study, we investigate habitat use by the Marbled Duck *Marmaronetta angustirostris* across natural, artificial, and accidental wetlands in Morocco using GPS telemetry data. We analysed high-resolution tracking data from wild individuals to quantify patterns of wetland use across seasons and to identify the main drivers structuring habitat use. Results show that Marbled Ducks exploit a large number of wetlands, strongly dominated by anthropogenic systems, particularly effluent-fed wetlands, wastewater treatment plants, and dams. In contrast, natural wetlands represented a smaller proportion of use. Wetland type emerged as the primary determinant of habitat use, with additional modulation by seasonal drought conditions, highlighting the influence of water availability on habitat use. These findings indicate that anthropogenic wetlands constitute an important habitat in the spatial ecology of the species and may partially buffer the effects of increasing water scarcity in Mediterranean landscapes. However, despite their growing importance, anthropogenic wetlands cannot be considered as a functional substitute for natural wetlands. Their use raises unresolved ecological questions, particularly regarding potential risks associated with pollutant exposure, pathogen presence, and disease transmission within wetlands. This study highlights the potential of integrating anthropogenic wetlands into conservation planning, while maintaining the protection and restoration of natural wetlands as a central priority.

Keywords: Marbled Duck; GPS telemetry; habitat use; anthropogenic wetlands; water scarcity; Mediterranean wetlands; movement ecology

Introduction

Global biodiversity is undergoing an unprecedented decline, driven by the cumulative effects of anthropogenic pressures and climate change (IPBES, 2019). Over recent decades, these pressures have intensified alongside human population growth and the expansion of industrial and agricultural activities, leading to the degradation of ecosystem structure, function, and resilience (Hersperger & Bürgi, 2009; Isbell et al., 2017; Newbold et al., 2018). Habitat loss, degradation, and fragmentation are the primary drivers of this crisis, with wetlands, in particular among the most affected biomes. Although they occupy only a small fraction of the Earth's surface, wetlands support a disproportionate share of global biodiversity and provide essential ecosystem services, including water regulation, nutrient cycling, and support for human livelihoods (Strayer & Dudgeon, 2010; Gardner & Finlayson, 2018). Nevertheless, extensive drainage, conversion, and hydrological alteration over the past century have led to widespread loss of wetland areas worldwide, and many remaining wetlands continue to experience intense anthropogenic pressure (Davidson, 2014; IPBES, 2019). These trends are particularly pronounced in the Mediterranean basin, a region of high conservation importance where wetlands occupy a limited area but support a high diversity of species relative to their spatial extent (Mittermeier et al., 2004; CEPF, 2024). Since the 1970s, the extent of natural Mediterranean wetlands has declined by approximately 50%. In contrast, artificial wetlands have expanded through the construction of dams, reservoirs, and agricultural ponds, contributing to increasing landscape artificialisation(MWO3, 2025). In North Africa, particularly in Morocco, artificial wetlands now represent a substantial proportion of total wetland area (approaching 38%), increasingly structuring the mosaic of waterbodies used by waterbirds and other taxa. This shift raises critical questions about their ecological value amid growing anthropogenic pressure and water scarcity (MWO3, 2025).

Another particular type of wetland, whose existence is often overlooked or poorly documented, is accidental wetlands. These wetlands are defined as unintentionally created waterbodies that form as a byproduct of anthropogenic activities such as effluent discharges from wastewater treatment plants, urban drainage, irrigation infrastructure, and mining operations (Palta, Grimm, & Groffman, 2017). Despite their unplanned origin, accidental wetlands can develop and maintain ecological functions comparable to those of natural wetlands, including habitat provision for species, nutrient cycling, water filtration, and social benefits for people (Palta, Grimm, & Groffman, 2017). Accidental wetlands, particularly those associated with wastewater effluent, may sustain waterbird populations in arid and semi-arid regions, where natural wetlands are highly variable or seasonally absent, but to our knowledge, no study has been conducted specifically on the importance of these habitats. Indeed, existing wetland classification frameworks commonly group all human-made wetlands under the broad category of "artificial" or "human-made" wetlands (Mahdavi *et al.*, 2018), thereby obscuring key ecological differences between intentional and unintentional anthropogenic wetlands (Mahdavi *et al.*, 2018). Recognizing these systems as distinct from engineered wetlands can provide a more accurate understanding of their importance for waterbirds and help assess their conservation value. Accidental wetlands are typically not recognized in wetland legislation such as the Ramsar Convention, and consequently receive little or no explicit protection status. By contrast, other artificial wetlands like wastewater treatment plants have been recognized under the Ramsar Convention and incorporated into protected-area networks, reflecting their importance for waterbirds and other biodiversity (Kumar *et al.*, 2023; Loyn *et al.*, 2023).

The development of animal-borne telemetry (bio-logging) has revolutionized the study of animal movement and behaviour by enabling the remote tracking of wildlife (Cooke et al., 2004; Kooyman, 2004; Cooke, 2008; Bograd et al., 2010). Advances in GPS and satellite telemetry have improved the precision, frequency, and duration of positional data, allowing the quantification of movement paths, home-range dynamics, dispersal, connectivity and habitat selection at fine spatial and temporal scales (Ponchon et al., 2013; Kays et al., 2015; Silvy, 2020). When combined with fine-scale satellite-derived habitat and landscape data, these technologies enable the characterization of dynamic space-use patterns and the identification of critical habitats and connectivity corridors throughout the annual cycle (Neumann et al. 2015; Batbayar et al. 2021). Such insights are particularly valuable for threatened species, for which movement studies can reveal key processes underlying population declines and inform extinction risk assessments and conservation planning (Runge et al. 2015; Scheele et al. 2018).

Combining positions of individuals from tracking data with habitat inference from remote sensing is especially relevant for cryptic and highly mobile species, such as the Marbled Duck, *Marmaronetta angustirostris*, a near-threatened nomadic species known for its spatio-temporal variability in habitat use (Salvador, Amat, & Green, 2023). The species is strongly associated with shallow ephemeral wetlands that are highly sensitive to water extraction, land-use change, and climate-driven drying (Salvador, Amat, & Green, 2023). Its movements and habitat use patterns thus provide a valuable framework for assessing the ecological consequences of wetland transformation and the role of accidental wetlands. The species is known to use artificial wetlands in Morocco and Spain, such as reservoirs and fish farms (Green, 2000*a*;

Green *et al.*, 2002), and has also been recorded using wastewater treatment plants (Ouassou *et al.*, 2021; Algadry *et al.*, 2022). In Morocco, a substantial proportion of wetlands where Marbled Duck were recorded during the International Waterbird Census between 2019 and 2023 were fed by sewage water, highlighting the growing importance of sewage-origin waters in its habitat use (Fig 1, Dakki et al., 2025). The use of these habitats where water and habitat quality are unknown raises key ecological and conservation questions, particularly regarding the extent to which these wetlands contribute to critical functions in the species' life cycle, as well as the potential risks associated with their use, including exposure to pollutants and pathogens (Anza *et al.*, 2014; Freitas *et al.*, 2024).

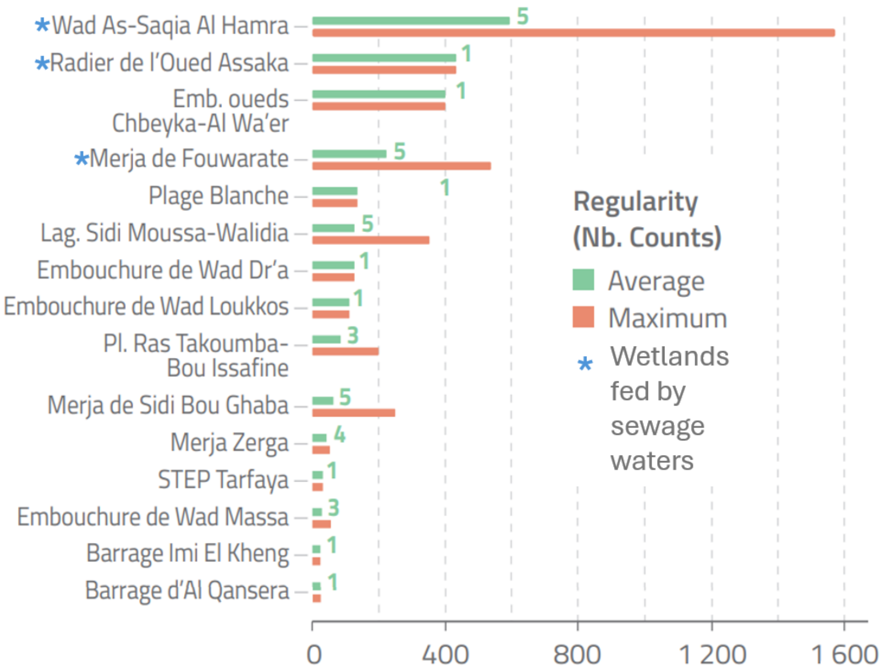

Figure 1. *Average number of Marbled duck counted per site during the International Waterbird Census in Morocco from 2019 to 2023 (figure adapted from Dakki et al., 2025). Asterisks indicate wetlands identified as sewage-fed based on field observations and wetland classification conducted in the present study. Green numbers in front of site bars indicate the number of visits during the 2019-2023 period. Orange bars represent the maximum recorded count per year during that period.*

Despite their importance, there remains limited quantitative evidence on how Marbled Ducks use natural, artificial, and accidental wetlands in North Africa. In particular, how anthropogenic waterbodies may compensate for the loss of natural wetlands under increasing water scarcity remains poorly documented.

In this study, we integrated GPS telemetry data from both Moroccan and Spanish individuals to evaluate the ecological role of these diverse wetland types. Specifically, we aimed at (1) comparing habitat use in North Africa across natural, artificial, and accidental wetlands; (2) identify environmental and climatic drivers underlying their use; and (3) assess the contribution of sewage-fed and other anthropogenic wetlands to Marbled Duck conservation under scenarios of increasing water scarcity, including their associated risks from pathogens, viruses and contaminants. We expect Marbled Ducks to have a greater relative use of artificial and accidental wetlands than natural wetlands, as these habitats provide relatively stable water and sometimes high productivity, especially wastewater treatment plants, effluent-fed wetlands, and dams, with increasing dependence on these wetlands during dry conditions. This study thus aims to clarify the functional role of anthropogenic wetlands in the spatial ecology of the Marbled duck and inform future conservation strategies.

Materials and Methods

Study system

The Marbled Duck is a medium-sized, slender waterfowl with a fragmented distribution across the western and central Palaearctic (Salvador, Amat, & Green, 2023). In the western Mediterranean, the population is distributed across North Africa and southern Spain, occupying both natural and artificial wetlands, and is typically associated with shallow wetlands, with a preference for brackish habitats). In Spain, the species is concentrated in two main regions: the wetlands of the southern province of Alicante and Doñana National Park and its surroundings (Pacheco-Guardiola *et al.*, 2025). In North Africa, the species ranges from southern Morocco in Saqia el Hamra, through Algeria and Tunisia to western Libya, where it was recorded breeding for the last time in 2012 at the Mallaha wetland (Etayeb *et al.*, 2014; Salvador, Amat, & Green, 2023*b*).

Tagging and tracking data

Between 2018 and 2025, individuals were captured and equipped with GPS-accelerometer tracking devices in Morocco and Spain. In Morocco, 11 adult wild individuals were captured between 2023 and 2025 at two wintering sites: the Sidi Moussa-Oualidia wetland complex and the Saqia El Hamra wetland (Fig 2). Birds were captured by trained ringers using whoosh nets and manually operated drop nets, both non-lethal techniques suitable for waterfowl. In Spain, 144 individuals were tagged between 2018 and November 2023 across two study areas (Fig 2) in southwestern (n = 51) and southeastern Spain (n = 93). The Spanish birds were captured using mist nets or baited cage traps fitted with modified funnels to prevent escapes (for more details, see Pacheco-Guardiola *et al.*, 2025). All captured birds were weighed, ringed with a standard metal ring, and, for visual identification, a PVC alphanumeric ring. Sex was determined in the field based on external morphology, including body size, head shape, and bill coloration (Green, 2000*b*). All capture, handling, and tagging procedures complied with national and international ethical standards and were conducted under permits issued by the relevant authorities in Spain and by the Agence Nationale des Eaux et Forêts in Morocco.

Birds in both countries were equipped with solar-powered GPS/GSM transmitters, primarily manufactured by Ornitela (n=26; Lithuania; https://www.ornitela.com/), with a smaller number (n=3) of Ecotone (Poland; https://ecotonetelemetry.com/) devices used in Spain. Transmitters were fitted using backpack-style harnesses made of Teflon ribbon (4 mm), a widely used attachment method shown to minimize impacts on survival and behaviour in waterbirds (Thaxter et al., 2014). The combined weight of the transmitter, harness, and rings was 11 g, corresponding to < 3% of body mass for all individuals with mean body mass ≈ 484g (min: 450g; max: 520g), well below accepted thresholds of for migratory birds (Phillips, Xavier, & Croxall, 2003). Tracking devices were remotely programmable via GSM/GPRS networks and configured to record GPS locations at intervals ranging from 5 to 120 minutes, depending on battery charge.

Data cleaning and pre-processing

GPS data were filtered and standardized before analysis. For Spanish birds, only those that performed trans-Mediterranean movements were kept for this study (n=18) and only fixes recorded in North Africa were included in the analysis. First, fixes with poor positional accuracy (HDOP > 5) were removed (Campion *et al.*, 2020). Flight locations were also excluded by retaining only fixes with ground speeds below 5 m/s. For habitat use analyses, the remaining locations were then resampled at 4-hours intervals, and individual tracks were constructed using “adehabitatLT” package in R version 0.3.29 (Calenge, 2011) to calculate movement metrics (e.g. time between fixes and distances). Fixes separated by temporal gaps exceeding 12 hours were discarded. Then fixes were counted per bird and season, defined as breeding (April to August) and wintering (September to March). Finally, we only retained seasons by bird-year-season combinations with at least 60 fixes. Individuals that did not meet this criterion were excluded (n=4; all from Spain).

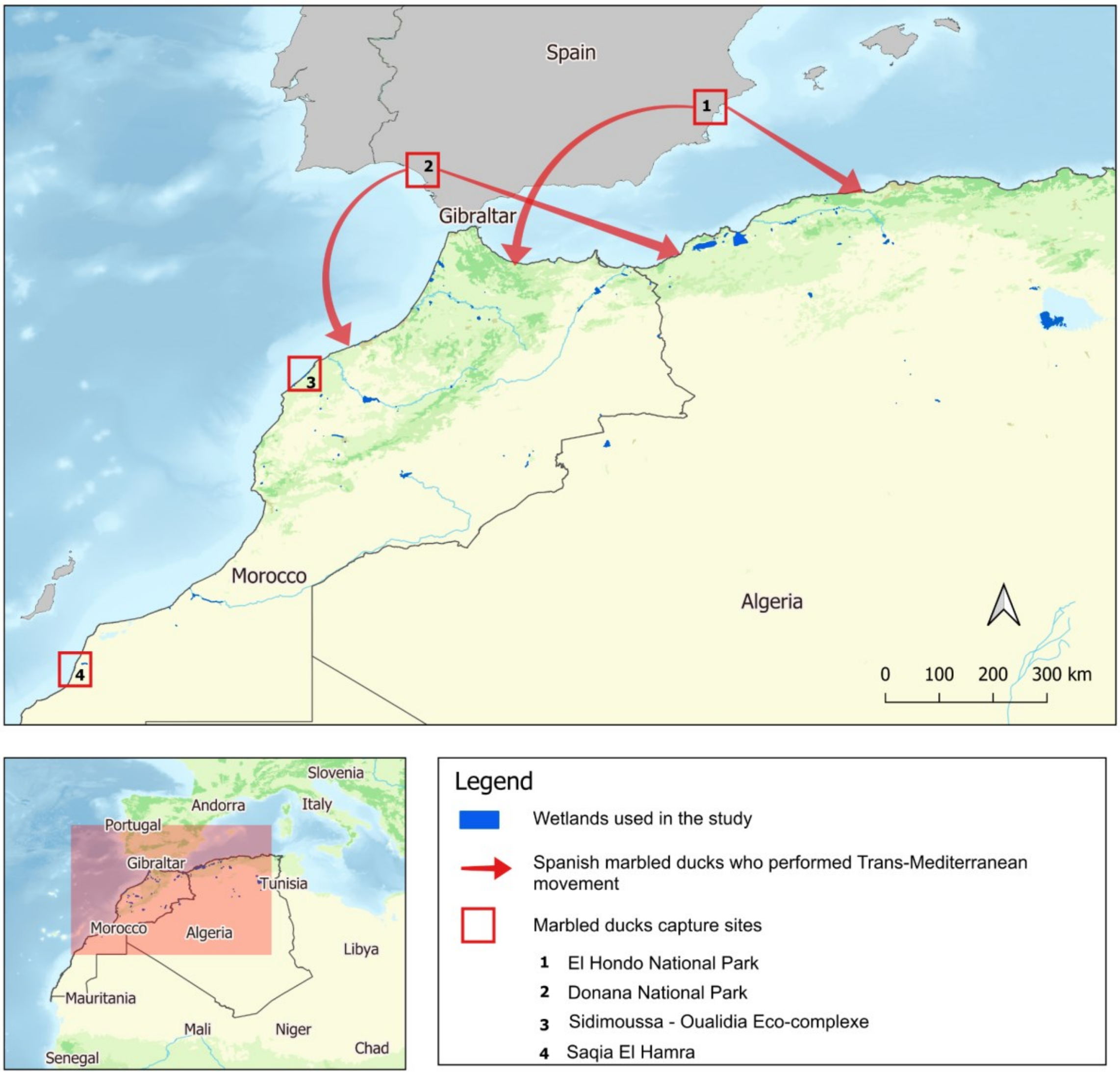

Figure 2. *Study area and capture sites in Morocco and Spain.*

Wetland inventory and classification

Wetlands were delineated through manual digitization in QGIS (version 3.40.11, QGIS Development Team 2024) based on visual interpretation of high-resolution satellite imagery (Google Earth, https://earth.google.com/) and GPS fixes from tagged individuals. We digitized all wetlands intersected by GPS fixes from our tracking data. Each polygon represented a unique wetland spatial unit and was assigned a unique identifier (wetland ID). These polygons constituted the spatial framework used in all subsequent habitat-use analyses. For each wetland, we extracted attributes describing environmental conditions, wetland characteristics (including origin and habitat type based on visual interpretation of satellite imagery), Ramsar designation status, and biological factors potentially influencing wetland use patterns

First, wetlands were classified into three wetland classes based on their origin: i) Natural wetlands, sustained primarily by climatic and hydrological processes, ii) artificial wetlands, deliberately created or managed for specific human uses and iii) accidental wetlands, which emerge unintentionally as a by-product of human activities such as wastewater discharge, infrastructure leakage, or overflow from engineered structures (Palta, Grimm, & Groffman, 2017).

Second, each wetland was assigned a more detailed wetland type describing its dominant habitat characteristics. Natural wetlands were classified as: i) rivers and watercourses; ii) estuarine and coastal wetlands (including lagoons) when located less than 10 km from the coastline; and iii) inland lakes, oases, freshwater marshes, and temporary ponds, when located 10 km or more from the coastline. Artificial wetland types included i) industrial activity ponds, ii) saltpans, iii) dams/reservoirs, iv) irrigation ponds or flooded agricultural fields, and v) wastewater treatment plants. Accidental wetland types included i) effluent-discharge-fed wetlands and ii) overflow/leakage-generated wetlands. Finally, wetlands overlapping a Ramsar site were identified as "Ramsar-designated", indicating internationally recognised importance for waterbirds (Ramsar Sites Information Service, https://rsis.ramsar.org/).

Habitat-use modelling framework

Habitat use was quantified as the number of GPS fixes recorded within each wetland for each individual-season combination. For individual i, wetland w, and season s, the response variable corresponded to the number of fixes recorded in wetland w during season s. To account for variable tracking duration and fix availability among individuals and seasons, we included the log-transformed total number of GPS fixes per individual-season combination as an offset term (Spelt *et al.*, 2019). This approach models relative wetland use while controlling for differential sampling effort.

Wetland use was analysed using generalized linear mixed models (GLMMs) with negative binomial distribution and a log link function. Individual ID and wetland ID were included as random effects. The general structure of the model was:

$$\boldsymbol{log}(\boldsymbol{\mu}_{iws}) = log(total\_fixes_{is}) + X_{ws}\beta + U_{i} + V_{w}$$

Where:

$\boldsymbol{\mu}_{iws}$ is the number of GPS fixes for individual i in wetland w during season s

$log(total\_fixes_{is})$ is the offset term accounting for sampling effort

X_{ws} is the design matrix of fixed effects, including main effects of environmental, spatial, and categorical predictors, as well as their interactions (e.g. Season x SPI, etc)

β is the vector of fixed-effect coefficients

$U_i \sim Normal(0, \sigma^2\_individual)$ is the random intercept for individual i

$V_w \sim Normal(0, \sigma^2\_wetland)$ is the random intercept for wetland w

Under this formulation, model coefficients describe how predictors affect the expected relative share of fixes allocated to a wetland, given individual tracking effort. Coefficients are reported on the log scale as estimates, where positive values indicate increased relative use and negative values indicate decreased relative use relative to the reference category. For ease of interpretation, coefficients are also expressed as incidence rate ratios (IRR), obtained by exponentiating the estimate. An IRR greater than 1 indicates higher relative use compared to the reference, while an IRR less than 1 indicates lower relative use. For example, an IRR of 2 means a wetland type receives twice the proportional allocation of fixes compared to the reference category, all else being equal.

We included a set of predictors describing environmental conditions, wetland characteristics, and biological factors potentially influencing wetland use patterns (Table S1). In addition to main effects, we tested a set of biologically meaningful interaction terms to evaluate whether climatic, habitat, management, and population effects varied across ecological contexts. A detailed description of all interaction structures evaluated is provided in Table S2.

Environmental predictors characterized drought and water conditions. Drought conditions were quantified using the Standardized Precipitation Index (SPI), which characterizes precipitation anomalies relative to long-term climatic norms (McKee, Doesken, & Kleist, 1993). SPI values are standardized around zero, with positive values indicating wetter-than-average conditions and negative values indicating drier-than-average conditions. Because SPI was extracted at each wetland's centroid location and averaged over each season, each wetland received a unique SPI value per season reflecting local precipitation anomalies relative to its own long-term average. Monthly precipitation data were obtained from the Climate Hazards Group Infrared Precipitation with Stations (CHIRPS, v2.0, Funk *et al.*, 2015) dataset from (https://data.chc.ucsb.edu/products/CHIRPS-2.0/) at 5 km resolution for 1995-2025 and extracted at wetland centroid locations. SPI was computed by fitting a gamma distribution to accumulated monthly precipitation time series and transforming cumulative probabilities to a standard normal variable (Guttman, 2007). SPI values were then averaged over biologically relevant seasons (see definition above). Water availability was quantified using the Normalized Difference Water Index (NDWI, McFeeters, 1996), derived from Sentinel-2 Surface Reflectance (Level-2A) satellite imagery accessed via Google Earth Engine (GEE) cloud platform (Gorelick *et al.*, 2017). NDWI was calculated as:

$$NDWI = \frac{P_{green} - P_{nir}}{P_{green} + P_{nir}}$$

Where p_{green} represents the green bands and p_{nir} represents the near-infrared bands of the Sentinel-2 data. NDWI values range from −1 to 1, with higher values indicating greater surface water presence. We filtered satellite imagery to the spatial extent of mapped wetlands, the study period (2019–2025), and removed images with more than 20% cloud cover.

For wetland characteristics, we classified wetlands by origin (natural, artificial, or accidental), wetland type (e.g., inland wetlands, coastal wetlands, dams, etc), and Ramsar designation. We also calculated landscape connectivity as the number of neighbouring wetlands within a 20 km buffer surrounding each focal wetland's boundary, to assess whether wetland attractiveness is influenced by local landscape context. A buffer of 20 km was defined based on the maximum daily movement distance of the marbled ducks in our study, which never exceeded 20 km during the non-migration period. Additionally, we included the latitudinal position of each wetland centroid as a spatial covariate. Wetland identity was included as a random effect to account for repeated observations and to capture site-specific heterogeneity.

Temporal and biological predictors captured individual and population-level heterogeneity, including: Seasons (breeding vs. wintering); population origin (individuals tagged in Morocco vs. Spain that undertook trans-Mediterranean migration to Algeria and Morocco). Individual identity was included as a random effect to capture inter-individual differences in movement behaviour and habitat use strategies.

All statistical analyses were performed using R statistical software, version 4.4.1(R Core Team, 2021). Models were run using package glmmTMB (Magnusson *et al.*, 2017), with different combinations of predictors based on the biological significance of the model. Model selection followed a multi-step process to select the best-fit model (Zuur *et al.*, 2009), using Akaike's Information Criterion (AIC). Models within $\Delta AIC \leq 2$ were considered to have equivalent support given the data. When several models showed similar support, they were examined based on their structure and the significance of parameter estimates. Before model fitting, multicollinearity among predictors was assessed using the variance inflation factor (VIF), and correlated variables (VIF > 7) were not included in the same model (Zuur, Ieno & Elphick, 2010). Model validation was performed by inspecting residual patterns and by assessing dispersion, zero-inflation, and uniformity of residuals using the DHARMa package (Hartig & Hartig, 2017). All final models showed no evidence of overdispersion or zero-inflation.

Results

The raw dataset included 162,907 GPS fixes from 24 Marbled Ducks (10 from Morocco, 14 from Spain) and encompassed 323 wetlands where at least one fix was recorded. Following the data filtering procedure, the restricted dataset retained 24,699 fixes from 21 individuals (including 10 from birds from Morocco and 11 from Spain) spanning 166 wetlands in Morocco and Algeria, across 2020-2025.

Modelling habitat use

Negative binomial GLMMs adequately addressed overdispersion (dispersion ratio = 0.42, p = 0.82) and provided a substantially better fit than Poisson models (Table S3), and were therefore retained for all analyses. Multicollinearity among predictors was low (all VIF < 2; Table S4).

Table X. *Model selection results for negative binomial mixed-effects models explaining the number of GPS fixes per wetland. Models are ranked by Akaike's Information Criterion (AIC); ΔAIC represents the difference relative to the best-supported model, and Akaike weights indicate relative model support. All models included random intercepts for individual identity and wetland identity.*

Model	Predictors	k	AIC	ΔAIC	weight
m7	**wetland type + origin + season * SPI + NDWI**	17	2395.4	**0**	0.215
m5	**wetland type + NDWI + season * SPI + ramsar + origin**	18	2396.5	**1.11**	0.123
m9	**wetland type + season * SPI + NDWI**	16	2396.6	**1.24**	0.116
m18	wetland type + origin * season + season * SPI + NDWI	18	2397.5	2.1	0.083
m12	wetland type + NDWI * season + season * SPI + ramsar + origin	19	2397.8	2.4	0.065
m15	wetland type + NDWI * season + season * SPI + ramsar + origin	19	2397.8	2.4	0.065
m4	wetland type + NDWI + season * SPI + origin + ramsar + neighboring wetlands	19	2397.9	2.51	0.061
m20	wetland type + origin + season * SPI + NDWI + ramsar * season	19	2398.1	2.76	0.054
m13	wetland type + NDWI + season * SPI + ramsar + origin + latitude	19	2398.4	3.08	0.046
m11	wetland type + NDWI + season * SPI + ramsar + origin +(1 | year)	19	2398.5	3.11	0.045
m3	wetland type + NDWI + season + SPI + ramsar + origin + neighboring wetlands	18	2398.9	3.58	0.036
m19	wetland type * origin + season * SPI + NDWI	25	2399.7	4.32	0.025
m8	wetland type * season + origin + season * SPI + NDWI	25	2399.8	4.41	0.024
m16	wetland type + NDWI + season * SPI + ramsar + origin + neighboring wetlands * season	20	2399.8	4.43	0.023
m1	wetland type + country + NDWI + season + SPI + ramsar + origin + neighboring wetlands	19	2400.9	5.57	0.013
m17	wetland class + SPI + NDWI * season	10	2404.3	8.93	0.002
m23	wetland class * origin + season * SPI + NDWI	13	2405.8	10.46	0.001
m21	wetland class * season + SPI + NDWI * season	12	2406.5	11.16	0.001
m22	wetland class * SPI + NDWI + season	11	2406.7	11.39	0.001
m2	wetland class + country + NDWI + season * SPI + ramsar + origin	13	2407.2	11.83	0.001

m14	wetland type * SPI * season + NDWI	40	2411.5	16.13	0
m10	wetland type + NDWI + season + ramsar + origin	16	2457	61.67	0
m6	wetland type + season * SPI + ramsar + origin	17	2629.2	233.88	0

Model selection identified model m7 as the best-supported model (AIC = 2395.4; Table S5), although models m5 and m9 also showed similar support (ΔAIC < 2). Diagnostic checks using DHARMa (Fig S1) indicated that both m7 and m5 provided an adequate fit to the data, with no evidence of residual dispersion. In contrast, model m9 failed goodness-of-fit diagnostics and was therefore not retained for inference (Fig S1). Model m7 is nested within model m5, differing only by the predictor Ramsar designation in m5. As Ramsar designation was not statistically significant and did not improve model fit, model m7 was retained as the final model. Across all well-supported models, wetland type, NDWI, and the interaction between season and SPI were consistently selected. Models including wetland type outperformed those using broader wetland classes, and revealed substantial differences in wetland use among specific types, particularly wastewater treatment plants, dams, and effluent-fed wetlands.

Several wetland types showed higher predicted use (Fig. 3), particularly dams and reservoirs (IRR = 8.22, Table S5), wastewater treatment plants (IRR = 6.99, Table S5), and effluent-discharge fed wetlands (IRR = 4.95, Table S5), all relative to the reference category (irrigation ponds/flooded agricultural fields). Rivers and estuarine/coastal wetlands were also used more than the reference wetland type, whereas inland freshwater wetlands and industrial water bodies showed weaker and less precise effects.

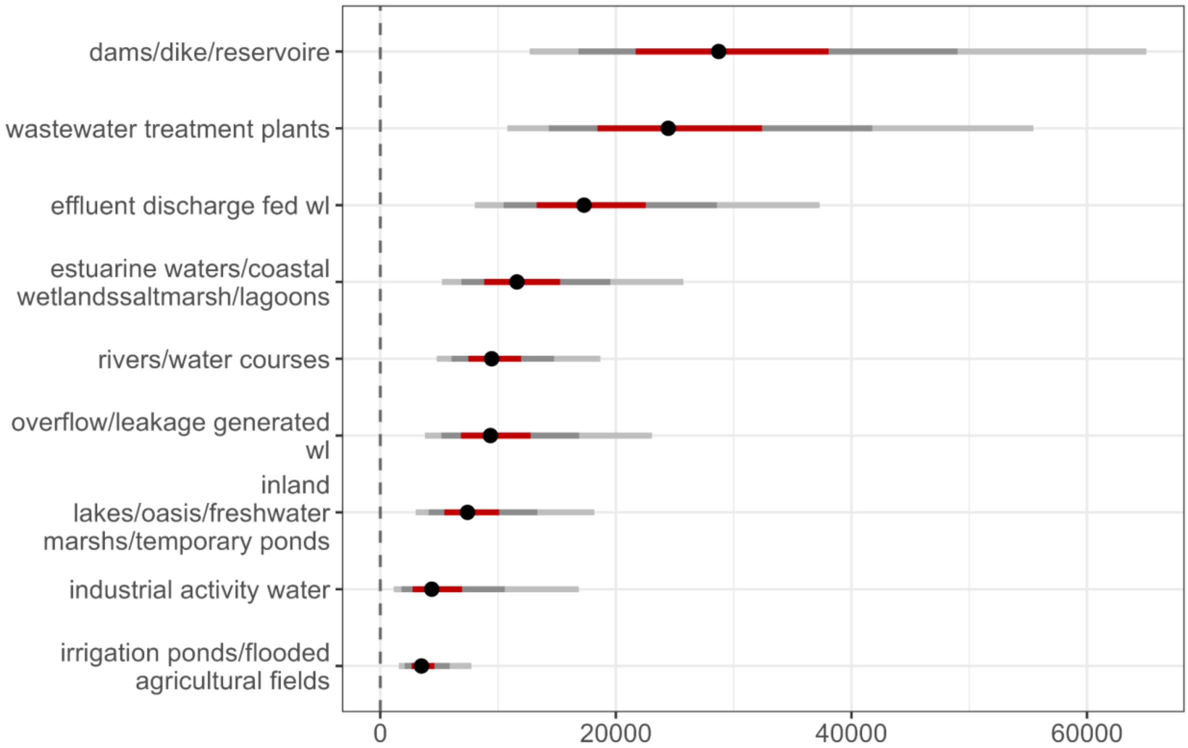

Figure 3. *Model-based marginal predicted wetland use by the Marbled duck across wetland types. Points represent the expected number of GPS fixes per wetland type. Horizontal lines indicate 50% (red), 80% (dark grey), and 95% (light grey) confidence intervals on the response scale. Estimates reflect relative differences in predicted use intensity among wetland types.*

Wetland use was further influenced by seasonal drought conditions, as indicated by an interaction between season and SPI (Fig. 4). During the breeding season, wetter conditions (higher SPI) were associated with greater concentration of fixes at individual wetlands (IRR = 1.29 per SD of SPI), suggesting birds use fewer wetlands more intensively under wetter conditions. whereas this relationship was weaker during the wintering season, as reflected by a negative interaction term (IRR = 0.67). NDWI was not significant and showed no clear effect on wetland use (Table S5). Birds originating from Spain allocated a larger proportion of their fixes to individual wetlands compared to Moroccan birds (IRR = 1.81, Table S5), suggesting Spanish migrants concentrate their activity at fewer sites. Model comparisons confirmed that most unexplained variability occurred at the individual wetland level, rather than at the individual level.

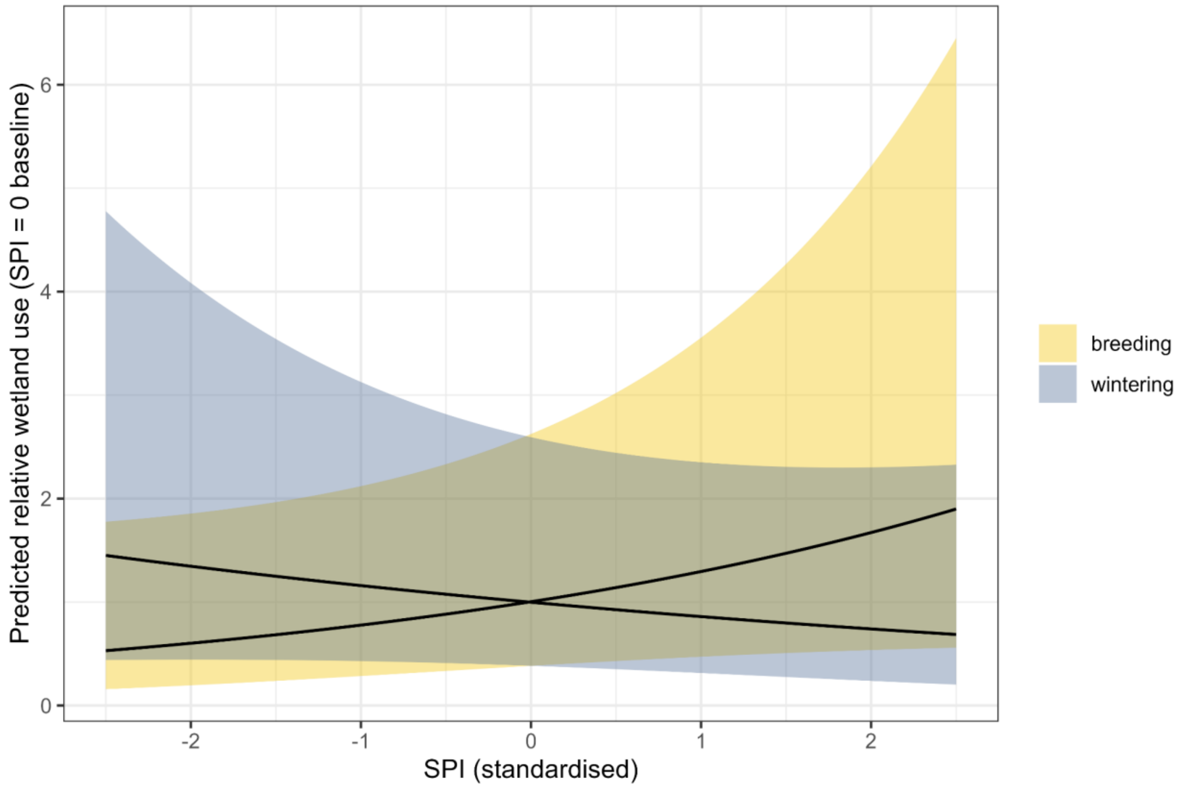

Figure 4. *Season-specific predicted effects of drought conditions on relative wetland use. Lines show model-based predictions from the best model (m7), expressed relative to the predicted wetland use at average drought conditions (SPI = 0) within each season.*

Discussion

Our study provides one of the first GPS-based assessments of Marbled Duck habitat use in North Africa. By integrating telemetry data from individuals originating from both Morocco and Spain, we show that Marbled Ducks rely heavily on anthropogenic wetlands, with dams, sewage treatment plants, and sewage-fed wetlands constituting a large proportion of used habitats during both breeding and wintering seasons. We further demonstrate that habitat use is structured by seasonal drought conditions, whereas local water availability (NDWI) and formal Ramsar designation status play a more limited role.

The Marbled Ducks' heavy use of anthropogenic wetlands partly contrasts with earlier studies, in which the species was strongly associated with natural wetlands. For instance, in 1997-1999, the species occurred predominantly in natural wetlands, mainly permanent brackish/saline lakes and mountain lakes, although it was also regularly recorded in reservoirs (Green *et al.*, 2002). Subsequent breeding studies showed that the species' wetland occupancy was positively related to the richness of emergent macrophytes and negatively related to altitude and distance from the coast, underscoring the importance of low-lying, natural fresh or slightly brackish wetlands with diverse emergent vegetation (Cherkaoui, Magri, & Hanane, 2016; Cherkaoui, Selmi, & Hanane, 2017). This suggests that mountain lakes currently play a limited role as breeding habitat compared to their importance in earlier studies. A similar pattern is observed in winter, where a survey of inland wetlands in the Saïss-Middle Atlas region did not detect Marbled Duck, despite its historical presence in the region, coinciding with recurrent drying and habitat loss in these mountain lakes (Squalli *et al.*, 2024).

International Waterbird Census (IWC) counts from 2015-2023 show that a substantial proportion of the Moroccan wintering population now occurs in wetlands supplied by sewage waters, such as Saqia El Hamra, Merja Fouarate, and Oued Assaka (Ouassou *et al.*, 2021; Dakki *et al.*, 2025). For example, during the period 2015-2019, up to 80% of the national winter count was recorded in anthropogenic wetlands, mainly those fed by sewage waters, such as Saqie El hamra and Merja Fouarate; sewage treatment plants (e.g., Guelmim STEP held 1748 individuals in 2018, which was 50 % of the national total that year) and large dams such as Moulay Abdelah and Al Massira. In contrast, natural wetlands, principally Sidi Moussa-Oualidia, Sidi Boughaba, and Merja Zerga, made up no more than 20% of the national counts (Ouassou *et al.*, 2021; Dakki *et al.*, 2025). These findings suggest a marked long-term increase in the use of artificial/anthropogenic wetlands relative to natural wetlands in Morocco.

In southeastern Spain, the species was mainly associated with shallow ponds with extensive Phragmites reedbeds, Scirpus stands, and salt marshes (Sebastián-González *et al.*, 2013). However, many of these wetlands form part of semi-artificial irrigation complexes that are managed for agricultural water supply (Sebastián-González *et al.*, 2013). A similar pattern of habitat artificialisation has occurred in the Guadalquivir marshes (Doñana), where over 80% of the original marsh has been converted to rice fields, aquaculture ponds, and salt pans. Here many waterbirds, including the Marbled Duck, rely on these artificial habitats while populations concentrated in the remaining natural marshes have declined (Rendón *et al.*, 2008; de Felipe *et al.*, 2024).

The lack of comparable habitat use studies in Algeria limits comparisons with our findings. However, some studies indicate that breeding Marbled Ducks have been recorded mainly in natural Saharan and steppe wetlands characterized by permanent water and abundant emergent vegetation, with occasional use of reservoirs and oases (Abdelaziz *et al.*, 2013; Aberkane *et al.*, 2014; Charchar, Bouchaâla, & Houhamdi, 2019). Similarly, no studies of habitat use are available from Tunisia. In Libya, breeding was noted for the first time in 2012 at the coastal

Mallaha saltmarsh (Etayeb *et al.*, 2014), and subsequent records indicate regular occurrence in the country, including breeding at the Al hadba wastewater treatment plant (Algadry *et al.*, 2022).

Many studies show that artificial wetlands are widely used by waterbirds and can partly compensate for natural wetland loss, although they rarely match natural sites in diversity or functional traits (Li *et al.*, 2013; Giosa, Mammides, & Zotos, 2018; Almeida *et al.*, 2020; Rajpar *et al.*, 2022). For the Marbled Duck, increased use of dams/reservoirs, wastewater treatment plants and sewage-fed wetlands, likely reflects a combination of multiple factors.

First, historical loss and degradation of natural wetlands has drastically reduced the suitable habitat of Marbled Ducks. Over 50 % of the species' suitable habitat may have been lost across its range during the 20th century, mainly due to extensive drainage, water diversion for agriculture, dam construction, and eutrophication (BirdLife International, 2022; Salvador, Amat, & Green, 2023). In Morocco, around a quarter of the national wetland area was lost between 1978 and 1999, especially low salinity wetlands, leading to the disappearance of 98% of seasonal mesohaline wetlands and a reduction of about one-third of seasonal Phragmites reedbeds, Scirpus stands marshes, which are important habitats for the Marbled duck (Green *et al.*, 2002). Another example is Lake Iriki, historically one of the most important breeding sites for the Marbled Duck, held hundreds of breeding pairs in the 1960s but has now vanished following the construction of the Al Mansour Ad-Dahbi dam, further reducing the availability of suitable natural breeding habitat (El Agbani et al., 1996).

Second, drought appear to be an important driver of habitat use. Across North Africa, increasing drought frequency linked to ongoing climate change has accelerated water loss from natural wetlands over recent decades, reducing their suitability for waterbirds (Khelifa, Mahdjoub, & Samways, 2022). These dynamics are likely to intensify: climate projections suggest that by 2050, approximately 90% of North African wetlands may become less suitable for waterbirds due to continued hydrological changes (Breiner *et al.*, 2022). In contrast, anthropogenic wetlands such as reservoirs, wastewater treatment plants, and effluent-fed systems often maintain relatively stable and predictable water levels, even under drought conditions. Our results are consistent with this mechanism: the positive relationship between SPI and predicted wetland use during the breeding season (i.e. the dry summer period) indicates increased use of wetlands that are under wetter conditions. Similar patterns have been reported in southwestern Spain's Doñana region, where a study found that wintering waterfowl concentrated in artificial fishponds during dry winters when natural marshes were not flooded, but returned to natural marshes in wetter years, illustrating how managed water bodies buffer hydrological variability and maintain habitat availability under drought (Kloskowski *et al.*, 2009). Similarly, in California, during extreme drought, waterbird densities were highest in deliberately managed flooded wetlands, whereas unmanaged natural wetlands with variable hydrology were used less intensively (Hartman *et al.*, 2025). Likewise, in China, at Poyang Lake, extreme drought has been shown to displace waterbirds from protected natural lakes into surrounding managed lakes and wetlands where water levels are artificially maintained, and food resources remain available (Wang *et al.*, 2025). A parallel finding comes from the Camargue (southern France), in which during a dry year with lower water levels in natural lagoons, Greater flamingos were found at twice the rate in managed salt pans compared to a wetter year, with those salt pans functioning as a refuge habitat (Béchet *et al.*, 2009). Together, these findings suggest that hydrological predictability may be an important determinant of the Marbled Duck habitat use under increasing climatic variability.

Third, high food availability in wastewater environments likely contributes to the attractiveness of sewage-fed sites. The reliance of Marbled Duck on wastewater treatment plants and effluent-fed wetlands suggests that these habitats play a potentially important conservation role under increasing water scarcity. These systems can be highly productive, with elevated nutrient loads supporting dense invertebrate and macrophyte communities providing food availability for waterfowl, particularly in arid landscapes where natural wetlands are dry (Zhang *et al.*, 2020). At a Ramsar-listed wastewater treatment plant in Australia, waterfowl numbers tracked nutrient inputs closely, declining when nutrient loads were reduced and increasing when nutrient-rich sewage was restored (Loyn *et al.*, 2023). In another example from Ghana, higher waterbird numbers were recorded in a fenced sewage facility than in a less polluted but heavily disturbed natural wetland, highlighting the importance of low disturbance in these systems (Holbech & Cobbinah, 2021). Likewise, wastewater systems along the Nile in Egypt and historical sewage ponds in Poland support large and diverse waterbird assemblages, particularly in otherwise dry or intensively modified landscapes (Orłowski, 2013; Noby *et al.*, 2025).

However, while anthropogenic wetlands may provide abundant resources, they may also expose birds to contaminants, pathogens, and heavy metals, raising potential long-term health and demographic concerns that may affect individual health and population dynamics. Sewage-fed wetlands and wastewater treatment plants often harbour high loads of avian pathogenic bacteria and can promote disease outbreaks under eutrophic conditions (Reid et al., 2019;

Alexander et al., 2024). For example, nutrient enrichment and carcass accumulation favour the growth of Clostridium botulinum, increasing the risk of avian botulism (Anza *et al.*, 2014). High bird densities and fecal-oral transmission in aquatic environments may also facilitate the circulation of avian influenza viruses and other waterborne pathogens (Kenmoe et al., 2024; Perlas et al., 2025). Beyond pathogens, these systems may expose birds to chemical contaminants and emerging pollutants, including heavy metals. Migratory shorebirds using a wastewater treatment plant showed higher per and polyfluoroalkyl substances (PFAS) and mercury concentrations than conspecifics in nearby natural wetlands, raising concerns about sub-lethal effects, particularly in immature birds (Ross et al., 2023). Wastewater wetlands can also act as hotspots for pharmaceutical residues, endocrine-disrupting chemicals, and antibiotic-resistant genes, which can have lethal effects on physiological and reproductive functions (Zhang et al., 2023; Zhao et al., 2024). Moreover, a multi-biomarker assessment study of passerines at an urban sewage facility revealed elevated genotoxic damage and erythrocyte abnormalities compared with individuals from protected forests, suggesting measurable sub-lethal physiological costs that may affect behaviour, reproduction, and survival (Freitas et al., 2024).

In Morocco, Merja Fouarate, and Saqia el Hamra are both supplied by polluted waters. Merja Fouarate is now classified as a highly organically polluted wetland, with 5-day biochemical oxygen demand (BOD_5) and ammonium values corresponding to organic pollution index (IPO) class 1 and 2, while earlier work similarly showed a strong organic pollution, driven by untreated domestic and industrial effluents (Chahboune *et al.*, 2012; Lemkimel, Slim, & Benssi, 2025). Similarly, Saqia El Hamra wetland contains nitrate that frequently exceeds 50 mg/L, above the World Health Organization (WHO) guideline, and is characterized by high ammonium, nitrite, organic load, and low oxygen, consistent with chronic contamination by untreated domestic sewage (Errich *et al.*, 2016, 2024). However, no ecotoxicological or demographic studies have yet quantified contaminant loads, health or survival of Marbled Ducks at these specific sites. It is therefore not possible to conclude that these wetlands are currently lethal, but the combination of poor water quality and known sensitivity of waterbirds to such pollutants indicates a high potential for sublethal effects. Targeted studies quantifying contaminant exposure and survival in Marbled Ducks using these wetlands are needed before robust conclusions can be drawn.

Future work should therefore (i) implement targeted ecotoxicological monitoring of Marbled Ducks and co-occurring species in wastewater wetlands, using non-invasive biomarkers (feathers, eggshells, faeces, blood indicators) to quantify metals, organic contaminants and emerging pollutants, and explicitly link these exposure metrics to fitness by contrasting key reproductive parameters (clutch size, hatching success, brood survival) between highly polluted and relatively unpolluted wetlands; (ii) characterize habitat quality in wastewater wetlands versus natural wetlands, quantifying food availability and emergent vegetation structure (iii) analyse wetlands connectivity and biovectoring processes, integrating movement data with pathogen/antimicrobial resistance surveillance to understand how birds move contaminants and diseases between wastewater wetlands, landfills, agricultural areas and natural sites. Overall, conservation strategies should prioritize the protection and restoration of high-quality natural freshwater wetlands in a climate change context while explicitly managing key anthropogenic habitats that currently support substantial fractions of the population.

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Supplementary material

Table S1 *: Definition, source, and ecological interpretation of variables included in the generalized linear mixed models and associated ecological hypotheses tested in wetland use analyses.*

Variable name	Variable type	Model role	Data source & extraction	Meaning	Question addressed
number of GPS fixes	Count	Response variable	GPS tracking data	The number of GPS fixes recorded within a given wetland during a season for an individual	How is wetland use distributed among wetlands?
total fixes	Continuous	Offset	GPS tracking data	Total number of GPS fixes available for an individual during a season	Controls for unequal sampling effort across individuals and seasons
SPI	Continuous	Predictor	Remote sensing (precipitation-based drought index)	Standardized Precipitation Index, reflecting drought severity	Does drought intensity influence wetland use intensity?
NDWI	Continuous	Predictor	Sentinel-2 remote sensing	Normalized Difference Water Index, proxy for water availability	Are wetlands with higher water availability used more intensively?
wetland type	Categorical	Predictor	Wetland inventory classification	Functional wetland type (e.g. lake, marsh, lagoon, dam)	Do Marbled duck preferentially use certain wetland types?
wetland class	Categorical	Predictor	Wetland inventory classification	Broad origin of wetlands (natural, artificial, accidental)	Does wetland origin influence habitat use?
Ramsar designation	Binary (Yes/No)	Predictor	Ramsar area spatial overlay	Whether the wetland is under Ramsar designation	Are internationally recognized Ramsar wetlands used more frequently than unrecognized ones?
season	Categorical	Predictor	Temporal classification	Breeding *vs*. wintering season	Does wetland use differ between breeding and wintering periods?
neighbour wetlands	Continuous (count)	Predictor	GIS buffer analysis (20 km radius)	Number of wetlands surrounding a focal wetland	Does landscape connectivity influence wetland attractiveness?
population origin	Binary (Morocco / Spain)	Predictor	Capture metadata	The country where individuals were originally captured	Do individuals from different populations use wetlands differently?
latitude	Continuous	Predictor	GIS (wetland centroid coordinates)	Latitudinal position of wetlands	Is there a latitudinal gradient in wetland use?
individual identity	Categorical	Random effect	Tag metadata	Individual bird identity	Accounts for individual-level heterogeneity in space use
wetland identity	Categorical	Random effect	Wetland inventory	Unique wetland identifier	Accounts for unmeasured differences in wetland attractiveness

Table S2 *: Conceptual grouping of interaction terms tested in the models*

Interaction category	Interaction terms	Ecological question addressed
Climatic modulation	season × SPI; NDWI × season	Do drought intensity (SPI) and/or local water availability (NDWI) influence wetland use differently between seasons?
Habitat-specific responses	wetland type × SPI; wetland type × season; wetland class × SPI; wetland class × season	Do wetland categories (type or class) differ in how wetland use responds to drought conditions and seasonal changes?
Population differences	wetland type × origin; wetland class × origin; origin × season	Do individuals from different capture origins (Spain vs Morocco) differ in their wetland selection patterns and/or seasonal use?
Management buffering	ramsar designation × season	Do Ramsar-designated wetlands get used differently between seasons?
Landscape context	neighboring wetlands z × season	Does landscape connectivity influence wetland use differently across seasons?

Table S3. *Overdispersion diagnostics for candidate error distributions*

Model	Distribution	Dispersion ratio	Pearson χ²	p-value	Interpretation
Model-P	Poisson	21.18	5168.12	< 0.001	Strong overdispersion
Model-NB	Negative binomial	0.42	–	0.82	No overdispersion

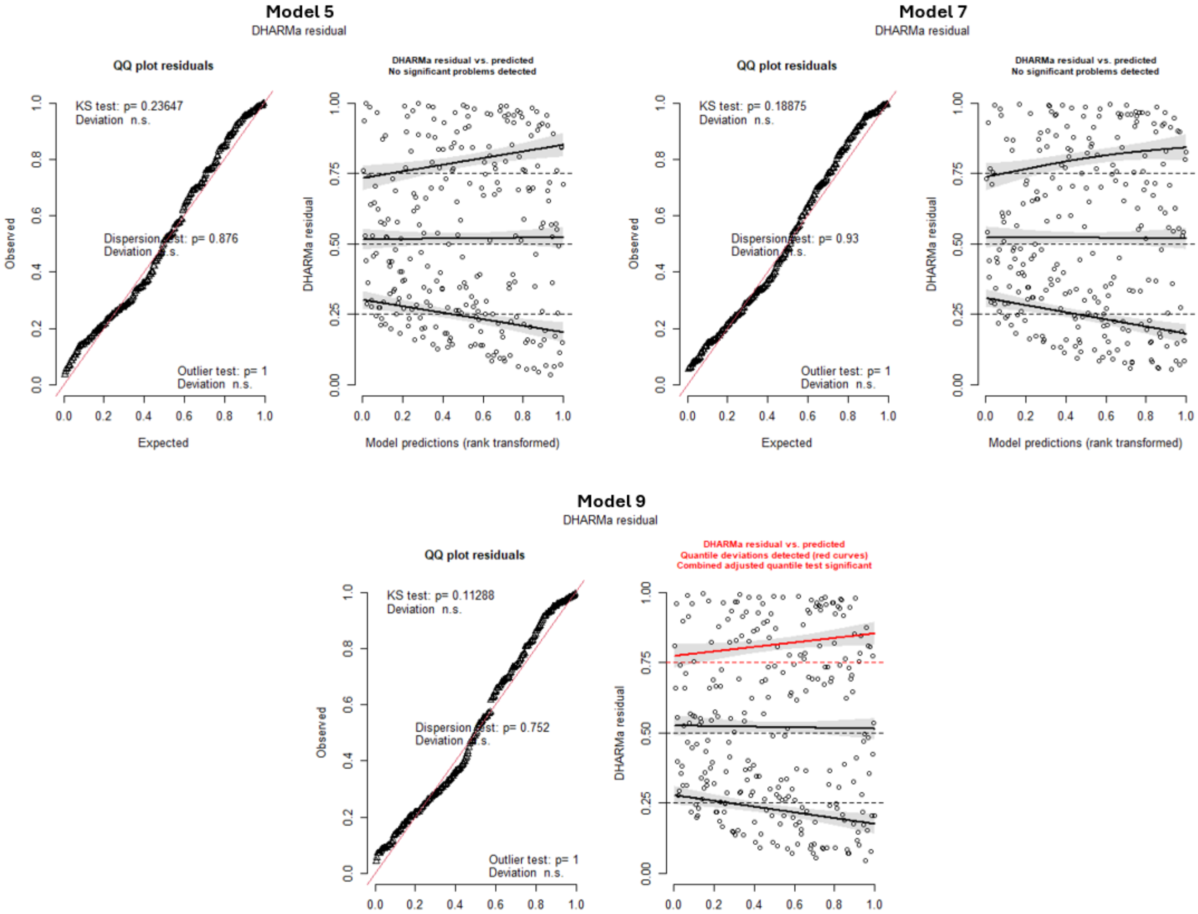

Figure S1. *DHARMa residual diagnostics assessing goodness-of-fit of candidate negative binomial GLMMs (Models 5, 7 and 9).*

Table S4. *Variance inflation factors (VIF) for fixed-effect predictors included in the candidate models.*

Predictor	VIF	95% CI (VIF)
origin	1.70	1.48–2.03
season	1.11	1.03–1.38
SPI	1.06	1.01–1.49
NDWI	1.30	1.17–1.54
latitude	1.67	1.46–1.99
ramsar designation	1.72	1.49–2.05
neighboring wetlands	1.55	1.36–1.84

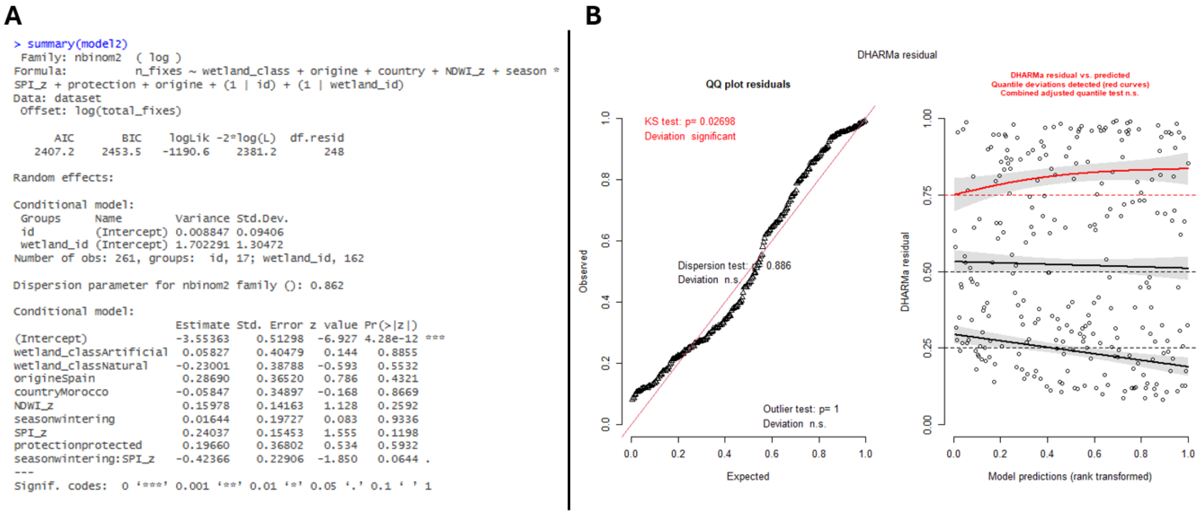

Figure S2. *Summary output (A) and DHARMa residual diagnostics (B) for the negative binomial GLMM including broad wetland class categories (Model 2).*

Table S5. *Model estimates from the best-supported model (m7). Estimates are shown on the log scale, with incidence rate ratios (IRR) indicating multiplicative effects on the expected number of fixes. Reference levels are irrigation ponds/flooded agricultural fields, the breeding season, and Morocco for origin. The model included random intercepts for individual identity and wetland identity.*

Predictor	Estimate	SE	z value	p value	IRR
dams/dike/reservoir	2.106	0.568	3.711	<0.001	8.218
wastewater treatment plants	1.945	0.557	3.489	<0.001	6.993
effluent discharge fed wl	1.599	0.546	2.927	0.003	4.948
estuarine waters/coastal wetlands saltmarsh/lagoons	1.2	0.553	2.17	0.03	3.319
rivers/water courses	0.995	0.501	1.987	0.047	2.705
overflow/leakage generated wl	0.984	0.574	1.714	0.087	2.675
inland lakes/oasis/freshwater marshes/temporary ponds	0.751	0.571	1.315	0.188	2.119
industrial activity water	0.223	0.776	0.288	0.773	1.25
Origin: Spain (ref: Morocco)	0.592	0.328	1.805	0.071	1.808
Season: Wintering (ref: Breeding)	0.085	0.194	0.438	0.661	1.089
SPI (z)	0.255	0.152	1.68	0.093	1.291
NDWI (z)	0.048	0.145	0.332	0.74	1.049
SPI*Wintering	-0.405	0.229	-1.76	0.077	0.667

Chapter 5 : General discussion

1. Reminder of main findings

This thesis aimed to improve our understanding of the ecology and conservation of the Marbled duck in Morocco by integrating population monitoring, movement ecology, and habitat use analysis. Although each chapter addresses a different ecological question, they are linked by a common focus on how habitat characteristics shape the species' breeding population, movement behaviour, and habitat use within increasingly modified wetland landscapes.

At the population scale, Chapter 2 provided the first standardised estimate of the national breeding population and identified key habitat features associated with brood abundance, particularly emergent vegetation cover and wetland type, highlighting the importance of shallow, densely vegetated habitats for breeding females.

Chapter 3 then examined spatial organisation at a finer scale by investigating how individuals organise their movements and behaviours within their daily use of habitat. This chapter revealed the existence of functional units linking roosting and foraging sites. The results showed that individuals may rely either on multifunctional wetlands or on spatially separated roosting and feeding areas. Environmental variables such as vegetation density, temperature, and proximity to human infrastructure were found to influence foraging site selection. The results of this chapter demonstrate that the conservation of the Marbled duck cannot rely on protecting individual wetlands in isolation, but must instead focus on maintaining functional wetland networks that provide complementary resources for the species.

Finally, Chapter 4 expanded the analysis to the landscape scale by examining habitat use across a wide diversity of wetland types throughout the annual cycle. This chapter revealed that Marbled ducks exploit a broad network of wetlands dominated by anthropogenic systems such as wastewater treatment plants, effluent-fed wetlands, and dam/reservoirs. In contrast, natural wetlands represented a smaller proportion of habitat use, although they remain critical components of the species' habitat. Habitat use was also modulated by seasonal drought conditions, highlighting the importance of water availability and climatic variability in shaping wetland use patterns. Together, these results indicate that anthropogenic wetlands currently play an important role in sustaining the species' spatial ecology, potentially buffering the effects of increasing water scarcity in Mediterranean environments.

Taken together, the three chapters provide complementary insights into how habitat characteristics influence Marbled duck ecology across different scales. While Chapter 2 identifies the habitat features that support breeding populations, Chapter 3 reveals how individuals organise their movements at a fine scale among habitats within a single wetland complex during the pre-breeding period, and Chapter 4 highlights the diversity of wetland types that sustain the species across seasons and under varying climatic conditions.

2. Implications for conservation and management

2.1. Conservation status of the Marbled duck's habitat in Morocco: past, present, and future

The national estimate of 382 [95% CrI:280–484] breeding pairs establishes the first national standardised demographic baseline for the species' population size for Morocco. Such estimates allow future monitoring programs to assess population trends, and evaluate the effectiveness of conservation actions (Nichols & Williams, 2006). In this context, the results of this study will serve as a key component in the development of the national action plan for the Marbled duck. Before implementation, this estimate can contribute to defining measurable conservation targets and identifying priority sites. During implementation, the sampling framework provides a repeatable monitoring protocol to track population responses to management actions (Henry & O'Connor, 2019). After implementation, repeated surveys using the same design would allow assessment of population trends and evaluation of conservation effectiveness (Moussy *et al.*, 2022).

The spatially structured sampling design also offers valuable insights for site-based conservation planning. Because surveys were conducted across a broad range of wetlands rather than only historic breeding strongholds, the probabilistic approach appears particularly suited to accounting for the nomadic behaviour of the species, allowing the detection of breeding activity at previously unrecorded sites such as Jazzouli dam (Table 1). However, randomly selected primary units may not systematically capture all historically important sites, which represents a limitation of this approach for identifying spatial strongholds. Combining the probabilistic survey with the exhaustive surveys conducted under the LIFE Cerceta Pardilla programme, coordinated by the Biodiversity Foundation of the Ministry for Ecological Transition and Demographic Challenge, which targeted known breeding sites and conducted simultaneously in Morocco, yielded a more comprehensive understanding of the breeding population distribution. Sites detected by both protocols, such as Sidi Boughaba, Merja Fouarate, and Mohamed V dam, likely represent the most consistently important breeding areas, while sites detected only through the probabilistic survey highlight the value of random sampling for discovering new breeding locations. A synthesis of breeding records from both surveys is presented in Table 1, which also indicates whether each site was detected by one or both protocols. These sites encompass a wide range of wetland types, including rivers, marshes, lakes, dams, ponds, and saltpans. Notably, several wetlands supporting breeding populations currently lack formal conservation status, despite their apparent importance for the national breeding population.

Table 1. *Wetlands where breeding Marbled duck broods were recorded during probabilistic surveys and/or the Spanish Marbled duck LIFE census in Morocco. For each wetland, the table reports its administrative region, wetland type (river, lake, marsh, dam/reservoir, pond, or saltpan), the number of broods recorded during the breeding surveys, the conservation status of the wetland including designation as a Ramsar site and/or Important Bird and Biodiversity Area (IBA), and the survey protocol through which the site was detected (probabilistic survey only, LIFE census only, or both).*

Wetland	Region	Wetland type	Broods count	Wetland status	Survey protocol	Notes
Oued Tensift -Marrakech	Marrakech-Safi	river	13	None	Life census	fed by sewage
Sidi boughaba	Rabat–Salé–Kénitra	lake	9	Ramsar; IBA	both	–
Merja fouarate	Rabat–Salé–Kénitra	marsh	7	Ramsar	both	fed by sewage
Mohamed V dam	oriental	dam	4	Ramsar; IBA	both	–
Oued yekkem	Rabat–Salé–Kénitra	river	4	None	Life census	–
Saline de Sidi-moussa	Casablanca–Settat	saltpans	3	Ramsar; IBA	both	–
Merja bargha	Gharb	pond	3	Ramsar; IBA	both	–
Oued noun assaka	Guelmim–Oued Noun	river	3	None	Life census	fed by sewage
Saqia Al Hamra	Laayoune	marsh	3	Ramsar; IBA	Life census	fed by sewage
Imi kheng dam	Souss–Massa	dam	2	None	Life census	–
Jazzouli dam	Souss–Massa	dam	2	None	Probabilistic	–
Diasra	Gharb	pond	2	Ramsar; IBA	both	–
Oued Draa - Oued Tantan confluence zone	Drâa–Tafilalet	river	2	None	Life census	fed by sewage

Sites such as Oued Tensift, Sidi Boughaba, and Merja Fouarate supported the highest numbers of broods during the surveys and should therefore be considered priority areas for conservation of the species. Beyond currently occupied sites, several wetlands that previously supported breeding populations, including El Hotba Marsh, the Souss-Massa mouth, and the Moulouya mouth, did not record any broods during the present study, likely reflecting recent drying or habitat degradation (El Agbani et al., 1996; Green et al., 2002), particularly in the context of recurrent and severe drought conditions affecting Morocco in recent years, which have substantially reduced wetland hydroperiod and water availability. More dramatic examples of habitat loss include Dayat Aoua in the Middle Atlas, which dried more than 15 years ago due to groundwater extraction for agriculture, and Lake Iriki (hundreds of breeding pairs were recorded in the 1960s), which disappeared in the 1990's following upstream dam construction). These examples illustrate how hydrological alterations can destroy suitable breeding habitats and underscore the importance of maintaining wetland hydrological regimes when designing long-term conservation strategies for the species.

Demographic consequences of indirect threats of habitat destruction are likely to reduce Marbled duck breeding success, brood survival, juvenile recruitment, and adult survival. Additionally, direct demographic impacts may arise from illegal killing and egg harvesting, both documented in multiple Moroccan wetlands (, despite the species being fully protected by law and not subject to legal harvest. Evidence from Spain suggests that poaching may have substantial demographic consequences, as non-natural mortality, particularly illegal shooting during the hunting season, can reduce survival enough to undermine population recovery . However, comparable quantitative information is lacking for North African populations, including Morocco where hunting pressure on waterfowl is likely of lower intensity than in Spain, and the nature and relative importance of other threats, such as predation by raptors, feral cats, or free-ranging dogs, may also differ substantially. Quantifying the demographic impact of these threats could benefit from population viability analyses (PVA), which provide a framework for evaluating extinction risk and comparing management scenarios under data uncertainty . Such analyses could be incorporated into the national action plan for the Marbled duck, where even preliminary simulations based on available data can help identify the most influential demographic parameters and guide conservation priorities. This approach has proven valuable for other threatened wetland-dependent species; for instance, stage-structured matrix models successfully predicted population decline of the snowy plover (Charadrius nivosus) and identified adult survival as the most influential demographic parameter (Cruz-López et al., 2017). For the Marbled duck in Morocco, a preliminary PVA could be parameterized using survival rates estimated from GPS-tagged individuals monitored in Chapters 3 and 4, and breeding success estimates derived from brood surveys in Chapter 2. Where data gaps remain, such as juvenile survival rates, parameters could be used from better-studied populations in Spain or estimated under explicit assumptions, with sensitivity analyses identifying which parameters most strongly influence population trajectory. The data collected in this thesis thus represents a valuable initial foundation for such modelling efforts, and longitudinal monitoring programs would progressively refine parameter estimates and improve the reliability of future demographic assessments.El Agbani *et al.*, 1996; Green *et al.*, 2002)(Pérez-García *et al.*, 2024)(Akçakaya & Sjögren-Gulve, 2000)(Pérez-García *et al.*, 2024)

The habitat use patterns identified in Chapter 4 also complement the breeding habitat highlighted in Chapter 2. Two of the wetlands supporting the highest numbers of broods, namely Oued Tensift and Merja Fouarate, are supplied with wastewater. This observation suggests that anthropogenic wetlands may contribute to breeding habitat availability in certain contexts, although their ecological quality and long-term suitability remain uncertain. Results presented in Chapter 4 extend this finding by showing that Marbled ducks use a broad network of wetlands dominated by anthropogenic systems. While natural wetlands remain essential for reproduction, anthropogenic wetlands may provide complementary resources, particularly during the breeding period when drought events reduce the suitability of natural wetlands, potentially increasing reliance on human-modified systems.

The reliance of the Marbled duck on anthropogenic wetlands, especially in dry years, is similar to findings from other regions, including coastal China and the Mediterranean (Spain), where artificial or managed wetlands can buffer waterbirds against drought and habitat loss, but rarely replicate the ecological quality offered by natural wetlands (Fan *et al.*, 2021; Feng *et al.*, 2025; Wang *et al.*, 2025, 2026). A broader historical perspective further supports this interpretation for Morocco. Long-term counts from the International Waterbird Census (1983-2023; Dakki *et al.*, 2025) conducted during mid-January reveal substantial shifts in the relative importance of Moroccan wetlands for wintering Marbled duck (Table 2). Notably, two of the wetlands supporting the highest numbers of birds in recent years, Merja Fouarate and the Saqia Al Hamra wetlands, are sewage-fed wetlands. Both sites were also identified as important breeding areas during the present study, highlighting their role in sustaining both breeding and non-breeding populations. Some wetlands also showed strong variability between decades in bird numbers, particularly temporary wetlands such as Sebkha Zima and Dayet Al Fahs. These wetlands can support important numbers of Marbled duck during favourable hydrological conditions but may become unsuitable in dry years, reflecting the high sensitivity of temporary wetlands to climatic variability (Grillas *et al.*, 2021).

Table 2. *Summary of International Waterbird Census counts of Marbled duck at major wetlands in Morocco across four decadal periods (1983–1992, 1993–2002, 2003–2012, and 2013–2023). For each site and period, the table reports the number of years surveyed, the mean count of individuals recorded during surveys, and the maximum count observed. Within each decadal period, grey shading reflects the relative importance of wetlands based on mean counts, with darker shading indicating higher mean counts relative to other sites surveyed during the same period. For sites that exceeded a maximum count of 300 individuals recorded over more than one year within a 10-year period and surveyed across two or more decadal periods, a descriptive change in counts between early and recent decades is indicated based on mean counts, with arrows suggesting an apparent increase (↗) or decrease (↘). '-' indicates that no surveys were available for the corresponding site and period..*

	Period 1983-1992			Period 1993-2002			Period 2003-2012			Period 2013-2023			Trend	Notes
site	years surveyed	mean count	max count	years surveyed	mean count	max count	years surveyed	mean count	max count	years surveyed	mean count	max count		
Dam Al Mansour Ad-Dahbi	-	-	-	3	64	170	3	17	26	1	14	14		
Dam Al Massira	-	-	-	2	1126	1973	4	90	136	2	127	220		
Dam Hassan Ad-Dakhil	-	-	-	-	-	-	1	339	339	1	36	36		
Dam Mohammed V	-	-	-	-	-	-	3	89	230	5	28	115		
Dam Moulay Abdellah	-	-	-	-	-	-	-	-	-	1	997	997		
Dayet Al Fahs	1	149	149	2	43	80	5	191	636	1	75	75		
Ouad Loukkos mouth	2	26	50	1	10	10	2	3.5	6	2	55	110		
Ouad Malwiya mouth	-	-	-	2	19	36	7	37	142	9	10	27		
Ouad Massa mouth	9	167	350	5	123	397	8	43	80	8	19	56	↘	
Ouad Souss mouth	-	-	-	1	5	5	-	-	-	2	6	6		
Sidi Moussa Walidia wetlands	7	346	920	8	510	1800	7	404	1340	10	143	351	↘	
lower Loukkos marshes	3	13	23	2	8	14	2	42	82	4	27	45		
Merja Zerga	2	10	17	3	34	60	7	84	130	10	74	200		
Merja Fouwarate	-	-	-	1	249	249	1	43	43	11	159	540	↗	Sewage fed
Merja Sidi Bou Ghaba	10	530	1400	7	194	734	6	70	185	11	64	280	↘	
Beach Ras Takoumba	-	-	-	1	550	550	2	36	52	4	61	200		
STEP Guelmim	-	-	-	-	-	-	-	-	-	3	612	1748		Sewage treatment
Sebkha Zima	3	215	336	4	135.5	250	4	291	950	2	231	450		
Saqia Al Hamra wetlands	-	-	-	3	60	110	8	351	1965	11	664	3557	↗	Sewage fed

Conversely, several important natural wetlands, such as the Oued Massa mouth, Sidi Moussa-Oualidia wetlands, and Sidi Boughaba, have experienced declines in birds counts in recent decades, suggesting that habitat degradation or hydrological alteration may have reduced their suitability. These sites are also amongst the most important sites for the breeding of the species in Morocco, making the identification of their main threats important for conservation planning. At the mouth of Ouad Massa, the dynamics of the sand barrier separating the river from the sea can strongly alter habitat conditions. When the sand barrier remains intact, the river mouth forms a terminal lagoon with freshwater or slightly brackish conditions that support emergent vegetation providing suitable habitat for waterfowl (El Agbani et al., 1996). However, when the barrier breaks and tidal exchange occurs, the area functions more as a salty estuary, leading to the disappearance of emergent vegetation and a shift in bird communities composition towards shorebirds rather than marsh-nesting species such as the Marbled duck (El Agbani *et al.*, 1996). On the other hand, Sidi Boughaba has experienced hydrological pressure from groundwater extraction associated with greenhouse agriculture surrounding the wetland and urban development. Recent remote sensing analyses over a 38-year period (1984-2021) quantified a loss in the lake's permanent water extent, with a significant central portion transitioning from permanent to strictly seasonal water (El Agbani *et al.*, 1996; Moukrim *et al.*, 2025).

In the Sidi Moussa-Oualidia wetland complex, anthropogenic pressures in addition to habitat degradation have been reported, including illegal killing or egg harvesting, intensive livestock grazing, cutting of emergent vegetation, expansion of salt extraction areas, sand extraction, and fishing activities, many of which occur both in winter and during the breeding season (El Agbani *et al.*, 1996; Green *et al.*, 2002). These activities can reduce the availability of nesting habitat, increase disturbance, and directly destroy nests. In addition, the expansion of saltpans at the expense of natural marshes has resulted in the loss of suitable wetland habitat (El Agbani et al., 1996).

Hydrological alteration also appears to play an important role. For example, El Hotba marsh, one of the wetlands within the Sidi Moussa-Oualidia complex and historically one of the most important sites for Marbled duck in Morocco, supporting up to 1,400 wintering individuals in the late 1990s (Green *et al.*, 2002) and regularly hosting breeding pairs, has experienced a substantial reduction in water extent in the last decade. Remote sensing analysis of water coverage (See supplementary. material for details on methods) indicates that the marsh has lost a significant proportion of its water surface and has frequently been nearly dry during the breeding season in the last decade (Fig. 1). This decline in water likely reduces habitat suitability for the species and may partly explain the decrease in Marbled duck counts in winter recorded in the Sidi Moussa-Oualidia complex (Table 2), where trends in bird numbers over the last decade appear to parallel the reduction in wetland water surface. Understanding the drivers of this hydrological decline, whether linked to increasing climatic aridity in the region, groundwater extraction for agriculture, or other forms of water management, is therefore essential to guide effective conservation and management actions aimed at restoring and maintaining suitable wetland conditions for the species.

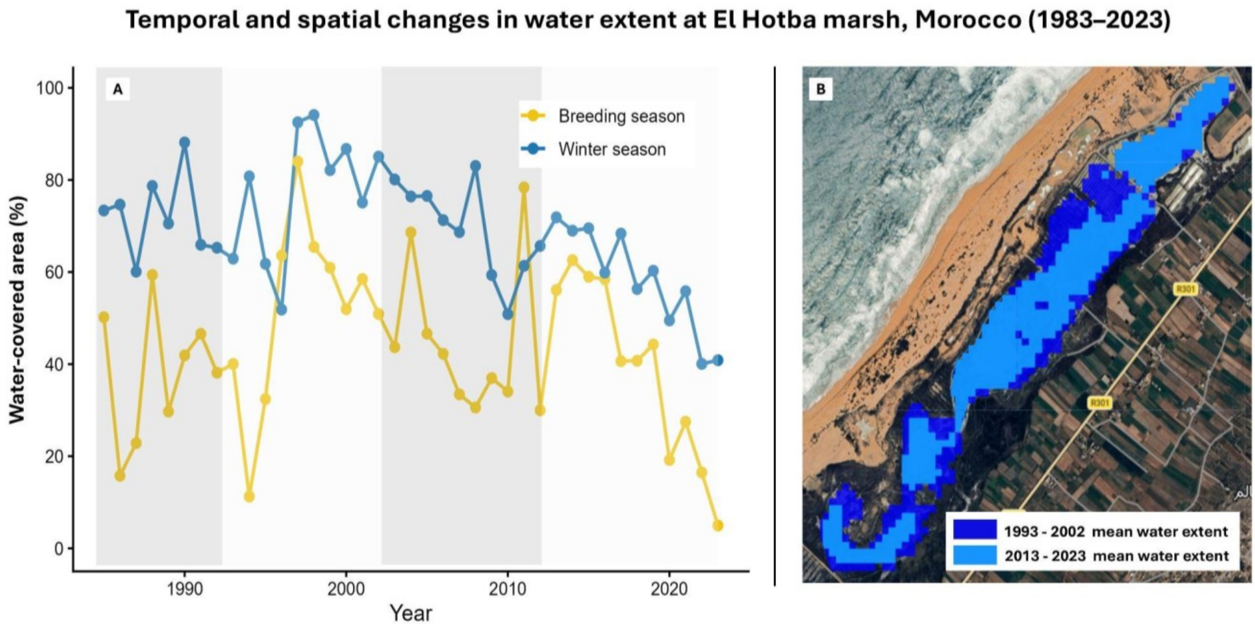

Figure 1. *Temporal and spatial changes in water extent at El Hotba marsh, Morocco (1983-2023). (A) Annual percentage of the wetland area covered by open water during the breeding season (May-August) and wintering season (September-March), derived from Landsat imagery. Grey shading indicates the four decadal periods used in the wetland importance in Table 2. (B) Comparison of mean open-water extent between two periods (1993–2002 and 2013–2023), illustrating changes in the spatial distribution of water within the marsh.*

Historically, several wetlands that supported large numbers of Marbled ducks during both breeding and wintering periods have been lost in Morocco, primarily due to large-scale drainage. In north-western Morocco, wetlands in the Loukkos and Gharb regions are estimated to have lost 34-93% of their area between 1912 and 2020, mainly due to agricultural conversion and water abstraction for irrigation (Falah, Dakki, & Mansouri, 2021). In the Gharb plain, extensive drainage resulted in the disappearance of vast marshland systems. Major wetlands such as Merja Boukka, Dawra, and Sidi Mohamed Ben Mansour were completely drained, while others, including the lower Loukkos marshes, were drastically reduced from approximately 25,000 ha to less than 1,000 ha (Morgan & Boy, 1982; El Agbani *et al.*, 1996). Similar processes have been reported in the Middle Atlas, where remote-sensing analyses of Dayet Aoua and Lake Ifrah revealed marked declines in water surface area, including episodes of complete drying, concurrent with a near fivefold expansion of irrigated agriculture (from c. 1,300 ha in 1985 to 7,070 ha in 2022) and major groundwater table declines (Bouhali, Amyay, & Chahdi, 2024). Repeated dry-outs have also been recorded at Aguelmam Afennourir, while in the Saïss-Middle Atlas region, 349 ha of wetlands were lost between 2003 and 2023 (Squalli *et al.*, 2024).

Without effective conservation and management measures to mitigate these pressures, the remaining natural wetlands in Morocco, such as El Hotba marsh, may follow similar trajectories of degradation, potentially becoming part of the historical wetland loss. In this context, conservation efforts should adopt a broader, integrative approach to wetland management, focusing not only on restoring degraded natural systems but also on strengthening multi-stakeholder protection frameworks and improving the management of anthropogenic wetlands. These priorities can be structured around three complementary axes: the restoration of natural wetlands, the reinforcement of wetland protection and conservation status, and the sustainable management of key anthropogenic habitats.

2.2. Restoration

2.2.1. Restoration approaches and priorities

The protection and restoration of degraded and lost natural wetlands remains the highest priority and could benefit not only the Marbled duck but also other threatened waterbirds sharing similar wetland habitats in Morocco, including the White-headed duck (*Oxyura leucocephala,* Endangered), Ferruginous duck (*Aythya nyroca*, Near Threatened), Common Pochard (*Aythya ferina*, Vulnerable), and Crested coot (*Fulica cristata*, Critically Endangered). Restoration studies from North America, Mediterranean and East Asia together show that lost or degraded wetlands can be rebuilt into highly productive duck habitats. Specifically, reflooding former floodplain lakes at Emiquon in Illinois rapidly generated over 3 million ducks and other waterbird use-days per year and more than 30% of regional use-days, demonstrating how restoring near-natural water regimes in a lost basin can instantly recreate key stopover and breeding habitat (Hagy *et al.*, 2017). Likewise, restoration of 38 shallow lakes in the highly drained Prairie Pothole Region of Iowa led to over 580,000 waterbirds and 78 species using restored lakes versus ~ 131,000 birds and 70 species on unrestored lakes, with semi-permanent basins, 40–50% emergent cover and large wetland area especially beneficial for ducks and other migrants (Vanausdall & Dinsmore, 2019). Similar wetlands restorations at East Dongting, Shengjin Lakes in China increased waterbird richness, functional diversity and densities of Anatidae, because mosaics of mudflats, sedge meadows and shallow water of varying depth were recreated, with planted or regenerating aquatic vegetation providing both food and cover (Zhou, Zhou, & Xu, 2020; Lei & Middleton, 2021; Zhang *et al.*, 2021).

While these global examples demonstrate the potential of wetland restoration for the conservation of waterbirds, the most direct example for the Marbled duck conservation lies in Spain, where the LIFE Cerceta pardilla project provided a valuable model for Marbled duck conservation. This project successfully restored over 3,600 hectares of wetlands, and included a population reinforcement programme through release of captive-bred individuals, leading to a substantial increase in the breeding population, with 172 breeding females and 1,427 chicks recorded in 2025, the highest levels recorded in two decades, and leading to the identification of new breeding areas in Andalusia, the Valencian Community, and the Region of Murcia (LIFE Marbled Teal project, 2024).

Replicating the restoration achievements of this project in Morocco would require, as a first priority, hydrological restoration. Rewetting drained systems and managing water levels can increase breeding habitat and abundance of ducks and other waterbirds . In Spain, targeted land acquisition, such as the purchase of 141 hectares at the El Espigar and La Raja estates in the El Hondo Natural Park, allowed for the removal of old irrigation infrastructure and the restoration of natural hydrology. Re-establishing seasonal flooding regimes or implementing environmental flow releases downstream of dams would help recreate dynamic, shallow water conditions similar to those recommended for Marbled ducks in El Hondo, where regulated water levels through the breeding season are needed to avoid nest flooding or rapid drawdown and to maintain brood habitat (Sebastián-González et al., 2013). Furthermore, the restoration of two old river meanders in the Brazo del Este Natural Area generated 50 hectares of essential refuge areas that sustain the ducks during unfavorable dry years, a concept that directly supports our Chapter 4 findings regarding the species' reliance on drought refugia. Given the species' reliance on highly modified and anthropogenic habitats in Morocco, this highlights the importance of establishing water management agreements with local irrigation stakeholders. These agreements, mirroring the successful models used with Spanish irrigation communities, are vital to ensure proper water circulation, maintain optimal flooding levels, and prevent eutrophication, specifically during the ducks' breeding season.(Fox *et al.*, 2025)

Beyond hydrological management, managers should restore the habitat's vegetation to maximize reproductive success and mitigate direct threats within these wetland networks. Restoring emergent vegetation stands such as Phragmites, Typha, Juncus and Scirpus directly addresses the habitat requirements identified in Chapter 2, as breeding females prefer densely vegetated, shallow ponds and avoid open water for brood-rearing . Consequently, management measures must limit the cutting or clearance of emergent vegetation during the breeding season. Additionally, as shown by the Spanish project, construction of artificial nest boxes and earthen breeding islets can provide predator-free zones for nesting and roosting, an approach shown to increase site attractiveness and breeding success for waterbirds in Mediterranean wetlands, without creating ecological traps . Finally, these structural improvements must be coupled with strict threat mitigation. To prevent newly restored sites from becoming ecological traps, Moroccan wetland management may incorporate strategies to decrease predator impact. Depending on the context, it may include protective fencing and capture-translocation programs targeting specifically free-ranging feral dogs and/or wild boars to protect nesting females and broods, as well as measures to prevent egg collection, a pressure documented in several Moroccan wetlands (see future directions section E below). (Sebastián-González *et al.*, 2013; Cherkaoui, Selmi, & Hanane, 2017)(Schwartz *et al.*, 2023)(Barasona *et al.*, 2021)

2.2.2. Priority sites for restoration and conservation

The Marbled duck habitat restoration and conservation measures in Morocco could be prioritised toward historically critical wetlands experiencing severe, ongoing degradation. At El Hotba marsh, habitat restoration should prioritize immediate threat mitigation, specifically by limiting overgrazing, vegetation cutting, and human disturbance during the breeding season. While active hydrological restoration is clearly needed to reverse the recent decline in water surface area, any physical intervention would benefit from being preceded by a thorough hydrological assessment to understand the exact drivers of water loss, whether climatic or anthropogenic. Similarly, reversing the degradation at Sidi Boughaba Lake requires immediate watershed-level policy enforcement. As recommended by Moukrim et al. (2025), this would include implementing strict regulations on groundwater pumping in the surrounding agricultural perimeters to halt the transition of permanent water bodies into seasonal ones. This could be complemented with the delimitation of buffer zones around the Ramsar perimeter to prevent further urban expansion from encroaching upon the wetland.

In addition, restoration strategies can look beyond existing degraded wetlands and also target the restoration of historically important sites that have been entirely lost, particularly in the Gharb region. This landscape-scale restoration can be guided by the recent work of Guelmami (2024), who utilized Earth Observation approaches to map over 7,000 km² of “potentially restorable wetlands” within the Sebou basin including numerous former temporary ponds that could be recreated with low to moderate effort. This spatial framework provides a direct, evidence-based pathway to identify and restore vanished marshland systems, such as Merja Boukka, Dawra, Merja Sidi Mohamed Ben Mansour, and the lower Loukkos marshes, which used to be important for the Marbled duck and other threatened Anatidae. This same remote-sensing approach can be extended nationwide to identify restorable habitats across other highly altered landscapes, such as the Middle Atlas and Souss region. Encouragingly, this type of large-scale hydrological restoration is already underway in Morocco, as evidenced by the ongoing project to restore Dayet Aoua in the Middle Atlas by Living Planet Morocco (Living Planet Morocco, 2024*a*).

2.3. Strengthening wetland protection in a changing climate

Strengthening the protection of key wetlands represents a second critical axis for the conservation of Marbled duck in Morocco. Formal designations such as Ramsar sites, Sites of Biological and Ecological Interest (SIBE), and Important Bird and Biodiversity Areas (IBA) have been shown to significantly improve wetland condition and waterbird populations (Gaget *et al.*, 2020). Analyses of more than 200 Moroccan wetlands indicate that, following Ramsar or SIBE designation, waterbird richness and abundance increased more rapidly in protected sites than in non-designated wetlands (Kleijn *et al.*, 2014). Similarly, at several Atlantic coastal wetlands, including Ad-Dakhla, Khnifiss and Souss, the establishment of strictly protected areas (National Parks and Protected Reserves under IUCN Category II) reversed previous declines and led to rapid increases in waterbird species richness and density (Cherkaoui *et al.*, 2018).

Despite this evidence, several wetlands identified in this thesis as supporting important breeding and wintering populations of the Marbled duck currently lack formal protection status (Table 1). Among these, Oued Tensift stands out as a priority candidate for designation, given the high numbers of broods recorded there during surveys. This protection deficit is not limited to Morocco. A recent gap analysis across 24 Mediterranean countries identified over 150 wetlands of international importance for wintering waterbirds that remain outside the Ramsar network (Popoff *et al.*, 2021), highlighting the scale of the challenge at the regional level. Moreover, given its Vulnerable status, the Marbled duck could represent a useful flagship species for guiding future wetland designation efforts in Morocco and the broader Mediterranean region (Simberloff, 1998).

In addition to strengthening the protected area network, climate change represents an increasing threat to the long-term viability of the Moroccan wetlands (Pérez-Cutillas & Salhi, 2024). The Mediterranean region is recognised as a climate change hotspot, where projected increases in temperature and aridity are expected to reduce surface water availability and shorten hydroperiods, particularly for shallow seasonal wetlands which represent the habitat type most important for the Marbled duck (Lefebvre *et al.*, 2019; Grillas *et al.*, 2021). Thermal adjustment of waterbird communities to climate warming is hampered by habitat conversion, which increases their climatic debt, whereas protected areas facilitate this adjustment by reducing additional anthropogenic pressures (Verniest et al., 2023). This interaction between climate vulnerability and protection status has direct implications for Morocco, where unprotected sites along the coast of North-West Africa were identified among those facing the highest thermal adjustment limitations under future climate scenarios (Verniest *et al.*, 2023). Furthermore, wetlands of international importance for waterbirds are more exposed to sea-level rise than other coastal wetlands (Verniest et al., 2024), meaning that coastal Moroccan sites might face compounding threats from both rising seas and inadequate legal protection.

These climatic pressures are likely to intensify existing conflicts over water resources (Kaiss *et al.*, 2025; Arnáez *et al.*, 2026). As surface water availability declines across the Mediterranean region, competition between conservation needs and human demands, including agricultural irrigation and urban water supply, may increase, potentially undermining wetland conservation efforts (Arnáez *et al.*, 2026). Water scarcity is already a significant challenge in Morocco, where agriculture accounts for approximately 85% of the country's water consumption (Arab Center, 2025). Integrating minimum ecological flow requirements into water governance frameworks, including river basin management plans and irrigation concession agreements, represent a key step toward reconciling competing demands on water resources. Ecological flows have proven effective in multiple river systems globally, with documented benefits for freshwater biodiversity, wetland connectivity, and ecosystem services (Arthington *et al.*, 2024). Encouragingly, a national guide on ecological flow has recently been developed through a partnership between the Directorate of Water Research and Planning, Living Planet Morocco, and international partners, aiming to define procedures for determining, applying, and maintaining ecological flow downstream of hydraulic structures in Moroccan watercourses (Living Planet Morocco, 2024*b*). Integrating this guide into the operational management of dams and river diversions affecting key Marbled duck habitat would represent a concrete step toward conserving the species' habitat.

A key consideration for the conservation of the Marbled duck is the existence of spatially structured functional units. As shown in Chapter 3, individuals may adopt two spatial strategies when using wetlands: some rely on multifunctional sites where both roosting and feeding occur, while others commute regularly between spatially distinct roosting and foraging wetlands. This behaviour has important implications for conservation planning, as strategies based solely on observations collected at a single site or during daytime surveys may overlook key habitats used by the species. While large protected wetland complexes, such as Ramsar sites in Morocco, are often extensive to encompass both roosting and foraging habitats, management within these complexes may not adequately account for nocturnal habitat use or foraging areas located outside protected boundaries. The data collected in Chapter 3 provide an example of this limitation: one individual tracked within the Sidi Moussa-Oualidia Ramsar complex undertook daily foraging flights of approximately 28 km to a sewage-fed wetland located outside the protected area boundary, returning to roost within the Ramsar site (Fig. 2).

Figure 2. *Daily commuting flights of a GPS-tagged Marbled duck between its roosting site within the Sidi Moussa-Oualidia Ramsar complex (A) and a wastewater fed wetland located outside the protected area boundary (B). Yellow lines represent individual GPS-recorded movement*

Similar patterns of spatially separated roosting and foraging functions have been documented in other waterbird systems. For example, shorebirds in the Yellow Sea depend on intertidal mudflats for feeding and supratidal ponds for roosting, leading to recommendations that these habitats be managed as interconnected ecological units (Jackson *et al.*, 2019). Nomadic ibis and spoonbills in Australia similarly exhibit distinct day-night habitat requirements, reinforcing the need to incorporate both roosting and foraging sites into conservation planning (McGinness *et al.*, 2024).

Within such networks, multifunctional wetlands that support both roosting and foraging may act as critical nodes. As shown in Chapter 3, Marbled ducks may adopt two distinct spatial strategies, some individuals relying on multifunctional sites while others commuting between spatially distinct roosting and foraging areas, a pattern also documented in other dabbling duck species such as Eurasian Teal . Recognising both natural and anthropogenic wetlands as components of these functional networks, as illustrated by the individual commuting 28 km from the Sidi Moussa-Oualidia Ramsar site to a sewage-fed wetland (Fig. 2), and managing them to maintain appropriate water levels, vegetation structure, and low disturbance levels, would therefore be important for sustaining Marbled duck populations. Finally, the context-dependent role of anthropogenic features such as roads and artificial light, sometimes facilitating nocturnal foraging but often generating disturbance and noise, highlights the need for nocturnal management, including limiting nocturnal disturbance, managing soundscapes, and preserving buffer zones around key wetlands .(Guillemain *et al.*, 2010)(Wu *et al.*, 2020)

2.4. Sustainable management of key anthropogenic habitats

As shown in chapter 4, anthropogenic wetlands, mainly dams, wastewater treatment plants and effluent-fed wetlands, constitute an important habitat of the Marbled duck. They should be also considered into Marbled duck conservation strategies, and management should make them safer and more suitable throughout the year. Studies across the globe show that artificial wetlands can support high waterbird richness and abundance when water depth, seasonal water-level regimes, vegetation structure, and disturbance are actively managed, and when they complement, rather than replace, natural wetlands . At key Moroccan reservoir/dams used by Marbled duck (Table 1 and Table 2), such as Mohamed V, Moulay Abdellah, and El Massira, it would be worth exploring how operating rules could be adjusted so that water level regimes follow more natural seasonal patterns, while remaining within the operating range required for energy production. Specifically, relatively high water levels in winter and spring followed by a gradual recession during the breeding period could help avoid nest flooding and maintain shallow brood-rearing areas. Combining such water-level management with targeted planting and protection of emergent and submerged vegetation can substantially expand nesting and foraging habitat, because many current regulation schemes keep water too high in winter and too low in summer, suppressing plant growth and reducing habitat heterogeneity . Shoreline reprofiling, creation of shallow shelves or vegetated islands, and local sediment-stabilisation structures can further restore ecotones and reedbeds that benefit waterbirds in regulated lakes . (Ma *et al.*, 2010; Qiu *et al.*, 2021; Ferreira *et al.*, 2024; Xu *et al.*, 2024)(Qiu *et al.*, 2021)(Fujimoto *et al.*, 2025)

Beyond dams, sewage treatment plants and effluent-fed wetlands are increasingly important for the Marbled duck in Morocco. Experiences from Africa, Europe and Australia show that, when nutrient rich water, macrophyte cover and disturbance are carefully managed, these systems can support high waterbird diversity. Evidence from a 20-year adaptive management study at a Ramsar-listed wastewater treatment plant in Australia showed that waterfowl numbers declined when nutrient-rich sewage inputs were replaced by cleaner recycled water, and increased again when moderate nutrient inputs were restored. Waterfowl abundance was positively related to moderate concentrations of ammonia (optimal: 20-30 mg N/L), nitrite (0.7 mg N/L), and phosphorus (18-41 mg P/L), with near-zero densities in nutrient-poor water and declines only at very high concentrations (Loyn et al., 2023). These nutrient loads likely sustain aquatic invertebrate and plant communities that form a major component of the birds' diet. The same study showed that later treatment stages (maturation and storage ponds), consistently supported higher waterbird densities and diversity than early treatment ponds, providing clear guidance for habitat design. Comparable patterns have been reported along the Nile in Egypt, where older pond-based treatment systems with open water and overflow basins support far richer and more abundant bird communities than modern, fully closed high-efficiency plants, emphasising that technical upgrades can inadvertently reduce habitat value if open-water units are not retained (Noby *et al.*, 2025).

The Australian study showed that waterfowl numbers fluctuated strongly with continental rainfall patterns, declining when extensive inland flooding created widespread alternative habitat and increasing when inland wetlands dried (Loyn et al., 2023). During major droughts (e.g. 2010–2011, 2016, 2020), the treatment plant functioned as a critical refuge, supporting large aggregations of waterfowl when many natural freshwater systems were unavailable. This was further illustrated by another study from the Bolivar wastewater treatment plant in South Australia (Breed *et al.*, 2020). During 2018–2020, which included one of the driest years on record in the Murray-Darling Basin, Bolivar regularly held several thousand ducks per visit, with mean counts of ~9,800 waterbirds and periodic peaks exceeding 7,000 Pink-eared ducks and 2,000 Grey teal; two nomadic dabbling duck species that that show ecological similarities with the Marbled duck in their opportunistic tracking of ephemeral resources (Kingsford, Roshier, & Porter, 2010). Both species are known to disperse widely from the arid and semi-arid zone during dry phases and to move to coastal refuge sites, then return inland to breed once conditions improve (Roshier, Asmus, & Klaassen, 2008). At Bolivar, high numbers of Pink-eared ducks and Grey teal in 2019 coincided with severe inland drought, whereas their numbers declined sharply following the breaking of the drought and likely dispersal back to inland breeding areas. Together with results from the Western Treatment Plant study, this reinforces that wastewater treatment wetlands can function as critical refuge nodes for nomadic Anatidae during dry periods, concentrating large numbers of individuals that have abandoned failing inland wetlands.

These findings provide a useful framework for the management of anthropogenic wetlands used by Marbled duck in Morocco. These systems require careful monitoring of potential ecological and sanitary risks. As discussed in detail in Chapter 4, waterbirds foraging and breeding in anthropogenic wetlands may be exposed to a diverse range of contaminants with potential consequences for health and population dynamics . In contrast to well-regulated systems such as the Western Treatment Plant , where strict effluent standards and water quality monitoring are in place, balancing biodiversity objectives with public health and coastal ecosystem protection, many North African wetlands receiving untreated or partially treated wastewater lack systematic monitoring. Regular monitoring of water quality and disease risk, including pathogen loads, contaminant levels in water and sediments, and health indicators in waterbird populations, is therefore essential, particularly for Moroccan sites such as Oued Tensift, Saqia El Hamra, and Merja Fouarate. Such monitoring could be integrated into adaptive management frameworks involving collaboration between water authorities, conservation agencies, and public health institutions. As emphasised by Murray & Hamilton (2010), anthropogenic wetlands should not be considered substitutes for natural wetlands, and reliance on them should not compromise broader wetland conservation efforts. Their long-term conservation value will ultimately depend on the extent to which biodiversity benefits can be balanced with water treatment objectives and ecological risk mitigation.(Murray & Hamilton, 2010)(Loyn et al., 2023)

The three complementary axes discussed above: restoring natural wetlands, strengthening wetland protection, and managing anthropogenic habitats, and their key management components are summarised in Figure 3.

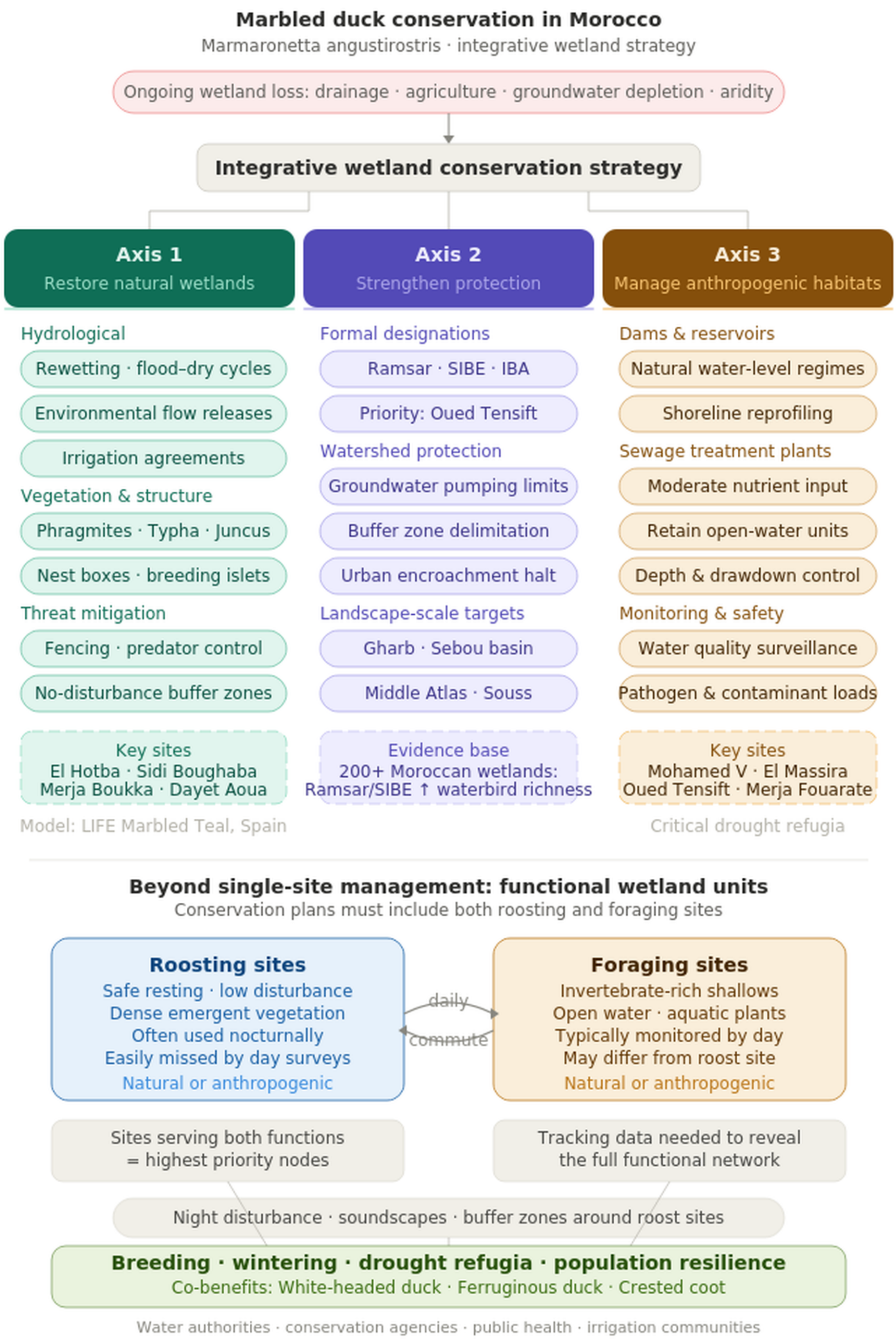

Figure 3. *Illustrative synthesis of conservation priorities for the Marbled duck in Morocco emerging from this thesis, structured around three complementary axes.*

3. Future directions

3.1. From Marbled duck to multispecies wetland monitoring

Assessing the effectiveness of the conservation actions outlined above will require long-term monitoring frameworks capable of detecting population trends and evaluating responses to management interventions . The probabilistic sampling framework developed in Chapter 2 could serve as a repeatable basis for assessing population size across large spatial scales and for enabling reliable comparisons through time. Importantly, this approach could be extended to adopt a multispecies monitoring perspective , as many wetlands used by the Marbled duck also host other breeding waterbirds of conservation concern, including the Ferruginous duck, White-headed duck, and Common Pochard. Multispecies survey designs and hierarchical community models have proven efficient for estimating abundance or occupancy of multiple waterbird and seabird species while sharing information across species, explicitly modelling detection, and generating composite indicators and trend estimates over time . When coupled with exhaustive targeted surveys of known important sites, this probabilistic framework could further help identify wetlands of national importance for breeding waterbirds and guide conservation actions such as habitat protection, restoration programs, or targeted management interventions , while accounting for the nomadic behaviour of the species and the potential discovery of new breeding sites as discussed above. (Nichols & Williams, 2006)(Guillemain *et al.*, 2025)(Whitlock, Lewis, & Peterson, 2020; Thaxter et al., 2025)(Adde *et al.*, 2020)

3.2. Habitat variables and mapping of suitable breeding habitat

One of the main limitations identified in Chapter 2 was the lack of fine-scale habitat layers, which constrained the extrapolation of brood abundance to the national scale. In the absence of such layers, population estimates relied solely on total wetland surface area, implicitly assuming that sampled and unsampled wetlands shared similar habitat characteristics. However, breeding suitability for the Marbled duck is likely determined by a combination of environmental factors including wetland type, hydroperiod, water depth, salinity, vegetation structure, and surrounding land use. Developing national-scale spatial layers describing these variables would therefore represent a major step toward improving population extrapolation and habitat-based conservation planning as demonstrated in other parts of the world . Advances in remote sensing now provide tools to generate such habitat layers. Satellite-derived indices such as NDVI and related vegetation metrics can be used to characterize vegetation structure, while other spectral products can provide information on water presence, wetland hydroperiod, and landscape context. In particular, emergent vegetation cover, mainly Typha sp., Phragmites sp., and Juncus sp., are a key component of breeding habitat for the Marbled duck and many other species . Proxies of emergent vegetation derived from satellite imagery, such as the Leaf Area Index (LAI), could be used to infer emergent vegetation density and spatial distribution at the national scale, enabling the construction of habitat suitability models capable of identifying potential breeding areas for the Marbled duck across Morocco . More broadly, these datasets could support multispecies habitat modelling approaches aimed at identifying wetlands of high conservation value for waterbird communities . Integrating habitat suitability modelling with probabilistic monitoring frameworks could further improve the detection of new breeding occurrences by incorporating prior species distribution information into the sampling design, an approach that has been shown to increase sampling efficiency for rare and elusive species . By compiling historical breeding-wetland records and overlaying them with current breeding records and hydrological, climatic, and land-use data, it would be possible to identify wetlands where rewetting, restoring emergent vegetation, or modifying water management could recreate suitable breeding habitat and re-establish functional wetland networks at national and Mediterranean scales .(Maleki *et al.*, 2016; Hamza *et al.*, 2024)(Ju & Bohrer, 2022; Koma *et al.*, 2022)(Hawman, Mishra, & O'Connell, 2023)(Sahour, Kemink, & O'Connell, 2021)(Chiffard *et al.*, 2020)(O'neal, Heske, & Stafford, 2008; Jr *et al.*, 2017; Duan *et al.*, 2020)

3.3. Demographic monitoring and data integration

A priority for future research would be to develop a demographic monitoring programme for the Marbled duck in Morocco. Breeding success and population size can fluctuate considerably between years due to variation in rainfall, hydrological conditions, and habitat availability, highlighting the need to link climate and hydrology with demographic responses . Long-term monitoring programs spanning multiple years will therefore be essential to capture interannual variability in breeding output and to assess population trends . In addition, incorporating demographic parameters such as nest success, brood survival, and fledgling recruitment would allow a more comprehensive assessment of the factors shaping population viability . Developing the appropriate field and analytical tools to estimate these parameters represents a critical next step. Capture-mark-recapture approaches based on ringing could provide robust estimates of survival and site fidelity, while brood survey protocols such as those implemented in Chapter 2 could contribute estimates of breeding success and recruitment. These parameters are subject to multiple sources of uncertainty, including interannual stochasticity, individual heterogeneity, and imperfect detection. Integrated population models (IPMs), which jointly analyse data from different sources within a unified statistical framework, offer a powerful approach to reducing this uncertainty and identifying which vital rates most strongly drive population dynamics . By simultaneously incorporating annual counts from monitoring programmes, survival estimates from tagged individuals, and productivity data from brood surveys such as those implemented in Chapter 2, an IPM could provide more precise estimates of population growth rate.(Ramírez *et al.*, 2018; Zhao, Boomer, & Royle, 2019)(Martínez-Abraín *et al.*, 2016)(Jarrett, Lehikoinen, & Willis, 2024)(Schaub & Abadi, 2011)

Such demographic studies could be complemented by advances in movement ecology. Modern biologging has enabled remote estimation of key demographic parameters (e.g. breeding performance, nest survival) and life-history states by combining high-resolution GPS and acceleration data . As demonstrated in Chapter 3, behavioural classification using machine learning approaches provides new opportunities to identify fine-scale habitat use patterns and activity budgets. Applying these approaches to breeding individuals may help identify nesting microhabitats, brood-rearing areas, and movement patterns between key habitats during the breeding season. Integrating demographic monitoring with behavioural and movement data would therefore provide a powerful framework for understanding how habitat conditions influence reproductive success and population dynamics, and for predicting population responses to environmental change.(Ferraz *et al.*, 2024; Lok *et al.*, 2025)

3.4. Regional connectivity and implications for the Moroccan population

The conservation of the Marbled duck cannot be fully understood within the boundaries of a single country, as the species forms part of a broader western Mediterranean population whose dynamics likely depend on movements across multiple regions. Recent tracking studies have revealed movements between Spain and Morocco (Pacheco-Guardiola *et al.*, 2025), providing direct evidence of trans-Mediterranean connectivity. Of 144 GPS-tagged individuals, only 18 crossed into Africa, and the majority were wild-born (n = 14), with only four originating from the captive breeding programme, indicating that long-distance dispersal is reduced in captive birds. Similarly, one individual ringed in the Sidi Moussa-Oualidia complex during this thesis was subsequently observed as part of a pair in Cadiz, Spain later in May, further supporting the existence of regular individual movements between Moroccan and Spanish populations. However, very little is currently known about movements between Morocco and other North African countries such as Algeria and Tunisia, and the broader spatial structure of the regional population remains poorly characterised. Expanding satellite tracking programmes across these regions would therefore be a major priority for future research. Tagging individuals across multiple breeding and wintering sites would allow researchers to better understand pre- and post-breeding dispersal, migratory strategies, and the role of key wetlands as stepping stones within broader habitat networks (Merken *et al.*, 2015; Pacheco-Guardiola *et al.*, 2025). Such data would also support the development of coordinated conservation strategies across countries (Lambertucci *et al.*, 2014).

The trans-Mediterranean connectivity also raises an important conservation question regarding the potential consequences of dispersal of captive-bred Spanish individuals for the genetic integrity of the Moroccan wild population. The genomic assessment of Ortego et al. (2024) provides a critical reference point. Populations from Spain and Iraq were assigned to distinct genetic clusters, and the captive populations from the two Spanish restocking centres showed genetic introgression from European zoo stocks, which were themselves founded with birds originating from the genotypically distinct Iraqi population. However, introgression from zoo stock into the contemporary wild population from Spain appears limited, suggesting captive-bred birds have restricted breeding success in the wild (Ortego *et al.* 2024). To date, the Moroccan population has not been genetically characterised; only three museum specimens from the 1926–1957 period were available and whether it constitutes a distinct management unit relative to the Spanish population remains essentially unknown. If Moroccan birds harbour locally adapted genotypes shaped by North African environmental conditions, introgression of captive-derived genetic material including contributions from geographically distant Iraqi zoo stocks could have adverse consequences for their adaptive potential (Champagnon *et al.*, 2012). The broader waterfowl literature offers a significant parallel: in Camargue (France), Champagnon *et al.* (2013) found significant rates of hybridization between wild and captive-bred mallards following decades of large-scale releases, and warned that, if continued at such scale, releases could irreversibly compromise the genetic structure and composition of European wild populations. While the scale of Marbled duck releases is far smaller, the underlying dynamic of uncontrolled gene flow from captive-adapted genotypes into locally adapted wild populations is analogous, and concerning given that current monitoring provides no means of detecting whether such processes are already underway in Morocco.

Addressing these uncertainties requires a proactive approach. Genetic characterisation of the Moroccan population is required to verify that is is not distinct from the spanish populations and establish a baseline against which future change can be detected. In this context, feather samples collected from 11 wild individuals during this thesis provide an initial foundation for future genomic analyses, which could help determine the genetic structure of the Moroccan population and assess its distinctiveness relative to the Spanish population. More broadly, these findings underscore the need to apply a transboundary perspective to Marbled duck conservation across the Western Mediterranean, ensuring that future captive breeding and release strategies formally account for the potential genetic consequences on North African populations.

3.5. Integrating ecological and social research

Addressing many of the threats affecting Marbled duck breeding habitats will likely require integrating ecological research with social and human-dimension studies. In Morocco and more broadly in the Maghreb region, there is a lack of information on local perceptions, attitudes, and interactions with waterbirds. Illegal killing has been identified as a major threat to waterbirds across the Mediterranean basin, with an estimated 11–37 million birds killed annually, including between 23,400 and 125,000 individuals in Morocco alone (Brochet *et al.*, 2016, 2019). In addition, egg harvesting has been reported in several Moroccan wetlands (Green *et al.*, 2002; pers. obs.), particularly by local communities, although its extent, motivations, and demographic impact remain poorly understood. Observations during this study suggest that such practices, including egg collection, vegetation cutting, and disturbance, may affect breeding success in some sites.

Future research would therefore benefit from incorporating social science approaches, such as semi-structured interviews and participatory surveys with local communities living near wetlands, to better understand the socio-economic and cultural drivers of these behaviours. Such studies could help quantify the intensity of pressures such as illegal killing and egg harvesting, identify their underlying motivations, and assess potential conflicts between conservation objectives and local livelihoods. This information would be valuable for designing effective conservation interventions, including awareness programs, participatory management, or community-based conservation strategies. Importantly, integrating social and ecological data would also allow the demographic consequences of these pressures to be evaluated. Quantifying harvest levels and disturbance could enable their incorporation into population models, such as matrix population models or integrated population models, to assess their impact on survival, reproduction, and population viability. Ultimately, combining ecological monitoring with social research offers a powerful framework for developing sustainable conservation strategies that both reduce pressures on Marbled duck populations and promote local engagement in wetland conservation.

4. Conclusion

This thesis provides a comprehensive, multi-scale assessment of Marbled duck ecology and conservation in Morocco, combining population monitoring, movement ecology, and habitat use analysis across spatial scales ranging from individual wetland complexes to the national and regional level. The results establish a demographic baseline for the Moroccan breeding population, reveal the importance of functional wetland networks encompassing both natural and anthropogenic habitats, and highlight the vulnerability of the species to ongoing wetland loss, climatic aridity, and growing importance of anthropogenic wetlands in its habitat use. Together, these findings provide a scientific foundation for the development of a national action plan and underscore the need for a transboundary conservation perspective that extends beyond Moroccan borders. Translating this knowledge into effective conservation action will require long-term demographic monitoring, habitat restoration, strengthened wetland protection, and the integration of social and human dimensions into management strategies. Ultimately, the conservation of the Marbled duck in Morocco represents a broader challenge, whose resolution will benefit not only this species but the wider waterbird communities that depend on these threatened ecosystems.

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Appendix

Remote sensing analysis of long-term hydrological dynamics at El Hotba marsh was conducted using the Landsat satellite archive within the Google Earth Engine (GEE) platform. We used Landsat Collection 2 Level-2 surface reflectance imagery from Landsat 4, 5, 7, 8 and 9, providing continuous coverage from 1983 to 2023 at a spatial resolution of 30 m. Images intersecting the wetland polygon were filtered and preprocessed by applying USGS surface reflectance scaling factors and masking clouds. Hydrological dynamics were quantified separately for two ecologically relevant periods: the breeding season (May-August) and the wintering season (September-March). Open-water surfaces were identified using the Modified Normalized Difference Water Index (MNDWI), calculated as (Green − SWIR1) / (Green + SWIR1), and pixels with MNDWI values greater than 0.1 were classified as water. Water extent was then calculated by summing the area of all water-classified pixels within the El Hotba marsh polygon (pixel size 30 × 30 m) and expressed as the percentage of the wetland area covered by water. This produced annual estimates of seasonal water availability from 1983 to 2023 for both breeding and wintering periods. To facilitate comparisons of water extent between periods were visualized using median annual composites and corresponding water masks.

Résumé substantiel

Introduction Générale

La biodiversité décline à un rythme alarmant sous l'effet combiné de plusieurs pressions comme la destruction des habitats, la surexploitation des ressources, et les changements climatiques. Parmi les milieux les plus affectés figurent les zones humides qui, bien qu'elles ne couvrent que moins d'1 % de la surface terrestre, abritent plus de 10 % de toutes les espèces connues. Environ 85 % de la superficie des zones humides existante au XVIIIe siècle a aujourd'hui disparu, et 65 % des zones humides restantes subissent des pressions humaines modérées à élevées. Dans le bassin méditerranéen, l'un des points chauds ("hotspot") de biodiversité les plus importants au monde; les zones humides ne couvrent qu'une faible proportion, mais elles détiennent plus d'un tiers de sa richesse spécifique. Les zones humides naturelles méditerranéennes ont diminué de près de moitié depuis les années 1970, tandis que les zones humides artificielles se sont étendues grâce à la construction de barrages et d'infrastructures hydrauliques. Cette transformation est particulièrement marquée au Maroc, où les zones humides artificielles représentent aujourd'hui environ 38 % de la superficie totale. Combinées à la pollution des eaux et à l'expansion urbaine, ces transformations ont négativement affecté le fonctionnement de ces milieux, menaçant ainsi les espèces qui en dépendent.

Les oiseaux d'eau comptent parmi les groupes les plus touchés par ces transformations. Plusieurs espèces dépendent des zones humides tout au long de leur cycle annuel pour la reproduction, l'hivernage et les haltes migratoires. Dans les régions arides et semi-arides, où la disponibilité en eau varie fortement dans l'espace et dans le temps, de nombreuses espèces ont développé des stratégies de déplacement flexibles, nomades, afin d'exploiter ces habitats temporaires et imprévisibles. Cette plasticité écologique rend difficile le suivi de ces populations et l'interprétation de leurs dynamiques, ce qui rend par conséquent difficile d'évaluer leurs statuts et de mettre en place des mesures de conservation.

La Marmaronette marbrée *(Marmaronetta angustirostris*) illustre parfaitement ces défis. Inscrite à l'Annexe I de la Convention sur les espèces migratrices (CMS), cette espèce quasi menacée occupe une aire de répartition fragmentée à travers son aire de distribution. La population de la Méditerranée occidentale, classée sous les catégories AEWA 1a et 1c, pour laquelle le Maroc représente une région essentielle de son aire de distribution, a connu un déclin marqué au cours des dernières décennies, principalement en raison de la perte des zones humides à cause du drainage, de la consommation de l'eau par les activités agricoles et des pressions anthropiques, comme le braconnage. Malgré cela, plusieurs dimensions essentielles de son écologie demeurent encore insuffisamment documentées, notamment des estimations fiables de la taille des populations, les stratégies de déplacement et l'utilisation de l'habitat sous des conditions climatiques variables, en particulier en Afrique du Nord.

Dans ce contexte, et pour combler ces lacunes, cette thèse mobilise deux cadres méthodologiques complémentaires structurés en 3 chapitres. Le premier cadre concerne l'estimation de la taille de la population nicheuse en tenant compte de la détection imparfaite, à l'aide d'un échantillonnage probabiliste analysé avec des modèles hiérarchiques. Cette approche probabiliste prend en compte le caractère nomade de l'espèce, et permet d'estimer l'abondance, puis d'extrapoler ces estimations à des zones non échantillonnées pour estimer la taille de population nicheuse au Maroc. Par ailleurs, les indicateurs d'habitats privilégiés par l'espèce pour sa reproduction sont identifiés.

Le second cadre repose sur l'exploitation des données issues de la télémétrie GPS et de l'accélérométrie tri-axiale. Ces outils permettent non seulement de localiser les individus, mais aussi de caractériser leurs comportements, d'identifier l'organisation fonctionnelle de l'espace et d'analyser l'utilisation des habitats à différentes échelles. Cette approche constitue la base des chapitres 2 et 3, consacrés respectivement à l'organisation comportementale et spatiale des individus en période non reproductrice, puis à l'utilisation des zones humides naturelles, artificielles et accidentelles en fonction des conditions climatiques.

Ensemble, ces trois chapitres apportent une vision complémentaire de l'écologie de l'espèce contribuant à mieux comprendre le statut de la population, son écologie spatiale et l'utilisation de son habitat. La discussion générale synthétise ces résultats afin d'en dégager les implications pour la conservation de l'espèce, notamment en matière de restauration et de protection des habitats, d'évaluation du rôle des zones humides anthropiques dans un contexte de déficit croissant en eau, et de définition des priorités futures de recherche.

Chapitre 1 : Estimation de la taille de la population nicheuse de la Marmaronette marbrée au Maroc

Les estimations fiables de la taille des populations comptent parmi les métriques les plus importantes en écologie de la conservation, constituant le fondement des évaluations de la Liste Rouge de l'UICN, des désignations de sites Ramsar et des plans nationaux de conservation. Ces estimations restent pourtant rares dans une grande partie de l'Afrique du Nord, où les contraintes logistiques, les infrastructures de suivi limitées et l'absence de protocoles d'inventaire standardisés rendent difficile l'évaluation du statut des espèces dépendantes des zones humides. C'est particulièrement le cas pour la Marmaronette marbrée, dont la population de Méditerranée occidentale a décliné de 46 % entre 2008 et 2018. Au Maroc, aucune estimation robuste de la taille de la population nicheuse à l'échelle nationale n'avait encore été établie, laissant une lacune critique dans les connaissances nécessaires à sa conservation.

Ce chapitre fournit la première estimation nationale des Marmaronettes marbrées nicheuses au Maroc. Les données ont été collectées sur deux années consécutives à l'aide d'un échantillonnage aléatoire à deux niveaux, dans lequel 35 unités d'échantillonnage primaires de 100 km² ont été sélectionnées aléatoirement à travers le pays, couvrant un large gradient latitudinal de l'oued Moulouya au nord jusqu'aux oueds sahariens au sud. Au sein de chaque unité primaire, des unités d'échantillonnage secondaires de 0,25 km² ont été prospectées (187 au total dans le Maroc), assurant une couverture large des différents types de zones humides au Maroc.

Afin de tenir compte de la difficulté inhérente à la détection des nichées, des modèles binomiaux hiérarchiques de type N-mixture ont été utilisés pour les analyses. Ces modèles estiment simultanément l'abondance réelle et la probabilité de détection à partir de données de comptages répétés, en distinguant explicitement la variation écologique de la distribution des nichées de la variation liée à l'observation. Le modèle retenu a estimé un total de 24 nichées sur les 47 km² de zones humides prospectées, avec une probabilité de détection moyenne de 0,71 (Intervalle de Credibilité (IC) à 95 %: 0,30–0,95), soulignant l'importance de prendre en compte la détection imparfaite dans les inventaires d'espèces difficiles à observer. Extrapolée à la superficie totale des zones humides nationales (748 km²), cette estimation a abouti à un effectif national de 382 nichées (IC 95 % : 280–484).

La végétation émergente s'est révélée être le prédicteur le plus important de l'abondance, en accord avec la forte association de l'espèce avec les formations denses de Phragmites, Typha et Scirpus pour la nidification et la dissimulation des nichées des prédateurs. Parmi les types de zones humides, les marais présentaient une abondance de nichées supérieures aux barrages, tandis que les rivières étaient associées à une abondance plus faible.

Ces résultats fournissent la première référence robuste de la taille de la population nicheuse au Maroc. Le cadre d'échantillonnage probabiliste et l'approche de modélisation développés ici pourraient être développés à d'autres espèces d'oiseaux d'eau et étendues à d'autres régions.

Chapitre 2 : Combinaison de l'accélérométrie et du suivi GPS pour caractériser les unités fonctionnelles de la Marmaronette marbrée

Comprendre où et quand les animaux s'alimentent, se reposent et se déplacent entre ces sites est au cœur de l'écologie du déplacement et de la conservation. Pour les espèces hautement mobiles, ces patrons demeurent toutefois difficiles à quantifier par les méthodes d'observation traditionnelles, en particulier lorsque l'activité se déroule la nuit ou dans des habitats difficiles d'accès. Les avancées récentes du bio-logging, notamment l'intégration de la télémétrie GPS et de l'accélérométrie tri-axiale, permettent désormais d'investiguer à fine échelle la manière dont les animaux organisent leur utilisation de l'espace. Chez les oiseaux d'eau, cette approche offre un cadre pour examiner le concept d'unités fonctionnelles, défini comme l'association spatiale entre des sites de repos diurnes, appelés zones de remise, et des zones d'alimentation nocturnes, appelées zones de gagnage. Ce concept revêt une importance particulière pour la conservation des oiseaux d'eau, dont certaines composantes de l'utilisation de l'espace peuvent être négligées dans la planification des mesures de protection.

Pour explorer ces questions, des données GPS et d'accélérométrie ont été collectées sur sixMarmaronettes marbrées sauvages suivies au Maroc durant la période d'hivernage. Plusieurs modèles d'apprentissage supervisé ont été entraînés sur un jeu de données annoté issu de trois oiseaux captifs, afin de classifier les données accélérométriques en cinq classes comportementales: vol, alimentation, autres activités en déplacement, lissage des plumes et repos. Le modèle le plus performant a atteint une précision globale de 89 % sur les oiseaux captifs, et a ensuite été appliqué aux données des oiseaux sauvages pour prédire leurs comportements et cartographier leur organisation spatiale.

Les analyses spatiales ont révélé une forte variation inter-individuelle dans l'organisation des unités fonctionnelles. Certains individus utilisaient des sites de remise et de gagnage spatialement distincts, avec des déplacements réguliers entre ces deux types de sites, tandis que d'autres utilisaient des zones humides multifonctionnelles au sein desquelles les deux comportements se produisaient dans le même espace. Ces résultats suggèrent que la Marmaronette marbrée adopte plusieurs stratégies d'utilisation de l'espace, reflétant une flexibilité comportementale face à la diversité des configurations de zones humides disponibles. Par ailleurs, les comportements présentaient un rythme nycthéméral marqué, avec un repos prédominant durant la journée et une alimentation principalement nocturne. Les sites de gagnage étaient caractérisés par des conditions environnementales et anthropiques spécifiques, avec la température, la densité de végétation (NDVI) et la distance aux routes comme les prédicteurs les plus importants.

Ces résultats soulignent la valeur de la combinaison des données GPS avec accélérométrie pour mieux comprendre l'organisation spatiale des oiseaux d'eau et les implications pour leur conservation. En particulier, ils mettent en évidence la nécessité de protéger des réseaux de zones humides spatialement connectées, intégrant à la fois des sites de remise et de gagnage, plutôt que de se concentrer sur des sites isolés. Cette approche constitue ainsi un outil pour améliorer la planification des mesures de conservation des espèces d'oiseaux d'eau mobiles, discrètes et difficiles à observer.

Chapitre 3 : Des zones humides naturelles aux zones humides alimentées par les eaux usées - utilisation de l'habitat dans un contexte semi-désertique

Les zones humides méditerranéennes sont de plus en plus modifiées en conséquence des modifications hydrologiques et de la raréfaction de l'eau, sous l'effet du changement climatique. Dans ce contexte, les zones humides artificielles se sont considérablement développées, reconfigurant profondément les paysages humides disponibles pour les oiseaux d'eau. Pourtant, la contribution de ces systèmes à l'écologie spatiale des oiseaux d'eau reste mal quantifiée, en particulier pour les espèces nomades dont l'utilisation de l'espace est hautement variable dans le temps et dans l'espace. Ce chapitre examine l'utilisation de l'habitat par la Marmaronette marbrée à travers un réseau de zones humides naturelles, artificielles et accidentelles (milieux humides formés involontairement comme conséquence indirecte d'activités anthropiques), en intégrant des données de suivi GPS d'individus capturés au Maroc et en Espagne et suivis à travers le Maroc et l'Algérie.

Les résultats montrent que les Marmaronettes marbrées exploitent un grand nombre de zones humides, avec une utilisation fortement dominée par les systèmes anthropiques, notamment les zones humides alimentées par les effluents des stations d'épuration et les barrages. En revanche, les zones humides naturelles représentaient une proportion plus faible de l'utilisation totale. Les conditions de précipitation saisonnière influencent également l'utilisation des habitats.

Ces résultats indiquent que les zones humides anthropiques constituent une composante importante de l'écologie spatiale de l'espèce et peuvent partiellement amortir les effets de la raréfaction croissante de l'eau dans les paysages méditerranéens. Cependant, malgré leur importance, les zones humides anthropiques ne peuvent être considérées comme un substitut fonctionnel aux zones humides naturelles. Leur utilisation soulève des questions écologiques non résolues, notamment concernant les risques potentiels liés à l'exposition aux polluants, à la présence d'agents pathogènes et à la transmission de maladies au sein de ces systèmes, dont les conséquences démographiques restent à quantifier.

Cette étude souligne le potentiel d'intégrer les zones humides anthropiques dans la planification de la conservation, tout en maintenant la protection et la restauration des zones humides naturelles comme priorité centrale. Elle met également en évidence la nécessité d'un suivi régulier de la qualité écologique et sanitaire des zones humides anthropiques utilisées par l'espèce, afin d'évaluer les risques associés à leur fréquentation et d'orienter les stratégies de gestion adaptées à l'échelle du réseau de zones humides marocain et nord-africain.

Discussion générale

Cette thèse visait à améliorer notre compréhension de l'écologie et de la conservation de la Marmaronette marbrée au Maroc en intégrant le suivi des populations, l'écologie du mouvement et l'analyse de l'utilisation de l'habitat à plusieurs échelles spatiales et temporelles. Les trois chapitres abordés dans cette thèse convergent vers un constat commun : les caractéristiques de l'habitat, comme la structure de la végétation, le type de zone humide et la disponibilité en eau, sont des déterminants centraux de l'utilisation des zones humides par l'espèce au Maroc.

Implications pour la conservation et la gestion

L'estimation nationale de 382 nichées constitue la première base démographique de référence pour l'espèce au Maroc. Ces résultats contribueront à l'élaboration d’une stratégie d'action nationale pour la conservation de la Marmaronette marbrée prévue dans les prochaines années. Le protocole d'échantillonnage probabiliste développé offre un cadre reproductible pour le suivi à long terme, permettant d'évaluer les tendances de population et l'efficacité des mesures de conservation. La combinaison des inventaires probabilistes avec les prospections sur 10 sites identifiés dans le cadre du programme LIFE Cerceta pardilla (LIFE19 NAT/ES/00090: 2021-2026) espagnol a permis d'identifier les sites les plus importants pour la reproduction au Maroc. Parmi ceux-ci, plusieurs (5 de 13) zones humides anthropiques ou alimentées par des eaux usées figurent parmi les plus productives, soulignant le rôle croissant de ces habitats pour l'espèce. À l'inverse, plusieurs zones humides historiquement importantes ont subi des pertes dramatiques liées aux altérations hydrologiques, à l'extraction des eaux souterraines et à la conversion agricole.

Les résultats du Chapitre 3 révèlent que les zones humides anthropiques, principalement les barrages, stations d'épuration et zones humides alimentées par les effluents, constituent une composante essentielle du réseau d'habitat de l'espèce, en particulier durant les années de sécheresse. Cette dépendance soulève des questions importantes concernant la qualité écologique et sanitaire de ces systèmes, notamment l'exposition potentielle des oiseaux à des agents pathogènes, des métaux lourds et des résidus pharmaceutiques, dont les conséquences démographiques restent à quantifier.

La conservation de la Marmaronette marbrée au Maroc repose sur trois axes complémentaires identifiés dans cette thèse. Le premier concerne la restauration des zones humides naturelles dégradées ou disparues, en s'appuyant sur les outils de télédétection pour identifier les sites restaurables comme ceux dans le bassin du Sebou. Des interventions hydrologiques prioritaires sont identifiées à El Hotba, Sidi Boughaba et dans la région du Gharb. Le deuxième axe porte sur le renforcement du statut de protection des zones humides clés. Plusieurs sites identifiés comme importants pour la reproduction ou l'hivernage de l'espèce sont actuellement dépourvus de protection formelle, notamment Oued Tensift. Le troisième axe concerne la gestion durable des habitats anthropiques, en particulier l'adaptation des règles d'exploitation des barrages pour favoriser des régimes hydrologiques plus naturels, et la mise en place d'un suivi régulier de la qualité de l'eau dans les zones humides alimentées par les eaux usées.

La question des unités fonctionnelles constitue une considération importante pour la conservation. Comme démontré au Chapitre 2, certains individus effectuent des vols d'alimentation quotidiens considérables entre leur site de remise et leur zone de gagnage. Un individu suivi dans le complexe Ramsar de Sidi Moussa-Oualidia effectuait ainsi des vols quotidiens d'environ 28 km vers une zone humide alimentée par les eaux usées située hors des limites de la zone protégée Ramsar. Cet exemple illustre les limites des stratégies de conservation centrées sur un seul site et souligne la nécessité de gérer des réseaux de zones humides intégrant à la fois les zones naturelles et anthropiques.

Perspectives de recherche

Plusieurs priorités de recherche ont été identifiées. Un programme de surveillance démographique dédié, combinant des approches capture-marquage-recapture et des suivis de nichées, permettrait d'estimer les paramètres vitaux clés, comme la survie, le succès reproducteur et le recrutement. L'intégration de ces paramètres dans des modèles de population intégrés (IPM) offrirait une approche adéquate pour relier les taux vitaux à la dynamique de population (Schaub & Abadi, 2011). Ces études pourraient être complétées par des approches de connectivité migratoire, combinant le suivi GPS, la classification comportementale et la télédétection de l'habitat. La connectivité trans-méditerranéenne, attestée par les études de suivi récentes et par la relecture en Andalousie d'un individu bagué dans le complexe de Sidi Moussa-Oualidia lors de cette thèse, soulève également des questions importantes concernant l'intégrité génétique de la population marocaine, considérant les lâchers massifs d’oiseaux issus de captivité en Espagne. La caractérisation génétique de cette population constitue une priorité, Des échantillons de plumes ont été collectés sur 11 individus capturés dans le cadre de cette thèse. Enfin, l'intégration de recherches sociales et humaines est indispensable pour mieux comprendre les pressions anthropiques sur les habitats de reproduction, notamment la collecte illégale d'œufs et le dérangement, et pour concevoir des stratégies de conservation participatives adaptées au contexte marocain

Conclusion

Cette thèse fournit la première évaluation multi-échelle de l'écologie et de la conservation de la Marmaronnette marbrée au Maroc. Les résultats établissent une base démographique de référence pour la population reproductrice nationale, révèlent l'importance des réseaux fonctionnels de zones humides englobant des habitats naturels et anthropiques, et soulignent la vulnérabilité de l'espèce face à la perte des zones humides, à l'aridité climatique et à la place croissante des habitats anthropiques dans son utilisation de l'espace. Ces résultats constituent un socle scientifique pour l'élaboration d'un plan d'action national et soulignent la nécessité d'une perspective de conservation transfrontalière. La conservation de la Marmaronnette marbrée au Maroc représente un défi plus large, dont la résolution bénéficiera non seulement à cette espèce mais aussi aux communautés d'oiseaux d'eau qui dépendent de ces écosystèmes menacés.

RÉSUMÉ

Les zones humides méditerranéennes comptent parmi les écosystèmes les plus menacés à l'échelle mondiale. Elles subissent des pressions croissantes liées aux prélèvements d'eau, aux changements d'usage des sols et à la raréfaction de la ressource hydrique sous l'effet du changement climatique. Ces pressions sont particulièrement aiguës en Afrique du Nord, où les oiseaux d'eau qui en dépendent présentent une vulnérabilité accrue. Parmi les espèces les plus concernées figure la Marmaronette marbrée (Marmaronetta angustirostris), une espèce quasi menacée, caractérisée par des déplacements nomades, et dont la population ouest-méditerranéenne a décliné de 46 % entre 2008 et 2018. Malgré cela, plusieurs dimensions de son écologie demeurent encore mal documentées, notamment la taille de sa population nicheuse, ses stratégies de déplacement et ses modalités d'utilisation de l'habitat. Les principaux objectifs de cette thèse sont donc d'établir une première référence robuste de la taille de la population nicheuse de la Marmaronette marbrée au Maroc; d'analyser la manière dont ses déplacements et son comportement sont structurés dans le temps et l'espace; et comment son utilisation de l'habitat est influencée par la variabilité climatique et par la transformation anthropique des zones humides, à travers trois chapitres complémentaires. Dans un premier chapitre, à l'aide d'un échantillonnage aléatoire à deux niveaux analysé par des modèles hiérarchiques, tenant compte de la détection imparfaite, nous avons estimé la population nicheuse nationale à 382 nichées [ICr 95 % : 280–484], fournissant la première estimation robuste à l'échelle nationale pour cette espèce au Maroc. La végétation émergente et le type de zone humide sont les principaux prédicteurs de l'abondance des nichées. Dans un second chapitre, en combinant télémétrie GPS et accélérométrie triaxiale, nous avons développé des modèles d'apprentissage supervisé permettant de classifier cinq catégories de comportements. La cartographie des zones de repos et d'alimentation révèle une organisation marquée entre remise diurne et alimentation nocturne, mais avec une forte variabilité interindividuelle dans l'utilisation fonctionnelle de l'espace. Enfin, dans un troisième chapitre, à partir du suivi de 24 individus capturés au Maroc et en Espagne, nous avons montré que le type de zone humide est le principal déterminant de l'utilisation de l'habitat, l'espèce utilisant majoritairement des zones humides d'origine anthropique. L'utilisation de l'habitat est également modulée par la pluviométrie. Dans son ensemble, ce travail apporte des connaissances nouvelles sur l'écologie spatiale de la Marmaronette marbrée en Afrique du Nord et fournit des bases scientifiques utiles à l'orientation des stratégies de suivi, de restauration et de conservation de l'espèce.

MOTS-CLÉS

Écologie de conservation, Marmaronnette marbrée, Zones humides méditerranéennes, Taille de population, Unités fonctionnelles, Utilisation des habitats.

ABSTRACT

Mediterranean wetlands are among the most threatened ecosystems globally, facing increasing pressures from water abstraction, land-use change, and climate-driven water scarcity. These pressures are especially acute in North Africa, where wetland-dependent waterbirds are especially vulnerable. Among the species most affected is the Marbled Duck (Marmaronetta angustirostris), a Near Threatened species characterised by nomadic movements, whose western Mediterranean population declined by 46% between 2008 and 2018. Despite this decline, several aspects of its ecology remain poorly understood, particularly in North Africa, including the size of its breeding population, its movement strategies, and its patterns of habitat use. The main objectives of this thesis were therefore to establish a first robust baseline estimate of the breeding population size of the Marbled Duck in Morocco, to analyse how its movements and behaviour are structured across time and space, and to examine how its habitat use is influenced by climatic variability and the anthropogenic transformation of wetlands, through three complementary chapters. In the first chapter, using a two-stage random sampling design combined with hierarchical N-mixture models that account for imperfect detection, we estimated the national breeding population at 382 broods [95% CrI: 280–484], providing the first robust national-scale estimate for this species in Morocco. Emergent vegetation and wetland type were identified as the strongest predictors of brood abundance. In the second chapter, by combining GPS telemetry with tri-axial accelerometry, we developed supervised machine-learning models to classify five behavioural categories. Mapping roosting and foraging areas revealed a marked pattern of daytime roosting and nocturnal foraging, together with strong inter-individual variation in functional space use. In the third chapter, using tracking data from 24 individuals captured in Morocco and Spain, we showed that wetland type is the main driver of habitat use, with the species relying predominantly on anthropogenic wetlands. Habitat use was also modulated by seasonal drought. Overall, this thesis provides new insights into the spatial ecology of the Marbled Duck in North Africa and offers a scientific basis for improving monitoring, habitat restoration, and conservation strategies for the species.

KEYWORDS

Conservation Ecology, Marbled duck, Mediterranean Wetlands, Population size, Functional units, Habitat use