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Stopover behaviour of migratory songbirds at a small desert oasis in Southern Morocco

Diplomarbeit

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Für Mama und deine Unterstützung auf allen meinen Wegen

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I, Marlene Colbow, declare that I completed the Diplomathesis independently and used only these materials that are listed. All materials used, from published as well as unpublished sources, whether directly quoted or paraphrased, are duly reported.

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Abstract

Every year millions of migratory birds travel from their breeding grounds in Europe across the Mediterranean Sea and Sahara Desert to their wintering grounds in Sub-Saharan Africa and back. In spring, breeding season follows the northward migration, so an energy-efficient migration or early arrival date at the breeding grounds can prove advantageous for an individual to ensure a successful breeding season.

Depending on species and individual factors birds use different migration strategies. Most of these strategies include at least one stationary period, a stopover, to rest and refuel depleted energy reserves.

The goal of this thesis was to determine the stopover behaviour of migratory songbirds at a small desert oasis in the Sahara Desert, what structures of the local vegetation they used and to investigate how external factors affected this behaviour.

To do so we conducted behavioural observations at the Yasmina oasis near Merzouga in Southern Morocco during the spring of 2024. We surveyed randomly selected tamarisks in the oasis and noted all birds that stayed in this tree during our observation session as well as their behaviour. We compared the occurrences of the different species and our three behavioural categories (Foraging, Movement or Resting) with data on temperature, wind, date, daytime and the characteristics of the tree.

The results confirmed findings from Maggini et. al. (1) – we observed the most birds foraging, but they showed more resting behaviour during midday, at high temperatures or strong winds. Additionally, they preferably used high trees with a dense foliage cover.

Zusammenfassung

Jedes Jahr ziehen Millionen von Zugvögeln von ihren Brutstätten in Europa über das Mittelmeer und die Sahara Wüste zu den Überwinterungsstätten in Subsahara-Afrika und zurück. Im Frühjahr folgt auf die Migration die Paarungszeit, sodass ein energie-effizienter Zug oder ein möglichst frühes Ankunftsdatum im Brutgebiet entscheidende Fitness-Vorteile für ein Individuum bringen können.

Je nach Spezies und Individuum nutzen die Vögel verschiedene Zugstrategien. Die meisten davon beinhalten mindestens einen intermediären Aufenthalt, einen sogenannten Stopover, um zu rasten und aufgebrauchte Energiereserven aufzufüllen. Je nach Jahreszeit, Spezies, Zugstrategie und individuellen Faktoren nutzen Vögel verschiedene Stopover Sites und verhalten sich dort unterschiedlich.

Das Ziel der vorliegenden Diplomarbeit war es, das Stopover-Verhalten von ziehenden Singvögeln in einer Oase in der Sahara Wüste zu dokumentieren und zu ermitteln, welche Strukturen sie nutzen und welchen Einfluss externe Faktoren auf das Verhalten haben.

Dafür führten wir im Frühjahr 2024 Verhaltensbeobachtungen in der Yasmina Oase nahe Merzouga im Süden Marokkos durch. Wir beobachteten zufällig ausgewählte Tamarisken in der Oase und notierten alle Vögel, die sich im Beobachtungszeitraum im Baum aufhielten sowie deren Verhalten. Das Auftreten der einzelnen Spezies und unserer drei Verhaltenskategorien (Nahrungssuche, Bewegung und Rasten) verglichen wir mit Daten zu Temperatur, Windstärke, Datum, Tageszeit und Eigenschaften des Baumes.

Die Ergebnisse bestätigen die Funde von Maggini et. al. (1) – wir beobachteten die Zugvögel am meisten bei der Nahrungssuche, aber sie ruhten vermehrt während der Mittagszeit, hohen Umgebungstemperaturen oder bei starkem Wind. Ausserdem nutzten sie bevorzugt hohe Bäume mit hoher Blattdichte.

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1. Introduction

1.1 Avian migration

1.1.1 Definition

Avian migration is defined as a type of bird movement "in which individuals make regular return movements at about the same time each year, usually in specific directions and often to specific destinations" (2). As opposed to resident birds, which stay at their breeding grounds all throughout the year, migrant birds travel from breeding grounds typically located in higher latitudes to non-breeding (wintering) grounds in lower latitudes as food availability and temperatures change with the seasons (2). These migrations often follow established routes, which can span continents and require birds to traverse different landscapes and climates (2). The routes birds take during migration differ greatly between species, populations, individuals and sometimes even seasons. Ornithologists differentiate between short-distance migrants and long-distance migrants. Short-distance migrants travel shorter distances, as their name suggests, within the same continent without crossing major ecological barriers. Long-distance migrants on the other hand travel between continents, often crossing geographical barriers such as deserts or seas and covering thousands of kilometres (2).

1.1.2 Diurnal or nocturnal migration

During migration, a bird's behaviour changes drastically compared to stationary seasons at wintering or breeding grounds.

While it might be expected for nocturnal species to migrate during the night, many usually day-dwelling (diurnal) species also migrate at night. They do so, even though they have no adaptations to night-flight like regularly nocturnal birds such as enhanced low-light vision (2). Of course, when crossing geographical barriers that do not allow stopping during the day (or night), for example bodies of water, birds continue their flight no matter the time of day (2).

There are substantial advantages to nocturnal flight. Flying during the night allows for time during the day for foraging and feeding while it lowers the risk of predation. Night-time flight is also less energy demanding because of denser air, less wind, and less turbulences. When necessary, birds can avoid hyperthermia and dehydration by flying at night at generally lower

temperatures and higher humidity. Lastly, in the dark the stars are available for orientation during the flight (2).

In ornithological studies this tendency for nocturnal flight becomes apparent in a phenomenon called “Zugunruhe” or migratory restlessness. Nocturnal activity exhibited by migratory birds at the appropriate time during migratory season even when kept in captivity is used as a marker for migratory activity (3). It even persists in absence of external clues, for example when putting birds in a dim room for more than 24 hours (4, 5).

The bird’s body condition greatly affects whether this restlessness occurs. A decrease in body mass also decreases migratory nighttime-restlessness, while an opportunity to refuel when fat stores are low makes it disappear completely (5).

The timing of Zugunruhe is determined by an endogenous pacemaker mostly driven by the production of melatonin in the pineal gland (4, 3).

1.1.3 Fuel deposition and phenotypic flexibility

Migration comes with significant behavioural changes for the birds. They fly much longer distances than in the non-migration seasons and undergo massive body changes to support this high-level endurance exercise (6, 7).

To prepare for these long-distance flights birds drastically increase their energy stores, mostly by accumulating body fat in subcutaneous adipose tissue. Small passerines for example, can deposit fat stores of 10-15 % of their lean body weight daily (8).

To do so, birds increase the amount of food they ingest by up to 40 % (hyperphagia) (8).

Some birds also change the contents of their diets to increase their body fat more efficiently. Chaffinches (*Fringilla coelebs*) switch from an insectivorous to an granivorous diet, while many songbirds switch from insects to mainly fruits during their autumn migration (8).

The migratory birds’ ability to adjust physiological and morphological traits in accordance to their needs during migration is called “phenotypic flexibility”. While “exercise-organs”, such as pectoral muscles, become hypertrophic in preparation for long-distance flight, “nutritional organs”, such as the gastrointestinal tract, become atrophic to get rid of unnecessary weight but reform within a matter of days once the bird has landed to refuel (7).

This phenotypic plasticity is an important adaptation of migratory birds in general, but especially in long-distance migrants with few opportunities for refuelling en route (2, 7).

1.1.4 Optimal migration theory

During migration, birds must balance the energy needed for flying or foraging at stopover sites as well as the time spent resting, foraging, and flying. They must make trade-off decisions between prioritizing a fast but energy-demanding journey (time-minimizing) or a slower but energy-conserving (energy-minimizing) way of traveling (9).

The decision, which of these two strategies to prioritize depends on many different factors, such as species, age, sex, body condition and external factors such as environmental influences, and can differ between seasons.

For example, birds tend to prioritize a faster journey during spring migration, when arriving at the breeding grounds earlier than conspecifics is especially beneficial to secure a territory and a mate, or when it is already late in the migrating season, to catch up with the bulk of conspecifics. Male birds tend to arrive earlier at the breeding grounds than females, so males are more likely to depart earlier for migration and minimize the time spent migrating. A female on the other hand might employ an energy-minimizing strategy to be in a better body condition when arriving at the breeding grounds, where she will be faced with the energy-demanding task of producing and laying eggs (6).

1.2 Stopover

1.2.1 Stopover sites

During migration only about one seventh of the time is spent flying, the rest of the time birds are stationary during so called “stopovers” (10, 6). The locations of these stopovers, called “stopover sites” can be on land, on water or in the air in airborne species (6).

In some avian species, individuals return to the same stopover sites each year during migration. This happens most often in birds which require highly specific environments to refuel, such as waterfowl or shorebirds (2). Most passerine species on the other hand migrate over large areas of suitable stopover habitat, so individual return rate to a specific stopover site is low (2).

We can differentiate between short and long stopovers: The first may only take a few hours and birds usually do not forage or feed during this time. The only purpose is to wait until dusk or dawn, when strictly nocturnal migrants will continue their migratory flight. When choosing a site for this kind of stopover, birds usually have very little requirements (2).

The latter occurs only one to four times during the whole migration at key staging areas along the route. These sites are used each year by many birds, different species and conspecifics from different populations alike, and can vary greatly in size, from less than one to more than a hundred thousand square kilometres (2).

According to the needs birds can fulfil at a stopover site, sites can be loosely sorted into three categories: “fire escapes”, “convenience stores” and “full-service hotels” (11).

“Fire-escapes” are sites used for short stops in emergency situations such as extreme weather conditions. They are infrequently used and provide no resources for refuelling but are nonetheless crucial for the survival of the individual bird. This type of stopover site is usually a small, isolated area surrounded by unusable landscape, such as islands within a large body of water (11).

“Convenience stores” are areas of varying size where birds can rest for one or two nights. Resources for refuelling are limited but can support birds on short flights to the next stopover site. Examples for this type of stopover site are parks or cemeteries surrounded by urban landscapes (11).

“Full-service hotels” are large areas such as national parks, where all resources such as food, water and shelter are available and abundant. They can support many different species and large numbers of birds. Birds staying here are able to refuel to top body condition (11).

1.2.2 Stopover functions and costs

The longer stopover periods can have multiple functions and may vary between species and individuals. The most important purpose is to refill the bird’s energy stores exhausted during the flight by foraging (refuelling). Stopovers may also be used to accumulate additional energy before particularly challenging parts of the migration route, for example crossing geographical barriers such as deserts or large bodies of water.

Other functions of stopover may be rest and recovery after migratory flight. This could include muscle recovery, catching up on sleep deficiency or restoring oxidative balance and

immune function lost due to the physically challenging endurance flight. Another possible purpose of stopover is the avoidance of unfavourable environmental conditions, such as strong winds, rain- or snowfall. Flying in these conditions can be very energy demanding, making it easier to just wait for the weather to pass before continuing the flight (6).

Stopovers also come with costs, for example the time spent at stopover instead of advancing on the migration route or the risks of predation or contracting infectious diseases (6). Another major cost is the energy expenditure for foraging. The resulting fuel deposition rate (a measure for foraging success, usually measured as the daily change in body mass) depends on the feeding conditions at the site. Not only do birds spend a considerable amount of time at stopover, they also spend about two thirds of the total energy used for migration during stopover (10).

Birds leave the stopover site once staying incurs more fitness costs than departure (6). Usually, birds leave the stopover site and continue their migration when they have sufficiently refilled their energy stores, unless weather conditions or other external factors prevent them from doing so (5). However, if the conditions at the stopover site are not optimal, it might be beneficial for a bird to leave the site while it still has energy stores available and to search for a site with more favourable conditions (6, 12, 13).

Just like the reasons for initiating a stopover, stopover duration and the decision of departure differ between migration routes, species, individuals, and stopovers (6).

Ultimately, stopovers aim to “minimize immediate and/or delayed fitness costs” (6). An immediate fitness cost would be the death of the animal, for example because of starvation or a traumatic fall because of adverse weather. A delayed fitness cost would be a lower chance for reproduction in the following breeding period (6).

1.2.3. Carry-over effects

Delayed fitness costs during migration can happen because of so-called “carry-over effects”. Carry-over effects are events or processes occurring in one season, that affect the bird’s fitness in the following season (14). Carry-over effects can be positive or negative, but more often negative carry-over effects are discussed.

For example, habitat loss or poor habitat quality in the wintering grounds can lead to higher mortality rates during the current wintering season. Additionally, surviving birds may enter the following breeding season in poorer condition, effectively carrying over the negative impact into the reproductive season which will result in lower chances of successful reproduction (15).

During spring migration, an important factor that may cause carry-over effects is the time of arrival at the breeding grounds (16). Birds need to time their arrival and the start of the breeding season with favourable conditions at the breeding grounds, such as food availability and temperature (17). For example, both Blue (*Cyanistes caeruleus*) and Great Tits (*Parus major*) as well as Pied Flycatchers (*Ficedula hypoleuca*) adjust the lay date of their clutches, so the time when their hatchlings require the most food coincides with the time when there are most caterpillars available (18, 17, 19). Since the breeding date of long-distance migrants is constrained by their arrival date at the breeding grounds (19), a delay during migration, such as a need for prolonged stopover, can reduce the chances of reproductive success in the following breeding season (16).

1.3 Trans – Saharan migration

1.3.1 The Afro-Palearctic migration system

The largest landbird migration system is the Afro-Palearctic migration system (2, 20), where every autumn billions of birds travel from breeding sites in Eurasia to their wintering grounds in Sub-Saharan Africa and return to their breeding grounds just in time for the vegetation green-up in spring (21).

This migration system can be divided into two major flyways: The Eastern flyway and the Western flyway. Birds breeding east of the 19th meridian primarily winter in East Africa and use the Eastern flyway which circumnavigates the Mediterranean Sea to the east and the Sahara Desert along the Nile valley. Birds breeding west of the 19th meridian primarily winter in West Africa and use the Western flyway, circumventing the Mediterranean Sea and Sahara Desert along the western coast (21).

On both flyways birds travel an average of 4500 – 5000 kilometres each way (21).

Although most birds choose to travel along the eastern or western edges of the Sahara desert, where environmental conditions are not as harsh, the Sahara is crossed by birds of different species at all longitudes (2).

Most birds following the Western flyway cross the Mediterranean Sea at Gibraltar, its shortest crossing, spanning only 15 kilometres. Many individuals, however, cross where the sea is much wider, requiring them to fly for up to two days non-stop without landing (2). This happens especially in spring when, due to time constraints, the birds choose a straighter trajectory to get back to their breeding areas.

1.3.2 Crossing the desert

Deserts like the Sahara Desert are inhospitable habitats for most birds and pose many challenges when flying over them. Long distances without food or water, high daytime temperatures and low humidity can lead to hyperthermia and dehydration, making it one of, if not the most challenging part of Afro-Palearctic migration (2).

Still, over three billion birds from more than 180 species cross the Sahara twice a year. The most numerous species crossing the Sahara, the Willow Warbler (*Phylloscopus trochilus*), is also one of the smallest and slowest birds. With an average speed of 34 kilometres per hour, an individual Willow Warbler must fly for up to 53 hours to cross the Sahara Desert (2).

There are many different strategies birds use to cross the Sahara: non-stop flight, diurnal flight with nocturnal rest, nocturnal flight with diurnal rest and occasionally multiple day stops at oases for refuelling (22, 23).

Crossing the Sahara without stopping is more common in some species - for example many herons and waders (23), but also Wood Warblers (*Phylloscopus sibilatrix*) – than in others. It is more common during spring migration, possibly to secure an advantage during the breeding season by reaching the breeding grounds earlier than conspecifics (22). In emergency situations such as extreme weather, even these birds may need to land in the desert. However, the incidence and significance of these “fire-escape stopovers” is not well studied (23).

Diurnal flight is a desert crossing strategy used by swifts and hirundines, which can forage and refuel while in flight (23, 2).

Most small passerines employ an intermittent flight strategy: flying during the night, sometimes prolonging their flight into the early hours of the morning and stopping during the

day (22). Some species of passerines sit motionless during the day in the shade of desert rocks without refuelling (23). This way they can cross the Sahara within a few nights (22, 2). This strategy is generally used by species adapted to mesophilic environments, such as wetlands or moist woodlands, from central or northern Europe, like the Willow Warbler (23).

Other passerine species, generally those more adapted to dry forests and scrubland from the Mediterranean, like the Western Subalpine Warbler (*Curruca iberiae*) or the Bonelli's Warbler (*Phylloscopus bonelli*), stop at xeric desert oases for multiple days, foraging and refuelling before continuing their migratory flight (23).

1.4 Stopovers in the desert

1.4.1 Who stops where?

When they are able to, mesophilic birds in poor body condition seem to specifically choose stopover sites closer to their natural habitat (higher humidity and more vegetation) for optimal conditions to refuel. In these species, individuals in good body condition are less selective, and some may stop at less optimal sites without refuelling only for one day or night (24).

On the other hand, xerophilic birds (24) generally land at desert oases similar to their home environment (23), regardless of body condition, and can spend several days at these sites (24).

1.4.2 Behaviour at desert stopover

Not all migratory birds stopping at the same desert oasis behave the same way.

Birds with an intermittent desert crossing strategy without stopovers to refuel may land at a desert oasis for one day but will not refuel even though food resources are available. Most likely the energetic expense to rebuild the digestive tract is too high and unnecessary, since these birds carry enough fuel to cross the desert without refuelling (23).

Those birds that stop to refuel stay for longer than one day, many stay for multiple weeks and spend most of the day foraging. However, the resulting fuel deposition rate differs between species. While xerophilic birds manage to gain weight at a low to moderate rate, those mesophilic birds that try to refuel tend to lose weight regardless of their foraging effort. Most likely these birds did not accumulate enough energy stores before starting the desert crossing and are now forced to stop and try to refuel in a suboptimal habitat. If they reach an oasis well

suited for their needs, they might be able to gain enough body fat to continue their flight, otherwise they may not be able to finish the desert crossing (23).

In nocturnal-migrating species, when an individual has refuelled sufficiently and restored its energy storages, it will reduce its activity during the day. This is most likely to preserve energy and to avoid predation during “unnecessary” foraging activity until it is time to leave the stopover site (5). Additionally, birds avoid spending precious water to cool themselves down while foraging in the sun when staying at stopover sites with a hot and dry climate.

It is important to understand that these desert oases are not “ecological junkyards” where only birds too weak to continue their migration are forced to land. On the contrary, some birds choose these sites actively and purposefully to rest and refuel in favour over other areas (24).

1.4.3 Environmental influences

Migratory birds decrease foraging activity at stopover during moderate to strong winds (1). This is likely due to decreased prey availability, as insects are less abundant during strong winds (25), making the energetic effort of flying and foraging in windy conditions not worthwhile for the birds.

The significance and effect of standing water at desert stopover sites on migratory birds is not fully understood.

Since birds have no sweat glands, the main ways of dissipating heat in small passerines are cutaneous and respiratory evaporative cooling. At moderate temperatures birds use both modes of evaporation equally, but with rising ambient temperatures and increasing heat stress the importance of respiratory evaporative cooling increases. Panting is the main mode of heat dissipation at high temperatures like those in the Sahara Desert (26).

To offset the evaporative water loss (EWL) in addition to water from metabolic processes, migratory birds at desert stopovers mainly obtain water via eating foods containing water (27).

Consuming additional water increases mass gain, eases digestion in birds and enhances food absorption by facilitating micro-anatomical and histological changes to the digestive tract (28).

One could assume that migratory birds foraging at desert stopover sites use standing water when available to assist refuelling and offset the water lost via cooling mechanisms.

Sapir et. al. (29) found that at a stopover site at the border of the Sahara, standing water had strong positive effects on fuel loads and fuel deposition rate of Blackcaps (*Sylvia atricapilla*), a forest-dwelling species while it had no effect on Lesser Whitethroats (*Curruca curruca*), which are more adapted to arid environments. They suggested that Blackcaps spend more time foraging when water is available instead of resting to avoid high water losses due to movement and that the water eased the digestion of these birds (29).

Four years later, Tsurim et. al. (30) found that fuel deposition rates of Blackcaps were higher when standing water was available. When water was not available, birds mainly consumed insects, which are rich in water but do not have a high fat content. Water allowed birds to switch to water-poorer but nutrient-rich diets such as fruits. Without water or insects, birds ate less overall and gained less body mass (30).

Paces et. al. (27) on the other hand saw no effect of water availability on Blackcap behaviour. Blackcaps were generally less active than Lesser Whitethroats. Both species were only rarely seen using the artificial water sources provided, which were mostly used by resident birds (27).

Similarly, the role of ambient temperature is still unclear. It would seem logical that rising temperatures, especially during the middle of the day when temperatures are highest, would force birds to cease all activities to avoid overheating and to decrease water loss.

Maggini et. al. (1) showed that migratory birds decrease their feeding efforts as temperatures rise from 20°C to over 30°C, while Jenni-Eiermann et. al (23) found no differences in activity at higher temperatures with the exception of Subalpine Warblers.

A possible explanation could be that depending on species and adaptation to arid environments, birds decrease their foraging efforts with rising temperatures, until reaching a threshold, at which efforts cannot be further decreased regardless of ambient temperatures.

Trans-Saharan migration and desert stopover are a remarkable feat accomplished by millions of birds each year. Currently, there are many things about the desert stopovers of migratory birds that we have not fully understood. There are many kinds of oases in the Sahara Desert, many of them are small, dry oases consisting of mostly tamarisks (*Tamarix* sp.) or similar plants without large human-made agricultural areas or open water supply. We know that migratory birds stop at these oases regularly and intentionally. However, the crucial structures within these oases, the way birds use them and how their behaviour differs between species is still largely unclear.

1.5 Aim/ Hypothesis

With this study we aimed to determine how external factors affect the behaviour of migratory birds at a desert stopover site during their northward spring migration.

First, we examined which features of the local vegetation and surrounding habitat are of importance to these birds. We looked at how environmental factors, such as temperature, wind and water availability, affected the bird's usage of the site and whether they would adjust their foraging activity with rising temperatures and windspeeds, as previously described. We investigated the vegetation types used by birds for different behaviours and whether this changed as the season progressed. We aimed at understanding whether these patterns are species-specific and observed the whole community of migrants and residents to this aim.

2. Materials & Methods

2.1 Timeframe

We collected our data during the spring migration season from 14th of March 2024 until 13th of April 2024 (31 days). This timeframe best fits the peak migration season of most species migrating over our study site.

2.2 Study area

We conducted our study at the oasis of Yasmina close to Merzouga, Morocco (31°12'N; 3°59'W). It consists of a dry lake that has not been filled with water for several years in a row but contains two small grey water ponds from the surrounding hotels as well as a patch of vegetation consisting mostly of tamarisk trees (*Tamarix sp.*). We identified and numbered the largest 154 individual tamarisks (modified work done by Aispuro et. al (31) – see Fig. 1) and also marked some with tags for better orientation in the field.

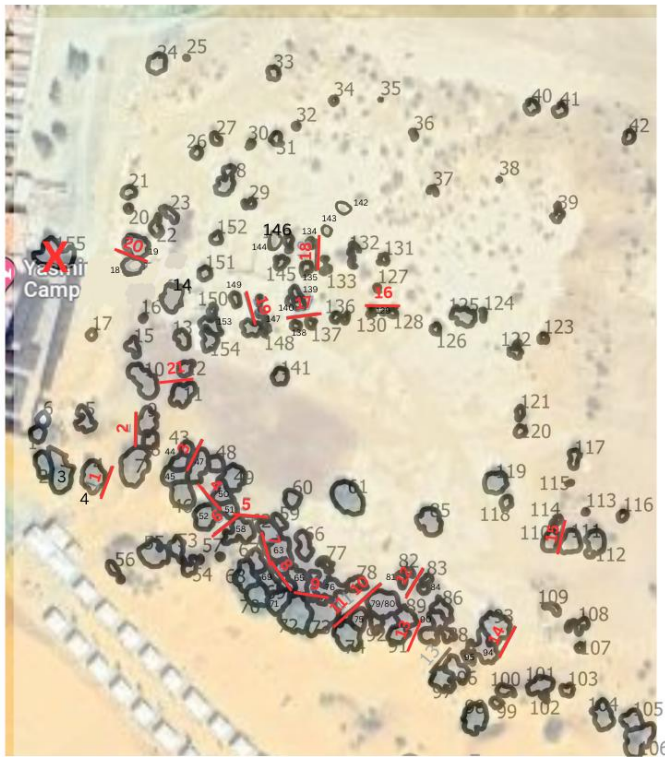


Figure 1 - Map of trees (black) and mistnets for bird capture (red) in the study area (Picture from Google Maps (32)). Numbers of nets and trees are indicated in the according colours.

We then categorized all tamarisks by height (in 2.5 m intervals) and visually estimated the density of foliage. We defined foliage density level zero as no or very little foliage, level one as up to 50 % leaf coverage, level two as up to 75 % leaf coverage and level three as (nearly) full coverage. According to those characteristics, the trees were assigned to twelve categories (A-L, see Tab. 1).

Table 1 - Categorization of tamarisk trees in the study area. Trees were categorized according to their height in steps of 2.5 m, and to foliage density with a score from 0 to 3 (see main text for a description). The number of trees in each category is indicated

Category	Height (m)	Foliage density	Number of trees in this category
A	0-2.5	0	3
B	2.5-5	0	15
C	5-7.5	0	3
D	0-2.5	1	14
E	2.5-5	1	39
F	5-7.5	1	8
G	0-2.5	2	13
H	2.5-5	2	32
I	5-7.5	2	3
J	0-2.5	3	2
K	2.5-5	3	20
L	5-7.5	3	2

Additionally, we measured the distance of each tree to the next greywater pool in metres. Trees number 14, 22 & 23 were < 1 m from the larger but temporary greywater pond and trees number 53 and 55 were < 1 m to the smaller but more permanent pond.

2.3 Observation protocol

We conducted bird observations sessions three times a day: in the morning (6:30-9:00), midday (10:30-13:30) and evening (16:30-19:30). Each time period, we observed randomly selected trees: eight trees in the morning and evening, four trees during midday.

We selected the trees using a randomized selection process and observed each tree and its closest neighbours for a five minute session, taking about one hour to finish one round of observations. Observations were made using a MINOX 8x42 monocular from ten to fifteen metres distance.

For every five-minute observation session, we also noted temperature in °C and wind speed (on a level from 0 to 3, see Tab. 2).

Table 2 - Definition of wind speed levels 0 to 3. Wind speed levels were categorized by their effect on the currently observed tree and its foliage.

Wind speed	Definition
0	No movement of leaves or branches
1	Movement of leaves
2	Movement of smaller branches
3	Movement of larger branches or whole tree (storm)

If during a five-minute session we observed a bird in the randomly selected tree or a neighbouring tree, we noted its species, the bird's behaviour (foraging, resting, movement) and interactions with other birds.

For species identification we used the book "Der Kosmos Vogelführer: Alle Arten Europas, Nordafrikas und Vorderasiens" (33).

We defined "Foraging" as actively searching for or consuming food or water, e. g. pecking at tree branches or the ground or sitting and eating a recently captured prey. "Resting" was defined as being stationary in a tree or on the ground without showing signs of foraging, e. g. sleeping, grooming, or generally sitting still. We defined "Movement" as the active movement of the bird within a tree or on the ground without any discernible foraging intent, e. g. jumping from branches, flying away from or flying into the tree. Interactions with other birds, e. g. mating or aggressiveness were also logged as movement and then we specified the interaction in an additional description box. We did not note down whether a bird was vocalizing while showing one of these behaviours and similarly did not record birds that we could hear vocalizing in the observed tree, if we could not see it.

2.4 Statistics & Analysis

The data collected during the fieldwork was analysed and plotted using R Statistical Software (v4.3.3, 2024) (34) and RStudio (35). We entered the data using the packages “readr” (36) and “readxl” (37) and visualized it using the packages “dplyr” (38), “egg” (39), “forcats” (40), “ggplot2” (41), “ggpmisc” (42), “ggpp” (43), “ggthemes” (44), “gridExtra” (45), “lubridate” (46), “padr” (47), “purrr” (48), “stringr” (49), “tibble” (50), “tidyr” (51) and “tidyverse” (52).

To determine whether the tree’s height or level of foliage had an impact on the likelihood of observing a bird, we employed a linear model. We used the absolute and relative numbers of sessions where a bird was observed as dependent variables and modelled how the independent variables tree height and foliage level affected them respectively.

Additionally, we ran multiple chi-square tests, to evaluate the association between wind speed and the absolute numbers of observations in the three behavioural categories for migrants and to compare the behavioural proportions of all migrants at different daytimes and in different tree categories.

3. Results

3.1 Overview

We carried out a total number of 746 observation sessions of focal trees.

Unfortunately, it was not possible to do sessions during all three time periods on some days, mostly due to weather problems (sandstorms). In total, we conducted 332 (44,5 %) observation sessions in the morning, 143 sessions (19,2 %) during midday and 271 sessions (36,3 %) in the evening.

During 423 of the 746 sessions, no birds were seen (56,7 %). Non-migratory House sparrows (*Passer domesticus*) and European Collared Doves (*Streptopelia decaocto*) were seen during 124 observation sessions (16,6 %), while migratory birds were seen during 202 sessions (27,1 %).

In total, we observed 20 different migratory species, the most observed migrants being Western Subalpine Warblers (*Curruca iberiae*) with 88 observations and Western Bonelli's Warblers (*Phylloscopus bonelli*) with 49 observations (see Tab. 3).

In total, we saw migrants foraging during 133 sessions (66,8 % of all migrant observations), moving 48 times (24,1 %) and resting 18 times (9,0 %). Resident species were observed foraging 24 times (19,4 % of all resident observations), moving 35 times (28,2 %) and resting 65 times (52,4 %).

3.1.1 Interactions

We recorded 49 interactions of birds, 30 interactions involved migrants. During one session we observed three Willow Warblers foraging together in the same tree. One time a Bonelli's Warbler showed aggressiveness towards a conspecific and once a willow Warbler was chased away by a House Sparrow. All other 23 interactions involved a Subalpine Warbler behaving aggressively towards either conspecifics or other species (two instances). This included the Subalpine Warblers chasing the other bird away from the tree or fighting with it (one instance).

Table 3 - List of all bird species observed in the study area during our protocol. The overall number of observations per species and their corresponding percentages of the total observations are indicated. Observations without birds seen are coloured red, resident species are printed in bold.

Species	Scientific name	Number of times seen	Percent of total observations
No birds seen	-	423	56,7 %
House Sparrow	<i>Passer domesticus</i>	111	14,9 %
Western Subalpine Warbler	<i>Curruca iberiae</i>	88	11,8 %
Bonelli's Warbler	<i>Phylloscopus bonelli</i>	49	6,6 %
Willow Warbler	<i>Phylloscopus trochilus</i>	15	2,0 %
European Collared Dove	<i>Streptopelia decaocto</i>	13	1,7 %
Olivaceous Warbler	<i>Iduna pallida</i>	7	<1 %
Northern Wheatear	<i>Oenanthe oenanthe</i>	5	<1 %
Barn Swallow	<i>Hirundo rustica</i>	4	<1 %
Willow Warbler /Chiffchaff	<i>Phylloscopus trochilus</i> / <i>Phylloscopus collybita</i>	4	<1 %
White-crowned Wheatear	<i>Oenanthe leucopyga</i>	4	<1 %
Woodchat Shrike	<i>Lanius senator</i>	3	<1 %
Common Redstart	<i>Phoenicurus phoenicurus</i>	3	<1 %
Common Whitethroat	<i>Curruca communis</i>	3	<1 %
Western Black-eared Wheatear	<i>Oenanthe hispanica</i>	2	<1 %
Western Yellow Wagtail	<i>Motacilla flava</i>	2	<1 %
Desert Wheatear	<i>Oenanthe deserti</i>	2	<1 %
Rufous-tailed scrub robin	<i>Cercotrichas galactotes</i>	2	<1 %
European Bee-eater	<i>Merops apiaster</i>	2	<1 %
Wood Warbler	<i>Phylloscopus sibilatrix</i>	1	<1 %
Great Gray Shrike	<i>Lanius excubitor</i>	1	<1 %
Melodious Warbler	<i>Hippolais polyglotta</i>	1	<1 %
Whinchat	<i>Saxicola rubetra</i>	1	<1 %
Total		746	

3.2 Tree category

The tree categories observed most often were those with trees between 2.5 m and 5 m height and medium-low to high foliage levels (levels 1 to 3; categories E, H, and K in Tab. 1)

This is not surprising, since categories E (186 observation sessions), H (159 sessions) and K (107 sessions) are the categories containing the most trees. On the other hand, there was no tree observed in category J (up to 2.5 m height and high foliage level 3 (see Tab. 1), which is one of the categories containing the lowest number of individual trees, only two trees.

We recorded the highest number of observation sessions with migratory birds (51 observations) in 2.5 m to 5 m high trees with level 3 foliage (category K in Tab. 1), which was 48 % of all observation sessions in this category (see Fig. 2).

The second largest number of migratory bird observations (45 times) was seen in trees which were 2.5 m to 5 m high and had level 2 foliage coverage (category H in Tab. 1). This accounted for 28 % of all observation sessions in this category (see Fig. 2).

When looking at the proportions of the total number of observation sessions and the number of migrant observations in each category, we observed the most migrants in trees between 5 m and 7.5 m high with level 2 foliage cover (category I in Tab. 1). Here we observed migratory birds 12 times (86 % of all observations in this category). Proportionally second most often we observed migrants in trees of 5 m to 7.5 m height and with level 3 foliage cover (category L in Tab. 1). Here we observed migrants 9 times (82 % of all observations of this category) (see Fig. 3).

We observed the most resident birds in trees of category E (2.5 m to 5 m high and foliage cover level 1). We observed resident birds 54 times (29 % of all observation sessions in this category) and they spent most of their time in this category resting (37 observations, 69 % of all resident species observations of this category) (see Fig. 2).

The highest proportion of resident species observations was tree category A (up to 2.5 m high and foliage level 0) with 60 % (9 times) of all observation sessions in this category. Here the resident birds exclusively spent their time resting (see Fig. 3).

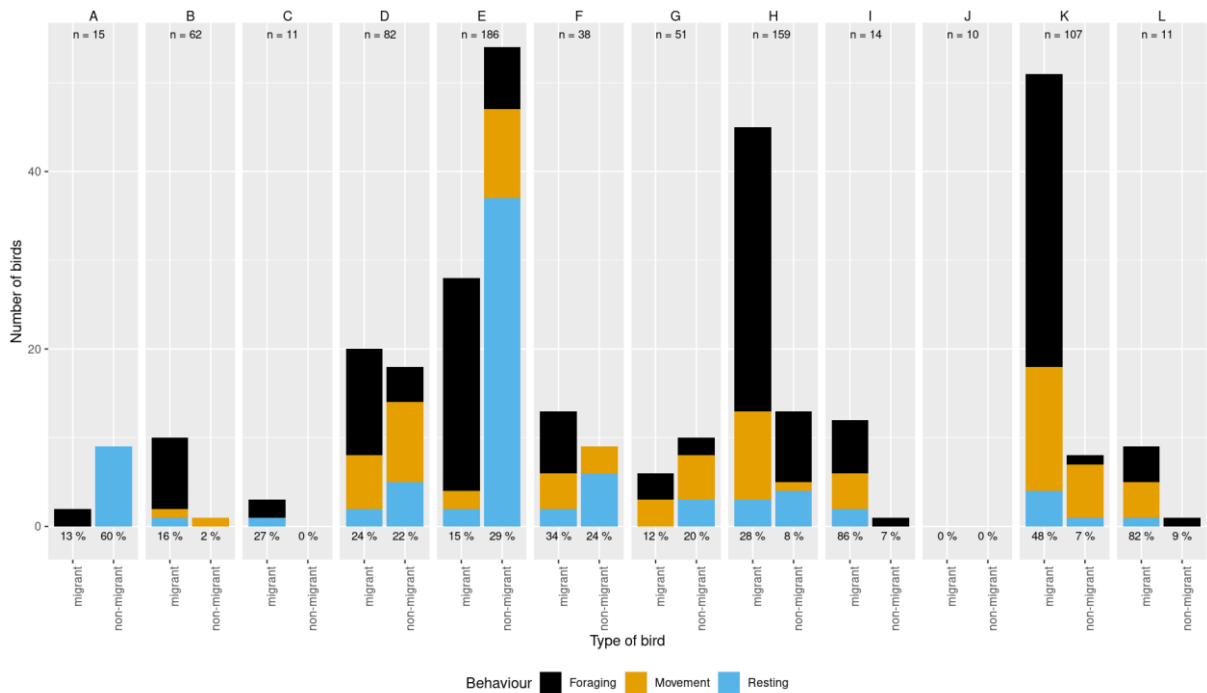


Figure 2 - Number of observations where migrants and resident birds were seen in each tree category. „n =“ indicates the total number of observations in each category. The percentage figure shows the proportion of the total observations, in which the respective birds were seen. Colours indicate the number of birds we saw displaying each behaviour.

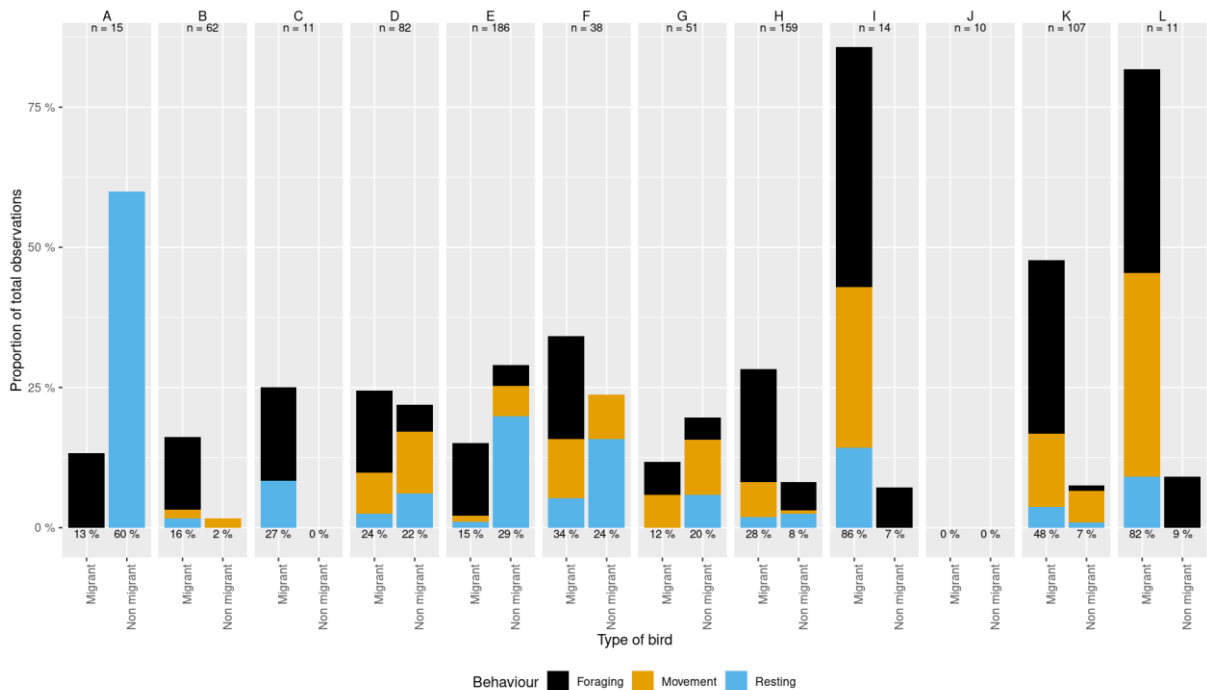


Figure 3 - Proportions of observations of each tree category in which migrants or resident birds were seen. „n =“ displays the total number of observations in this category. The percentage figure shows the proportion of total observations where migrants or residents were seen. Colours indicate the proportions of birds we saw displaying each behaviour.

For more details on the proportions of behaviours from migrants we saw in the different tree categories see Annex 1.

Regardless of the tree category, most of the migrant observations showed foraging behaviour, although in some categories the proportion of observations showing movement may be equal. Resting behaviour was observed the least number of times in every tree category.

We performed a chi-square test to see if the proportions of observed migrant behaviour differed depending on the tree category. The results showed no significant association ($X^2 = 18.557$, $df = 20$, $p\text{-value} = 0.551$) indicating that the observed differences in behaviour are likely due to chance.

3.2.1 Effect of tree height and foliage density

Modelling the absolute numbers of observations produced no significant results.

Modelling the relative numbers however, meaning the proportions of observations with migrant birds versus all observation sessions, showed that both tree height and foliage density were significant predictors of the number of birds observed. Both variables showed a positive association with the proportion of observations with migrants, indicating that migrants were observed more often in higher trees and with increasing foliage density. Tree height had a larger effect size and was more robustly associated with the number of observations than foliage density (Tab. 4).

The multiple R-squared value of 0.115 indicates that 11.5 % of the variability in tree choice of the migrants is explained by height and foliage level, while the adjusted R-squared of 0.102 accounts for the number of predictors, suggesting a modest model fit. Despite this, the F-statistic of 9.371 and a p-value of 0.0001 confirm that the model is statistically significant.

Table 4 – Results of the linear model describing the effect of tree height and foliage density on the proportion of observations where we saw a migrant.

Coefficients	Estimate	Std. Error	t-value	Pr (> t)
(Intercept)	-13.946	9.422	-1.480	0.141
Tree height	15.630	4.338	3.603	< 0.001
Foliage density	6.332	2.581	2.453	0.015

3.2.2 Distance to water

In the trees 14, 22 and 23 (<1 m from the temporary water) we saw 32 birds during 37 total observation sessions (86 %). Eleven birds out of these 32 were migrants (30 % of all observation sessions), 21 observations were residents (57 % of all observation sessions).

Seven out of these eleven migrants we observed foraging (63 % of all migrant observations in those trees), while two each were observed moving and resting, respectively (18 % of all migrant observations).

In trees number 53 and 55 (<1 m from the permanent pond) we saw 21 birds during 24 total observation sessions for these trees (88 %). 20 out of these 21 observations were migrants (83 % of all observation sessions), a resident bird was only seen one time (4 % of all observation sessions).

We observed 16 migrants foraging (80 % of the migrant observations in those trees) and four migrants moving (20 % of the migrant observations in those trees).

3.3 Time of day

We most often observed migrants in the morning (123 times, 37 % of all morning observation sessions). In the evenings we observed them 44 times (16 % of all evening sessions) and during midday they were observed 32 times (23 % of all midday sessions) (Fig. 4 and Fig. 5).

We observed the most resident birds in the evenings (103 birds, which is 38 % of all evening observation sessions). In the mornings we observed 20 resident birds (6 % of all morning sessions) and during midday one resident bird (less than 1 % of all midday sessions). It was a House Sparrow foraging. In the evenings the observed resident birds mostly spent their time resting (63 times, 61 % of all evening resident bird observations) (Fig. 4 and Fig. 5).

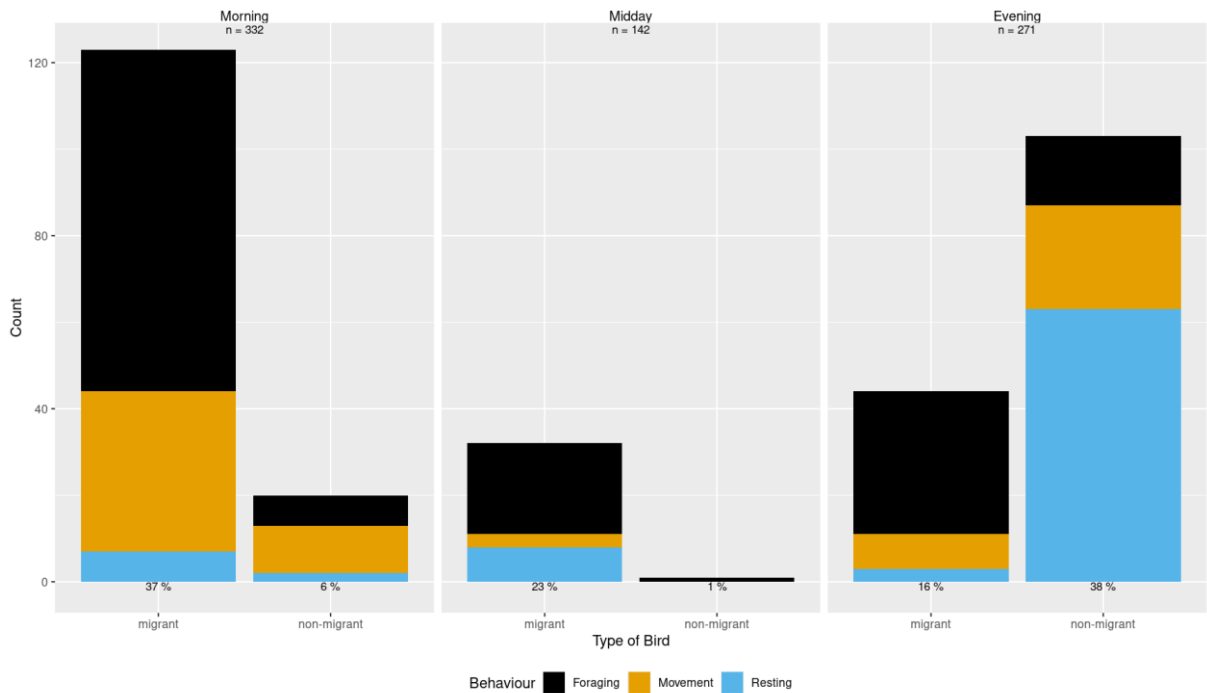


Figure 4- Absolute numbers of migrants and resident birds observed in the morning, midday or evening. „n =“ indicates number of total observations in this time frame. The percentage figure shows the proportion of total observations where a migrant or resident bird was seen. Colours indicate the number of birds showing each behaviour.

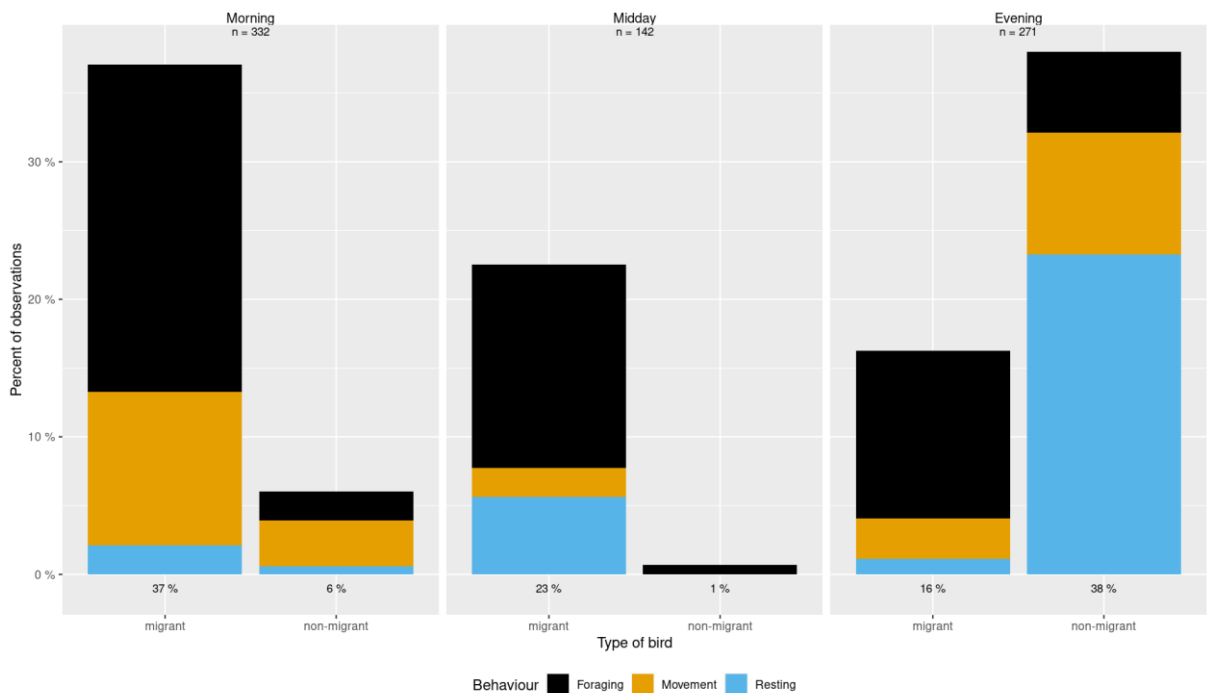


Figure 5 - Proportions of observations in the morning, midday or evening when we saw migrants or resident birds compared to the total number of observations made per time period. „n =“ indicates the total observations in this timeframe. The percentage figure shows the proportion of the total observations in which birds were seen. Colours indicate the proportions of birds showing each of the three behaviours.

Table 5 - Proportions of behaviours observed in the morning, during midday or in the evening when we saw migrants exhibit the three different behaviours. The total migrant observations in each time frame are indicated.

Daytime	Foraging	Movement	Resting	Total migrant observations
Morning	64%	30%	6%	123
Midday	66%	9%	25%	32
Evening	75%	18%	7%	44

Tab. 5 shows that we saw proportionally more resting migrants during midday than during the morning and evening. The proportion of foraging observations is very similar, irrespective of time of day.

The chi-square test comparing the behavioural proportions of all migrants at different daytimes shows that the relative behavioural make-up significantly differs between the three time periods (X-squared = 16.688, df = 4, p-value = 0.002).

When comparing two of the three time periods, morning and evening did not differ significantly in the proportions of behaviours observed (X-squared = 2.332, df = 2, p-value = 0.312).

Midday and morning differed significantly (X-squared = 14.01, df = 2, p-value = 0.001) while the difference between midday and evening was close to statistical significance (X-squared = 5.453, df = 2, p-value = 0.065).

3.4 Date

The number of daily observation sessions varied greatly, mostly due to weather effects.

We recorded the highest number of sessions on April 7th, 2024 with 54 observations.

On March 16th, March 24th, and April 9th no observation sessions could be made.

As seen in Fig. 6, the number of migrants observed increased slightly but statistically significantly over time ($p = 0.019$).

In Fig. 6, the number of resident birds observed appears stable over time, while the number of observations without birds seems to decline, however these relationships are not statistically significant.

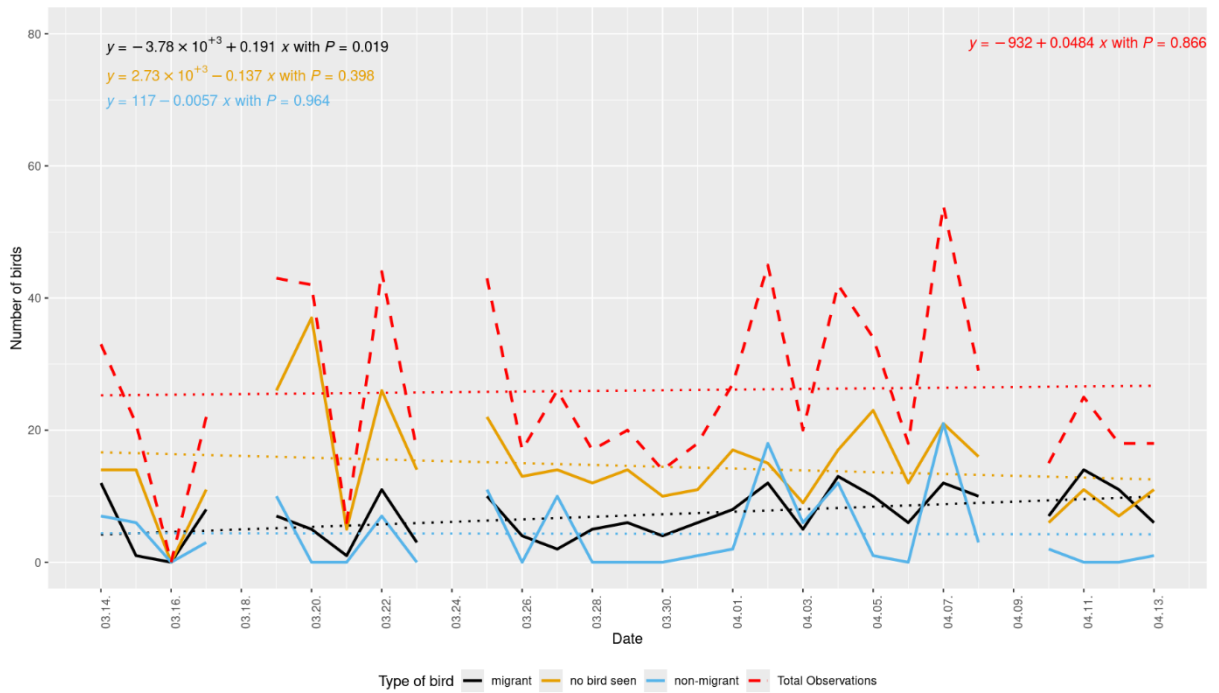


Figure 6 – The number of observations over time. Colours indicate the total observations, whether a bird was seen and if it was a resident or migratory species. Dotted regression lines for each category are displayed in the corresponding colours, including their regression equations and respective p-values in the upper corners.

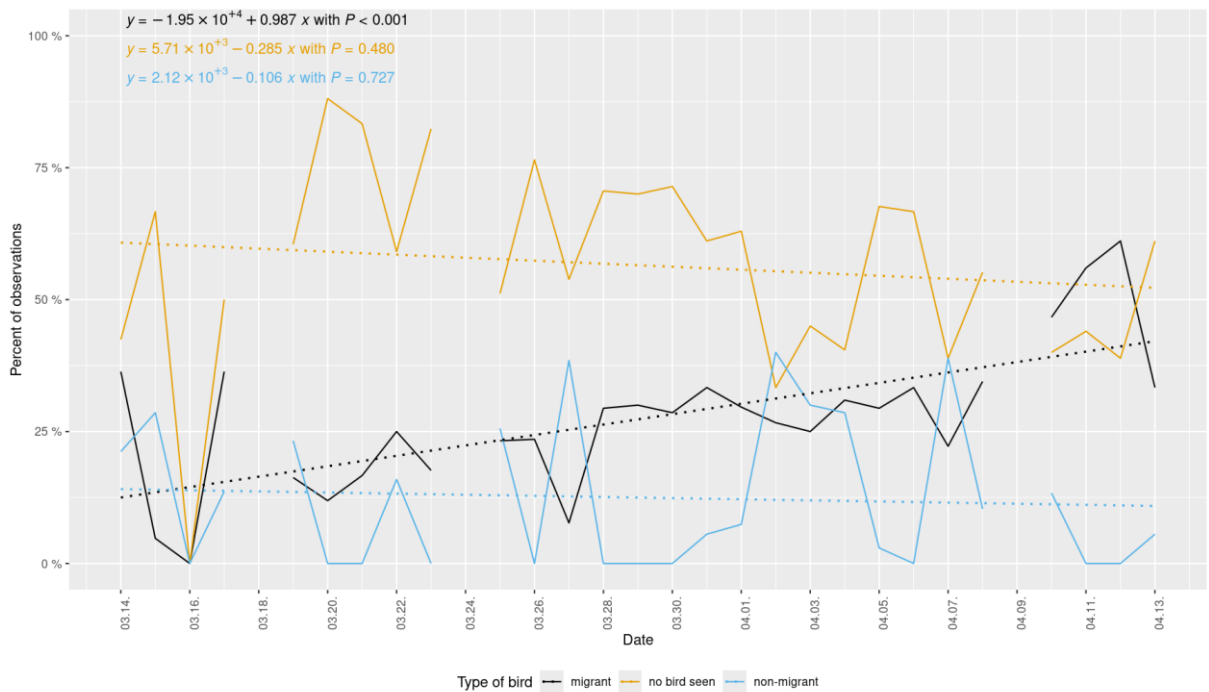


Figure 7 - The proportions of observations in comparison to the total number of observations over time. Colours indicate whether a bird was seen and if it was a resident or migratory species. Dotted regression lines for each category are displayed in the corresponding colours, including their regression equations and respective p-values in the upper lefthand corner.

As seen in Fig. 7, the proportion of migrants observed significantly increased over time ($p < 0.001$). The proportion of resident birds observed varied daily and the trend over time appears stable. The proportion of observations without bird sightings seems to decrease but the relationship was not statistically significant ($p = 0.281$).

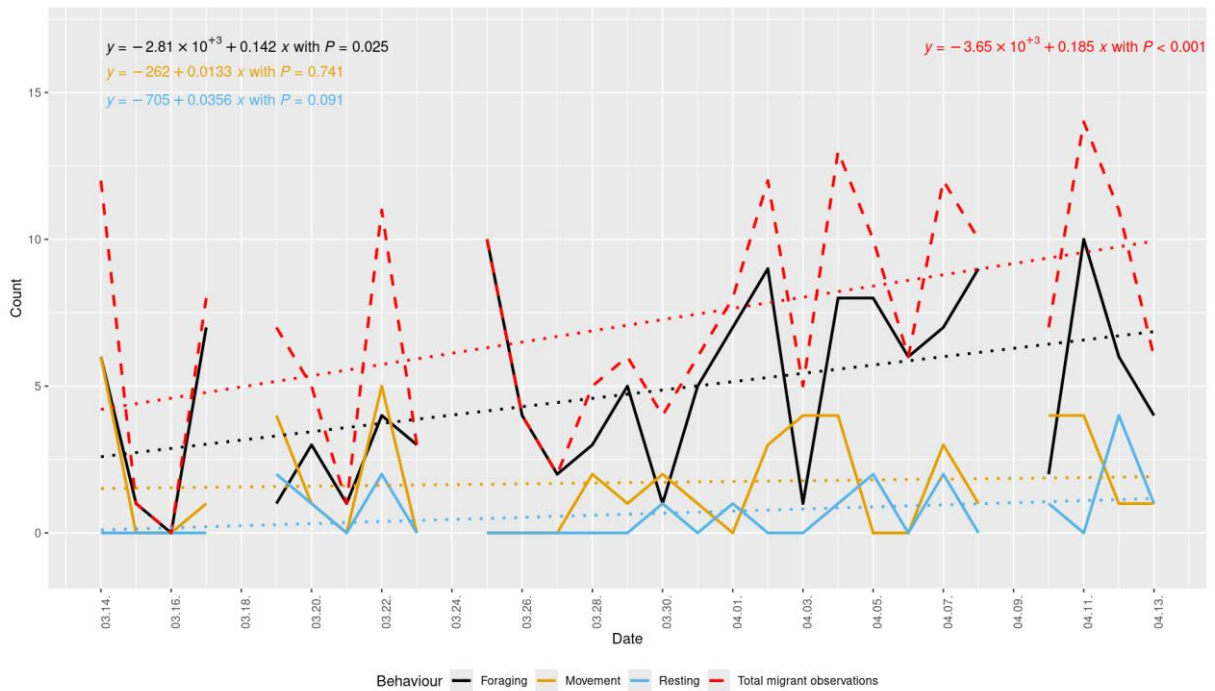


Figure 8 - The number of migrant observations over time, colours indicate total migrant observations and whether we saw the bird foraging, moving or resting. Dotted regression lines for each category in the corresponding colours are displayed, including their regression equations and respective p-values in the upper corners.

When looking at the behaviour of migrant birds specifically (Fig. 8), the number of foraging observations per day increased significantly over time ($p = 0.025$), similarly to the total number of migrant bird observations per day.

The number of resting and movement observations also appear to increase slightly, although not as strongly as the number of foraging observations. However, both these relationships are not statistically significant.

When looking at the proportions of the three different behaviours to the total migrant observations (see Annex 2), none show any statistically significant relationships.

3.5 Wind

We performed most observation sessions at windspeed level 2 (284 sessions). 204 sessions took place at level 0, 160 sessions at level 1, and 98 sessions at level 3.

We observed the most migrants (68 birds) at windspeed level 2. We saw 59 migrants at windspeed level 0, 38 migrants at windspeed 1, and 34 migrants at windspeed 3 (Fig. 9).

The highest relative number of migrant observations was at windspeed level 3 (35 % of all sessions in this category, see Fig. 10). At the same windspeed level we saw the smallest proportion of resident birds: only during 3 % of sessions at this level. At windspeed level 1 we saw migrants in 29 % of all sessions, at windspeed level 2 and level 3 we saw migrants in 24 % of all sessions at that wind level respectively (Fig. 10).

We observed 33 resident birds at windspeed 0 (16 % of all observation sessions at that windspeed level), 39 residents at windspeed 1 (24 % of all sessions at that level), 49 times at windspeed level 2 (17 % of all sessions) and three times at level 3 (3 % of all sessions at that level) (Fig. 9 and Fig. 10).

Table 6 - Proportions of migrant observations at each windspeed level , when we saw migrants exhibit the three different behaviours. The total migrant observations at each windspeed are indicated.

Windspeed	Foraging	Movement	Resting	Total migrant observations
0	66 %	31 %	3 %	59
1	71 %	16 %	13 %	38
2	72 %	21 %	7 %	68
3	53 %	29 %	18 %	34

Tab. 6 shows the proportions of migrants observed showing the three different behaviours at the different windspeeds. At all windspeed levels the majority of the migrants we observed were foraging, while the minority of migrants observed were resting. At windspeed level three the proportion of migrants observed foraging is the smallest (53 %) while the proportions of movement (29 %) and resting behaviour (18 %) are highest.

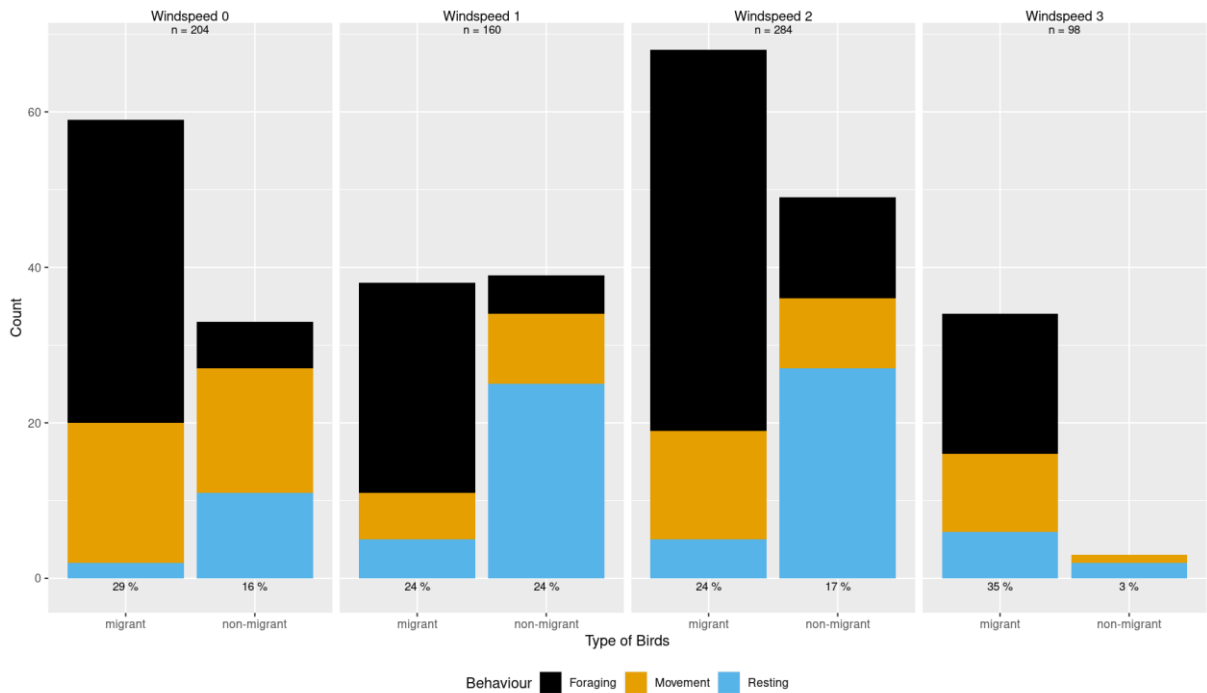


Figure 9 - Numbers of migrant and resident observations at each windspeed level , „n =“ indicates the total number of observations at this level. The percentage figure shows the portion of the total observations at this windspeed level where a respective birds was seen. Colours indicate the number of corresponding birds displaying each behaviour.

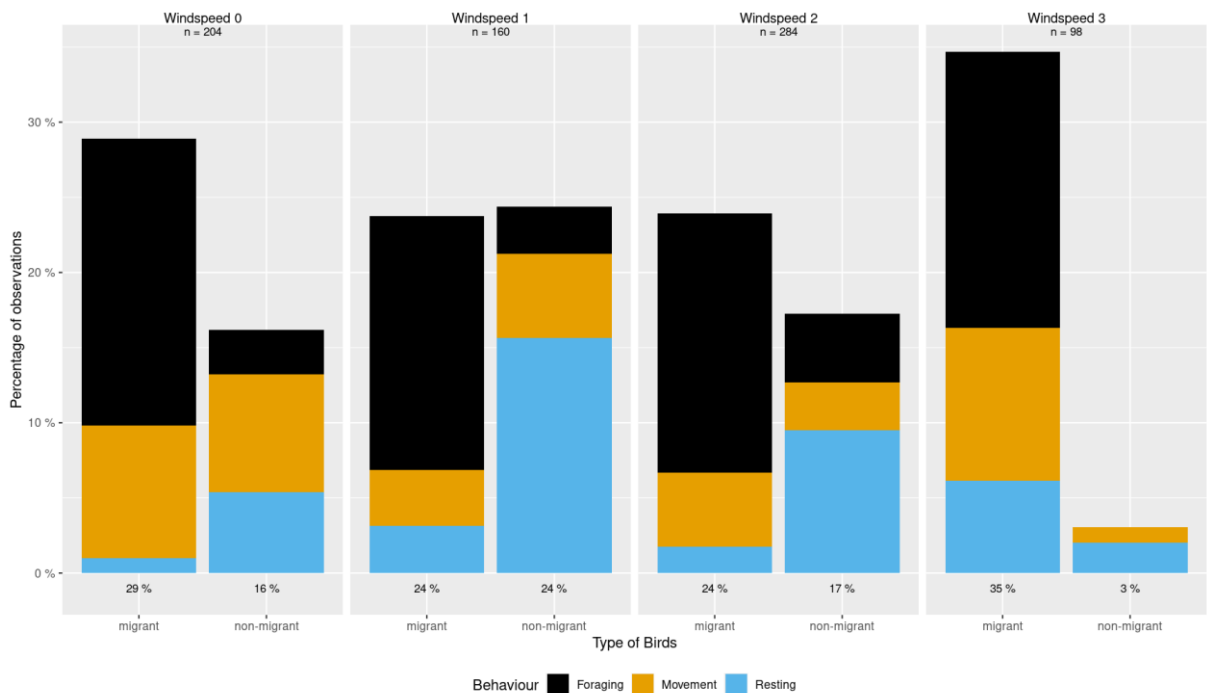


Figure 10 - Proportions of observations at each windspeed level where we saw migrants or resident birds compared to the total number of observations made at each windspeed level. „n =“ indicates the total observations at each level. The percentage figure shows the proportion of the total observations in which birds were seen. Colours indicate the proportions of birds showing each of the three behaviours.

The chi-square tests revealed no significant association between windspeed and foraging behaviour ($X^2 = 4.117$, $df = 3$, $p\text{-value} = 0.249$) or movement behaviour ($X^2 = 3.740$, $df = 3$, $p\text{-value} = 0.291$).

For resting behaviour, the test approached significance ($X^2 = 6.369$, $df = 3$, $p\text{-value} = 0.095$), but the result may be unreliable due to the small dataset and thus small expected counts in some categories. This suggests a possible weak association, but further investigation is needed.

3.6 Temperature

The temperatures during the study period ranged from 10 °C to 34 °C. Highest temperatures were logged during midday, while the colder temperatures occurred during morning and evening observation sessions.

The number of sessions varied with each temperature and so did the proportions of migrants, resident birds or no birds sighted.

The number of residents we observed seems to increase with temperature, while the number of migrants observed seems to decrease slightly. However, neither relationship is statistically significant (Fig. 11).

When looking at the proportions of migrant and resident sightings (Fig. 12), the proportion of migrant observations decreases significantly with rising temperatures ($p = 0.001$). The proportion of resident birds observed on the other hand increases significantly with rising temperatures ($p = 0.028$).

Both Foraging and Movement behaviour in migrants seem to decrease with rising temperatures when looking at the absolute numbers. However, none of the three relationships are statistically significant (see Annex 3). The number of migrants we observed differed at each temperature but at all except two temperatures we observed migrants more often foraging than moving or resting (see Annex 4).

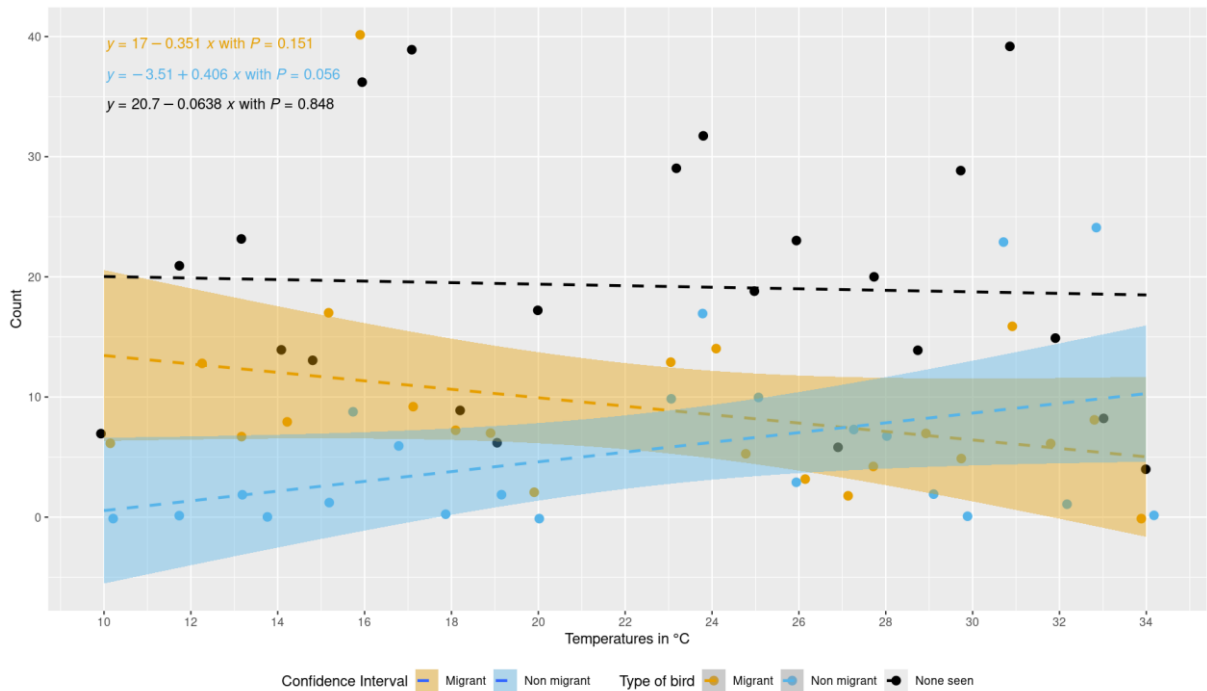


Figure 11 - Number of observations as a function of temperature. Colours indicate whether we observed a bird and if it was a migrant or resident. Regression lines and confidence intervals (0.95) of the data are displayed in the respective colours and the corresponding regression equations and p-values are indicated in the upper lefthand corner.

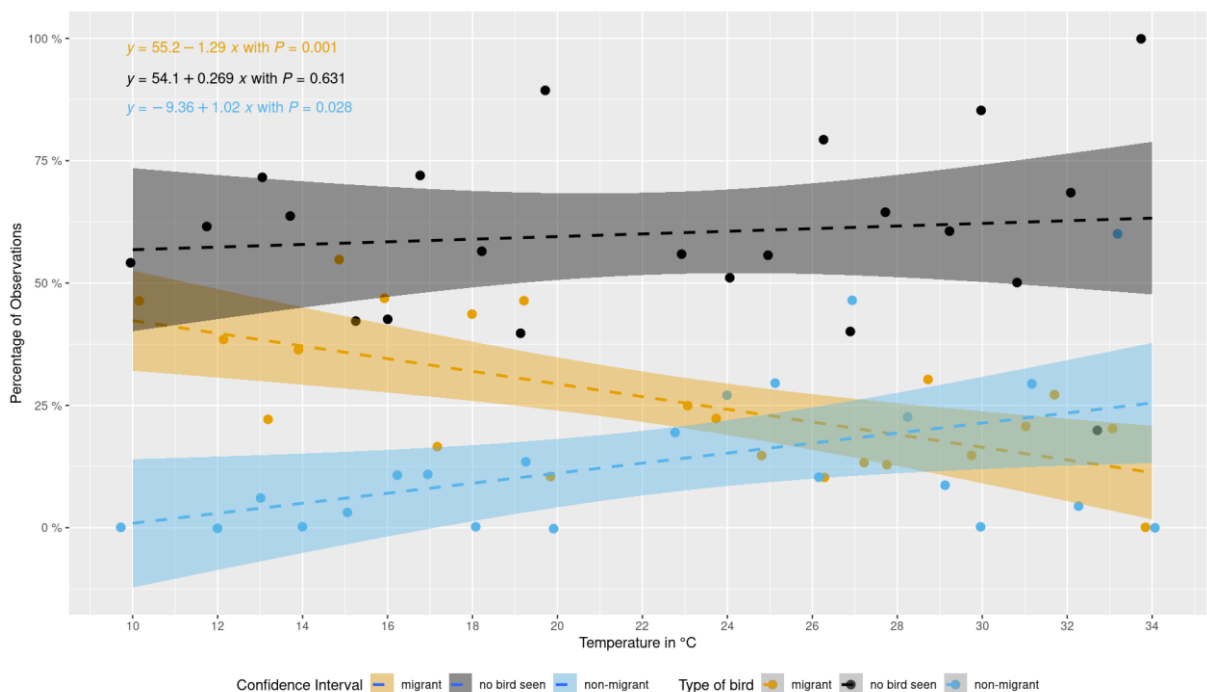


Figure 12 - Proportions of the observations as a function of temperature. Colours indicate whether we saw a bird and if it was a migrant or resident species. Regression lines and confidence intervals (0.95) are displayed in the corresponding colour and the regression equations including their p-values are indicated in the upper lefthand corner.

When looking at the proportions of the three behavioural categories with the total migrant observations, resting behaviour seems to increase with rising temperature and the relationship is approaching significance. The two other behaviours seem to decrease slightly but show no statistically significant relationships with temperature (see Fig. 13).

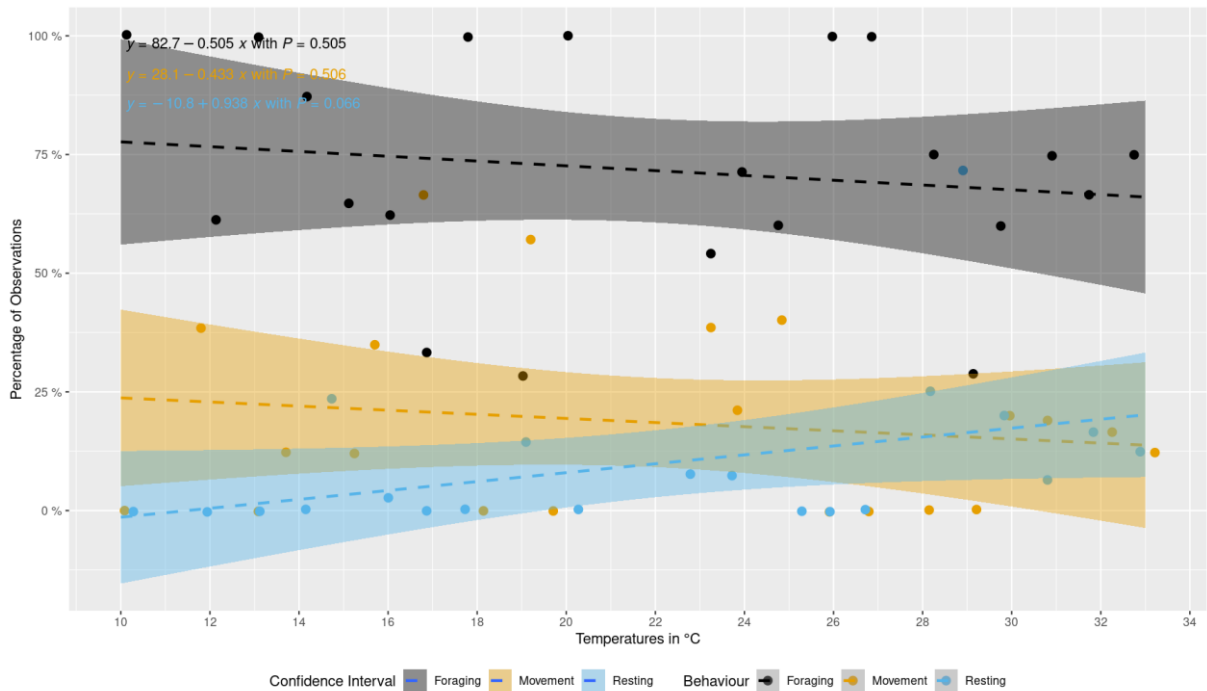


Figure 13 - Proportions of all migrant observations where the three behaviours were seen by temperature. Colours indicate the different behaviours. Dashed regression lines and confidence intervals (0.95) are displayed in the corresponding colours. Regression equations and p -values are included in the upper lefthand corner.

3.7 Species-specific observations

The three migrant species we observed most often were Western Subalpine Warblers (*Curruca iberiae*), observed 88 times (11.8 % of all observation sessions), Western Bonelli's Warblers (*Phylloscopus bonelli*), observed 49 times (6.6 % of all sessions) and Willow Warblers (*Phylloscopus trochilus*), observed 15 times (2.0 % of all sessions). Additionally in four instances it was not possible to distinguish if the bird was a Willow Warbler or Chiffchaff (*Phylloscopus collybita*). These four observations were included into the Willow Warbler category for the following calculations.

3.7.1 Tree category

When looking at the tree categories with the most observations of these three species specifically, we see the same pattern as with all migrants. Categories E (2.5 m to 5 m high and foliage level 1), H (2.5 m to 5 m high and foliage level 2) and K (2.5 m to 5 m high and foliage level 3), which were the categories with the most observation sessions overall, also have the most observations of these three species (Fig. 14).

Similarly to the overall migrant population, we saw these species mostly foraging, regardless of tree category.

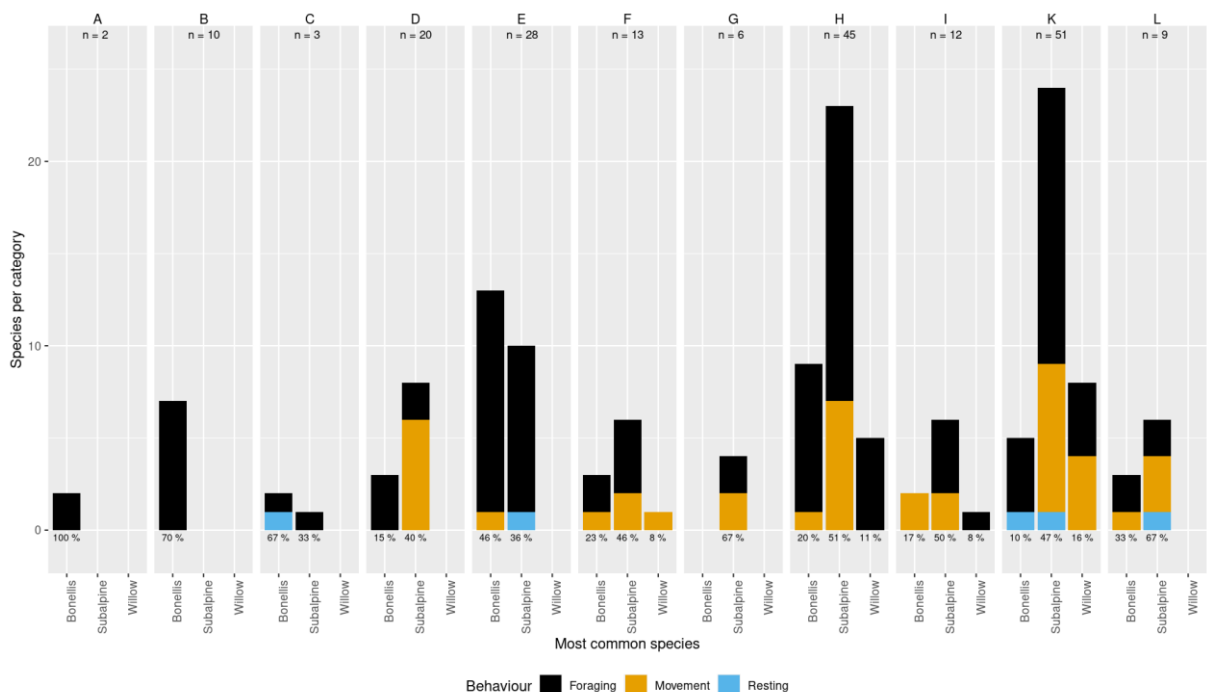


Figure 14 – Observation numbers of the three most common species by tree category. “n =” indicates the number of all migrant observations in this category. The percentage figure shows the proportion of all migrant observations where we saw the respective species.

3.7.2 Date

Looking at the number of observations of these three species over time, we can see that Bonelli's Warblers and Willow Warblers show the same trend as the overall migrant population, with observations increasing significantly as the season progresses. On the contrary, observations of Subalpine Warblers decrease significantly as the season progresses (Fig. 15).

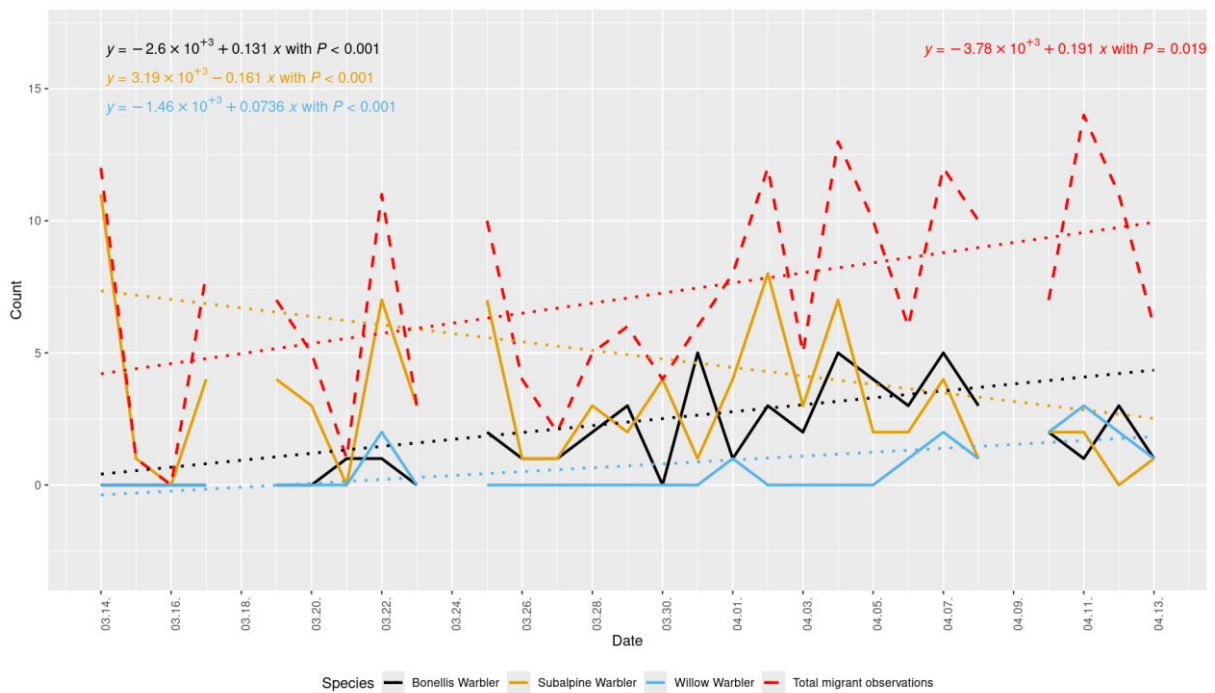


Figure 15 - Numbers of observations of the three most common species over time. Dotted regression lines are displayed in the corresponding colours and regression equations including p-values are indicated in the upper lefthand corner.

3.7.3 Temperature

When looking at the observations of the three species in relation to the temperature, the number of sessions where we saw Bonelli's Warblers or Subalpine Warblers seem to decrease. The numbers of Willow Warblers appear mostly stable with different temperatures; however, none of the relationships are statistically significant (Fig. 16).

When looking at the proportions of the three species with all migrant observations at different temperatures Bonelli's Warblers still seem to decrease, while Subalpine Warblers are mostly stable, and Willow Warblers show a slight increase. However again, none of the relationships are statistically significant (Fig. 17).

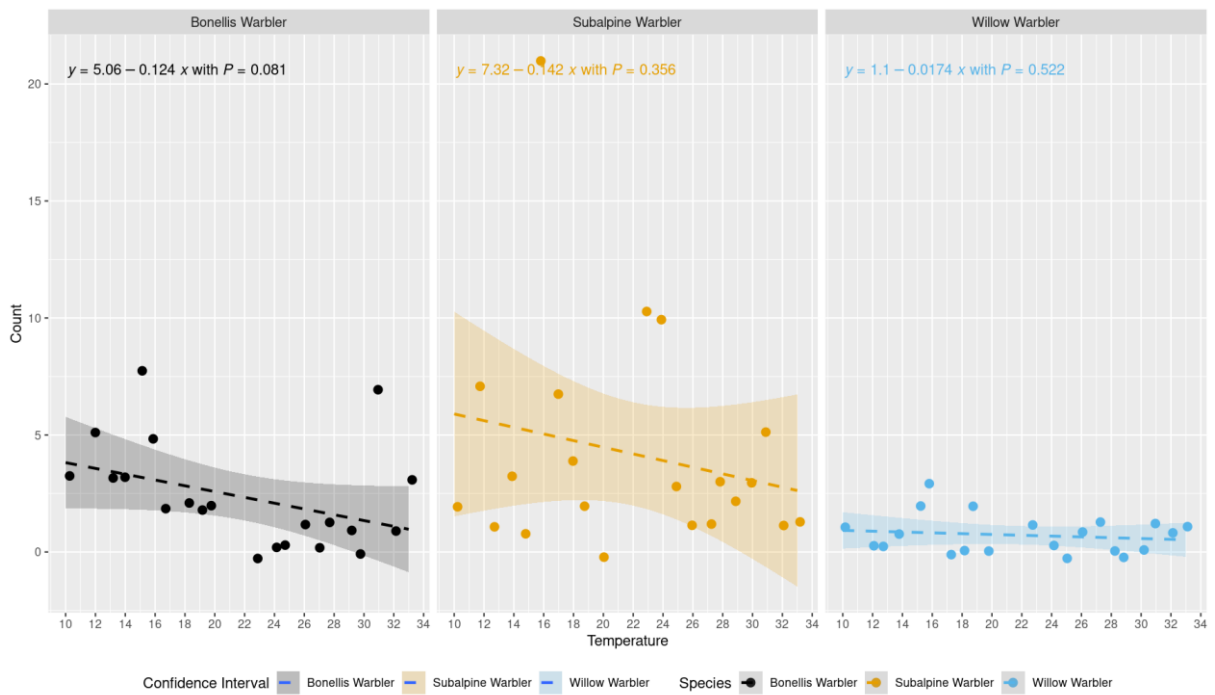


Figure 16 - Numbers of observations of the three most observed migrant species as a function of temperature. Dashed regression lines and confidence intervals (0.95) are displayed in corresponding colours and the regression equations and p-values are included at the top.

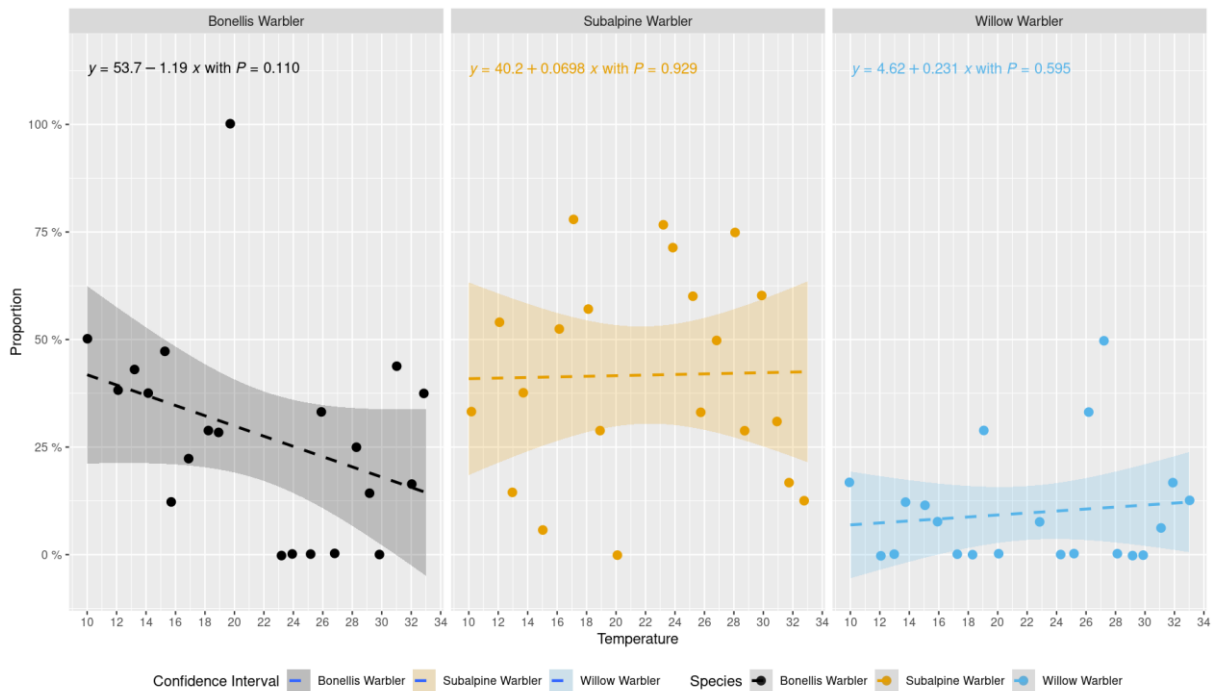


Figure 17 – Proportions of observations of the three most observed migrant species and overall migrant observations as a function of temperature. Dashed regression lines and confidence intervals (0.95) are displayed in corresponding colours and the regression equations and p-values are included at the top.

4. Discussion

4.1 Tree Category

With this study, we aimed to explore which structures of the site, namely which trees, migrants used at all or preferably.

In absolute numbers, most migrants were observed in trees which were 2.5 m to 5 m high with the two highest levels of foliage density (Category H and K), while proportionally, migrants were most often observed in trees higher than 5 m with a level 2 or 3 foliage cover (Category I and L).

The relative numbers show that migrants prefer tall trees with lots of foliage and the linear model confirms this, as both vegetation and tree height have significant impact on where the birds are observed, but height has a larger influence than vegetation level.

While migrants seemed to prefer the highest trees in the area with the most foliage cover, the fact that they frequently used the slightly smaller trees instead of leaving the site to find a more suitable habitat, suggests that these shorter trees can still adequately fulfil the migrants needs and are thus used when the tall trees are unavailable, for example due to a high density of birds at the site.

The numbers of migrants we saw differed between the tree categories, however the relative proportions of the migrant's behaviour did not. This suggests that birds prefer to reside in taller trees with more foliage, but that they still spend the same amount of time and effort foraging when staying in shorter, less covered trees.

Previous studies of migrants at stopover and wintering sites showed evidence to support an anti-predator hypothesis, where migrants chose staging areas that provided shelter from predation over those with greater foraging opportunities (53, 54). The same reasons might cause the trends for tall, highly vegetated trees we see in our data. Significant foliage cover can hide birds from predators, while tall trees provide vantage points to look out for airborne predators while efficiently protecting from ground-level predators.

However, Aispuro et. al. (31) showed that Western Subalpine Warblers at the same stopover site prefer trees with less foliage cover and hypothesized that this might be because it enables the highly territorial males of this species to better defend their territories.

We did note multiple instances where Subalpine Warblers showed aggressive behaviour towards other species, so it is possible that other migrants are deterred from trees with lower foliage cover by the Subalpine Warblers and opt for trees with higher foliage instead.

We observed the large majority of migrants foraging, which is in accordance with the results from earlier studies on the same subject (23). The differentiation between Movement and Foraging is not always clear. A bird might move around in an effort to find food, but without success and would thus be recorded as moving, not foraging. It is important to keep that in mind when interpreting the results on these two behaviours. In reality birds might have been foraging even more often than we recorded.

Resident species were most often observed in trees of category E (2.5 m to 5 m high, level 1 foliage), and spent most of their time in this category resting. This can be easily explained as the resident population of house sparrows would roost in trees number 26 to 31, which are both in this category. We often observed the house sparrows in large numbers in these trees during the evening, which explains that most evening observations of resident birds are resting (61 % of all evening resident bird observations). A large part of these observations are the same house sparrows in trees number 26 to 31.

While migrants clearly preferred tall trees with dense foliage cover, for resident species no such high preference was observed. We also noticed that the residents often used the trees and structures of the neighbouring hotel gardens to rest and forage, something the migrants did only occasionally. Similarly, we only observed three resident birds at the highest wind level, and they were not foraging, likely because the resident birds used the hotel area as shelter from strong winds.

Resident birds are more familiar with the site and its occurrences of resources and predators than migrants, so they do not need to be as cautious as migrants when choosing their roosting sites. Additionally, they have other priorities than the migrants who need to refuel rapidly and then rest under cover until they can continue their migration.

To the house sparrows, their flock may also provide them with a form of safety from predators, so they do not need to hide in tall, highly covered trees like the migrants.

4.1.1 Distance to water

In all trees close to water, we observed proportionally more birds than in the other trees in the area (88 % and 86 % of the total observation sessions).

Comparing this to the overall percentage of bird observations – 16,6 % resident birds and 27,1 % migratory birds – it can be concluded that generally birds preferred trees in close proximity to water.

In trees close to the permanent pond the overwhelming majority of birds we observed were migrants (83 % of observation sessions in those trees) while in the trees close to the temporary water we observed more residents (30 % of sessions were migrants, 57 % of the sessions were residents).

This might be because the trees near the temporary pond (14, 22 and 23) all have a relatively low foliage cover and are thus not favoured by the migrants, while residents seem to have less problems with less vegetated trees.

On the contrary, a large number of migrants used the trees near the permanent water. Both trees near the permanent pond belonged to the category K (2.5 m to 5 m with the highest foliage density). These results are in line with our previous conclusions, that migrants prefer tall trees with dense vegetation.

In the trees close to the temporary water we observed 63 % of all migrants foraging. In trees close to the permanent pond 80 % of the migrants we saw were foraging. This is a higher proportion of foraging migrants than in the whole study area (66,8 %), suggesting that the area around the permanent pond is a more suitable foraging ground for migrants. One reason might be that insects - the main food source of these migrants - tend to aggregate around bodies of standing water and in trees with high leaf coverage, like those around the permanent pond (55).

But water is also known to ease digestion (28) and may increase fuel deposition rates in birds (29, 30). We cannot discern with certainty why migrant birds prefer to forage in trees in close proximity to permanent water pools, but most likely it is an interplay of all aforementioned reasons.

4.2 Time of day, Temperature and Date

With this study, we also wanted to determine if other environmental factors like wind and temperature had an effect of the behaviour of the birds at the stopover site.

We most often observed migrants in the morning. This was also the time that we performed the most observations sessions overall, but the relative numbers also show the largest proportion of sessions where we recorded migratory birds in the morning, while the majority of bird sightings in the evening are the resting resident House Sparrows. This suggests that there are either more migrants at the site in the mornings or that they are most active during that time. It is possible that we observed migrants arriving at the stopover site after prolonging their nocturnal flight into the morning hours (22). Our data also shows that migrants behave differently during midday, spending more time resting and making them harder to spot for the observer. This leads to the conclusion that migrants are more active in the morning and use the cooler hours to forage.

In contrast, we observed less migrants overall during midday and observed proportionally more of them resting than during the morning and evening. Similarly, with rising temperatures we observed migrants less often and resting behaviour seemed to increase.

This suggests that some birds avoid foraging activity during the midday, most likely to decrease water loss and the risk of hyperthermia (1) and spend more time resting in areas inaccessible for observation, for example deep within highly vegetated trees.

Maggini et. al. (1) found the time of day had no effect on the activity of our three most observed species. However, in this study they measured activity via peck rate during foraging while we observed the behaviour in general. It could be possible, that birds do not forage as frequently during midday and spend more time resting, but if they forage, they do so at the same rate as during other times of the day.

Still, the proportion of foraging observations is the highest of the three behaviours, no matter what time of day, suggesting that even at the high temperatures of the midday some migrants were able to forage. These might be xerophilic species, which are more adapted to foraging in arid environments, like Maggini et. al. suggested (1).

Yet, the numbers of observations of both Bonelli's Warblers (a species adapted to forests and woodland) and Subalpine Warblers (a species adapted to dry shrubland) seem to decrease with temperature. However, temperatures generally rise as the season progresses and Subalpine Warblers stopover at Yasmina earlier in the season, when it is not as warm and are observed less during the latter, hotter part of the season.

Both the absolute numbers and proportions of migrants observed increased statistically significantly over time. Similarly, the number of foraging observations per day increased significantly over time. This might be a result of the observer getting more proficient at spotting birds or it might show an actual increase in birds at the site as the season progresses, as mid to late April is generally the main migration season over Yasmina with the highest catch rate.

Bonelli's Warblers and Willow Warblers showed the same trend as the overall migrant population, with observations increasing significantly as the season progresses. Observations of Subalpine Warblers decreased significantly as the season progresses, likely because Subalpine Warblers migrate earlier and start breeding earlier in their Mediterranean breeding grounds.

4.3 Wind

We observed the most migrants at moderate windspeed, which was also the most common windspeed. Foraging behaviour of migrants was proportionally lowest at high windspeed while resting behaviour was highest. This is not surprising, since it is likely more difficult for birds to move around and forage during strong winds due to increased movement of leaves and branches, as discussed by Maggini et. al (1). Additionally, arthropod prey availability and detectability may decrease with increasing winds (25), making foraging during strong winds more energy consuming and less successful as windspeeds increase.

Although we could not find significant association between wind speed and foraging, tests approached significance for resting behaviour.

The data suggests that migrants spend less time foraging and more time resting in high wind conditions, like Maggini et. al. (1) suggests, but due to the small sample size we cannot statistically confirm these results.

4.4 Conclusion

In conclusion, we can say that many birds from different Afro-Palearctic migrant species actively choose these small stopover sites in the desert of Northern Africa. Maggini et. al. (56) showed that the majority of birds landing at these small desert oases are not in need of immediate refuelling but could continue their migration further towards the Mediterranean coast. They are not forced to land there by poor body condition.

The birds use the tamarisks at the stopover site – preferably tall trees with lots of foliage. Trees around water attract more birds, they are generally larger and have more foliage, thus providing more shelter and foraging opportunities than smaller trees with less foliage. Water can also ease digestion and increase fuel deposition rate when consumed.

As migrants at these desert stopover sites spend most of their time foraging – not just resting during day, waiting to continue their nocturnal flight once the sun sets – we can assume that their use of these stopovers to refuel, even if not immediately necessary, aids in successfully completing their migration.

Higher temperatures have proven to reduce foraging activity. Global rising temperatures caused by climate change will likely make refuelling at this kind of desert stopover site less effective and migration more difficult for birds dependent on refuelling during their desert crossing. They might take longer to cross the desert or not be able to cross it at all. We can already see the repercussions of this happening – the numbers of long-distance migratory birds are declining more rapidly than those of short-distance migrants or non-migratory birds (57, 58). While birds migration and stopover behaviour is flexible to a certain extent (59), the loss of stopover sites in general (60, 61) but also those tall trees specifically poses an additional threat to the birds trying to rest and refuel during their migration.

To better protect these migratory birds, we need to provide them with possible stopover sites that have high trees with lots of foliage to provide shade and shelter and that offer opportunities for efficient fat deposition. An example of this kind of site close to our study site in Yasmina is a palm plantation in Igrane, where we observed large numbers of migrants during our study period.

We hope that with this research, we could gain some new insights and support the research made by others into how birds spend their time during stopover in the Sahara and that it can help conserve these sites and protect the birds using them.

4.5 Limitations

The design of this study comes with some limitations, which we acknowledge but tried to mitigate as best as possible.

Firstly, this thesis mostly studies migratory birds as a whole, although there are many differences between the species in stopover behaviour, duration, date etc. This approach was chosen due to a lack of data for many species. For the three species, that we had a reasonable amount of data, we investigated the species-specific patterns, but it should be kept in mind that these three species make up the majority of the migrants we observed, so the general results are likely highly influenced by the behaviours of these three species.

Secondly, some birds were probably missed by the observer, regardless of their behaviour, especially in trees with dense vegetation or very large trees. Since these types are still the trees with the most birds observed, it can be assumed that the preference for these types of birds is correct and potentially even stronger than the data shows.

Resting birds are harder to spot than those who are foraging or moving. We tried to mitigate this by observing a tree for five full minutes, even if it seemed empty at first glance, to give the observer a better chance to spot the resting birds. Still, it is very likely that the number of resting birds shown here is lower than the real number and that migratory birds might spend more time resting than we have recorded here. However, relative differences within the behaviours should mirror closely the real difference, since we maintained a strictly standardized observation protocol.

Additionally, it is plausible that birds spend more time resting during harsh weather conditions such as sandstorms. However, those same weather conditions did not allow for observation sessions, likely further decreasing the number of resting birds recorded.

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7. Annex

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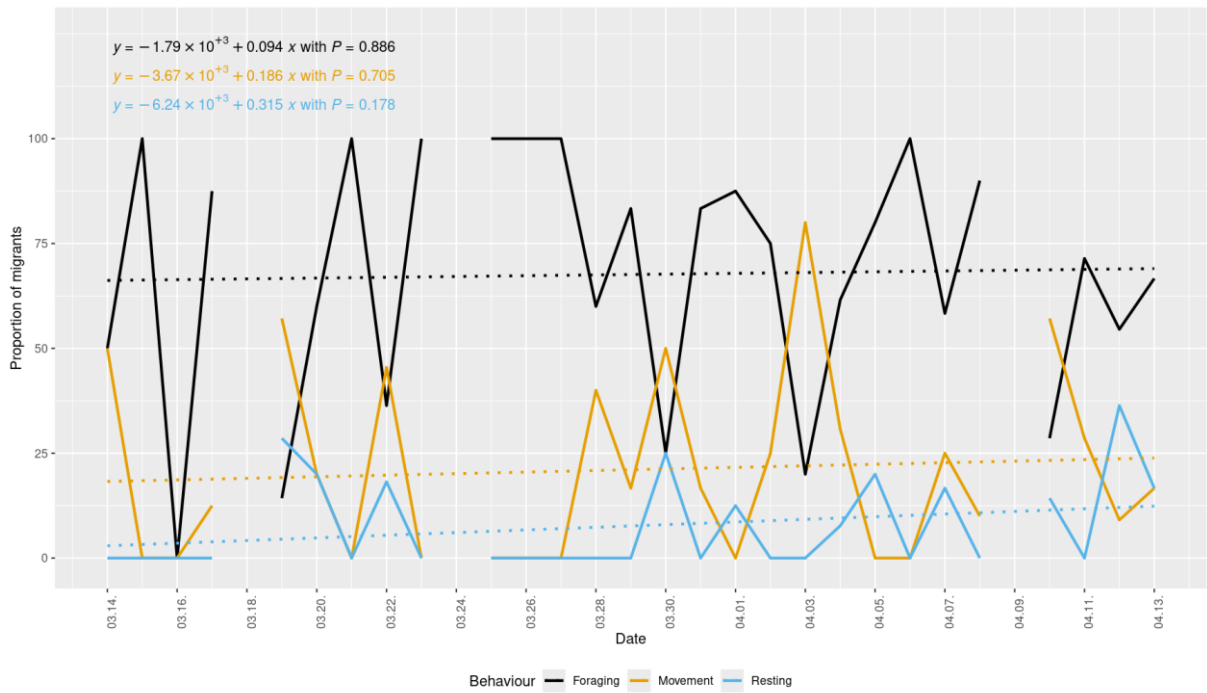
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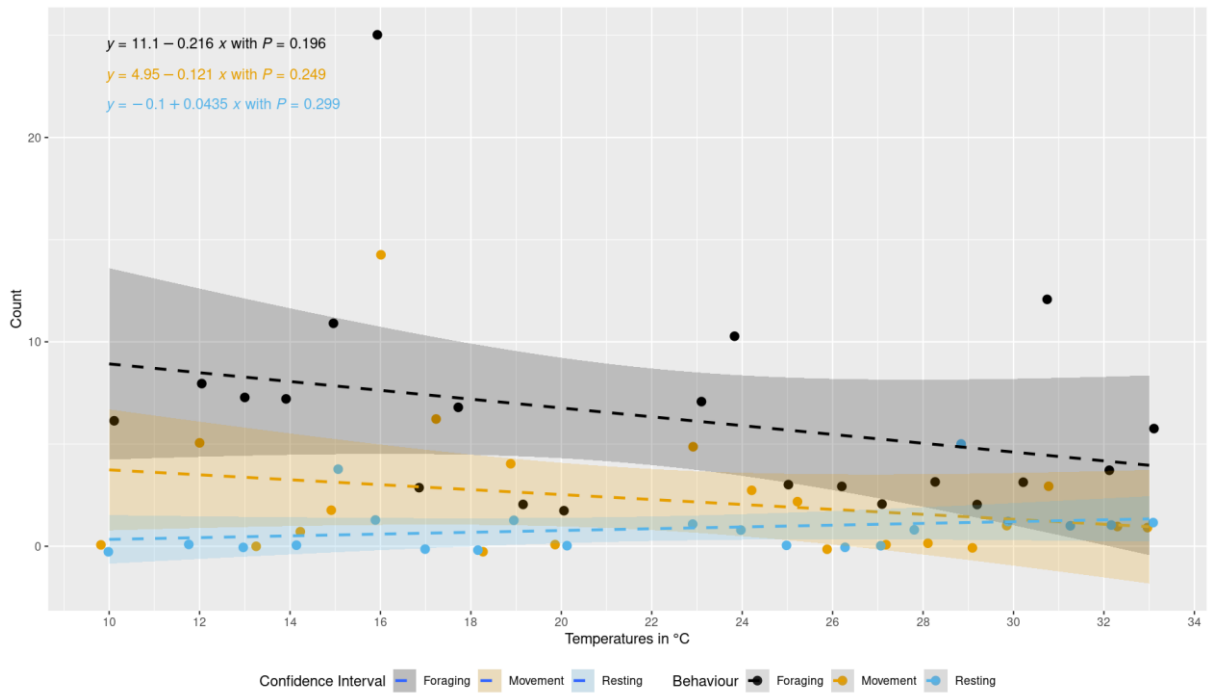
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Annex 1 – Proportions of the three behaviours observed in migrants per tree category. The total migrant observations in each tree category are indicated.

Tree Category	Foraging	Movement	Resting	Total migrant observations
A	100 %	0 %	0 %	2
B	80 %	10 %	10 %	10
C	67 %	0 %	33 %	3
D	60 %	30 %	10 %	20
E	86 %	7 %	7 %	28
F	54 %	31 %	15 %	13
G	50 %	50 %	0 %	6
H	71 %	22 %	7 %	45
I	50 %	33 %	17 %	12
J	-	-	-	0
K	65 %	27 %	8 %	51
L	44 %	44 %	11 %	9



Annex 2 - Proportions of the three behaviours observed in migrants over time compared to all migrant observations. Dotted regression lines are displayed in the corresponding colours. Regression equations including p -values are shown in the upper lefthand corner; none are statistically significant.



Annex 3 – Absolute numbers of migrant behaviours at different temperatures. Colours indicate the three behaviours. Dashed regression lines and confidence intervals (0.95) are shown in the corresponding colours. Regression equations and the respective p-values are included in the upper lefthand corner. None are statistically significant.

Annex 4 - Proportions of migrant behaviour at different temperatures, compared to the total number of migrant observations at each temperature. Total number of migrant observations at each temperature are included.

Temperature (°C)	Foraging	Movement	Resting	Total migrant observations
10	100 %	0 %	0 %	6
12	62 %	38 %	0 %	13
13	100 %	0 %	0 %	7
14	88 %	13 %	0 %	8
15	65 %	12 %	24 %	17
16	68 %	38 %	3 %	37
17	33 %	67 %	0 %	9
18	100 %	0 %	0 %	7
19	29 %	57 %	14 %	7
20	100 %	0 %	0 %	2
23	54 %	38 %	8 %	13
24	71 %	21 %	7 %	14
25	60 %	40 %	0 %	5
26	100 %	0 %	0 %	3
27	100 %	0 %	0 %	2
28	75 %	0 %	25 %	4
29	29 %	0 %	71 %	7
30	60 %	20 %	20 %	5
31	75 %	19 %	6 %	16
32	67 %	16 %	16 %	6
33	75 %	13 %	13 %	8