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Bachelor thesis

Breeding dietary preferences of an endangered raptor: the Montagu's Harrier

Öland's agricultural landscapes: a buffet of birds

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Abstract

The intensification and modernization of agriculture in the increasingly intensive agricultural landscape is one of the greatest threats to biodiversity in Europe and causes a continuous loss and degradation of natural habitats. This threat claims thousands of lives annually, especially of species that have become reliant on these areas for breeding, such as ground-breeding farmland birds. In addition, this causes a severe reduction in food resources for farmland birds. Among these threatened species is the endangered Montagu's Harrier, which has experienced a sharp decline in several European countries, prompting extensive conservation measures. As a step towards saving the species, gaining insight in its diet is vital, as this factor strongly impacts their breeding success. Despite there is a lot of knowledge about their diet in vast parts of their breeding range, information about the prey preferences of Swedish Montagu's Harrier's is very limited. To determine which are the key prey species for the population, collection and analysis of pellets and prey remains were conducted during the 2023 breeding season on Öland, which is Sweden's second-largest island and home to two-thirds of the nation's Montagu's Harriers. In total, 78 pellets and 38 prey remains containing 233 prey items were collected, and the results revealed that the population strongly relies on birds (76% of biomass consumed), while mammals were of less importance (22%). Insects and other prey items (≈1% each) contributed only minimally to the diet. The population thus stands out from other populations across Europe in its prey selection, indicating the need for increased and/or expanded protection of potential prey birds and their habitats, given that many bird species rely on a variety of habitats on the island. Further knowledge about the Montagu's Harrier on Öland will be required to conserve the species as a part of the biodiversity it contributes to.

Key words

Circus pygargus, pellet analysis, farmland bird, decline, Sweden.

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1 Introduction

Many bird species are experiencing an escalating rate of changing living conditions, largely due to human actions (Heldbjerg et al. 2018; Reif & Hanzelka 2020; Rigal et al. 2023). This trend not only contributes to the decline of birds locally (Heldbjerg et al. 2017), but also jeopardizes their survival globally (Burns et al. 2021). Among the species most severely affected, especially in Europe, are farmland breeding birds – as a consequence of the intensification of agricultural practices (e.g. Donald et al. 2001). This situation is aggravated by the loss and/or deterioration of favorable natural habitats across Europe, which in turn has forced many species to become increasingly dependent on farmland habitats (Szentirmai et al. 2010). One such species is the Montagu's Harrier *(Circus pygargus)* (Millon et al. 2002), a medium-sized ground-nesting raptor *(Fig. 1)* with a large Palaearctic breeding distribution (Arroyo et al. 2004), with its main breeding population in Europe – predominantly located in France, Poland, Russia, Spain and Ukraine (BirdLife International 2021).

Figure 1. Male Montagu's Harrier *(Circus pygargus)* on Öland, Sweden. Photographer: Markus Tallroth (2024).

Traditionally, the Montagu's Harrier breeds in scrublands, as well as in dense, tall herbaceous vegetation in meadows or sparsely growing reeds (Rodebrand 2011), preferably in or near moist areas (Friberg & Forslund 2019), but also in marshes, grasslands, lowland heaths, steppes (Terraube et al. 2010) shrublands (Arroyo et al. 2004), dunes (Schlaich 2019), wetlands (Mirski et al. 2016), moorlands (Schlaich 2019), sedges (Wiącek 2015), hay meadows (Koks et al. 2007) and peat bogs (Wiącek 2009). In the last decades there has been a notable shift in breeding habitats across Europe from natural habitat to farmland (Arroyo et al. 2002; Friberg & Forslund 2019; Kitowski et al. 2021; Mirski et al. 2016; Rodebrand 2011). The reasons behind this shift are not conclusively known, but it has been argued that loss or degrading of natural nesting habitats (Koks et al. 2007; Rodebrand 2011; Trierweiler & Koks 2009) along with overgrowth of such areas contribute (Rodebrand 2011).

Being a ground-nesting bird species, the Montagu's Harrier is highly selective when it comes to choosing nest location, given the trade-off they face between nest safety and nest accessibility (Limiñana et al. 2006). The vegetation should neither be excessively high or low, nor too sparse or too dense (Rodebrand 2011). This has resulted in agricultural land becoming the most suitable habitat for Montagu's Harriers breeding requirements (Rodebrand 2011). Several crops, like winter barley and winter wheat, have an optimal density and height in late spring when the Montagu's Harriers arrive at their breeding grounds (Arroyo et al. 2004; Limiñana et al. 2006). Occasionally, they may nest in semi-colonies (e.g. Fuentes et al. 2023; Guixé & Arroyo 2011), provided that the breeding habitat can support several pairs in a small area (Fuentes et al. 2023). They often nest far from where they forage, which, on average, may be as far as 3.5-9.9 kilometers away (Guixé & Arroyo 2011; Krupiński et al. 2021).

The crop types attracting the highest number of Montagu's Harriers are early-harvested crops like grassland and alfalfa (Poprach et al. 2013) and cereral crops (e.g. Arroyo et al. 2003; Arroyo et al. 2004; Friberg & Forslund 2019; Poprach et al. 2013; Åberg 2024) such as winter barley, winter rye, spring/winter wheat and rapeseed (Åberg 2024). In case of nesting in crops, this means that nest (including eggs and juveniles) and even females are in danger of being destroyed during harvest (Arroyo et al. 2003; Friberg & Forslund 2019). As a result, many European countries, including Sweden, have established and implemented conservation programs for the species with the objective of secure its long-term survival (Rodebrand 2011; Friberg & Forslund 2019). The most effective method is to protect nests located in crops, and this can be achieved in several different ways (Berger-Geiger et al 2019; Ferrarini et al. 2023; Santangeli et al. 2014; Santangeli et al. 2015). A common method involves using a one-meter-high electrified fence around the nest – where the size of the fence can vary and be adjusted to specific needs (e.g. Friberg & Forslund 2019; Koks et al. 2007; Åberg 2024). This not only prevents ground predators from reaching the nest, but also safeguards the nest during the farmers' harvest(s) (Ferrarini et al. 2023; Santangeli et al. 2015). Nest protection and preventing predator access are important factors for Montagu's Harriers success rate in terms of breeding (Koks et al. 2007).

The species' reliance on such a man-made environment renders it particularly exposed to any changes that occur in these type of habitats (Arroyo et al. 2002). This poses a significant problem for the species as these habitats often experience lower breeding success than nests in natural areas (Koks et al. 2007) as these fields are harvested once or multiple times during the species breeding season (Poprach et al. 2013; Åberg 2024). Due to nest losses and low reproductive output, birds that nests in crop can thus not sustain stable population levels (Koks & Visser 2002). This trend is evident across Europe, resulting in a concerning decline in Montagu's Harrier populations (Butet & Leroux 2001; Rutkowski et al. 2015; Szentirmai et al. 2010) to a point where it today is classified as threatened, and even (critically) endangered, in several countries (Rutkowski et al. 2015) including Sweden (SLU Artdatabanken 2020) and the Netherlands (van Kleunen et al. 2017). This situation even once escalated to the extent where the species was temporarily extinct from the Netherlands (Zijlstra & Hustings 1992).

The Montagu's Harrier still remains viable on a global scale (BirdLife International 2021), but there is, as earlier concluded, a concern across a vast part of Europe regarding the species' long-term survival. This represents a matter of special concern considering that the species is listed in Annex I of the European Bird's Directive (2009/147/EC), signifying its classification as particularly threatened and requiring special conservation efforts (Koks et al. 2007; Terraube & Arroyo 2011). Something that has led to critical actions and measures to mitigate the decline of tomorrow's Montagu's Harriers (e.g. Rodebrand 2011; Terraube & Arroyo 2011).

The reproductive success of the species relies not only on the protection of nests, but also on the availability of food resources during the breeding season (e.g. Millon & Bretagnolle 2008; Newton 1979; Newton 1998; Schlaich 2019), which determines the outcome of the breeding and hence number of fledglings (e.g. Newton 1979; Millon & Bretagnolle 2008). In this way, their diet forms a central aspect of their ecological niche (Terraube & Arroyo 2011). Therefore, understanding the varying relative importance of different prey species/groups to the Montagu's Harrier is valuable, as this ultimately affects their populations (Terraube & Arroyo 2011). Which, in turn, affects population dynamics and how to form the most effective conservation measures (Terraube & Arroyo 2011).

The Montagu's Harrier is the smallest species of its genus (Leroux & Bretagnolle 1996), weighing only 295-345 ± 25-30 g (AnAge 2024; Leroux & Bretagnolle 1996), and thus feed on smaller sized prey; including birds, rodents and insects (e.g. Kitowski et al. 2021; Limiñana et al. 2012; Terraube & Arroyo 2011; Wiącek 2015). It is often considered a generalist rather than a specialist (Arroyo 1997), and can thus change its diet opportunistically depending on the availability of different prey types (Arroyo 1997; Terraube & Arroyo 2011). In other words, they do not typically rely on a particular food resource, regardless of how common it is (Terraube & Arroyo 2011). However, prey abundance of particular species, such as voles, have been shown to have large effect on breeding output, and thus locally it may behave as a specialist (Koks et al. 2007; Salamolard et al. 2000).

While the most important prey may differ between studies, birds (primarily passerines), insects (mostly *Coleoptera* and *Orthoptera*), mammals (mainly lagomorphs and smaller rodents), reptiles (such as lizards), amphibians and eggs (primarily bird-eggs) are normally part of the harriers' diet during the breeding season (e.g. Arroyo 1997; Kitowski et al. 2021; Koks & Visser 2002; Koks et al. 2007; Limiñana et al. 2012; Mirski et al. 2016; Terraube & Arroyo 2011; Wiącek 2015). Across studies, the most predominant prey found in their diet are voles (Arroyo 1997; Kitowski et al. 2021; Mirski et al. 2016) – such as the common vole *Microtus arvalis* (Koks & Visser 2002; Koks et al. 2007; Millon et al. 2002; Mirski et al. 2016; Wiącek 2015) and the European water vole *Arvicola amphibius* (Kitowski et al. 2021). Other important prey species are pipits, e.g. meadow pipit *Anthus pratensis* (Koks & Visser 2002; Terraube & Arroyo 2011), larks, e.g. skylark *Alauda arvensis* (Arroyo 1997; Koks & Visser 2002; Millon et al. 2002; Mirski et al. 2016; Terraube & Arroyo 2011; Underhill-Day 1993) and buntings *(Emberizidae)* and finches *(Fringillidae)* (Arroyo 1997; Terraube & Arroyo 2011). Moreover, several studies have identified yellow wagtails *Motacilla flava* (Koks & Visser 2002; Millon et al. 2002), starlings *Sturnus sp.* (Arroyo 1997; Koks & Visser 2002; Underhill-Day 1993),

Iberian hares *Lepus granatensis* (Arroyo 1997; Onofre 2020; Terraube & Arroyo 2011), Algerian psammodromus *Psammodromus algirus* (Arroyo 1997; Onofre 2020) and *Tettigonia sp.* (Arroyo 1997; Onofre 2020; Mirski et al. 2016) as key components of Montagu's Harriers' diet.

However, the distribution range is large (Arroyo et al. 2004) and the breeding habitats are diverse and changing. Therefore, more diet studies are needed, especially in areas where the population is small and threatened. One such population is the Swedish population (Friberg & Forslund 2019; Rodebrand 2011). There are extremely few and limited suitable breeding sites left for Montagu's Harriers in Sweden, with the majority of the breeding concentrated to just a handful of locations (Friberg & Forslund 2019; Rodebrand 2011; Åberg 2024). Öland, Sweden's second-largest island, represents one of the last remaining and most significant strongholds for the Swedish Montagu's Harriers (Friberg & Forslund 2019; Rodebrand 2011; Åberg 2024). The island is home to approximately 65-70% of the country's harriers during the breeding season (Rodebrand 1996; Åberg 2024), that normally occurs from May (Rodebrand 1996; Rodebrand 2011; Åberg 2024) through August (Rodebrand 1996; Rodebrand 2011).

Despite the fact that the majority of Swedish Montagu's Harriers have bred on Öland for an extended period (Friberg & Forslund 2019; Rodebrand 2011) and that the population on the island has been extensively studied, no substantial study has been conducted regarding the populations' diet. The previous studies, such as the Swedish conservation program for the Montagu's Harrier, have mainly been conducted with the aim of conserving the Swedish population as whole (Rodebrand 2011). The knowledge of the Montagu's Harriers' diet on Öland is currently based solely on field observations (Friberg & Forslund 2019).

The Swedish harriers are believed to primarily feed on voles, e.g. the common vole and the European water vole (Friberg & Forslund 2019), other small rodents (such as the wood mouse *Apodemus sylvaticus*) (Friberg & Forslund 2019; Rodebrand 2011) and passerines, like meadow pipit, yellow wagtail and skylark, during the breeding season (Friberg & Forslund 2019). It is, however, believed that also larger mammals such as leverets, bird eggs (Friberg & Forslund 2019), larger insects and reptiles (primarily lizards) play an important role as prey for Swedish Montagu's Harriers (Friberg & Forslund 2019; Rodebrand 2011). This assumption is based on the documented diet of the species' in countries nearby – like the Netherlands, given the similarity in climate between Sweden and the Netherlands (Friberg & Forslund 2019).

Thus, a critical piece of knowledge is missing and remains unknown about one of Sweden's most endangered bird species – i.e. what the adult Montagu's Harriers, and indirectly their offspring, feed on. This understanding is crucial given the escalating decline (Heldbjerg et al. 2018; Rigal et. al 2023) and local extinctions of many farmland species (Chamberlain & Fuller 2000), especially in intensified and modernized agricultural landscapes (e.g. Donald et al. 2001; Fuentes et al. 2023 ; Krupiński et al. 2021). Such losses can impact not only the harriers' prey selection (Arroyo et al. 2002; Mirski et al. 2016), but also ultimately their survival and reproductive success (Arroyo et al. 2002; Fuentes et al. 2023). Where the latter is directly

determined by how many chicks successfully fledge and the condition of these fledglings (e.g. Corbacho et al. 1997).

Given the lack of comprehensive knowledge about the Swedish Montagu's Harriers' diet, along with their increased need for protection in agricultural landscape, as well as the rapid decline of many species in these landscapes, it is imperative to study the species' diet during the breeding season in this region. Especially given that Öland represents one of the last and most vital habitats for the Swedish population. Studying prey choices and preferences is thus of outmost importance, since ongoing conservation efforts will be required as long as the species continues to breed in agricultural landscapes and continues to face the impact of modern agricultural practices (Friberg & Forslund 2019).

An understanding of the species' prey selection during the breeding season on Öland can provide insights into which habitats on the island that might safeguard the species survival. Something that will aid in developing and implementing effective measures critical for securing the future of tomorrow's Montagu's Harriers. This study therefore aims to address this knowledge gap in order to contribute to the survival of the species and indirectly the preservation of biodiversity in the Swedish landscape.

1.1 Study question and hypotheses

Which prey species serve as the primary and most significant food sources for the Montagu's Harrier during its breeding season on Öland? Additionally, the study aims to investigate if the food preferences of the species vary across different locations and phases of the breeding season.

The study's first hypothesis is that the primary and most significant food resources are expected to resemble the diet composition observed in nearby countries, such as Poland and the Netherlands, as well as the few field observations conducted in Sweden. This means that the diet of Swedish Montagu's Harriers should predominantly consist of small mammals, mainly rodents, such as voles, but also to some extent passerines (e.g. larks, pipits, wagtails and starlings), lagomorphs, insects (primarily *Tettigonia sp.*), amphibians, reptiles and bird eggs. This is supported by earlier Dutch (Koks & Visser (2002), Koks et al. (2007)) and Polish (Kitowski et al. (2021), Mirski et al. (2016), Wiącek (2015)) studies.

The assumption made associated with this hypothesis is based on the geographical proximity of Öland, the Netherlands and Poland, which therefore experience relative similar climates (Ricklefs & Relyea 2021; Soininen et al. 2007) and comparable ecological communities (Soininen et al. 2007), ultimately leading to a shared set of prey species (Ricklefs & Relyea 2021). This phenomenon is driven by the fact that abiotic factors shape biotic conditions, resulting in more uniform species assemblages in nearby regions (Ricklefs & Relyea 2021).

The second hypothesis is that the species' diet preferences will differ between nest locations and throughout the different phases of the breeding season. The composition of the species' diet will most likely be adjusted to align the annual cycles of different groups of prey, but also

certain prey species. Especially given, as previously mentioned, that the Montagu's Harrier is an opportunistic predator that favors the most abundant prey available at the moment. This means that specific prey groups will be favored when they are most abundant during the breeding season, which in turn depends on the timing of the preys' arrival to Sweden, when their nesting beings, when they give birth or hatch.

Considering the timing of when the majority of passerines arrive on Öland and when their nesting begins, along with the peak birth season for small mammals, and the periods with highest abundance of insects, amphibians, reptiles and bird eggs, the diet of Montagu's Harriers should fluctuate as follows. It is likely that the percentage of captured mammals, particularly voles, will increase as the breeding season progresses, given the growing number of individuals within each prey species during the summer months. This has been found in neighboring countries (Poland and Germany) (Mirski et al. 2016; Ylönen et. al 1991). Regarding birds, since they are often difficult to capture, raptors typically catch chicks and/or juveniles (Mirski et al. 2016). As a result, the Montagu's Harriers are expected to capture most birds and bird eggs during June (before the study's data collection starts) when there is a higher availability of eggs and juvenile birds, i.e. more easily caught individuals, in the landscape (Mirski et al. 2016). Throughout the summer, the percentage of birds in the diet is therefore excepted to decrease as juvenile birds grow up.

Regarding insects, such as orthopterans, the number of insects is expected to peak later in the summer since they become adult, and also most abundant, at this time (Mirski et al. 2016). Insects rely on heat for normal body function (Ricklefs & Relyea 2021). Reptiles and amphibians are expected to increase as the season progress (Mirski et al. 2016), as these species also require heat in order to function (Ricklefs & Relyea 2021). For this reason, insects, reptiles and amphibians are expected to be most abundant in the harriers' diet during the warmest period of the summer.

The explanation why the diet most likely will vary between different breeding pairs is linked to the fact that individuals can exhibit different dietary specializations (Terraube et al. 2014). That is a result of morphological differences affecting the ability to efficiently capture different prey (Rincón et al. 2007; Terraube et al. 2014), combined with their individual patterns of habitat use and foraging behaviors, as well as landscape variations impacting the abundance of different prey (Terraube et al. 2014). There are thus intra-population phenotypic differences (physiological and morphological), together with spatial and temporal heterogeneity in food abundance and/or diversity, as well as varying levels of experience (Terraube et al. 2014). This leads to different habitats harboring distinct species compositions (Ricklefs & Relyea 2021), and thus depending on where the harriers forage, the frequency and composition of prey will differ among breeding pairs.

1.2 Ethical considerations

Given the species' confirmed sensitivity to disturbance, particularly in early stages of the breeding season (e.g. Millon et al. 2002), ethical considerations were imperative before starting the fieldwork. This resulted in the proactive decision to prioritize the well-being of the species

over maximizing collection of material for the study. During the actual fieldwork, I actively made sure to minimize potential disturbances by refraining from searching for pellets and prey remains near a nest when the male or female was in sight. If either of them returned or spotted my presence, I would try to hide as much as possible in the tall, dense vegetation or quickly retreat to my vehicle that was strategically parked at a safe distance from the nesting site. This was done to prevent causing unnecessary stress. I always moved slowly and cautiously to minimize the risk of detection. This principle was paramount and followed consistently during each visit.

Throughout the breeding season, I was extremely careful not to reveal any details about the species and its nesting's, refraining from disclosing specific nesting sites. This precaution was, and remains, critical for the species' protection, particular considering its endangered status. Any information deemed inappropriate for public disclosure, such as details about locations of recurring important nesting sites on Öland, will be excluded from the study to ensure that the Montagu's Harriers remain secure.

1.3 Study relevance and social implications

The study plays a critical role in enhancing our understanding of the Montagu's Harrier and the factors crucial for its persistence in Sweden. Hopefully, the study will aid in more effective conservation efforts for the species, with the ultimate goal of improving the Montagu's Harriers' conservation status from its current status. Enhanced knowledge about the species, as intended with this study, could ultimately have the potential to contribute to preserving biodiversity and better ecological balance on Öland. Additionally, it offers valuable insights into how species may respond to human activities, especially within agricultural landscapes. Without adequate knowledge about the species, including its current and future needs as well as threats, we are at loss if this charismatic bird continues to decline.

2 Materials and methods

2.1 Study area

The study was conducted during the 2023 breeding season in southeastern Sweden on the southern half of Öland, with the majority of the nests located on the southwestern part of the island. Öland is approximately 130 km long and 20 km wide and is located on a limestone plateau (Betzholtz et al. 2010). The area is dominated by arable land, alvar grassland, coastal meadows and wetland areas, yet the study was restricted to arable land. The rationale behind this decision was to ensure that the Montagu's Harriers nesting in natural habitat with *Cladium mariscus* marshes *(Fig 2a-b)* or patches of shrubby cinquefoil *Dasiphora fruticosa (Fig. 3)* remain undisturbed from human intrusion (Åberg 2024). Approaching a nest, for example, may give rise to the formation of pathways that enhance ground predators' ability to locate the nests (Åberg 2024). Despite this, the nests in arable land, that predominantly consists of pasture (lucerne) and cereal crops such as rape, barley, winter wheat, winter rye, were visited due to the need of putting up protective fences during harvest.

Figure 2. Natural breeding habitat for Montagu's Harriers in a *Cladium mariscus* marsh. Photographer: Jouko Rikkinen (n.d.) – picture A and B.

Figure 3. Natural breeding habitat for Montagu's Harriers in patches of shrubby cinquefoil *(Dasiphora fruticose)* on Öland, Sweden. Photographer: Stefan Svenaeus (n.d.).

2.2 Study population and breeding sites

2.2.1 Localization

The monitoring of Montagu's Harriers on Öland has been conducted since 1942, with exceptions for the periods 1982-1995, 1997-2003, 2009, 2011, 2013-2014 and 2016 (Friberg & Forslund 2019; Åberg 2024). The methodology for locating and identifying initiated breeding attempts of the species on the island is therefore well-established and standardized after undergoing minor adjustments to adapt to changing patterns in the species habitat preferences (Friberg & Forslund 2019; Åberg 2024). Breeding attempts are typically identified towards the

end of May each year (around week 21), when the majority of nesting of the Montagu's Harrier commences on Öland (Friberg & Forslund 2019; Åberg 2024). The detection is carried out through a selection of inventory points based on previously known sites with advantageous observations spots and breeding conditions, as well as on observations reported via the citizen science observation platform Artportalen (www.artportalen.se) or through other means – such as personal contacts (Åberg 2024). Since 2023, the use of a DJI Mavis 3T drone equipped with a thermal camera was also used to locate nesting sites (Åberg 2024).

The most reliable indication that nesting is about to begin is observing a female carrying nesting material in her beak (Åberg 2024). By following her movements, one can track where she deposits the material (Åberg 2024). Alternatively, witnessing a male delivering food to a female, which temporarily leaves the nest where she's already incubating eggs, is a useful way to discover a nesting site (Friberg & Forslund 2019; Åberg 2024). In 2023, approximately 50 locations were monitored, with 42 confirmed as actual nesting sites (Åberg 2024). Once a nesting site was roughly located, the drone was flown up to a height of 50 meters to find the brooding female and to precisely determine the nest's location with GPS-coordinates. This was done in order to mark out a 10x10-meter square more easily around the nest before the first harvest of the crop, which for lucerne typically occurs around the 25th of May in Sweden (Åberg 2024). Once each field was mown, an electric fence (12.5x12.5-meter) was installed around the nest *(Fig. 4)*. Ideally, this was done immediately after the mowing (Åberg 2024). This was completed before the 15th of June for all nest located in lucerne, whereas nests in winter wheat were not discovered and protected until around the 24th of July. For the two pairs in winter wheat, cages made of mink netting with a diameter of 1.5 meters were placed around the nests approximately two weeks after the chicks hatched, due to the later harvest of the crop during the summer season on Öland (Åberg 2024)

Figure 4. A protected Montagu's Harrier nest on a mown lucerne field on Öland, Sweden. Photographer: Clara Lindström (2023).

2.2.2 Monitoring

All initiated breeding attempts on Öland were regularly monitored to observe whether each breeding attempt was advancing or not. It is crucial to determine whether the breeding has been interrupted or failed for any reason, especially for pairs nesting in lucerne (Åberg 2024). This is because the protective fences need to be removed as soon as possible in order to minimize disruptions to the farmer's second and third harvests (Åberg 2024).

The monitoring was carried out either through the use of the drone flying at an altitude of 50 meters above the nests (Åberg 2024) or by observing the presence of ongoing nesting during monitoring (from a vehicle) of the individuals' plucking posts (see under 2.4 for the definition of the term) near the nest. This reduced disturbances around the nest site and minimized the risk of attracting predators to the nest through created pathways by us humans. The nesting activity was also indirectly monitored during the collection of prey remains (see 2.5) from the harriers.

2.3 Breeding pair selection

The selection of breeding pairs included in this study was partly based on the contact with farmers/landowners, but also on locations where the project already had identified specific pairs and their plucking posts (see 2.4). Additionally, two of the breeding pairs included in the study

were selected because their males (Bernt and Johan) were GPS-tagged in 2023. These pairs consisted of a pair north of Kastlösa (number 6) and the southeastern nest in Grönhögen (number 4) *(Fig. 5)*.

The study included in total a solitary male and 12 out of the 31 breeding pairs that successfully raised at least on fledgling out of a total of 42 breeding attempts during 2023. Among these 12 pairs, ten nested in lucerne, whereas the remaining two pairs nested in winter wheat fields. The map below *(Fig. 5)* displays the exact locations of the solitary male and the breeding pairs included in the study.

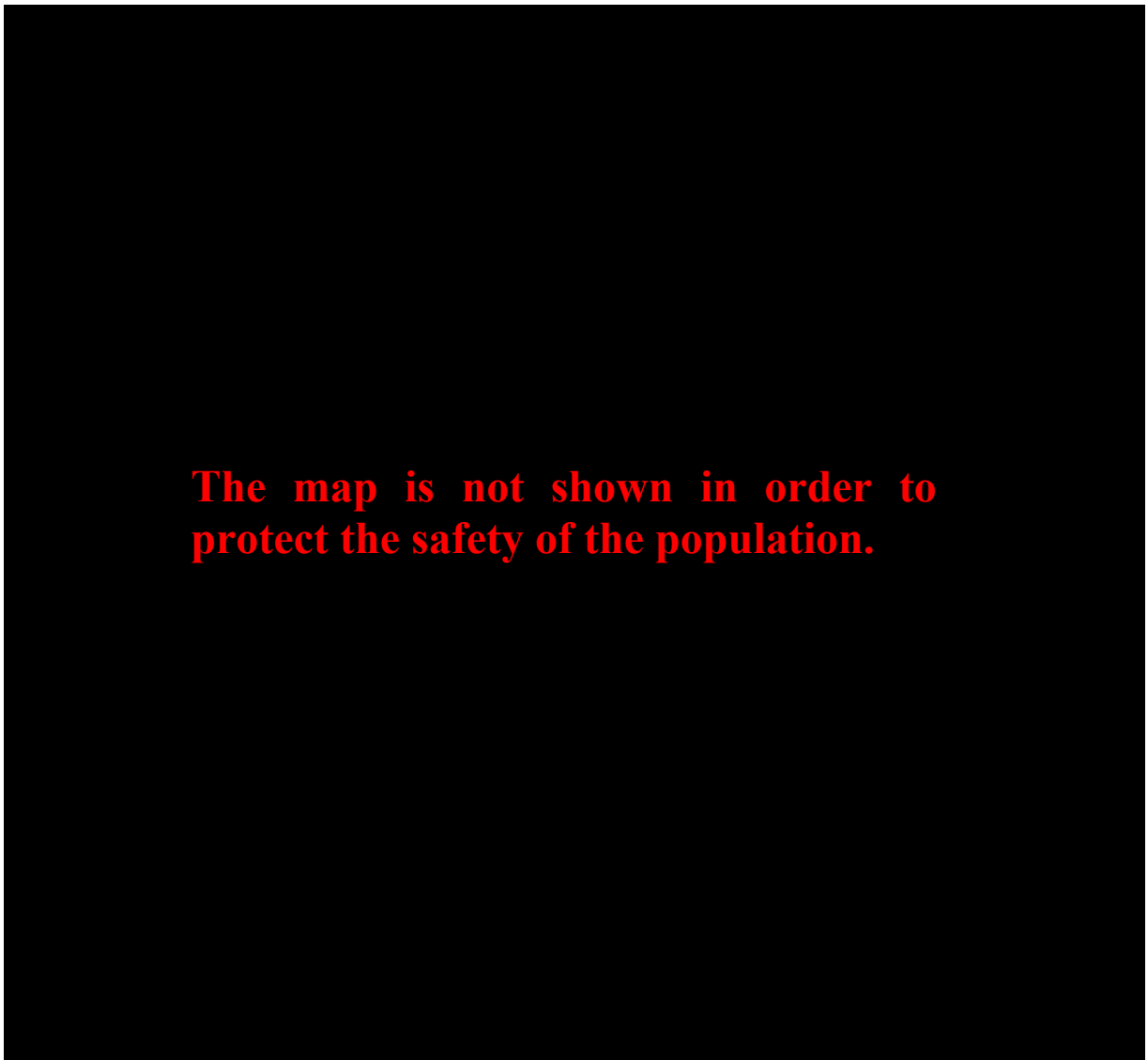

Figure 5. Locations of a solitary male and 12 nests of breeding Montagu's Harriers where pellets and prey remains were collected on Öland, Sweden, in 2023. Note that the point representing the breeding pair in Resmo is the same as for the solitary male located at the same field.

2.4 Plucking posts

Montagu's Harriers, being raptors, also face the risk of attracting other (avian or ground) predators as a consequence of the scent of dead prey (A. Åberg, personal communication, 23-05-25). As a result, adult Montagu's Harriers refrain from consuming or plucking prey to their chicks at the nesting site (A. Åberg, personal communication, 23-05-25). Instead, they establish

a designated plucking site, often a meter-high perch *(Fig. 6a-b)*, a stone wall or a branch *(Fig. 7a-b)*, (e.g. Vintchevski & Yasievitch 2009) which is located some distance away from the nest (typically at least 40-50 meters away) (A. Åberg, personal communication, 23-06-15), where they can pluck (Vintchevski & Yasievitch 2009), consume part of the prey and bring the rest to their offspring (A. Åberg, personal communication, 23-05-25). Another reason for the plucking sites is the difficulty that otherwise arise for the adult to have time to eat or pluck apart the prey inside the nest with the chicks trying to access it (A. Schlaich, personal communication, 24-04-05). This plucking post is also utilized for regurgitate prey remains in the form of pellets (Mirski et al. 2016), given that Montagu's Harriers cannot completely digest all parts of their prey (Sánchez-Zapata & Calvo 1998; Underhill-Day 1993) – such as bones, feathers, beaks and claws.

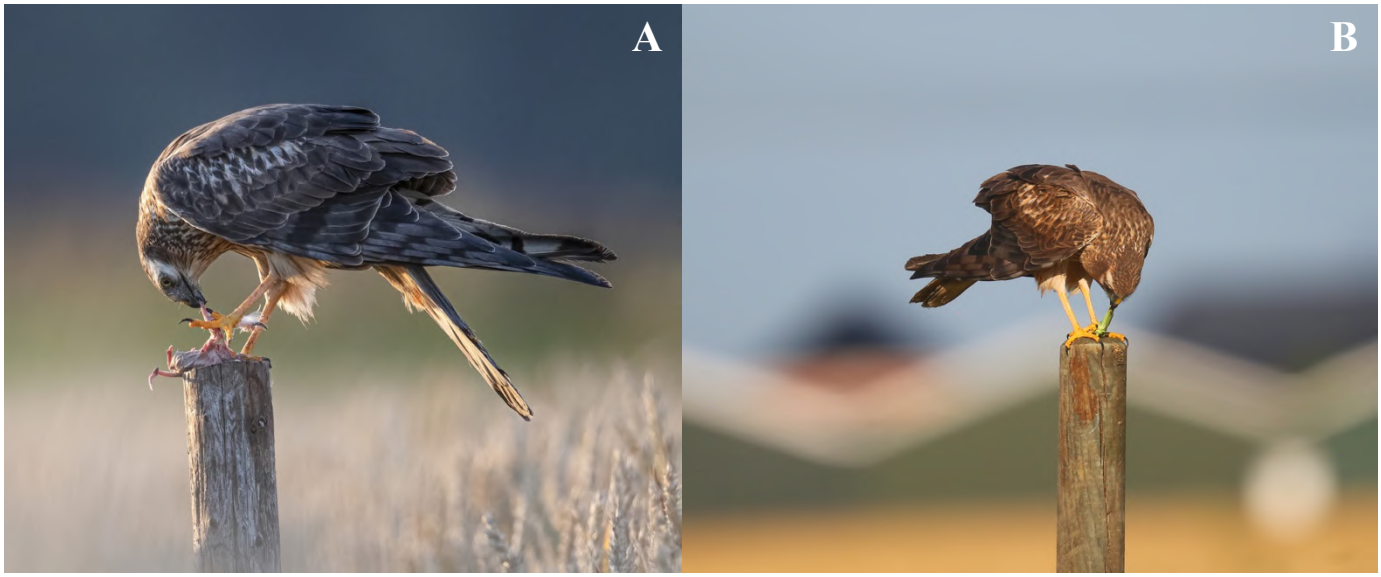

Figure 6. Two female Montagu's Harriers *(Circus pygargus)* consuming and dividing prey (a vole in A and a grasshopper in B) at their respective plucking site. Photographers: Jan Ploeger (2021) – picture A, and Theo van Kooten (2022) – picture B.

Figure 7. Two female Montagu's Harriers *(Circus pygargus)* at potential plucking sites. Photographer: Anders von Brömssen (2022) – picture A and B.

In this study, these plucking posts were located until around mid-June by either Anders Åberg, myself, or the volunteers. This was achieved by observing the birds with binoculars, typically from inside a vehicle, during the incubation period when the male either hands over prey to the female and/or when he himself sits nearby – often at the plucking post keeping watch over the breeding site. This approach allowed the localization of most plucking posts. In two cases where no distinct plucking post was identified (nest number 2 and 10) *(Fig. 5)*, meter-high perches *(Fig. 8a-b)* were raised by mid-June around 40 meters away from the nest along the field's edge. This was done to simplify the collection of pellets *(Fig. 9a)* and other remnants of prey *(Fig. 9b)*.

Figure 8. Installed perches situated close to Montagu's Harriers nest north of Resmo (left) and in Mysinge (right), on Öland, Sweden. Photographer: Clara Lindström (2023).

Figure 9a. Pellets and prey remains from Montagu's Harriers on Öland, Sweden. Photographer: Clara Lindström (2023).

Figure 9b. Prey remain Eurasian skylark *(Alauda arvensis)* from a Montagu's Harrier on Öland, Sweden. Photographer: Clara Lindström (2023).

2.5 Collection of pellets and prey remains

During the breeding season of 2023 on Öland 78 pellets and 38 prey remains *(Tab. 1)* were collected on nine locations with 12 nests *(Fig. 5)*. The three nests located in Grönhögen were considered to belong to the same location, as were the two nests found in Nedre Ålebäck *(Fig 5 ; Tab. 1)*. This is due to that is was impossible to differentiate which pellet and prey remain that originated from which Montagu's Harrier pair at each location. Therefore, the three nests in Grönhögen and the two nests in Nedre Ålebäck have been combined respectively in Table 1.

Table 1. Total number of pellets and prey remains over four periods during the 2023 breeding season on Öland, Sweden, divided per location.

Nest	Total number of pellets	Total number of prey remains	Total number of pellets 1 July – 10 July	Total number of prey remains 1 July – 10 July	Total number of pellets 11 July – 20 July	Total number of prey remains 11 July – 20 July	Total number of pellets 21 July – 30 July	Total number of prey remains 21 July – 30 July	Total number of pellets 31 July – 12 August	Total number of prey remains 31 July – 12 August
Grönhögen (3 nests)	67	18	19	5	24	3	22	9	2	1
Karlevi	1						1			
Kastlösa	3	5	2			1		3	1	1
Klinta		2						1		1
Kvinnsgröta N		1		1						
Lunda		2								2
Mysinge		1				1				
Nedre Ålebäck (2 nests)	2	7	1	1		1	1	2		3
Resmo	5	2	4	2	1					
Total	**78**	**38**	**26**	**9**	**25**	**6**	**24**	**15**	**3**	**8**

The retrieval of pellets and other prey remains occurred roughly twice a week between July 1st and August 12th. The collection usually took place from 9:00 AM and 4:00 PM. Upon arrival at each field containing one of the study nests, the car was parked a good distance away from the protected square with the nest inside. The area was then scanned with binoculars to ensure that no Montagu's Harriers were visibly present on-site in order to minimize the risk of disturbing the male or female.

Once it was confirmed that no adult harriers were present, the gathering of materials could begin. To collect the material, plastic gloves and freezer bags were used. The material was placed in the same bag provided it was not bloody or sticky in any other way, and that it belonged to the same date and location – which also was noted on each plastic bag. While in the field, the materials were collected mainly by searching along field and road edges, on and around stone walls and beneath perches – both recently installed by us and/or pre-existing ones like fence posts and similar structures. But also, to some extent inside the nest during ringing of the chicks. If the male or the female returned, or if the female noticed me from the nest, I would carefully try to hide in the terrain or quickly retreat to the car.

2.6 Storage of collected field material

After each completed field day, the collected pellets and prey remnants were briefly examined. The material was then placed back into labeled freezer bags to be stored frozen until the 20th of August. Freezing the material was necessary to prevent insect larvae from hatching inside the pellets.

Between August 20th and 21st, the frozen material was thawed and dried at room temperature for about 30 hours. Following this, all pellets and prey remains were placed in regular envelopes, labeled with the location and date of collection, as well as the number of nests present at the site at the time of collection – since three nests were lost (nest number 2, 3 and 7), due to predation, during the summer. The envelopes were then stored dry at room temperature.

2.7 Analysis of pellets and prey remains

2.7.1 Analysis in Sweden

All feathers obtained from prey remains collected during the summer of 2023 underwent examination at Linnaeus University's zoonotic laboratory. The species identification of the feathers was facilitated through the use of the website Featherbase (https://www.featherbase.info/en/home). These identifications were later verified in the Netherlands.

2.7.2 Analysis in the Netherlands

The collected material from the harriers during the breeding season was ultimately analyzed from January 23rd to 25th with the assistance of the Dutch Montagu's Harrier Foundation in Zuidlaren, located near Groningen in the Netherlands. On-site, Dutch experts work with the

Montagu's Harrier and have dedicated many years to studying the Dutch Montagu's Harrier population, including activities such as collecting pellets and other prey remains. This enabled species identification to be carried out with high accuracy and reliability.

Data on the contents of pellets and other remnants of prey were documented following a protocol designed for the Dutch Montagu's population *(Appendix 1)*. This follows a standardized method for investigating the diet of raptors, such as Montagu's Harriers. The dimensions, both length and width, of the pellets were measured using a ruler. The contents were separated using brushes and tweezers. The contents were sorted based on type of prey, and then the composition of each pellet was estimated in terms of the percentage distribution of its contents. The number of each prey species was also recorded. Prey were classified into four main categories (birds, insects, mammals and other), and efforts were made to identify each prey to the most precise taxonomic level as possible. Species identification was achieved by analyzing structures such as fur, feathers, teeth, bones, jaws/mandibles, beaks and claws *(Fig. 10a-d)*.

Figure 10. Prey items (A – skull from a yellow-necked mouse *(*Apodemus flavicollis*),* B – feathers from a yellowhammer *(Emberiza citrinella)*, C – mandibles from great greeen bush crickets *(Tettigonia viridissima)* and D – remains of a wart-biter *(Decticus verrucivorus)*) from the Montagu's Harrier on Öland, Sweden. Photographer: Clara Lindström (2024).

Identification of prey species was done using Featherbase (in case of birds) and expert knowledge (in case of birds and mammals). Insects discovered in the pellets were photographed

and later identified in Sweden (see 2.7.3). Photographs *(Fig. 10a-d)* were taken with a VEVOR digital microscope equipped with an HD-screen capable of magnifying objects up to 1300x.

2.7.3 Species determination of insects

The microscope-captured photographs were taxonomically identified by experts Geoffrey Lemdahl and Oskar Kindvall. Geoffrey, an expert in species determination of *Coleoptera,* determined photographs containing *Coleoptera sp.,* while Oskar, an expert in species belonging to *Orthoptera,* determined the photographs within his area of expertise.

2.7.4 Calculation of prey biomass

To establish the biomass for each prey species, an average live weight (according to available literature, see *Appendix 2*) was multiplied with the number of prey found (Trierweiler & Hegemann 2011). Note that in cases where multiple sources provided varying weighs for the same species, a weight representing the mean of the available literature was chosen *(Appendix 2 ; Tab. 2)*. All the former was calculated as these variables are standardized for investigating raptor, for example Montagu's Harrier, diet (e.g. García & Arroyo 2005; Trierweiler & Hegemann 2011).

2.8 Excel

Tables and figures were all created in Excel, where the percentage of number and biomass of each prey species as well as category was calculated. The data was categorized into four main categories – bird, insect, mammal and other – where the diet was analyzed over the entire breeding season, as well as within intervals of 10-13 days and among breeding pairs.

3 Results

3.1 Diet of Öland's Montagu's Harriers

In 78 pellets of Montagu's Harriers collected during the breeding season 2023 on Öland *(Tab. 1)*, 2.2 prey items were found on average, with a variation ranging from 1-14. The pellets contained a total of 175 prey items, with pellet size ranging between 9 to 26 mm in width (mean 15.3 mm) and 18 to 75 mm in length (mean 35.4 mm). Additionally, 38 prey remains were found *(Tab. 1)*.

A total of 233 prey items were identified, averaging 62.3 gram each, totaling 8125.4 grams collectively *(Tab. 2).* The pellets and prey remains from the Montagu's Harriers contained 105 birds (45.1%), 95 insects (40.8%), 25 mammals (10.7%) and 8 other preys (3.4%) *(Fig. 11 ; Tab. 2)*. Of the total biomass, birds made up 76.1%, while insects accounted for 1.0%, mammals for 22.0% and other prey species for 0.8% *(Fig. 11 ; Tab. 2)*. There were 43 prey species identified in the diet of Montagu's Harriers, with the most common prey in terms of quantity and overall biomass being passerines *(Passeriformes sp.) (Tab. 2)*. Followed by grasshoppers *(Caelifera sp.)* in terms of numbers, but followed by European rabbits *(Oryctolagus cuniculus)* in terms of total biomass *(Tab. 2)*.

Table 2. Prey species of the Montagu's Harrier on Öland, Sweden during summer 2023 found in pellets (n=78) and prey remains (n=38) sorted by species group and descending numbers.

Prey species	Latin name	Number	Percentage of number (%)	Individual average biomass (g)	Total biomass (g)	Percentage of biomass (%)
Bird	*Aves*	105	45,1	161,6	6187,0	76,1
Bird sp.	*Aves sp.*	4	1,7	161,6	646,2	8,0
Non-passerine		6	2,6	368,0	2331,8	28,7
Black headed gull	*Chroicocephalus ridibundus*	1	0,4	306,0	306,0	3,8
Grey partridge	*Perdix perdix*	2	0,9	492,0	984,0	12,1
Hooded crow or rook	*Corvus cornix or Corvus frugilegus*	1	0,4	499,0	499,0	6,1
Northern lapwing	*Vanellus vanellus*	1	0,4	218,5	218,5	2,7
Pigeon sp.	*Columbidae sp.*	1	0,4	324,3	324,3	4,0
Passerine	*Passeriformes*	95	40,8	32,6	3209,0	39,5
Eurasian skylark	*Alauda arvensis*	13	5,6	36,8	478,4	5,9
Eurasian tree sparrow	*Passer montanus*	2	0,9	20,5	41,0	0,5
European starling	*Sturnus vulgaris*	3	1,3	74,0	222,0	2,7
Passerine sp.	*Passeriformes sp.*	72	30,9	32,6	2344,1	28,8
Pipit sp.	*Anthus sp.*	1	0,4	21,3	21,3	0,3
Reed bunting	*Emberiza schoeniclus*	1	0,4	18,4	18,4	0,2
Wood lark	*Lullula arborea*	2	0,9	26,9	53,8	0,7
Yellowhammer	*Emberiza citrinella*	1	0,4	30,0	30,0	0,4
Insect	*Insecta*	95	40,8	0,5	81,1	1,0
Insect sp.	*Insecta sp.*	10	4,3	0,9	8,5	0,1
Beetle	*Coleoptera*	26	11,2	0,2	19,0	0,2
Beetle sp.	*Coleoptera sp.*	14	6,0	1,3	18,2	0,2
Click beetle sp.	*Elateridae sp.*	1	0,4	<0,1	<0,1	<0,01
Dor beetle	*Anoplotrupes stercorosus*	2	0,9	0,2	0,35	<0,01
Harpalus sp.	*Harpalus sp.*	2	0,9	<0,1	<0,1	<0,01
Leef beetle sp.	*Chrysomelidae sp.*	1	0,4	<0,1	<0,1	<0,01
Pill beetle sp.	*Byrrhidae sp.*	1	0,4	<0,1	<0,1	<0,01
Poecilus sp.	*Poecilus sp.*	1	0,4	<0,1	<0,1	<0,01
Pterostichus sp.	*Pterostichus sp.*	1	0,4	0,1	0,1	<0,01
Pterostichus versicolor	*Pterostichus versicolor*	1	0,4	0,1	0,1	<0,01
Ten-spotted ladybird	*Adalia decempunctata*	1	0,4	<0,01	<0,01	<0,01
Weevil sp.	*Curculionidae sp.*	1	0,4	<0,01	<0,01	<0,01
Orthoptera	*Orthoptera*	56	24,0	1,1	53,0	0,7
Cricket sp.	*Gryllidae sp.*	2	0,9	0,4	0,7	<0,01
Grasshopper sp.	*Caelifera sp.*	27	11,6	0,3	8,1	<0,1
Great green bush-cricket	*Tettigonia viridissiima*	17	7,3	1,8	30,6	0,4
Ortohptera sp.	*Orthoptera sp.*	9	3,9	1,3	11,6	0,1
Wart-biter	*Decticus verrucivorus*	1	0,4	2,0	2,0	<0,1
Other		3	1,3	0,2	0,6	<0,01
Damselfly sp.	*Zygoptera sp.*	1	0,4	0,4	0,4	<0,01
Hymenopteran sp.	*Hymenoptera sp.*	1	0,4	0,2	0,2	<0,01
Shield bug sp.	*Carpocoris sp.*	1	0,4	<0,1	<0,1	<0,01
Mammal	*Mammalia*	25	10,7	64,3	1791,0	22,0
Lagomorph	*Lagomorpha*	6	2,6	214,0	1284,0	15,8
European rabbit (leveret)	*Oryctolagus cuniculus*	6	2,6	214,0	1284,0	15,8
Rodent	*Rodentia*	19	8,2	39,4	507,0	6,2
European water vole	*Arvicola amphibius*	1	0,4	120,0	120,0	1,5
House mouse	*Mus musculus*	1	0,4	20,5	20,5	0,3
Mouse sp.	*Murinae sp.*	11	4,7	20,5	225,5	2,8
Rodent sp.	*Rodentia sp.*	3	1,3	19,6	58,8	0,7
Wood mouse sp.	*Apodemus sp.*	2	0,9	26,4	52,8	0,6
Yellow-necked mouse	*Apodemus flavicollis*	1	0,4	29,4	29,4	0,4
Other		8	3,4	6,1	66,2	0,8
Egg sp.	*Ova sp.*	7	3,0	9,0	63,0	0,8
Snail sp.	*Gastropoda sp.*	1	0,4	3,2	3,2	<0,1
Total		233	100,0	62,3	8125,4	100

There was a difference in the average proportion of the four main categories – birds, insects, mammals and other preys – between quantity and biomass *(Fig. 11)*. Birds and mammals contributed a smaller proportion to the Montagu's Harriers' diet in terms of quantity compared to biomass, whereas insects and other prey items showed the opposite relationship *(Fig. 11)*. Birds were a substantial component of the diet regardless of whether the diet was quantified by count or biomass *(Fig. 11)*. Insects comprised a large portion of the total captures, but their biomass contribution was negligible *(Fig. 11)*. Mammals showed a moderate presence in terms of count, but their contribution to the Montagu's Harriers' diet was more pronounced when considering their actual biomass *(Fig. 11)*. Other prey items had relatively minor impact on

both count and biomass, particularly in the latter measure *(Fig. 11)*. The individual average weight of birds was 161.6 g (s.d. ±177.4 g), while the individual average weights for insects, mammals and other prey items were 0.5 g (s.d. ±0.6 g), 64.3 g (s.d. ±75.3 g) and 6.1 g (s.d. ±4.1 g), respectively.

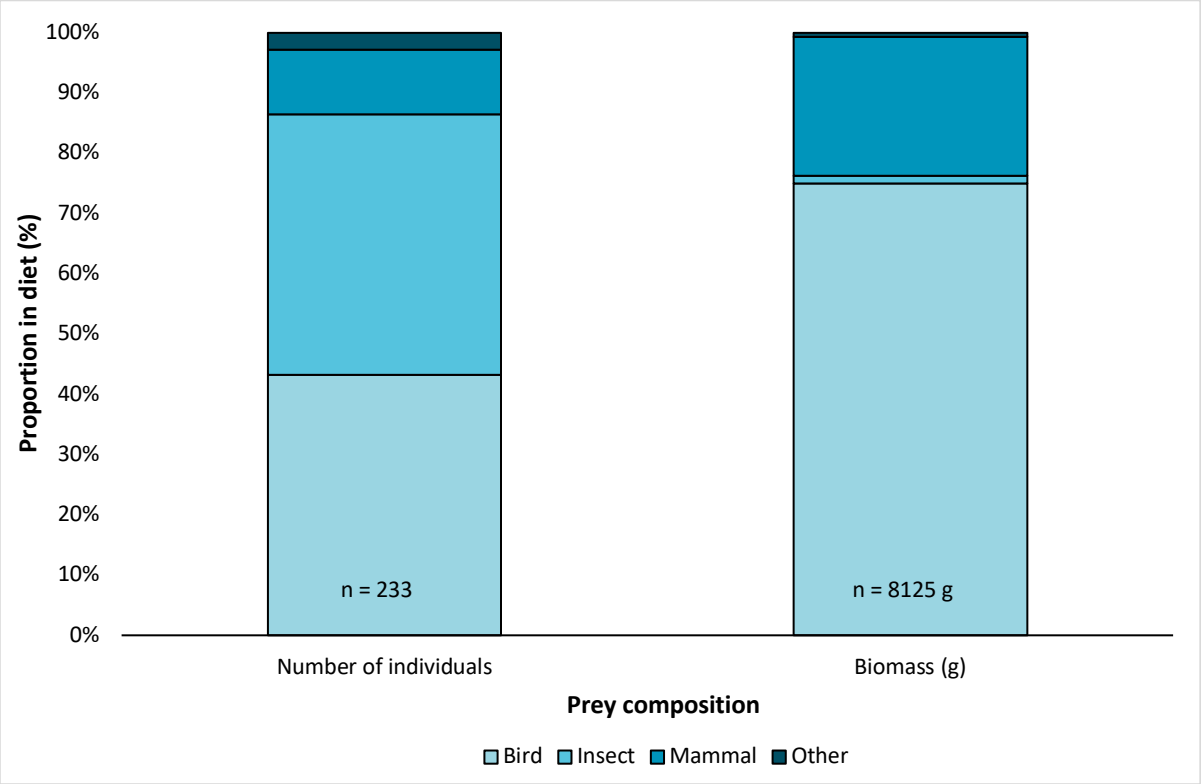

Figure 11. Proportional distribution of four categories of prey species by number and biomass found in pellets (n=78) and prey remains (n=38) of Montagu's Harriers on Öland, Sweden. Birds (n_{number} = 105; $n_{biomass}$ = 76.1%), insects (n_{number} = 95; $n_{biomass}$ = 1.0%), mammal (n_{number} = 25; $n_{biomass}$ = 22.0%) and other (n_{number} = 8; $n_{biomass}$ = 0.8 %).

The results above indicate that biomass offers a better indication of the importance of different prey categories to the Montagu's Harrier during its breeding season on Öland. Therefore, only this parameter will be displayed in the subsequent results of the study.

3.2 Seasonal variation in diet

Between July 1st and August 12th, 78 pellets and 38 prey remains were found *(Fig. 12 ; Fig 13 ; Tab. 3)*. Shortly after this date, the majority of the Montagu's Harriers had begun their migration towards Africa, that typically starts around the second half of August (Rodebrand 2011).

During each specific period of the 2023 breeding season, 10 to 32 birds were identified, while 5 to 45 insects, 2 to 10 mammals as well as 0 to 4 other prey items were found during the same four periods *(Tab. 3)*. Birds were clearly the most common prey category in each period during the summer, making up between 64.3% and 89.0% of the total biomass found *(Tab. 3)*. Insects, on the other hand, ranged from 0.4% to 2.5%, whereas mammals, clearly being the second most

common prey category, ranged from 10.1% to 32.3% *(Tab 3).* Other prey items varied between 0% to 1.0% of the total biomass during the breeding season *(Tab. 3)*.

Between 31st of July and 12th of August, the Montagu's Harriers caught the highest percentage of bird biomass, whereas the same pattern occurred for the insect prey category during the period of 11 of July to 20th of July *(Tab. 3).* The highest percentage of mammal and other prey item biomass was found between 11th of July and 20th of July and 1st of July until 10th of July, respectively *(Tab. 3)*.

Table 3. Percentage of total biomass of Montagu's Harrier diet during four periods throughout the 2023 breeding season on Öland, Sweden, classified into four prey categories. Note that the number of prey items corresponding to this biomass is specified in the table.

Prey category	1 July – 10 July	11 July – 20 July	21 July – 30 July	31 July – 12 August
Bird	72.2% (n = 32)	64.3% (n = 29)	87.9% (n = 33)	89.0% (n = 10)
Insect	0.4% (n = 12)	2.5% (n = 45)	0.9% (n = 34)	0.9% (n = 5)
Mammal	26.4% (n = 9)	32.3% (n = 10)	10.6% (n = 4)	10.1% (n = 2)
Other	1.0% (n = 4)	0.8% (n = 2)	0.7% (n = 2)	0% (n = 0)
Total	100% (n=57)	100% (n = 86)	100% (n = 73)	100% (n = 17)

3.2.1 All nests

Birds constituted by far the predominant prey category in the Montagu's Harriers' diet throughout all the four periods during the breeding season *(Fig. 12).* Mammals clearly represented the second largest biomass source during the season, though notably less than birds' contribution to their diet during this time *(Fig. 12)*. The difference in biomass contribution between birds and mammals was smallest during 11 July – 20 July but reached its peak during 31 July – 12 August *(Fig. 12)*. Both insects and other prey items constituted a negligible portion of the total biomass consumed by the harriers, with insects contributing slightly more biomass during the last three periods of the 2023 breeding season *(Fig. 12)*. Other prey items were completely absent from July 31st *(Fig. 12)*.

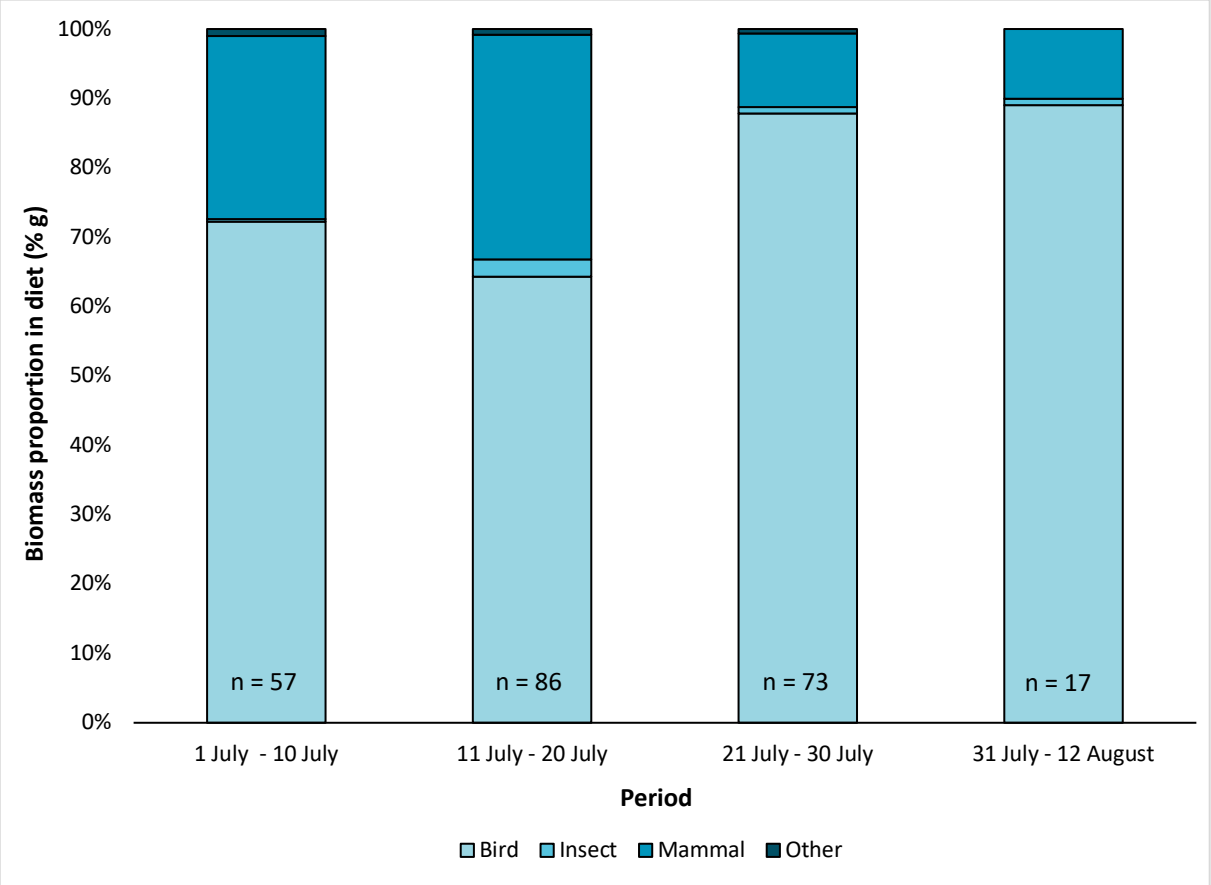

Figure 12. Proportional distribution of biomass of four categories of prey species over 10-13-day intervals for Montagu's Harriers on Öland, Sweden. The number of prey items is given in the bars.

3.2.2 Locations with prey items throughout the entire breeding season

During the breeding season, pellets and prey remains were found exclusively at the nesting sites in Grönhögen, Kastlösa and Nedre Ålebäck during all four periods of the summer *(Fig. 13)*. The highest number of prey items was found in Grönhögen (n = 190), followed by Nedre Ålebäck (n = 15) and Kastlösa (n = 11) *(Fig. 13)*. This corresponded 5286 gram for Grönhögen, 781 gram for Nedre Ålebäck and 661 gram for Kastlösa. A total of 48 prey items (2509 g) were located during the first period, 82 prey items (1936 g) in the second period, 72 prey items (2007 g) in the third period and 14 prey items (276 g) during the fourth and last period.

Birds were by far the most predominant prey type by biomass (75%) for the Montagu's Harriers in Grönhögen, Kastlösa and Nedre Ålebäck throughout the breeding season, with the exception for Kastlösa between July 21st and July 30th *(Fig. 13).* At the specific dates in Kastlösa, only insects were found captured by the harriers *(Fig. 13)*. The second most important prey category overall for these locations were mammals (23%), whereas insects (1.3%) and other prey (0.7%) had a practically negligible role in the overall biomass contribution *(Fig. 13)*.

The percentage of biomass from birds reached its peak during the period July 21st to July 30th across all three nesting sites together, but was lowest during July 11th to July 20th. The proportion of mammal biomass was highest during the period of July 11th to July 20th and lowest during July 21st to July 30th. Insects contributed the most biomass during July 11th to July 20th,

but the least during July 31st to August 12th. Other prey items were absent during July 31st to August 12th, while they reached their peak during the period of July 1st to July 10th *(Fig 13)*.

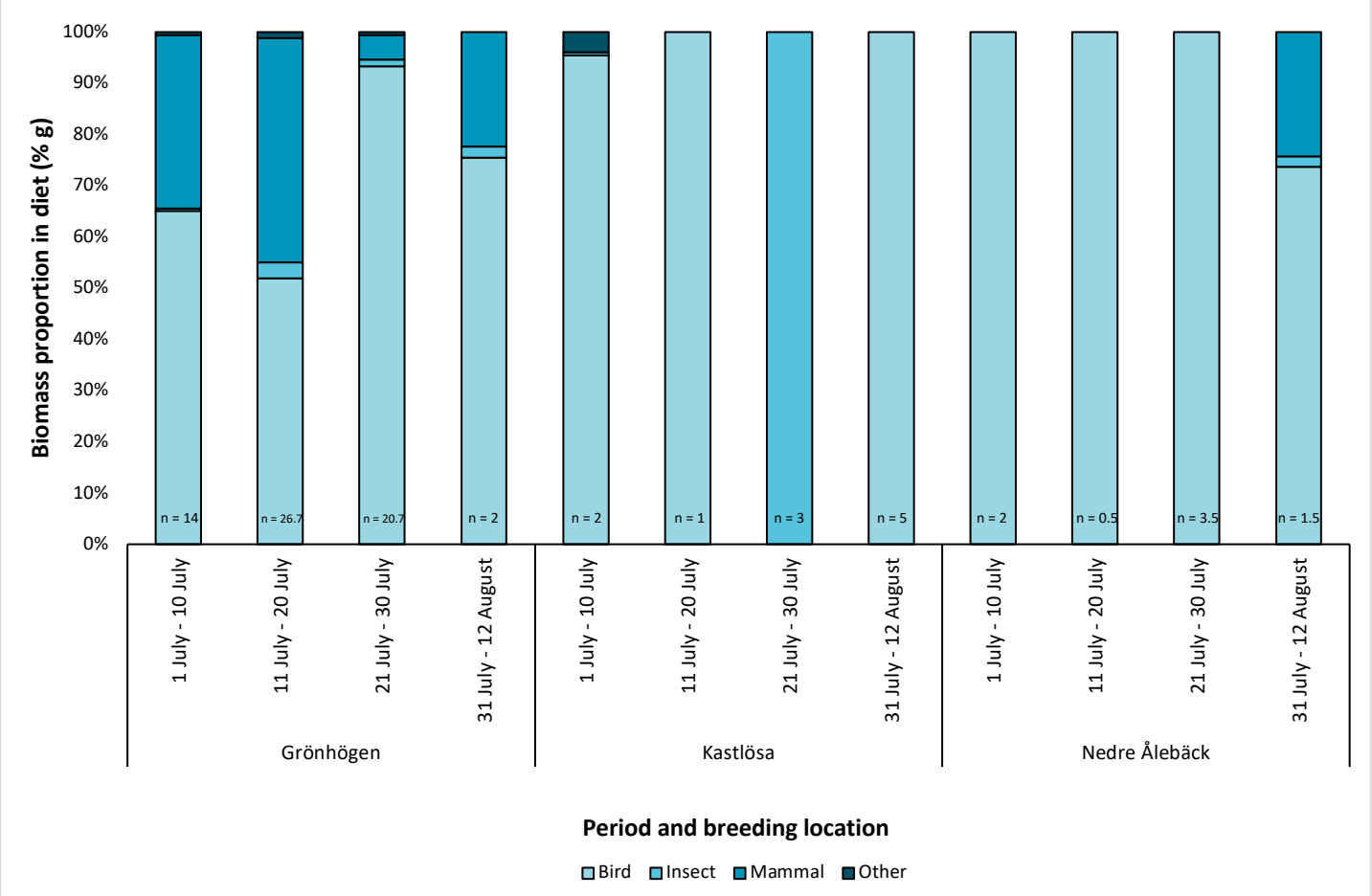

Figure 13. *P*roportional distribution of four categories of prey species by biomass over 10-13-day intervals for Montagu's Harriers on Öland, Sweden. Note that Grönhögens and Nedre Ålebäcks bars are divided by three ($n_{nest} = 3$) and two ($n_{nests} = 2$) respectively, as these locations contained semi-colonial breeding. The number of prey items is given in the bars.

3.3 Variation in diet between breeding pairs

Birds constituted the most prevalent prey category in terms of biomass at all breeding sites except for Karlevi, where mammals where the predominant type *(Fig. 14)*. Some nests had solely captured birds based on the collected material, whereas nests with several prey categories (Grönhögen, Karlevi, Kastlösa, Nedre Ålebäck and Resmo) had mammals as the second most common prey category based on biomass (except for Karlevi where mammals, as noted, was the predominant type) *(Fig. 14)*. Insects and other prey constituted a small proportion of the biomass in all nests *(Fig. 14)*.

The prey composition between different nest varied clearly, although most nests had few located prey items *(Fig. 14)*. The variation was more pronounced in nests where a greater number of prey items was found (Grönhögen, Kastlösa, Nedre Ålebäck and Resmo) *(Fig. 14)*.

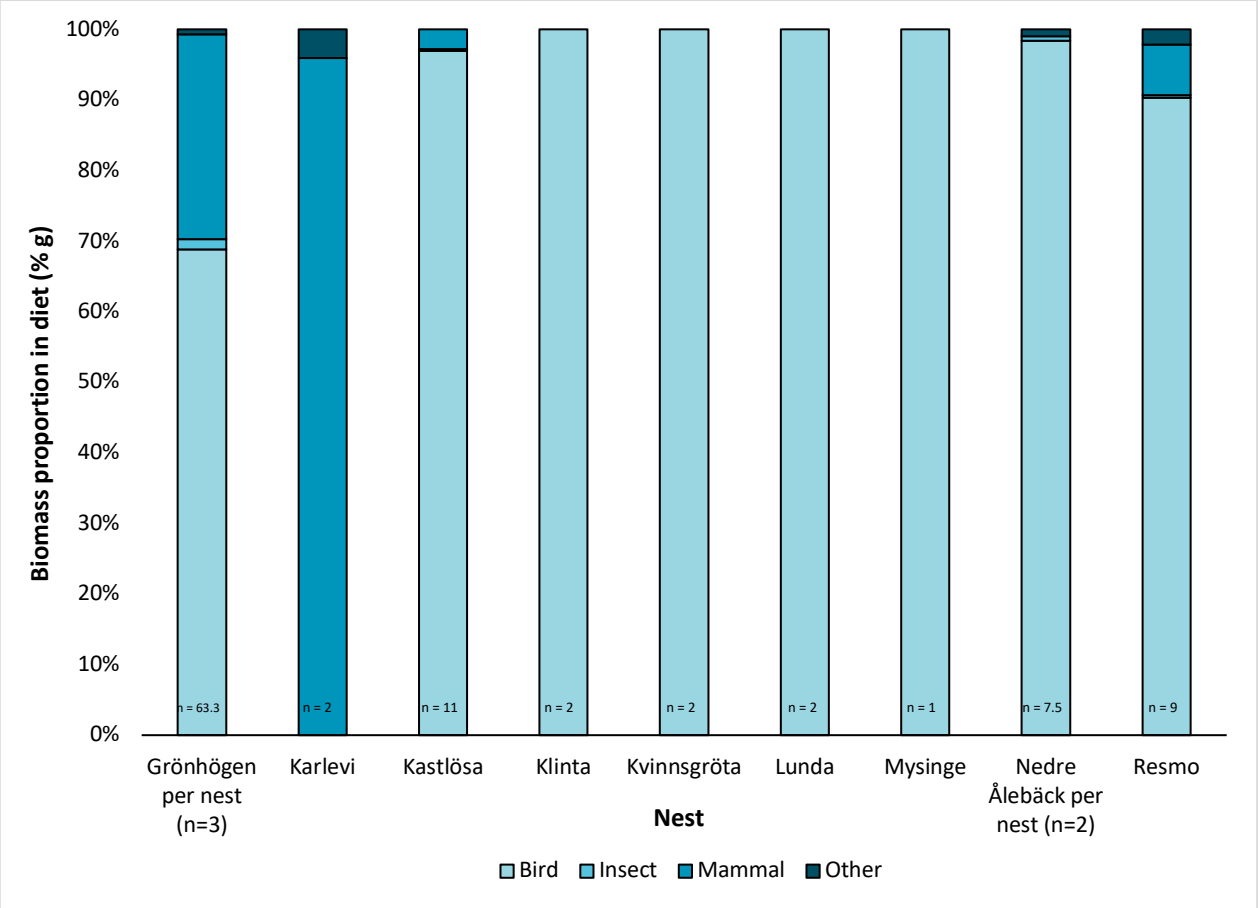

Figure 14. Proportional distribution of four categories of prey species by biomass between breeding pairs (n=12) of Montagu's Harriers on Öland, Sweden. Note that Grönhögen's and Nedre Ålebäck's bars are divided by three and two respectively, as these locations contained semi-colonial breeding. Also, note that a solitary male is included in the breeding pair in Resmo. n_{total}; birds (n = 76.1%), insects (n = 1.0%), mammal (n = 22.0%) and other (n = 0.8%). The number of prey items is given in the bars.

4 Discussion

The prey selection of Montagu's Harriers on Öland, Sweden, showcases a unique composition of preferred prey during the breeding season compared to previous studies in other countries. In the summer of 2023, the investigated Montagu's Harriers diet consisted of a total of 43 prey species, including eight passerine species, five non-passerine species, eleven beetle species, five species of *Orthoptera*, three other insect species, six rodent species, one lagomorph species, one snail species, as well as some prey listed at higher taxonomic levels due to identification issues. Among these, birds *(Aves sp.)*, grey partridges *(Perdix perdix)*, passerines, skylarks and leverets of the European rabbit *(O. cuniculus)* were among the most important prey items based on biomass, whereas passerines, skylarks, beetles, grasshoppers, great green bush crickets *(Tettigonia viridissima)* and mice *(Murinae sp.)* were prominent in terms of quantity.

4.1 Prey selection of breeding Swedish Montagu's Harriers

The results indicate distinct differences in the importance of prey species and categories, both in terms of quantity and biomass. However, birds were the most important category in both

aspects. Insects were notable in terms of quantity but had minimal impact on biomass. Mammals accounted for just over a tenth of the number of prey but nearly a quarter of the total biomass. Other prey items were negligible in both number and biomass. These findings emphasize that biomass is the best indicator for the importance of different prey categories, regardless of their frequency among the collected material. This is supported by previous studies, for example by Arroyo (1997), Kitowski et al. (2021), Koks et al. (2007), Mirski et al. (2016) and Onofre (2020), that show that the number of prey items is irrelevant if the prey do not provide enough biomass, i.e. food and energy.

Based on countries nearby and knowledge of the Montagu's Harrier population on Öland, it was predicted that the population would predominantly rely on voles and to some extent passerines, but also to a certain degree on larger mammals, lizards, larger insects and bird eggs. However, unlike in many parts of the breeding range of the species', particularly in Europe (e.g. see García & Arroyo 2005; Kitowski et al. 2021; Koks et al. 2007; Onofre 2020; Wiącek 2015), the Öland population showed a distinct preference, for birds as its primary prey. In this area, both passerines and non-passerines were important prey in terms of biomass. However, passerines dominated as the main prey by number. Hence, passerines were captured much more frequently than non-passerines. This is logical, given that passerines typically contribute less biomass per prey compared to non-passerines, that generally weigh considerably more per individual (see Table 2; AnAge 2024; Baldwin & Kendeigh 1938). Also, the fact that skylarks were the most common bird species found in the harriers' pellets and prey remains can most likely be explained by the species' high numbers in southern Sweden compared to many other bird species (Birdlife Sweden 2021). This significant presence of skylarks on Öland and in the Montagu's Harriers diet may thus reflect the previously mentioned generalist and opportunistic feeding strategy of the species, opting for the most abundant, hence most accessible, prey in their landscape.

The aspect that birds constituted such a substantial proportion of the Montagu's Harriers diet, both in terms of number (45.1%) and biomass (76.1%), has not been observed in other studies. Earlier research across different parts of Europe has shown that birds normally contribute approximately 12-33% (e.g. see García & Arroyo 2005; Kitowski et al. 2021; Koks et al. 2007; Onofre 2020; Terraube & Arroyo 2011; Wiącek 2015), and in some cases up to around 42% (see Mirski et al. 2016), of the total biomass in the harriers' diet. The strong preference of Öland's Montagu's Harriers for birds over other prey types may be linked to Öland's high bird diversity in various environments, including agricultural land. The island is recognized as one of Europe's best locations for birdlife – primarily due to its rich variety of habitats and landscapes, that includes wetlands, meadows, forests, alvar grasslands, as well as coastal areas (Betzholtz et al. 2010) and coastal meadows (Betzholtz et al. 2010; Friberg & Forslund 2019). This variation in habitats thus attracts a wide range of bird species to breed, roost or live all year around, something that is evidenced by the observation of around 400 bird species on the southern tip of the island (Ottenby bird observatory n.d.).

Surprisingly, mammals, especially rodents (such as voles), played a far less significant role in the diet of our Montagu's Harrier population than initially thought based on observations as

well as the importance of voles during good vole years in nearby countries, such as the Netherlands. Although mammals comprised 22.0% of the total biomass, they only made up 10.7% by number. This indicates that the captured mammals were quite heavy, which also is confirmed by the distribution of lagomorphs and rodents in the study. In fact, leverets from European rabbits, weighing 214 g each (see Table 2 ; Appendix 2), comprised approximately 76% of the mammal biomass. This emphasizes the minimal contribution of rodents (6.2%) to the Swedish Montagu's Harriers' diet in 2023. Determining whether this was due to a poor vole year on Öland is challenging, but given consideration to the mild summer in southern Sweden in 2023, conditions were likely rather favorable for rodents, without extreme heat and/or drought. This is because many rodent species in Sweden primarily feed and rely on vegetation and smaller insects (Artdatabanken SLU – A n.d.; Artdatabanken SLU – B n.d.; Artdatabanken SLU – C n.d.; Artdatabanken SLU – D n.d.), that are more difficult to find during hot and dry summers compared to a mild and moist summer, like last year. If this low contribution of rodents was attributed to a substantial portion of material not being recovered, that may have included some mammal remains, it is hard to determine definitely, but the possibility exist and should be acknowledged.

Another potential explanation for why the Montagu's Harrier's were not more reliant on rodents may be attributed to that birds might have been more abundant during last summer. Resulting in a dominance of birds in prey selection owing to the species' opportunistic nature, i.e. foraging behavior. Possibly, bird populations had a high breeding success in the mild summer conditions on Öland last year which could have led to an increased avian prey availability beyond normal levels. The Montagu's Harrier's preference for bird could also, and perhaps even more likely, be tied to Öland's diverse bird and wildlife populations, especially in agricultural areas, including vast areas of grazed land. This abundance likely results in a large number of ground-nesting passerines, which in turn would explain the dominance of bird in their diet. However, no information on prey availability has been collected in this study in conjunction with the fact that the study's sample size may have influence the results. It would therefore be interesting to investigate harrier prey and prey availability in several years to determine if avian prey is as important as we think now.

The relatively low contribution of insects (1.0%) to the captured biomass by the harriers during their breeding on the island is unsurprising, considering the small size of these prey items, despite their abundance. Thus, it is not viable to primarily target these prey when other more profitable prey are available (Kitowski et al. 2021), as the needs of the breeding pairs and their offspring are too high to be adequately met by insects (Terraube & Arroyo 2011) at this latitude for survival and to maintain good condition before the autumn migration to North Africa. It therefore does not become profitable for them (Kitowski et al. 2021), as there are too many beaks to feed, that instead can be fed by other abundant and more profitable prey, such as birds and mammals. This effect is likely amplified as a result of that birds and mammals offer high-energy food that is easier to assimilate compared to other prey (Wiącek 2015), like insects (Terraube & Arroyo 2011). In fact, insects are the least energetically profitable prey category as a consequence of their low to medium contribution of energy combined with their relatively high handling time for harriers (Terraube & Arroyo 2011).

This means that even though insects were numerous (45.1%), their minimal size, i.e. biomass (1.0%), made them not crucial for the survival and rearing of the chicks. However, this does not imply that insects are useless and unimportant, as they often serve as vital initial prey for the chicks as they learn to hunt and divide prey themselves (Kitowski 2005; Kitowski et al. 2021). The breeding pair typically supply, for instance insects to their chicks as a part of their learning process to become an independent predator (Kitowski 2005). In addition, females often hunt for insects in the vicinity of the nest where they can still keep watch over the brood but also contribute to the feeding of the offspring (A. Schlaich, personal communication, 24-05-16).

Several other countries in Europe, exhibit notably higher invertebrate contributions (e.g. see Mirski et al. 2016; Onofre 2021) than Öland. For instance, previous studies by Mirski et al. (2016) and Onofre (2021) have shown that insects contributed 20.8% of the diet's biomass in Poland and 32.9% in Spain. The low contribution in some regions, like Öland, may partly be explained by that most insect parts can be digested by Montagu's Harriers, resulting in an underrepresentation of this category in pellets and prey remains (Kannan et al. 2022). Conversely, other categories – like mammals – can be overrepresented (Redpath et al. 2001) as many parts cannot be digested (Lewis et al. 2004) and also may be regurgitated in several pellets (Lewis et al. 2004; Trierweiler & Hegemann 2011).

Moreover, the fact that invertebrate contribution generally decrease further north in Europe could relate to the distribution of insects, with more insects found in the southern part of Europe (Onofre 2020). That is due to shorter, less warm summer in the northern part of the continent (Onofre 2020), potentially reducing the contribution of insects among the Swedish population of Montagu's Harriers. Yet, this fails to explain why Poland, in such proximity to Öland, exhibited notably higher prevalence of insects in the diet of their Montagu's Harriers. The former might be attributed to differences in agricultural landscapes. Studies conducted in Poland, e.g. see Mirski et al. (2016), have revealed findings indicating that Montagu's Harriers nesting in less intensively managed areas with lowers levels of intensive and modern agriculture have a greater proportion of insects in their diet, compared to the population on Öland.

It is not surprising that other prey items, i.e. bird eggs and a snail, were uncommon in the diet of Swedish Montagu's Harriers (only 3.0% and 0.4% in number, and 0.8% and 0.1% in biomass, respectively). This can partly be explained by the species' typical diet, that does not include mollusks (see section 1), but also the fact that the majority of prey bird eggs had already hatched during the period of the study (1st of July – 12th of August). Yet, this does not exclude the possibility that bird eggs could have been more important earlier in the breeding season, in May and June, when the egg abundance is higher. The result of the small contribution of other prey items is also not remarkable given that previous studies (e.g. Kitowski et al. 2021; Mirski et al. 2016; Onofre 2020; Terraube & Arroyo 2011; Wiącek 2015) in Europe have shown that bird eggs usually only contribute 10% of the diet during the breeding season. This may be due to the same reasons mentioned above concerning insects, that these prey types are less profitable than others.

The lack of amphibians and reptiles, especially lizards, in the diet of Swedish Montagu's Harriers, despite their presence in other European regions and field observations (before 2023) in Sweden, can most likely be explained by the following reasons. It is possible that amphibians and reptiles constituted such a small portion of the Montagu's Harriers' diet that their remains were not detected in the study's collected material. The fact that not all prey material can be located is a general challenge for these kind of studies, especially at nests where little material is recovered. This also applies to this study and all four prey categories. In this study, the collection of prey material was mainly limited by that breeding pairs 1 and 9-10 had chosen unfavorable plucking sites, such as out in lucerne fields or in the middle of cornfields, but also by that pair number 11 and 12 were found late during the breeding season. That resulted in that not all material could be found and thus was lost to the study.

Other reasons contributing to the absence of reptiles and amphibians in the study could be that there might have been low abundances of these prey categories, despite the mild summer weather, making it less worthwhile for the harriers to pursue them. Or that especially high abundance of bird led to this result. Alternatively, the Montagu's Harriers in the studied population might simply prefer other prey items that they perceive as more valuable, and hence, more worthwhile.

4.2 Seasonal fluctuations in Montagu's Harriers prey selection

4.2.1 All nests

The prey selection of all the breeding Montagu's Harriers on Öland varied throughout the summer, with birds consistently representing the most important prey in terms of biomass. Mammals clearly ranked as the second most important prey during all periods, while insects and other prey items contributed a small portion of the total biomass during each period. This result is consistent with the overall diet of summer 2023 and is, as previously discussed, most likely attributed to a high abundance of birds during last year's breeding season. Birds being the most abundant prey category, while also being a high-energy prey (Wiącek 2015), probably led the opportunistic harriers to encounter birds more frequently than other prey, and thereby captured them to a greater extent.

The observation that the percentage of birds captured within each period peaked towards the end of the summer contradicts one of the hypotheses of this study and the majority of results from previous studies (see e.g. Kitowski et al. 2021; Mirski et al. 2016). However, it is important to note that the percentages of the actual number and biomass captured during the first period (1st of July – 10th of July) was almost equivalent to that of period two (11st of July – 20th of July). Additionally, a similar number of birds were captured, but with higher biomass contribution, during period three (21st of July – 30th of July) compared to period one and two. This implies that the predicted hypothesis, i.e. that the proportion of captured birds are highest early in the summer and decline over time, is inconsistent with the actual findings.

However, the rationale behind the similar captures of bird prey during period one and two, the higher rate during period three and four could be attributed to the following three explanations. (1) Larger parts of the bird prey material may have remained undiscovered than other prey remains during period one and two, despite in reality being more abundant, which would support the study's hypothesis. The perception that prey categories appear more (or less) important than they actually are (that depends on to which extent a prey can be digested), alongside the practical limitation of never being able to recover all pellets and prey remains from Montagu's Harriers, are a general problem for these kind of studies. (2) Öland has a consistent high supply of bird prey that fluctuates slightly over time. The birds are also relatively easy to capture until the end of the summer (period four), before many begin their autumn migration. (3) Other prey items, such as smaller mammals, may have been more abundant (due to their typical cyclical patterns (Salamolard et al. 2000)) and easier to capture during period one and two than during the last two periods. If they were easier to capture during period one and two, could be attributed to a higher availability of juvenile mammals earlier during the breeding season (Arroyo 1997), that also are easier and less risky to attempt to capture (Terraube & Arroyo 2011). This could have resulted in mammals representing a larger part of the biomass during 1st of July – 20th of July.

The most likely explanation to the seasonal variation in bird prey composition might be a combination of incomplete recovery of pellets and prey remains across periods, a consistent availability of birds on Öland through the breeding season and fluctuations in the population of other prey species and their abundance during the summer. This suggests that conclusions should be drawn with caution regarding why a specific prey category's seasonal variation does not align with theory. However, these factors may have resulted in the Montagu's Harrier's shifting the proportions of birds in their diet over time, a trend that has been documented in other studies (e.g. Arroyo 1997; García & Arroyo 2005; Kitowski et al. 2021; Koks et al. 2007; Mirski et al. 2016; Wiącek 2015). As one type of prey is captured more frequently during a specific period, there is a natural corresponding decrease in the capture of other prey categories (Wiącek 2015). Thus, there is an interplay between different prey categories, where the Montagu's Harrier selects the most accessible and easiest prey to capture at that particular moment. Especially as it quickly can adjust its choice of prey (Arroyo 1997).

As for the proportion of mammals, they contributed the highest proportional biomass percentage during period two. As the summer progressed, they became increasingly uncommon in total percentage of the harriers' diet and this finding is partly in contrast or directly contradicts results from the Netherlands and Poland (see van Laar 2013 and Mirski et al. 2016). The result also contradicted the expected trend of a rise in mammal occurrence in the diet as the summer progressed, indicating that the recovered prey items from mammals did not align with the hypothesis. This trend may be influenced by several factors. Early in summer, many mammals reproduce rapidly, resulting in higher population levels (Erlinge et al. 1983; Ylönen et al. 1991). Conversely, as the season advances, more mammal prey species begin reproducing (Ylönen et al. 1991), although many are preyed upon early in their lifecycle (Hansson & Henttonen 1989). But also, as summer progresses, the risk of getting eaten by a predator intensifies (Erlinge et al. 1983) and more mammals get exposed to predators and/or die as a

result of human agricultural activities, such as mowing (Schlaich et al. 2015). The described factors, along with the fact that the heaviest mammals (leverets) were nearly exclusively caught at the beginning of the summer, i.e. before they became too heavy and risky to hunt, could provide an explanation for the seasonal pattern of mammals observed in the study.

Furthermore, when examining why the mammals contributed varying percentages during each period, it is likely related to their availability compared to other prey categories, with bird prey abundance probably playing a large role. When for example mammal populations increase, they will also be targeted more frequently due to their increased prevalence, and vice versa. Therefore, the explanation may vary depending on whether you analyze the total percentage contribution of the mammal category over the breeding season or if one compare the percentage within each period.

Given the minimal contribution of insects and other prey items to the total biomass across all four periods, despite substantial variations in their numbers between periods, it is challenging to discuss and/or draw conclusions about their actual variation during the Montagu's Harriers' breeding season. It is, however, notable that a higher number of insects was recovered during the middle of the summer (11th of July – 30th of July), i.e. the warmest period, – supporting the hypothesis that insects require warmer conditions, thus being most abundant during that time. By this point, most insects have reached adulthood and can be captured more easily compared to earlier or later in the summer (Jiguet 2002), especially if the weather is mild – as it was last summer. Hence, both categories most likely remained uncommon throughout all four periods as a result of their limited significance when more high-energy prey, that is easier to assimilate, were available.

The differences in prey composition over the breeding season's periods between Poland, the Netherlands and Öland (Sweden) are noteworthy. In Poland, findings indicate that 33.3% of the prey biomass are mammals, 41.6% are birds and 20.8% are insects, with the remaining 4.3% falling into other prey categories (Mirski et al. 2016). In contrast, a Dutch study by Koks et al. (2007) showed that approximately 52% of the prey biomass was small mammals, 23% larger mammals, 22% birds and the remaining 5% belonged to other prey categories. This differs from the results presented about the diet of Montagu's Harriers on Öland. Additionally, in Poland, the proportion of mammals increased over the season, while birds decreased from the beginning of July, and insects, depending on insect order, peaked either in June or July (see Mirski et al. 2016). Conversely, in the Netherlands, mammals dominated, but their contribution to the overall diet fluctuated and peaked towards the end of the breeding season (see van Laar 2013). Birds and insects also fluctuated, although birds were clearly the second most common prey during each period (see van Laar 2013).

The seasonal difference observed on Öland compared to Poland and the Netherlands, despite its geographical proximity, are likely explained by two factors. Once again, the harrier's opportunistic nature drives them to target the most accessible prey, which likely varies between previous studies and this study. The dominance of birds on Öland throughout each period, unlike the other countries, probably stems from the island's status as one of Europe's best

habitats for breeding birds, owing to its landscape diversity compared to many other European locations and regions. This unique aspect of Öland suggests that conditions in the other areas may have been less favorable for supporting such a rich diversity and abundance of birds. Resulting in Polish Montagu's Harriers hunting birds and mammals in agricultural landscapes, while Dutch agricultural areas primarily supported mammals. For instance, the Dutch landscape is characterized by intensive agriculture, which is species-poor, causing the Montagu's Harriers to depend on voles, especially during peak vole years (Koks et al. 2007). This means there are not enough alternative prey, like birds, unlike the situation on Öland. Earlier studies (e.g. Terraube & Arroyo 2011) also indicate that Montagu's Harriers shift from a bird-based diet only when profitable. This was thus likely not the case on Öland.

The fluctuations in prey and the varying trends among the different prey categories are most likely also influenced by the fact that populations differ from each other (Ricklefs & Relyea 2021) including those of Montagu's Harriers (e.g. Arroyo et al. 2007; Kitowski et al. 2021; Wiącek & Niedzwiedz 2005). Different populations often specialize in unique ways to meet specific environmental conditions, adjusting to their ecological niche, the level of competition they encounter locally (which varies between countries) (Ricklefs & Relyea 2021) and making local adjustments to maximize their breeding success (Salamolard et al. 2000). These factors thus play a role to the different seasonal prey preferences observed among the Montagu's Harriers in Sweden, Poland and the Netherlands.

4.2.2 Nests in Grönhögen, Kastlösa and Nedre Ålebäck

The locations where pellets and prey remains were discovered during all four periods were Grönhögen, Kastlösa and Nedre Ålebäck. The prey composition varied not only between the locations in the same period, but also in how the prey choices changed over the breeding season. All sites and periods were dominated by birds, with the exception of period three in Kastlösa, where only mammals where recovered. The prevalence of birds can likely be attributed to the entire population likely having better access to birds as prey than other types of prey, influencing their prey choices.

Nevertheless, it is important to consider that few prey items were found in each period at Kastlösa and Nedre Ålebäck, potentially altering our understanding of the prey composition. Therefore, Grönhögen is probably the only site where enough material is collected to discuss how these semi-colonial breeding pairs actually selected prey. The other two locations are too uncertain, due to their low sampling size, to draw any conclusions about how the diet changed over the summer and how/why the composition of the three locations differed.

The three nests in Grönhögen consistently showed a preference for birds as their primary prey, with mammals clearly being the second most common prey type. Insects and other prey items contributed little to the prey biomass in this location, although insects were slightly more common than other prey were. The distribution of birds and mammals almost mirrored those seen across all nests, but mammals were more common in Grönhögen during all periods (except period three), and they also increased during period four. However, it is important to note that the data from Grönhögen during the last period was based only on six prey items, that is much

fewer than the 42, 62 and 80 prey items found during the other periods. This skewed distribution in sample size casts doubt on the accuracy of the true prey distribution during this last period. With that in mind, the overall trend in Grönhögen was relatively consistent with the result when all nests were analyzed together. This is reasonable as this location constituted a substantial portion of the recovered material, thereby forming the bases for the discussion, conclusions and explanations presented in section 4.2.1.

The substantial contribution of birds in the extensive material recovered from Grönhögen may not only be explained by their likely high abundance and consequent ease of capture, but also by the proximity of the three nests to the southern tip of the island and thus Ottenby bird observatory which is recognized as one of Europe's best stopover- and breeding sites for birds (Wilhelmsson et al. 2020). This likely resulted in a landscape close to the nest that was rich in birds that could be captured.

4.3 Variation in prey selection within the Öland population

All 12 nests, except the nest in Karlevi, where mammals were the primary prey, showed a dominance of birds in their prey selection. Nonetheless, several nests (nest number 1 and 9-12) had few prey items found – either as a consequence of unfavorable plucking sites or late discovery of nests. This makes it challenging to draw conclusions about several nests in the population on Öland and regarding their primary prey choice, whether it was birds or another prey category. One can only speculate about their true prey preferences during the breeding season.

Among the nests studied, only Grönhögen, Kastlösa, Nedre Ålebäck and Resmo had a higher number, and thus biomass, of prey items. In these seven nests, mammals were the second most common prey, though once again substantially less compared to birds. Additionally, both insects and other prey items were uncommon, but other prey were somewhat less uncommon than insects in terms of biomass. However, these seven nests represented more than half of the nests studied, implying that birds were likely favored as the primary prey category for nest number 1 and 9-10 as well. This is supported given the relatively large distance between these seven nests. For instance, Grönhögen's nests and Nedre Ålebäck's nests were the nests furthest apart in this study (50 km as the crow flies), yet they shared birds as their primary prey choice.

Despite the four categories of prey following the same trend as in earlier discussed results, there seem to be individual differences between the nests/locations regarding the proportion contributed by these categories to the total biomass. For example, Grönhögen exhibited a notably higher biomass of mammals compared to Nedre Ålebäck, that was the location where the second most material was collected during the breeding season. The slight variations in the distribution of each prey category among the locations may stem from inherent individual differences and specialization within a population. Previous studies (see Terraube et al. 2014) have demonstrated that within the same Montagu's Harrier population, certain individuals may act as specialist while others act as generalists. Furthermore, local variations in prey densities and competition, along with individuals' differing hunting experiences and skills, may also contribute to the outcome. This was discussed in section 1.1 might derive from morphological

differences that affects the ability to efficiently capture different types of prey (Rincón et al. 2007; Terraube et al. 2014), together with their individual patterns of habitat use and foraging behaviors, but also the fact that landscapes differ – that in turn affects the abundance of different prey (Terraube et al. 2014).

The minor differences observed between the seven nests may thus be influenced by intra-population phenotypic differences, physiological as well as morphological, but also spatial and temporal heterogeneity in prey abundance and/or diversity, along with different levels of experience (Terraube et al. 2014). This might explain the relatively small differences observed among the nests that had a higher quantity of material collected during last summer.

4.4 Concluding remarks

Birds consistently served as the primary prey for Montagu's Harriers on Öland in 2023, regardless of the aspect under investigation. Mammals clearly represented the second most important prey category, although they were far less common than birds. Insects and other prey items did not contribute significantly to the harriers' diet based on biomass, but they might still be vital for the development of chicks into proficient predators. This highlights that the population largely relies on several prey types, especially birds, for its survival on the island. That, in turn, is a critical insight to consider that should guide future measures for the species and its conservation in the landscape of Öland. Especially given that the prey composition appears to be unique to Öland compared to other parts of Europe.

Also worth highlighting is that the three nests in Grönhögen contributed with the majority of the collected material from the population. This sheds light on the prey distribution further south on the island, where these birds were hunting. Determining if the entire island population relied on birds during the summer of 2023 is harder, especially since five nests did not yield a lot of prey material. However, at the seven nests where more prey biomass was found, birds were consistently identified as the primary prey, despite considerable distances between them – indicating a likely trend across all nests included in the study.

It would have been beneficial for the study if the collected prey material had been more evenly distributed across the 12 nests. Unfortunately, this was beyond my control as Montagu's Harriers do not always select plucking sites where pellet and prey remains are easily detectable. Challenges in accessing plucking sites also complicated the collection of prey material. Including more nests in the study would have provided a more comprehensive understanding of their prey choices/preferences, benefiting the knowledge of the entire population as well as variations between breeding pairs. However, last summer, it was necessary to accommodate needs and opinions of local farmers to participate in the Montagu's Harrier project. This aspect should be considered into future initiatives in order to maximize collection of pellets and prey remains.

4.5 Conclusions and future implications for Montagu's Harrier conservation on Öland

The fact that birds constitute the primary prey for the Montagu's Harriers on Öland underscores the unique nature of this population compared to other Montagu's Harrier populations, which have never displayed such an extensive reliance on birds in their diet. This population likely reflects its unique location and environment – fulfilling not only the Montagu's Harriers requirements but also those of many other birds species. Given that many bird species on the island rely on wetlands, (coastal) meadows, forests, coastal areas, the unique alvar grasslands as well as farmland, several different areas on Öland would need protection and/or increased protection to safeguard the prey species that the harriers depend on. This, in turn, would aid in conserving this charismatic raptor, that contributes not only to recreation experiences but also to the stability of ecosystems as well as the unique composition of biodiversity on Öland.

To ensure an effective conservation of Montagu's Harriers, their habitats and the species they rely on during the breeding season, more research into the species, particularly its prey preferences on the island, is pivotal. The variability in prey choice observed between years in previous studies across Europe underscores the need for a deeper understanding of what sustains the harriers on Öland. This knowledge is crucial for confidently implementing effective conservations measures, beyond those already established.

Furthermore, the study should also be expanded to include sporadic breeding locations of Montagu's Harriers in Sweden outside Öland to assess whether the Öland population exhibits unique food preferences or if Swedish Montagu's Harriers overall display distinctive prey choice. Especially given that the Montagu's Harriers on Öland exhibit a strong fidelity to their birthplace (i.e. they typically breed on Öland if they were born on the island) (Rodebrand 1996). An initial step in expanding the study could involve study the entire Öland population, including nests located on the northern half of the island and/or in natural habitats. It is imperative in such cases to consider and collaborate with involved parties, especially farmers, to address their interests simultaneously as conducting research aimed at understanding potential differences in prey preferences within, and potentially beyond, Öland.

Thus, it will require concerted efforts and future research initiatives to continue the successful work with the Montagu's Harrier on Öland. This includes preserving one of the species' most critical and last remaining breeding grounds in Sweden and acquiring knowledge about the population to facilitate the implementation of even more effective measures in the future. Although Montagu's Harriers on Öland constitute only a small fraction of the biodiversity on the island, they symbolize something much greater – humanity's determination and capacity to bring about real change. Ultimately, this can contribute in the long run to saving much of what has been lost or is currently at risk of being lost, giving tomorrow's Montagu's Harriers an opportunity to reclaim their former numbers and habitats.

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6 Appendices

6.1 Appendix 1

Appendix 1. Standardized Dutch protocol for documenting data on pellet and prey remains from birds, such as Montagu's Harriers *(Circus pygargus)*.

Prey remain form year 20...

Grauwe Kiekendief
Kenniscentrum Akkervogels

nr	date	species	place (nest code)	found near	type	lenght	width	prey type	percentage
		MoH		N nest P pole F field edge O other	p pellet r remain	mm	mm		%

6.2 Appendix 2

Appendix 2. Literature used to determine the average individual live weight of prey in the Montagu's Harrier diet on Öland, Sweden.

Prey species	Latin name	Literature
Bird sp.	*Aves. sp.*	Average weight of all birds species in the study.
Black headed gull	*Chroicocephalus ridibundus*	AnAge (2024).
Grey partridge	*Perdix perdix*	AnAge (2024).
Hooded crow or rook	*Corvus cornix or Corvus frugilegus*	AnAge (2024) – average weight of the two species.
Northern lapwing	*Vanellus vanellus*	AnAge (2024).
Pigeon sp.	*Columbidae sp.*	AnAge (2024) – average weight of *Columba* livia, Columba *oenas*, *Columba palumbus* and *Streptopelia decaocto*.
Eurasian skylark	*Alauda arvensis*	Average weight based on AnAge (2024), Kitowski et al. (2021) and Mirski et al. (2016).
Euraisian tree sparrow	*Passer montanus*	AnAge (2024).
European starling	*Sturnus vulgaris*	AnAge (2024).
Passerine sp.	*Passeriformes sp.*	Average weight of all passerines in the study.

Pipit sp.	*Anthus sp.*	AnAge (2024) – average weight of and *Anthus* cervinus, Anthus *petrosus*, *Anthus pratensis*, *Anthus spinoletta* and *Anthus trivialis*.
Reed bunting	*Emberiza schoeniclus*	AnAge (2024).
Wood lark	*Lullula arborea*	AnAge (2024).
Yellowhammer	*Emberiza citrinella*	AnAge (2024).
Insect sp.	*Insecta sp.*	Average weight based on Kitowski et al. (2021) and Schlaich et al. (2021).
Beetle sp.	*Coleoptera sp.*	Average weight of all beetle species in the study.
Click beetle sp.	*Elateridae sp.*	Evans (1972).
Dor beetle	*Anoplotrupes stercorosus*	Jay-Robert et al. (2003).
Harpalus sp.	*Harpalus sp.*	Honek et al. (2003).
Leef beetle sp.	*Chrysomelidae sp.*	Kang & Krupke (2009).
Pill beetle sp.	*Byrrhidae sp.*	Farrell (1974).
Poecilus sp.	*Poecilus sp.*	Lang et al. (2012).
Pterostichus sp.	*Pterostichus sp.*	Lang et al. (2012).
Pterostitchus versicolor	*Pterostichus versicolor*	Average weight based on Booij et al. (1994) and Lang et al. (2012).
Ten spotted ladybird	*Adalia decempunctata*	Dixon (1959).
Weevil sp.	*Curculionidae sp.*	Average weight based on Martinek et al. (2017) and Reardon & Spurgeon (2002).
Cricket sp.	*Gryllidae sp.*	Finke (2015).
Grasshopper sp.	*Caelifera sp.*	Average weight based on Mitchell et al. (2014) and Schlaich et al. (2021).
Great green bush cricket	*Tettigonia viridissiima*	Mirski et al. (2016).
Orthoptera sp.	*Orthoptera sp.*	Average weight based on Fielding & DeFoliart (2008) and the average weight of all *Orhoptera* species in the study.
Wart-biter	*Decticus verrucivorus*	Average weight based on Cherrill & Brown (1990) and Mirski et al. (2016).
Damselfly sp.	*Zygoptera sp.*	Oliveira-Junior et al. (2022).
Hymenopteran sp.	*Hymenoptera sp.*	Ulrich (2006).
Shield bug sp.	*Carpocoris sp.*	Pereira et al. (2017).
European rabbit	*Oryctolagus cuniculus*	AnAge (2024).
European water vole	*Arvicola amphibius*	AnAge (2024).
House mouse	*Mus musculus*	AnAge (2024).
Mouse sp.	*Murinae sp.*	Schlaich et al. (2021).
Rodent sp.	*Rodentia sp.*	Average weight based on Kitowski et al. (2021) and Mirski et al. (2016).
Wood mouse sp.	*Apodemus sp.*	AnAge (2024).
Yellow necked mouse	*Apodemus flavicollis*	AnAge (2024).
Egg sp.	*Ova sp.*	Mirski et al. (2016).
Snail sp	*Gastropoda sp.*	Hurst (1936).