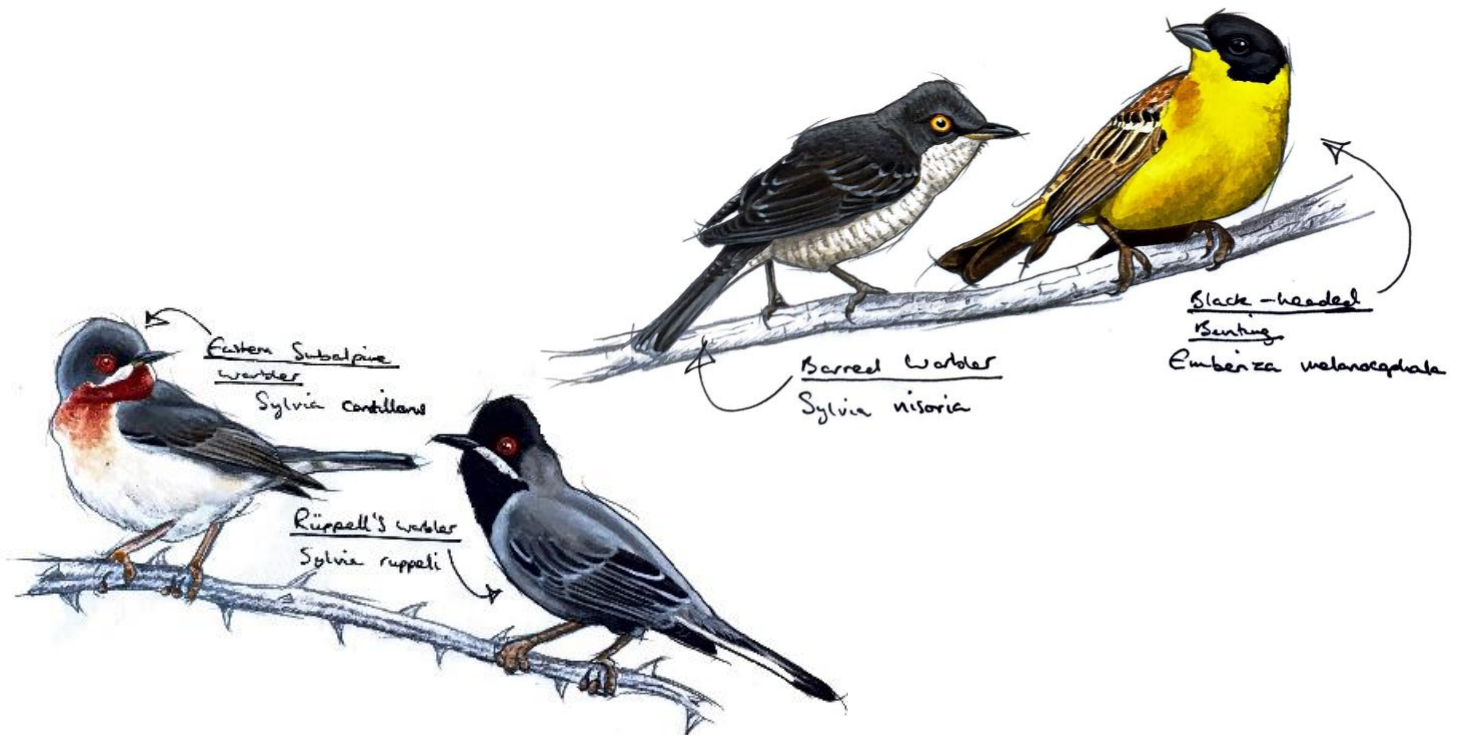


# Bird and Insect migration through Cyprus and the eastern Mediterranean region



Submitted by

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# Abstract

Twice each year, vast numbers of birds and insects undergo poleward migrations. Species which cross between Europe and Africa must negotiate traversing the Mediterranean region. Many birds are known to avoid crossing seas and therefore in the east they bypass the Mediterranean by taking an overland route and migrating through Israel, Lebanon and Syria. However, some birds do make the sea crossing and use Cyprus as a steppingstone between Africa and Europe. Despite widespread knowledge of this route, no dedicated studies on bird migration have been carried out in the north of Cyprus, and no season-long assessments of insect migrants has been carried out on the island. From March through to May of 2019, a team of five University of Exeter students surveyed insect and bird spring migration occurring through the northeast peninsular of Cyprus over a 39-day period; this survey was to be repeated in spring 2020, but the COVID-19 pandemic rendered fieldwork impossible. In **Chapter 1** observations of bird migration on Cyprus were contextualised by comparing them with ornithological radar data from Israel (a known migratory hotspot), then assessing broad migration trends and the effect of wind on bird migration intensity. In agreement with existing studies, larger birds like raptors were less impacted by wind currents than smaller birds such as songbirds. Moreover, when beneficial tailwinds were scarce, songbirds chose to migrate in lower wind speeds. Migration traffic rates for day-migrating birds were found to be proportionally greater over the Karpaz peninsular than in the Hula valley of Israel. Thirdly, temporal migration patterns for raptors over Cyprus and Israel correlated significantly. **Chapter 2** takes a natural history focus by detailing the taxonomic assemblages of migrants recorded on Cyprus, and then discussing the implications of our findings. Higher than expected numbers of migrating crag martins (*Ptyonoprogne rupestris*), common kestrels (*Falco tinnunculus*) and pallid harriers (*Circus macrourus*) for Cyprus were recorded during our spring survey. Observed numbers for pallid harriers suggest that the Karpaz peninsular may possibly be Europe's most significant flyway for the species. These provisional findings are of great conservation importance as pallid harriers are listed as a globally near threatened species on the IUCN Redlist. In addition, the first African migrant butterfly (*Catopsilia florella*) on Cyprus since 1986 and the first ever

Cyprus record of the ladybird *Harmonia quadripunctata* were recorded. Furthermore, evidence of mass migratory behaviour in the flies *Delia platura* and *Stomoxys calcitrans* is presented, both of which were not previously considered migratory. Observations of signs of illegal bird trapping at the Cyprus study sites is discussed anecdotally.

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## Author's Declaration

All chapters in this thesis were written by Edward Walliker with comments provided by Professor Jason Chapman and Dr Karl Wotton (my supervisors).

All Cyprus data were collected by Edward Walliker, William Hawkes, Olivia Forster, Boya Gao and Kate Lacey. Israel Radar data was collected by Professor Nir Sapir (and team), who granted access to Edward Walliker. Preparation and processing of insect data (**Chapter 2**) was carried out by William Hawkes. All data analysis and thesis preparations were undertaken by Edward Walliker. Data collection, processing, analysis and thesis preparation were overseen by Professor Jason Chapman.

All images and illustrations were produced by Edward Walliker unless stated otherwise.

# General Introduction

## Introduction to migration

The term migration often conjures images of many animals of the same species undergoing a long journey. Indeed, one of the widely accepted definitions is that migration is when a population of a particular species embarks on annual to-and-fro trips between a breeding ground and wintering ground (Newton, 2003). This definition however excludes many other examples, particularly of the most important and numerous terrestrial migrants, insects (**1.3**). In this writeup I will use a broader definition originally proposed by Kennedy in his classic 1985 paper, and then promoted and expanded upon by Dingle (2014) and Dingle & Drake (2007). This definition posits that migration is characterized as a persistent, straightened out movement during which an individual ignores cues that are usually attractive, such as those associated with feeding and reproducing (Dingle, 2014). The main strength of this definition is that it focuses less on distance travelled and population outcomes (such as degrees of dispersal), and more on behaviour at an individual level, the level on which natural selection acts. Finally, the Dingle & Kennedy definition also excludes ranging and commuting movements, which may cover vast distances and involve many individuals but are driven by immediate cues such as feeding and reproducing, and thus no inhibition of cues is occurring.

Migration can broadly be described as an adaptive response to seasonal or geographic variation in resources. Each migratory movement is thought to be driven by benefits to one or more of the following: feeding opportunity, survival (e.g. avoiding of unfavourable climates) and reproductive success (Heape, 1931). Therefore, migration is particularly abundant at higher latitudes (Newton & Dale, 1996). Here annual cycles lead to large differences in duration and intensity of solar energy received on each hemisphere over a temporal scale, resulting in seasonal periods of extreme favourability and unfavorability (Choe, 2019). In the northern hemisphere (e.g. northern Europe) this results in very cold winters and temperate summers, in the southern hemisphere (e.g. sub-Saharan Africa) this produces wet and warm winters, but very hot, dry summers. Many species travel

to high latitudes to take advantage of these periods of high productivity and long days, then escape before the onset of poorer climates, or in the case of many insects, diapause (Johnson, 1969). These temporary plentiful regions also present good breeding sites as they tend to have less competition due to winter's low carrying capacity (Shaw, 2016). Breeding at high latitudes can also result in lower predation: nest predation in shorebirds decreases at higher latitudes (McKinnon *et al.* 2010). Migration is not restricted to high latitudes however; for example, globe skimmer dragonflies (*Pantala flavescens*) follow the monsoon rains around tropical regions, and reproduce in temporary puddles with no predators in an attempt to reduce competition and predation for their nymphs (Anderson, 2009).

Migration may also evolve in order to escape high pathogen and parasite levels. For example, migratory monarch butterfly (*Danaus plexippus*) populations have significantly lower pathogen levels than sedentary populations. This is due to migrants constantly moving on from heavily infested regions ('migratory escape') and highly infected individuals dying on the journey ('migratory culling'); thus the migrant population maintains lower parasite levels than it would if it were sedentary (Bartel *et al.* 2011, Bradley & Altizer, 2005). Migration may also be a way to escape high pathogen levels. Parasite abundance and diversity is highest in lower latitudes, this combined with high competition and predation levels is likely why many species don't remain in these areas year-round (Hansson *et al.* 2014). The interaction between pathogens and migrants appears to be complex and not yet fully understood. It has been theorised that comparatively greater investment into flight capability, energy storage and subsequent longer periods actively flying may negatively impact on immune systems in both migratory birds and insects (Bonte *et al.*, 2012; Chapman *et al.*, 2015; Hansson & Akesson, 2014; Milner-Gulland *et al.*, 2011). Conversely it has been theorised that annual exposure to two or more faunas of parasites (as opposed to resident populations exposure to one parasitic fauna) and (in some cases) higher conspecific densities should result in migrants having superior immune systems to resident species. Supporting evidence has been found for both theories (Eikenaar & Hegemann, 2016; Møller & Erritzøe, 1998; Wilson *et al.*, 2001), indicating that the migratory

host-pathogen relationships may highly case specific or simply poorly understood.

## **Bird migration**

Birds are the best studied of all migratory groups. The extensive research on birds is likely due to a combination of their high visibility, often remarkable journeys, and because they are much loved by people (Dingle, 2014). Examples of these include the Arctic tern's (*Sterna paradisaea*) biannual pole-to-pole migrations spanning 22,000 km per leg, and the Amur falcon's (*Falco amurensis*) extreme to-and-fro routes between China and Southern Africa (Egevang *et al.* 2010; Bildstein, 2006). Whilst most avian migration isn't as spatially extensive as these examples, it is certainly taxonomically extensive. A probable underestimate of 19% of all bird species are known to make regular annual movements away from their breeding distributions (Somveille *et al.* 2013). These species exhibit an impressive array of morphological adaptations and behaviours to enable migration.

Birds can be described as true navigators, by which we mean that on the journey, adult birds are aware of their current location in relation to a target destination. Birds are capable of true navigation via a combination of physiological adaptations, experience, and finely-tuned methods of orientation. These sets of orientation methods are split into innate or near innate cues (wherein no learning, or only a small degree of learning is required) and learnt cues, and are discussed in more depth below.

The primary innate modes of orientation are achieved via the use of celestial and magnetic cues. Celestial cues are visually sourced from light patterns in the sky such as the sun, stars and polarised light patterns. These are highly predictable and can be used for navigation in conjunction with the earth's rotation (Foster *et al.* 2018). Diurnally migrating birds use the sun's azimuth direction in conjunction with an internal clock to determine their flight direction (Chernetsov, 2016). Many small birds such as passerines migrate at night to reduce energetic costs and predation, and therefore use the stars to navigate. Such nocturnal migrants are

capable of learning the position of the centre of stellar rotation, which allows them to identify the direction of the geographical poles and use this to orientate (Emlen, 1967). Magnetic cues are acquired from the earth's geomagnetic field, in this the field's polarity (direction of north and south), inclination (the field's angle to/from the horizon), intensity (strongest at the poles, weakest at the equator), and declination (angle between the magnetic and geographical poles) can be determined. Magnetic cues are imperceptible to humans, but in birds are believed to be visually received, this has been supported by restlessness in migratory birds as they exhibit more head-scans in absence of a magnetic field (Mouritsen & Hore, 2012; Mouritsen *et al.*, 2004). These navigational cues do not act independently of each other, but instead are frequently used in conjunction. Depending on external conditions magnetic or celestial cues may be favoured, for example if stars are visible, celestial cues may be used and vice versa. Furthermore, changes in declination angle during travel lead to magnetic sense requiring recalibration, this is achieved at sunset via celestial cues (Cochran *et al.* 2004).

Learning combined with various navigational mechanisms further assist in navigation during migration. Evidence for use of an olfactory map has been shown in birds such as pigeons and shearwaters. In this, odour plumes are used to create a chemical map of regions allowing birds to accurately return to e.g. breeding grounds (Gagliardo, 2013; Lefeldt *et al.*, 2014). Birds are also able to remember a network of local features (or a 'mosaic map') to better pinpoint a destination. This has been demonstrated in juvenile chaffinches (*Fringilla coelebs*) which were unable to relocate their natal grounds in following seasons after being restricted to a subsection of their breeding range and then relocated (Sokolov *et al.*, 1984). This indicates that free roaming across unconfined swathes of breeding (and wintering grounds) is essential for the creation of a mosaic map and subsequent successful return. Some migrants use landmarks such as rivers as markers to help compensate for wind drift (Bingman *et al.*, 1982). Consistent variation amongst migration routes of marsh harriers (*Circus aeruginosus*) has presented evidence that distinct landmarks are learnt from previous migratory trips (Vardanis *et al.*, 2011). Finally, the magnetic sense has a further, more precise application – a 'magnetic map'. Herein a bird remembers

magnetic intensity, inclination and declination (of e.g. breeding grounds) to create a bicoordinate map or effective magnetic signature of a region (Chernetsov, 2016). This has been demonstrated in thrush nightingales as they increased their feeding when artificially exposed to a magnetic field replicating that of Egypt's, the last stopover before crossing the Sahara Desert (Fransson *et al.* 2001).

The migrations undergone by birds come with many risks and costs, however these have been offset by a plethora of physiological and behavioural adaptations. Firstly, energetic costs are reduced by low skeletal masses and the ability to fly (an energetically efficient method of transport) (Butler, 2016). Many migrants have evolved higher aspect ratio wings to increase efficiency over distance. This has been observed in partial migrants such as blackcaps (*Sylvia actricapilla*) in which sedentary populations have broader and shorter wings than migrants (Linossier *et al.*, 2016; Fiedler, 2005). Before the onset of migration resources are reallocated by reducing the size of liver, kidneys, intestines and stomach to promote hypertrophy of heart and pectoral muscles (Piersma, 1998). Some species are so morphologically adapted for flight that migration is not energetically costly. For example, common swifts (*Apus apus*) remain on the wing for all life stages except reproduction and are such excellent flyers that their legs have been reduced making it more difficult to land than fly, and thus migration is not an energetically expensive task (Hedenström *et al.*, 2016; Åkesson *et al.* 2012). Behaviourally, one of the main ways in which birds reduce costs is via use of stopover sites. These areas present opportunities to lay down fat and moult worn feathers (Leu & Thompson, 2002; Hutto, 1998; Jehl, 1990). Stopovers are crucial in anticipation of crossing geographical barriers such as large water bodies and mountain ranges. Similarly, some species have evolved to buffer energetic costs whilst travelling; for example, Amur falcons are believed to coincide their crossing of the Indian Ocean with migratory dragonflies on which they may feed (Anderson, 2009). Finally, some of the main benefits acquired from completing multiple migrations in a lifetime are learning and experience. Experienced raptors crossing between Europe and Africa have 2% mortality rates, far lower than the 31% of juveniles that die en route (Strandberg *et al.* 2009). Moreover, moving in groups and following behaviours improve juvenile survivorship. Large species such as great white pelicans (*Pelecanus onocrotalus*)

are a good example of this, often moving in V-formations with juveniles further back, expending less energy (Weimerskirch *et al.*, 2001).

Birds chiefly migrate either by day or by night (however some species migrate during both). Smaller birds such as songbirds tend to migrate nocturnally, and these make up the bulk of migrants in terms of numbers and individuals. Larger birds such as raptors, cranes and pelicans undergo diurnal migration. Each strategy presents a number of potential benefits to the individuals. Migrating at night allows for daylight hours to be spent foraging (for diurnally active species), resulting in offset of energetic costs (Alerstam, 2009). Nocturnal migration also reduces exposure to predators whilst travelling because most are active during the day (Alerstam, 2009; Lank, 1989). Thirdly, climatic conditions are usually more favourable at night, and thus birds experience less turbulent winds and cooler temperatures, further reducing energetic costs (Kerlinger & Moore, 1989). Many diurnally migrating birds dynamically soar on thermals. This involves very little flapping flight and greatly reduces energetic costs (Hedenström, 1993). Many diurnal migrants such as falcons, swifts and swallows migrate using flapping-flight, however multiple representatives of these groups have been found to feed on the wing during migration (e.g. on insects). This fly-and-forage strategy reduces the need for stopovers and may be more beneficial and widespread than previously thought (Strandberg & Alerstam, 2007). Diurnal migrants also have a greater ability to locate their conspecifics (more important for juveniles), as well as assess the suitability (or unsuitability) of potential stopover sites (Alerstam, 2009). The latter could be greatly important for mitigating potential costs and risks whilst resting.

### **Insect migration**

Insects are perhaps the least studied migratory group despite being the most abundant in terrestrial ecosystems. This is largely due to their small sizes making them difficult to observe and quantify, leading to a bias towards larger species such as butterflies and dragonflies, and economically significant species such as agricultural pests. Multiple insect orders have been found to contain migrant species, for example: Lepidoptera (butterflies and moths), Odonata (dragonflies),



Diptera (true flies), Orthoptera (grasshoppers and crickets), Hemiptera (true bugs), Coleoptera (beetles) and most recently, Hymenoptera (bees) (Fijen, 2020; Dingle, 2014). The majority of insect migrations fundamentally differ from those of birds by typically being multigenerational (meaning that the annual migration circuit comprises of at least two, and often three or more, generations) (Chapman *et al.*, 2015; Stefanescu *et al.*, 2013). One well-known exception to this general rule is provided by the Bogong moth (*Agrotis infusa*) in Australia which travels to the Australian Alps each spring to diapause, and returns to its lowland breeding grounds in a single generation (Warrant *et al.*, 2016). However, the reasons to migrate remain the same as those for birds, and insects also exhibit a large array of physiological and behavioural adaptations.

Unlike birds, insects are not true navigators, they simply orientate towards a chosen heading without the goal of a predetermined destination (Mouritsen, 2018; Mouritsen *et al.*, 2013). Orientation methods for individual species are comparatively understudied and mostly limited to a select few 'classic' insect migrant species, such as the monarch butterfly. Monarchs use a time-compensated sun compass, in which an internal clock in conjunction with the sun's position is used to determine the preferred migration direction towards its winter diapause site in Mexico (Mouritsen & Frost, 2002). In addition, research from the Reppert group has indicated that polarized light patterns and magnetic information may also be used; similar to birds, these cues are likely differentially prioritised under different conditions (Guerra *et al.*, 2014; Reppert *et al.*, 2004). Finally, the lack of taxonomic scope of orientation research on insects means that the cues and mechanisms are largely undefined, for example we do not know with certainty how nocturnal migrating insects orientate in low light, we only know that they do (Chapman *et al.*, 2015).

The multigenerational nature of insect migration without a predetermined destination may seem risky and can sometimes be described as a form of 'hedge-betting', however insects have evolved a number of ways to offset the potential costs (Holland *et al.*, 2006). Firstly, insect migrants reduce risks by often being generalists in terms of resources required for reproduction and development. For example, painted lady butterflies (*Vanessa cardui*) use multiple

larval foodplants such as nettles and mallows which are widely distributed and frequently common making finding them more likely (Stefanescu *et al.*, 2013; Ackery, 1988). Migrant insect species also produce more eggs than resident species, potentially to offset higher mortality rates during migration (Chapman *et al.*, 2015). Many insects temporarily pause reproduction to prioritise storage of fuel in the form of fats for locomotion (Haunerland, 1997). This is known as the oogenesis flight syndrome and it improves the chances of the eventual high egg-load being laid in a suitable location (Rankin *et al.*, 1986). Conversely, unlike high-latitude resident species, many migrants constantly move and reproduce year-round, resulting in higher reproductive productivity over the course of the year (Chapman *et al.*, 2015). As with birds, the evolution of flight greatly facilitates insect migration, the most extreme example being aphids which may spawn a predominantly migratory winged generation from a flightless parent generation depending on stressors as a means of evolutionary escape (Taylor *et al.*, 1979). Finally, to counter their often low mass and flight power, many insects selectively choose to migrate in wind currents aligning with their preferred heading. By flying high (>150 m above ground level) in favourable winds silver Y moths (*Autographa gamma*) achieve high travel speeds (>25 m/s) and can travel great distances over the course of a single night (Chapman *et al.*, 2010; Chapman *et al.*, 2008).

Similar to birds, insect migration occurs both by day and night. Insect migration at night is considered to generally occur at high altitudes where an individual's flight speed is added to the wind speeds. If the direction of wind currents align with a preferred heading this can be greatly beneficial to insects. Furthermore, on days when high altitude winds are in an unfavourable direction, nocturnal migrants have been found to not migrate, and instead wait for nights with more favourable wind directions (Chapman *et al.*, 2008). In arid regions following of winds is particularly advantageous as it transports migrants to atmospheric convergence zones where rains are more likely (Chapman *et al.*, 2015). Diurnal migration of insects occurs at both low altitudes (below flight boundary layer) and high altitudes. It was previously thought that some species only migrated close to the ground, however now it is thought that usage of high altitudes is also mediated by wind directions. Diurnal high-altitude migration presents similar benefits to nocturnal high-altitude migration (i.e. greater speeds and distances achieved) if

wind directions are favourable. Diurnal migration at lower altitudes reduces the impact of winds on individuals. Lower wind speeds mean migration in head and crosswinds is achievable, and the risk of drift is greatly reduced. Furthermore, low altitude flight increases opportunity for feeding, reproduction, oviposition (and the likelihood of encountering foodplants) (Chapman *et al.*, 2015). The main costs of low-altitude migration are lower travel speeds, increased flight cost and exposure to diurnal insectivorous predators such as larger insects (e.g. dragonflies) and vertebrates (Chapman *et al.*, 2015).

### **Importance of migration**

Insect and bird migrants are composed of representatives from many trophic levels. Many insects such as locusts are herbivores and therefore feed primarily on plant matter at every life stage. The vast majority of bird migrants are predatory and feed on a broad range of prey items. Furthermore, due to the multi-staged lifecycles of insects (and to a lesser extent seasonal dietary changes in birds) temporal changes in diet are not uncommon in migrants (e.g. the marmalade hoverfly (*Episyrphus balteatus*) hoverfly is an aphid predator in the larval stage but feeds on pollen as an adult fly). Resultingly, mass seasonal influxes of migrants covering a range of trophic levels can have a great impact on local ecosystems. On a small scale, temporary influxes of organisms present local predators with a highly important and plentiful food source (Bauer & Hoyer, 2014). Due to the seasonal predictability of such movements, some predators such as Eleonora's falcons (*Falco eleonora*) have shifted their breeding season to coincide with the autumn migration period to exploit southward movement of songbirds (Walter, 1979). Mass migrations also transport vast quantities of nutrients in the form of waste such as faeces and corpses. This is particularly significant for insects as entire generations die during migration (Chapman *et al.*, 2015). Insect bodies are 10% nitrogen and 1% phosphorus, by dry weight, both important limiting nutrients for plants (Elser *et al.*, 2000), consequently mass deaths of insect migrants greatly benefit local plant ecosystems (Landry & Parrott, 2016). An estimated 3.5 trillion insects migrate over the southern United Kingdom annually at altitudes of above 150 metres. If these densities are consistent across continents, insect migration accounts for the most important

annual animal movement in terrestrial ecosystems (Hu *et al.*, 2016). Many insect migrants (and a handful of bird migrants) feed on pollen and nectar and therefore can act as pollinators. Transport of pollen grains over large distances greatly increases genetic flow between plant populations, and further benefits plant communities (Paschke *et al.*, 2002). Finally, due to the sometimes vast distances (and high population densities) involved with migration, there is an increased potential for spread of pathogens and parasites (Krauss & Webster, 2010). They are also exposed to a broader range of parasites (and pathogens) and therefore increase the likelihood of introducing a novel parasite (or pathogen) to a resident ecosystem (Altizer *et al.*, 2011; Waldenström *et al.*, 2002).

Due to their broad range of ecological impacts it is unsurprising that many bird and insect migrant species are of high socioeconomic value to humans. Birds are becoming of increasing value for ecotourism; however, this is currently only relevant for larger species such as greater flamingo (*Phoenicopterus roseus*) in locations such as Cyprus and Tanzania. Insects in particular are of great importance in agriculture. Migratory pollinators benefit agricultural crops in much the same way they help wild plant populations, increased genetic diversity has been shown to increase plant health and crop yield (Doyle *et al.*, 2020). Many insect migrants also provide an effective biological control service, for example some hoverfly larvae and ladybirds (*Coccinellidae*) have been found to greatly reduce aphid numbers in crops (Schmidt *et al.*, 2003; Hindayana *et al.*, 2001; Dixon & Dixon, 2000; Dixon *et al.*, 1997). Many insects are also considered to be agricultural pests. Herbivorous species such as desert locusts (*Schistocerca gregaria*) directly consume vegetation and in high densities can be extremely damaging. A desert locust swarm on the horn of Africa was estimated to have on a daily basis consumed enough vegetation to feed 400,000 people for a year (MacKenzie, 1985). As previously mentioned, many migrants are vectors, and bring disease to crops and livestock. A famous example of this are aphids, which feed on plants by sucking sap through a needle-like stylet (whilst simultaneously injecting saliva); in this way they introduce a broad range of pathogens (particularly mosaic viruses) to a broad range of important crops (such as: beans, brassicas, capsicum, carrots, celery, lettuces, sweetcorns and sweetpotatoes) (Valenzuela & Hoffmann, 2015; Jones, 2004). Migrant pathogen vectors may also

impact on humans directly. Recent evidence has suggested that both *Anopheles* and *Culex* mosquitos are also migrating at high altitudes utilising favourable winds, perhaps explaining the annual recurrence of Japanese encephalitis and malaria in regions where the mosquito vector and disease are not found year-round (Dao *et al.*, 2014; Huestis *et al.*, 2019; Satterfield *et al.*, 2020).

## **Declines and conservation of migration**

Migratory species, like much of the world's biodiversity are in decline (Wilcove & Wikelski, 2008). This is due to a number of causes, all of which are anthropogenic. Humans are already responsible for the extinction of some migrants such as the passenger pigeon, which was wiped out primarily by active hunting, despite at one point being the most abundant bird species in North America (Bucher, 1992). Forms of pollution such as light and electromagnetic negatively affect orientation in many species, particularly those which migrate at night (Grubisic *et al.*, 2018, Van Doren *et al.*, 2017). However, despite migration evolving in response to temporal changes in climate and habitat, it is habitat destruction and climate change that are impacting on migration most heavily. This is due to the speed and magnitude at which they are occurring. The nature of large temporal distributions presents the problem of differing conservation practices between countries and regions. Only 9% of migrant bird species are adequately protected across their global range, far less than the 45% of non-migrants (Runge *et al.*, 2015). High site fidelity and the importance of stopover sites places some bird species in particular risk as has been seen for waders in the wake of China's extensive development (22,000 km<sup>2</sup>) on the mudflats of the Yellow Sea (Studds *et al.*, 2017). Effective conservation of birds must involve protection of habitats at all stages of their journey, particularly wintering, breeding and stopover grounds (Higuchi, 2012). Climate change increasing extreme weather events poses additional difficulty for migrants, particularly on passage, however these can be offset by prolonged stay at stopovers (for birds) and selective flight timing (in insects). Climate change is primarily affecting migrant birds by creating shifts in seasonal timings and consequently suboptimal breeding timing. This poor timing generally means lower food availability, and thus lower fledgling success or in the case of red knots (*Calidris canutus*), smaller fledgling

size resulting in their beaks becoming less able to reach their mollusc food in sediment on the wintering grounds (Van Gils *et al.*, 2016; Both & Visser, 2001).

### **Migration in the Mediterranean / Introduction to study site**

An estimated 2.1 billion birds migrate between Europe and Africa, all of which must traverse the Mediterranean region (Hahn *et al.*, 2009). Birds and (some) insects have been found to either avoid crossing geographic barriers (such as mountains or vast expanses of water) or cross them via the shortest possible route (Alerstam, 2001; Brattström *et al.*, 2008; Wikelski *et al.*, 2006). For birds this has led to the formation of migratory bottlenecks at points along particular 'flyways', where great numbers of migrants are funnelled through small geographic regions which align with favourable routes. In the Mediterranean, flyways occur along routes which incorporate the shortest sea-crossings. Frequently in the Mediterranean, islands are used as 'stepping-stones' between continents during migration and provide a vital stopover site to break up the sea crossing. Cyprus is the only large island in the eastern Mediterranean Sea, and is an important stopover site for an estimated 150 million birds annually (Hellicar *et al.* 2014). Unfortunately, perhaps many Mediterranean islands are better known for the volume of illegal killing of migrant birds which occurs on these islands. This also takes place on Cyprus. An estimate of at least 2 million songbirds are illegally caught and killed on Cyprus every year (BirdLife Cyprus, 2019). The focal species is the blackcap which is plucked and boiled to be served as the traditional delicacy 'ambelopoulia'. Capture of blackcaps is achieved by means of indiscriminate methods such as limesticks and illegal mist netting (and playback devices). At least 1 million blackcaps are believed to be killed across the Mediterranean each year (Brochet, *et al.*, 2016). Despite passing of laws, the illegal capture of songbirds undoubtedly persists and is now an underground industry worth an estimated 15 million Euros per year (Shialis, 2017). Insect-focused research in the vicinity of Cyprus is broadly focused on agricultural pest species, and thus the true composition and scale of insect migrants in Cyprus is not fully known (Campion *et al.*, 1977).

Our primary field site is located on the tip of the Karpaz peninsular of Cyprus (coordinates: 35.692824 N, 34.584572 E). The site is surrounded by sea on all sides except to the south-west, and the nearest landmasses are Syria to the east (108 km), Turkey to the north (110 km) and Israel to the southeast (465 km). The habitat at the site is a combination of scrub and rocky ground. The site was selected due to Jason Chapman observing great numbers of migrant hoverflies arriving in spring 2018. Data from Israel, obtained by a vertical looking radar will be used to compare observations between locations.

## **Aims**

In this thesis I aim to look into the migratory patterns of the eastern Mediterranean with a particular focus on both Cyprus and birds. I will analyse broader regional patterns by comparing observations on Cyprus with those recorded on the mainland in Israel. Abundances at each site will be compared to evaluate and contextualise the scale at which migration is occurring in Cyprus. Temporal migration patterns in Israel and Cyprus will be compared to infer region-wide patterns and furthermore be used to theorise routes for birds arriving in Cyprus. The effect of local wind patterns on migration will be tested to discover the impact wind has on different bird families. Finally, the taxonomic assemblages for both bird and insect migrants in Cyprus will be presented and the significance of these findings will be discussed.

# **Chapter 1: A comparison of spring migration patterns between Israel and Cyprus by using ornithological radar data and on-the-ground observations**

## **Abstract**

Each year, Israel and other countries bordering the Mediterranean sea to the east host vast quantities of migrant birds as they travel between Africa and Europe. This is largely driven by the tendency for many birds to avoid travel across large expanses of water. Despite this, the eastern Mediterranean island of Cyprus is also a migratory hotspot. This is thought to be because some birds use Cyprus as a stepping-stone across the sea. Little is known of Cyprus's place in bird migration across the eastern Mediterranean other than species assemblages and that a great many birds pass through. In this chapter, findings from Cyprus are contextualised by comparing them with data from a famous eastern Mediterranean migration hotspot, the Hula Valley of northern Israel. Furthermore, the effect of wind currents on bird migration at each site is assessed. In Cyprus, bird abundance was found to increase in the presence of headwinds. In Israel, songbird migration was found to increase when wind speeds decreased. Larger birds such as raptors were found to be less affected by wind currents. Whilst not truly greater, migration traffic rates on Cyprus were found to be proportionally greater than those of Israel. Temporal seasonal trends between raptor groups at both sites correlated significantly for simultaneous days. These findings were used to hypothesise vertical assemblages of bird migration over Cyprus and to consider the cross-Mediterranean route taken by migratory birds arriving at Cyprus.



## Introduction

Twice every year billions of birds make poleward journeys to exploit temporarily plentiful resources and multiple other benefits (Dokter *et al.*, 2018; Gilg & Yoccoz, 2010; Hahn *et al.*, 2009). A probable underestimate of 19% of all bird species undergo annual movements, northwards in the spring and southwards in the autumn (Somveille *et al.* 2013). These migratory journeys vary greatly in scale from short, often within-country movements and changes in altitude to extensive intercontinental movements, sometimes spanning the length of the globe (Barcante *et al.*, 2017; Egevang *et al.*, 2010). Different bird groups also adopt different strategies of migration (Alerstam, 2009). Songbirds, as well as most physically smaller bird families migrate at night in cooler temperatures, whereas larger birds such as storks, cranes and birds of prey migrate during daylight hours utilising thermals to soar, reducing energetic flight costs (Baudinette & Schmidt-Nielsen, 1974). Some smaller birds like swifts and Swallows also migrate diurnally as they are particularly well adapted for flight and spend much of their life aloft (Lockley, 1969).

In order to reduce risk and energetic costs, most migrating birds avoid major geographic barriers such as large bodies of water (Berthold, 2001). In the Western Palearctic this has resulted in the routes of many migrant species converging to involve the shortest crossing of the Mediterranean. This has led to multiple geographic bottlenecks and 'flyways' where vast numbers of birds are funnelled through small regions. In Europe, the three best known flyways are: the western flyway that crosses the Mediterranean at the Gibraltar strait, the central flyway that crosses between Tunisia and Italy, and the eastern flyway that skirts the Mediterranean via the 'Levant' region and Turkey. On a smaller scale but for the same reasons migratory birds are known to follow valleys in mountain ranges and coastlines aligning with their track direction (Alerstam & Pettersson, 1977; Bruderer & Liechti, 1999). Israel lies on the eastern flyway and is famous for passages of large diurnal migrants. Over a million raptors and storks travel through Israel each year, including the entire global population of lesser spotted eagles (*Clanga pomarina*) and Levant sparrowhawks (*Accipiter brevipes*)

(Leshem & Yom-Tov, 1996). Cyprus is the only large island in the eastern Mediterranean Sea and also a migration hotspot. An estimated 150 million birds use it as a stopover point each year (Hellicar *et al.*, 2014). Whilst some species avoid crossing the sea altogether, many use Cyprus as a steppingstone into Europe in the spring (and vice versa in the autumn) (Flint & Stewart, 1992).

Climate presents multiple challenges to migratory birds such as unpredictable temperatures and precipitation (Richardson, 1978). However, one of the greatest challenges is posed by the medium in which they travel, air currents (Chapman *et al.*, 2011; Liechti, 2006). Wind direction and speed can greatly impact on birds in flight. Unfavourable wind directions greatly increase energetic costs of migration, reduce travel speed and can result in considerable drift (Chapman *et al.*, 2011). Conversely, wind currents aligning favourably with a migrant's intended track direction can be greatly beneficial (Karlsson *et al.* 2011). Migrant birds morphologically reduce energetic costs via fat deposition and hypertrophy of muscles crucial for flight (Piersma, 1998). Birds can further minimise potential expenditure by not only refuelling and resting at stopover sites, but also by waiting for more favourable conditions (Hutto, 1998). Songbirds in particular are known to wait for nights when air currents have a tailwind component or are weak, but will depart regardless of suitability after a number of days (usually 6-8) due to the costs of late arrival (Åkesson & Hedenström, 2000; Kokko, 1999; Weber *et al.*, 1998). Conversely, some migrant species such as Osprey (*Pandion haliaetus*) have shown no selectivity for winds (Thorup *et al.*, 2006).

Recording of bird migration comes with multiple difficulties. The main difficulty quantifying nocturnal migration is that the darkness greatly reduces visibility and thus active observation of nocturnal migrants is nearly impossible. Techniques such as audio recording of flight calls and counting numbers passing across the moon have been used to estimate nocturnal migration intensities (Nisbet & Drury, 1969; Schrama *et al.*, 2007). Both of these approaches come with multiple drawbacks: not all nocturnal migrants call in flight, and those that do are not constantly calling; secondly due to silhouetting species identification is usually impossible, the lunar cycle and cloud cover reduce repeatability and cannot be carried out for extensive periods due to moon movement changing the area of

sky you are counting against, and resulting in lower estimates. The main method used to monitor nocturnal migration is mist netting (Peckford & Taylor, 2008). Many migration monitoring stations are situated in known stopover regions, and resultingly catch a sample of birds replenishing fat reserves or undergoing stationing flights (Bonter *et al.*, 2007). The main drawbacks of this monitoring technique are that unless a recapture, it is difficult to tell if an individual is migrating for some species, and more crucially (with the exception of stations situated in high altitude mountain passes) birds actively migrating typically fly at high elevations and thus are not caught (Komenda-Zehnder *et al.*, 2010). Diurnal migrant species are easier to count as they can be actively observed, and thus simple census counts are effective. However, in favourable conditions some birds attain altitudes of >1 km (particularly those which soar on thermals such as raptors and storks), making them very difficult to see and identify (Sparr *et al.*, 2000). In recent years many of these shortcomings have been mitigated by usage of vertical-looking ornithological radars (Bauer *et al.*, 2017). Radars constantly record the number and altitude of everything that passes (with the exception of very small insects and objects) and do not require the capture or handling of any subjects (Nilsson *et al.*, 2018). Furthermore, characteristics such as size, speed and wingbeat-frequency are factored in to categorise passing objects. Radars aren't without drawbacks either, very low-flying birds are not detected and the categorisations in place are broad and far from species-level (Komenda-Zehnder *et al.*, 2010). Consequently, a combination of methods may reduce the shortcomings of a single survey method and be the most effective way to monitor migration intensity and composition.

In the northern hemisphere there is a large skew towards migration studies conducted during the autumn period. This is perhaps due to a combination of several factors: firstly migration is on a slightly larger scale due to the addition of fledgelings (and tagging studies are often derived from birds tagged on the nest), secondly weather conditions are more favourable for observing diurnal migrants due to less cloud cover in hotspots (e.g. Spain and Israel), and thirdly there is far more migration research conducted in the northern hemisphere than the southern hemisphere and scientists are more likely to collect data from a starting point (i.e. when birds leave in the autumn), rather than when migration terminates (i.e. after

arriving in spring)(Chapman, 2020 pers.comm.). Despite this, the spring migration period has greater time constraints and far higher costs associated with late arrival (Nilsson *et al.* 2013). Individuals that arrive earlier experience less competition at breeding grounds, have significantly greater reproductive performance and have more time to raise young in preparation for the autumn journey south (Kokko, 1999; McNamara *et al.*, 1998; Van Noordwijk *et al.*, 1995). As climate change increases, better understanding of the factors governing arrival timing at breeding grounds is of great importance for conservation.

Little is known of Cyprus's place in the eastern flyway other than species assemblages and that a great many birds pass through (Hellicar *et al.*, 2014). Almost all extensive observational surveys on Cyprus have been conducted during the autumn, and all were carried out in the southern part of the island (Frost, 1994; Roth & Corso, 2005; Roth, 2008; Wilson, 2005). I was therefore interested in asking a number of questions:

1. On what scale does spring bird migration occur through the north of the island and is it comparable with the abundance of birds migrating along the overland route through the Levant?
2. Where do the birds that pass-through Cyprus cross from? Perhaps from a known mainland hotspot like Israel?
3. To what extent do weather conditions impact on local and wider-scale migration patterns?

In this study I compare radar data on bird migration traffic rates through the Hula Valley of northern Israel with on-the-ground counts of birds migrating through the north-east tip of Cyprus (approximately 465 km to the NNW) during the same spring migration period. Here I assess the similarities and differences between the migratory traffic rates of different bird groups over different timeframes to infer larger migratory patterns across the eastern Mediterranean. Additionally, I assessed the effect of weather patterns on the variability of migration. Consequently, this paper improves understanding of how migration patterns in Cyprus compare to those in Israel.

## Materials and Methods



**Figure 1:** Map of the eastern Mediterranean Sea indicating study site locations (Red Circle: Karpaz peninsular of Cyprus, Blue Circle: Hula Valley of Israel)

### Study Sites

Data was collected in spring of 2019 between 28/03/19 – 05/05/19 at two study sites located on the Karpaz peninsular (or ‘Pan-handle’) of northern Cyprus (**Figure 1**). Study site 1 was located at the very tip of the peninsular ( $35^{\circ} 41' 33.45''$  N,  $34^{\circ} 35' 3.64''$  E), site 2 was located at the Oasis Hotel ~21 km west of the tip ( $35^{\circ} 37' 31.86''$  N,  $34^{\circ} 22' 30.04''$  E). The peninsular aligns with a northeast by southwest axis and is surrounded on all sides except to the southwest by the Mediterranean Sea. The nearest landmasses are Syria to the east (108 km),

Turkey to the north (110 km), Lebanon to the southeast (186 km) and Israel due south (465 km). For the same time period radar data was obtained from a Birdscan MR1 X band vertical-looking radar situated in the Hula valley (33° 7' 35.39" N, 35° 36' 39.87" E) in northern Israel (**Figure 1**). Hula valley itself aligns with a north by south axis and is ~6 km across, ~25 km long, and 90 m above sea level. The Israel site is 291 km SSE of site 1 in Cyprus.

## Data Collection

All Cyprus bird and insect migration data were collected by a team of students from Exeter University: myself, William Hawkes, Olivia Forster, Kate Lacey and Boya Gao. To record diurnally migrating birds in Cyprus, we stood atop a raised section of site 1 during three daily 45-minute counts at 10:00, 12:00 and 14:00. During these counts we recorded the number and direction of every bird that passed excluding gulls (*Larus sp.*) and peregrines (*Falco peregrinus*) as they were breeding at the site and therefore not migrating. If species-level identification could not be achieved, the bird would be identified to genus-level e.g. *Circus sp.* for unidentified ring 'ringtail' (female/immature plumage) harriers. Daily migration traffic rates were extrapolated from counts during these survey periods, as described below.

As it was not possible to survey them whilst migrating, nocturnal migrants that had interrupted migration in Cyprus were surveyed via morning and evening counts due to their greatly reduced activity during the heat of the day. A 30-minute constant effort survey at 07:00 for site 2 and at 17:00 for site 1 was undergone along an established ~1 km transect each day. Every bird observed was recorded and identified, birds heard calling but not observed were not recorded as it was difficult to ascertain numbers solely by auditory cues. Whilst this is obviously not a direct measure of bird migration activity, it was hoped that morning and evening counts of migrant birds on the ground may provide an indirect proxy for expected migration activity on the previous or following night. However, I recognise this is a far from perfect method as the number of grounded birds will be heavily influenced by meteorological conditions such as rainfall and wind direction/speed, and will not necessarily vary with actual migration activity.

The Israeli Birdscan radar collected altitudinal migration data via both short pulse emissions (which monitor migration activity between 50-800 m) and long pulse emissions (which monitors elevations above 800 m). However, in this study we omitted long pulse data as <10% of migration activity was recorded >800 m. The radar automatically categorises objects that pass through the vertical-pointing beam based on their echo signatures, and objects classified as birds are further categorised based on their flight style, wing-beat frequency and size characteristics (Schmid *et al.*, 2019).

To make data from each site more comparable, the Cyprus bird migration data were compared against the most appropriate radar categories: day-flying raptors were compared with the radar category of diurnal 'Large Single Bird', and both diurnal and nocturnally migrating songbirds were compared with the radar category of 'Passerine'. However, this did mean that we removed all data for swifts 'Apus sp.' (a very abundant migrant) from Cyprus as their flight characteristics are distinct from passerines and no distinct category was provided for swifts (Chapman, 2020 pers.comm). For brevity, henceforth both Cyprus's birds of prey and Israel's 'Large Bird' category will be referred to as raptor(s), and all smaller diurnal migrants, and nocturnal migrants will be referred to as passerines as these are representative of the largest portion of each group. Furthermore, to increase comparability Cyprus data was converted into an estimate of migratory traffic rate (MTR) (Schmaljohann *et al.*, 2008). A migratory traffic rate is an estimate of how many individuals pass across a line of pre-established length during a set time, e.g. 'X birds/km/h'. There was little change in numbers observed during different timed diurnal surveys and due to the three 45-minute surveys only accounting for a fraction of the total day, daily counts were converted into a per-minute value and scaled up to create an MTR for between 07:00-18:00. Due to birds following coastlines, no birds were observed further than 50 metres either side of our position at the tip and so the Israel radar MTRs (calculated for 1 km) were divided by 10. The overwhelming majority of diurnal migrants observed in Cyprus travelled at altitudes below 100 m above ground level, and I am confident that none of the birds we recorded were above 200 m. Instead of MTRs, true numbers of recorded birds were used for both for nocturnal

comparisons as active migration was not observed on Cyprus, and therefore using an estimate of migration rate over time would be false.

### **Weather Data**

Wind data were obtained from the National Centres for Environmental Prediction database (NCEP) for north-eastern Cyprus and northern Israel. Data for both wind speed and direction were obtained. I tested for differences in speed and direction for different times of the day, but changes were minimal and so wind data for 12:00 each day was used for diurnal migrant analysis. Both directions and speeds were not found to be substantially different between ground level and 300 m and so ground-level data was used. In Cyprus, due to the coastal-following and the orientation of the peninsular ( $65^\circ$ ) the desired direction of migration was northeast (Alerstam & Pettersson, 1977). In Israel, the Hula valley aligns north by south and thus the preferred migratory heading for spring was north ( $0^\circ$ ). Wind direction data was converted so that downwind direction was directly comparable with the migration track direction, and made suitable for linear analysis by using a scale of  $0^\circ$  to  $180^\circ$ , where '0' represented the location-specific optimal direction. For Cyprus 0 was  $65^\circ$ , and for Israel 0 was  $0^\circ$  (and resultingly a true wind direction of e.g.  $270^\circ$  (easterly winds), would be converted to  $155^\circ$  and  $90^\circ$  for analysis for Cyprus and Israel respectively). Thus, the converted wind scale provided a linear measure of how favourable the wind was for migration at each location, ranging from 0 (perfectly aligned with the intended migration direction (or tailwinds)) to 180 (, which completely opposes the intended flight direction (headwinds)).

### **Statistical Analysis**

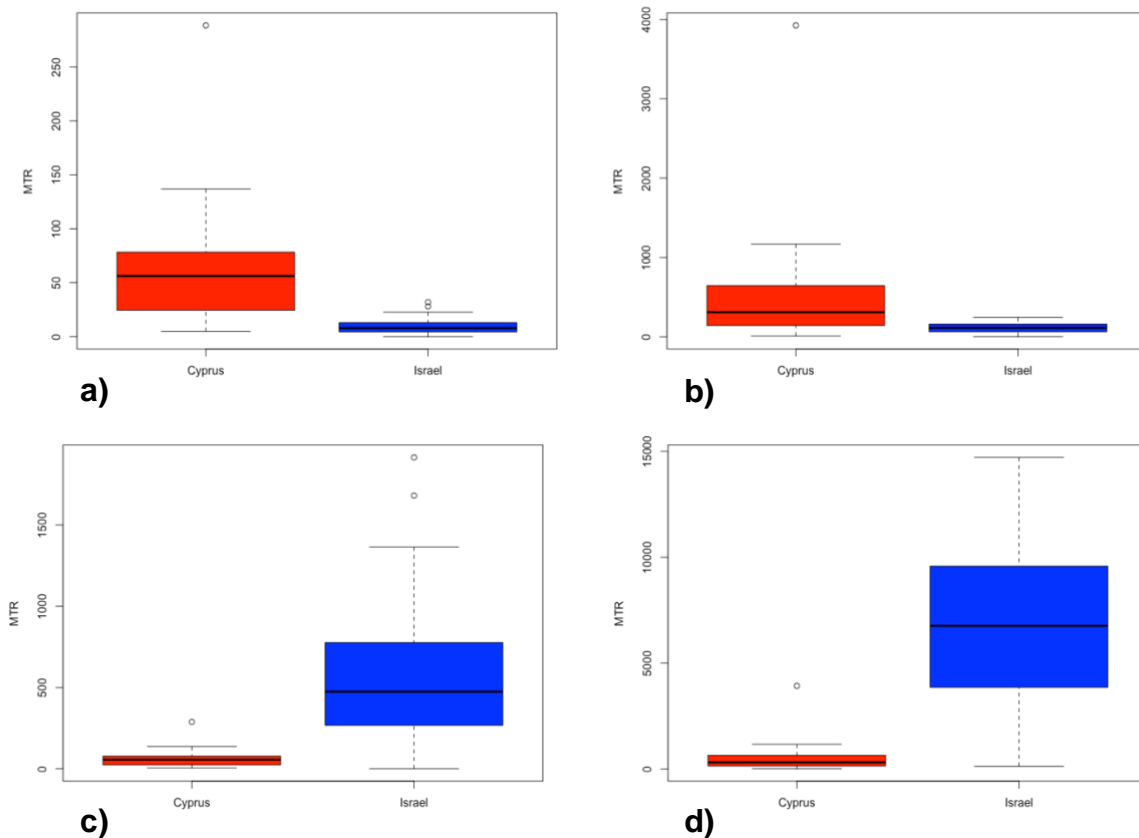
All statistical analysis was performed using R studio for Mac Version 1.3.1.093 (R Core Team, 2020, <http://www.rstudio.com/>). Differences in daily MTRs were tested for using paired t-tests. The effect of wind on migration was tested for using analysis of variance to select the generalised linear models that best fit variations in migratory traffic rates as a result of wind. For Cyprus, only values for north-easterly movement were used because to use a quasipoisson distribution



all values must be non-negative and instances of reverse migration (movement southwest) were uncommon. For Israel no directional data was provided by the radar and so absolute MTR values were used since the vast majority of birds are likely heading north. A further analysis of variance was conducted to test for comparative abundances between altitude bands (50-800 m) in Israel. Pearson's product moment correlation coefficient tests were used to look for temporal relationships between groups between Cyprus and Israel. Cyprus MTRs were compared with Israel MTRs for the same day and 2 days either side for diurnal groups (passerines and raptors). For nocturnal migrants MTRs were not used as we did not actively observe nocturnal migration in Cyprus. The same correlations were performed except instead of same day, totals for Cyprus were compared against migration radar totals (exact numbers recorded over the radar, not an estimate across a 1 km transect) from the previous night in Israel (19:00-6:00) and consequently 2 nights either side of that. Days on which the radar did not function, or we were unable to survey were excluded from analysis. Distances were calculated using an online distance calculator (Georg, 2018).

## Results & Discussion

Average daily migration traffic rates for both diurnal groups were significantly higher in Cyprus than they were in Israel (raptors:  $t(29) = 5.5475$ ,  $p < 0.001$ , passerines:  $t(29) = 3.1355$ ,  $p = 0.004$ ). The mean daily MTR (between 07-18:00 across 100 m) for raptors was 64.9 for Cyprus and 9.8 for Israel <200 m above ground (**Figure 2 (a)**). Mean daily MTR (between 07-18:00 across 100 m) for diurnally migrating songbirds was 528 in Cyprus and 112.9 in Israel below 200 m (**Figure 2 (b)**). Furthermore, Cyprus's mean daily 0-200 m MTRs were greater than the sum of daily means at all four altitude bands (50-800 m) in Israel which was 25.2 for raptors and 211.3 for songbirds. Whilst these findings seem surprising, when considered in context they make more sense. For Cyprus, 100 m represents the total length of the region through which migration was occurring, but for Israel 100 m only accounts for a small portion of the Hula valley which is ~6 km across (east to west) (Werber, 2020 pers.comm.). When scaled to account for the entire valley's width, the daily 50-200 m mean MTRs for



**Figure 2:** A comparison of mean daily <200 M MTRs (Migration Traffic Rates) between Cyprus and Israel **(a)** Daily raptor MTRs per 100 m **(b)** Daily passerine MTRs per 100 m **(c)** Comparison of daily raptor MTRs across Karpaz tip (100 m) and total width of the Hula Valley (6 km) **(d)** Comparison of daily passerine MTRs across Karpaz tip (100 m) and total width of the Hula Valley (6 km)

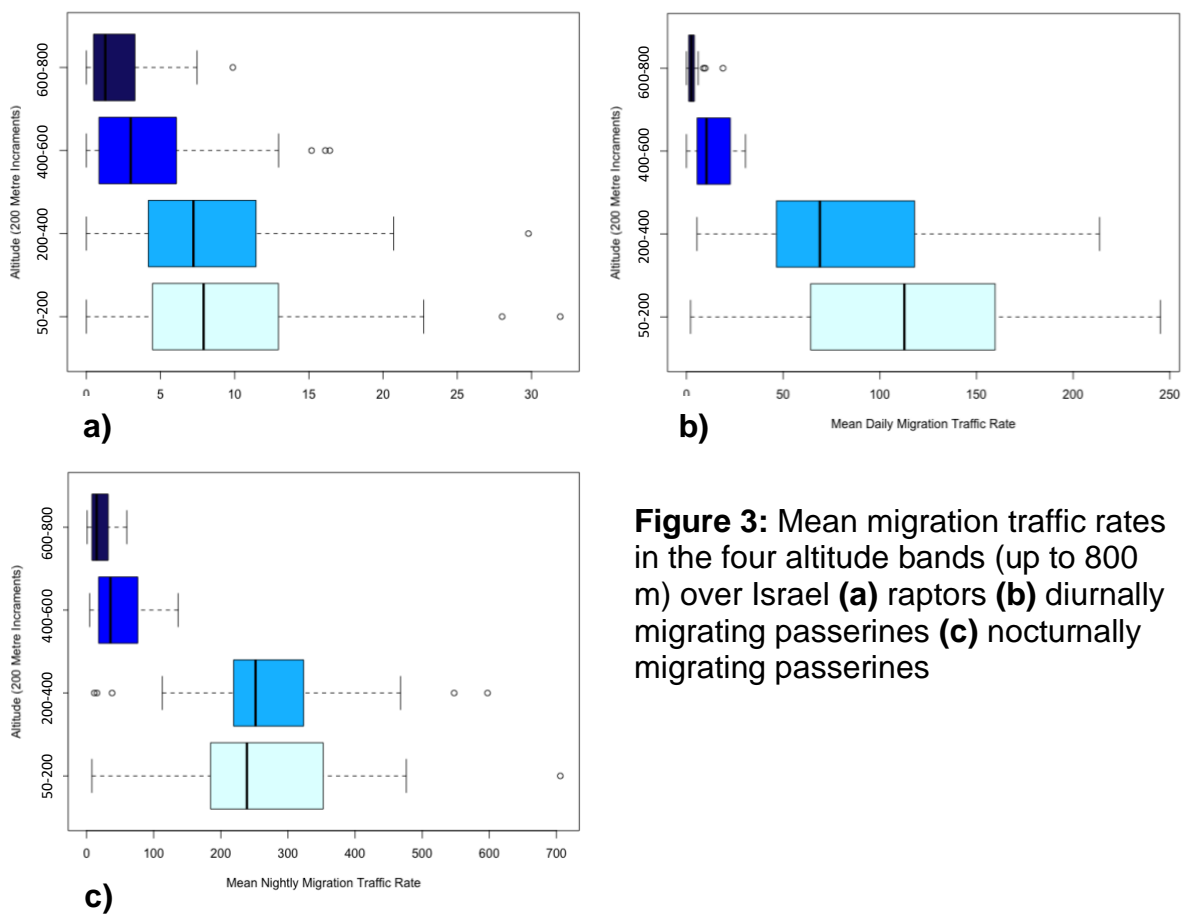
Israel far surpasses those of Cyprus (raptors:  $t(29) = 6.444$ ,  $p < 0.001$ , mean Israel MTR: 590.2, passerines:  $t(29) = 8.953$ ,  $p < 0.001$ , mean Israel MTR: 6778.9 **(Figure 2 (c, d))**). Nevertheless, the MTRs for diurnal migrants on Cyprus are remarkably large for birds crossing just a 100 m stretch. These patterns are likely being caused by the peninsula acting as a migratory bottleneck or funnel. The vast majority of diurnal migrants departed land at the peninsular tip to avoid a longer sea-crossing. The observations at the tip represented a culmination of multiple local-scale migration strategies (i.e. followed southern coastline, northern coastline, stayed over land) and furthermore unlike at the Israel site, there simply was no other land to fly over resulting in a proportionally higher volume crossing a narrow area. Fundamentally, the vast volumes of migration over Israel are caused by the same reasons, but on a far larger scale. For Israel, the

Mediterranean lies to the west, and the Arabian desert lies to the south and east (Safriel, 1968). This combined with the Egypt land-bridge connecting Asia and Africa to the south has resulted in Israel itself becoming a migratory bottleneck.

The average number of nocturnal migrants recorded per day in Cyprus was lower than the mean nightly 50-200 m radar number (Cyprus: 55.2, Israel: 646.7), however this is less comparable as nocturnal migrants in Cyprus were not recorded actively migrating. The primary reason for comparing nocturnal groups was not to compare respective abundances, but instead to assess correlations in temporal patterns.

The radar recorded a significant difference in traffic rates at different altitude bands. Both diurnal passerine migrants and raptors exhibited similar trends in altitude (**Figure 3**). The volume of diurnal migrants was significantly different between elevations (Raptors:  $F(3,116) = 10.88, p < 0.001$ ; Passerines:  $F(3,116) = 47.14, p < 0.001$ ). Tukey's Post Hoc tests revealed that traffic rates were not significantly different between 50-200 m and 200-400 m, or between 400-600 m and 600-800 m but differed significantly between all other elevations for raptors ( $p < 0.05$ ), and differed significantly between all elevations except 400-600 and 600-800 for passerines ( $p < 0.05$ ). The greatest volume travelled below 200 m (mean raptors = 9.84, mean Passerines = 112.98 (**Figure 3 (a, b)**)) and the traffic rates reduced considerably above 400 m. Nocturnal passerines displayed similar altitudinal trends, a significant difference was observed across all altitude bands ( $F(3,116) = 79.716, p < 0.001$ ) and they flew slightly higher. Tukey's Post Hoc tests were carried out. Numbers at both altitude-bands below 400 m were significantly different from those above 400 m ( $p < 0.001$ ), but not each other. Again, the highest MTRs occurred at altitudes of 50-200 m (mean = 259.33) and 200-400 m (mean = 266.77) (**Figure 3 (c)**). Using these findings to infer altitudinal assemblages over the Karpaz peninsular of Cyprus would not be entirely accurate as the geography of the sites differ in a few ways. In a 2018 study comparing radar findings between many sites, Bruderer *et al.* found that multiple factors impact on vertical distribution, particularly: proximity to mountains, sea-crossings and winds. The study found that at sites immediately after a sea-crossing such as Mallorca (an island similarly surrounded by the Mediterranean),

the largest volume of migration occurs below 200 m; and at montane site (or those close to mountains) most migration occurred at much higher altitudes (~800 m above ground-level). Due to the relatively low-lying geography (~90 m elevation) and little mountain presence of the Hula valley, it is unsurprising that most migration occurred at low elevations. However, the extent recorded at these elevations was unexpected. 90% of all recorded 50-800 m diurnal migration occurred below 400 m, 52% below 200 m. Whilst similar in trends to other findings in Israel and further south in Egypt, this skew towards lower elevations was far greater than was expected (Bruderer *et al.*, 2018; Dinevich & Leshem, 2012). Due to the extreme and unexpected nature of the Israel radar findings, I think it is unwise to use them to estimate altitudinal assemblages over Cyprus, however I would predict that the findings would be similar to those observed on Mallorca wherein ~30% of all birds migrate below 200 m and ~50% migrate below 500 m.

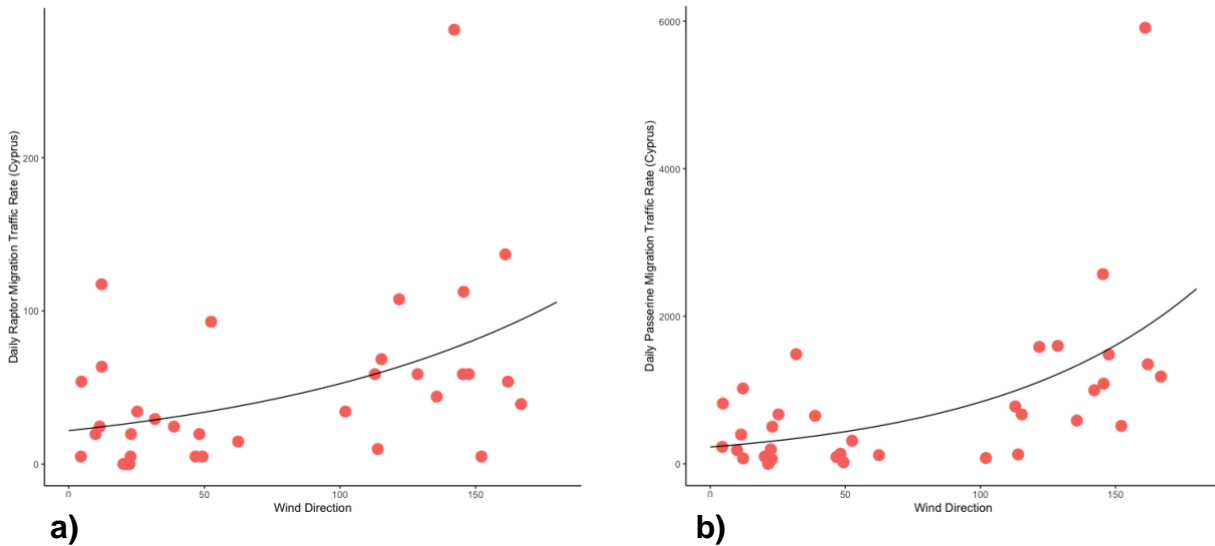


**Figure 3:** Mean migration traffic rates in the four altitude bands (up to 800 m) over Israel (a) raptors (b) diurnally migrating passerines (c) nocturnally migrating passerines

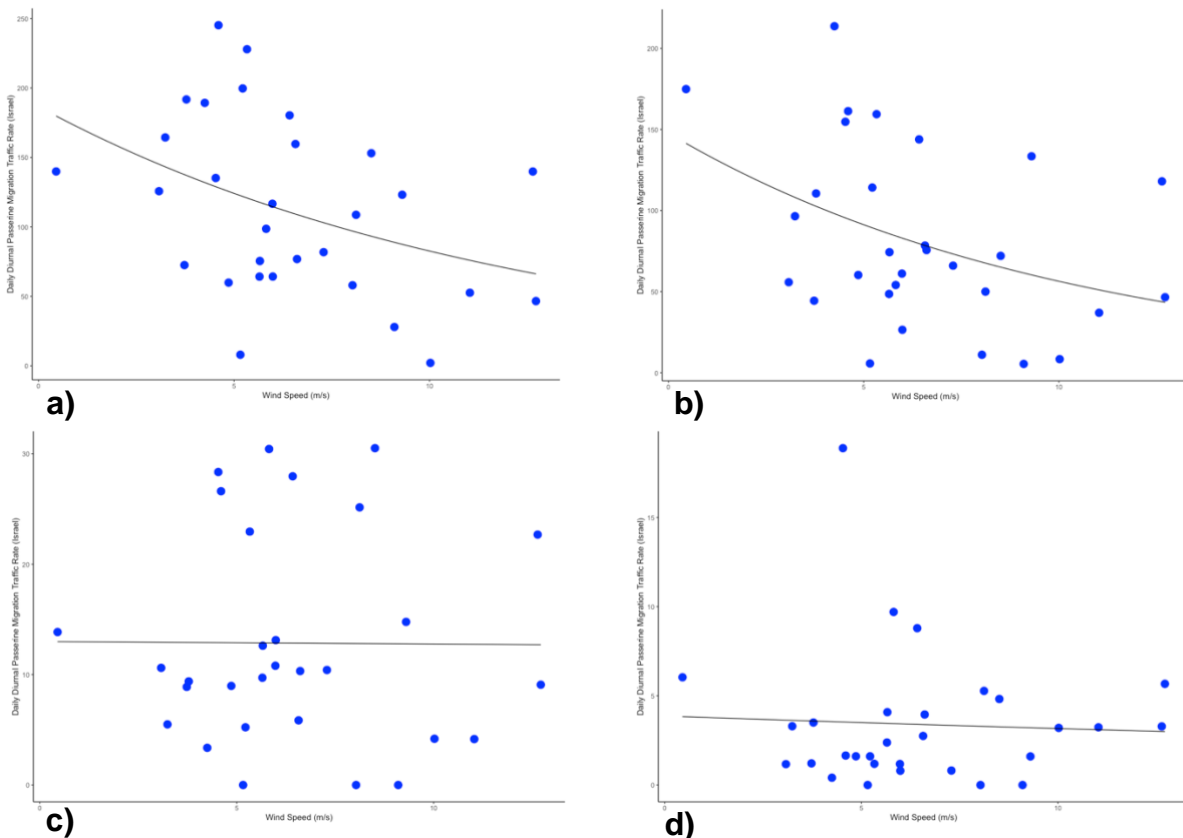
Wind currents had slightly different effects on diurnal migration in Cyprus and Israel. There was a statistically significant effect for wind direction on migration

traffic rates for both raptors ( $f(1,33) = 7.81, p = 0.009$ ) and diurnally migrating passerines ( $f(1,33) = 12.84, p = 0.001$ ) in Cyprus (**Figure 4 (a, b)**). There was a positive effect for both groups (Raptors: est. = 0.009, S.E. = 0.003; Passerines: est. = 0.01, S.E. = 0.002), indicating that they were in higher abundance in headwinds (winds with a north-easterly component). Wind speed had no significant effect on either group in Cyprus. Wind direction and speed had no effect on MTRs of raptors in Israel. Wind speed however had a significant overall effect on diurnal passerines in Israel ( $f(1,118) = 3.95, p = 0.049$ ). There was a negative interaction (est. = -0.081, S.E. = 0.04) indicating that as wind speeds increased, migration traffic rates decreased (**Figure 5**). Whilst groups appear to have behaved differently between sites, it may be the slightly differing conditions that best explains these findings. Average wind speeds were slightly lower in Cyprus than in Israel (Cyprus: 4.47m/s, Israel: 6.39m/s), but variety of wind directions was higher. Easterly winds were virtually absent during the study period in Israel, this may have been caused by sheltering from a small patch of mountains to the valley's west (Chapman, 2020 pers.comm.). Winds in Israel most frequently had a westerly component (westerly winds on 22 out of 39 days, mean direction: 250°) and often did not change direction for multiple consecutive days, presenting migrant birds with challenging crosswinds which can result in increased drift in flight (Liechti, 2006). Less wind-selective raptors and other large birds were seemingly not affected by this. However, such consistently unfavourable wind directions probably lead to smaller songbirds not waiting for favourable tailwinds, but instead waiting for days on which the wind was at its lowest speeds, resulting in the largest numbers migrating in ~5m/s or lower winds, much slower than their average self-powered flight speeds (~11 m/s) (Alerstam *et al.* 2011; Liechti & Bruderer, 2002). In Cyprus, our findings appear to be inverted, suggesting that both raptors and smaller diurnally migrating groups actively select for costly headwinds (Erni *et al.*, 2002; Karlsson *et al.* 2011). This would only make sense in the context of benefitting from earlier arrival at breeding grounds (Shamoun-Baranes *et al.*, 2017). However, in the more variable wind directions and lower average wind speeds it is more likely that we simply saw more migrants in headwinds due to them being driven down to ground-level where winds are usually weaker (Liechti, 2006). Conversely, on days of favourable tailwinds we possibly missed many migrants as they flew at higher

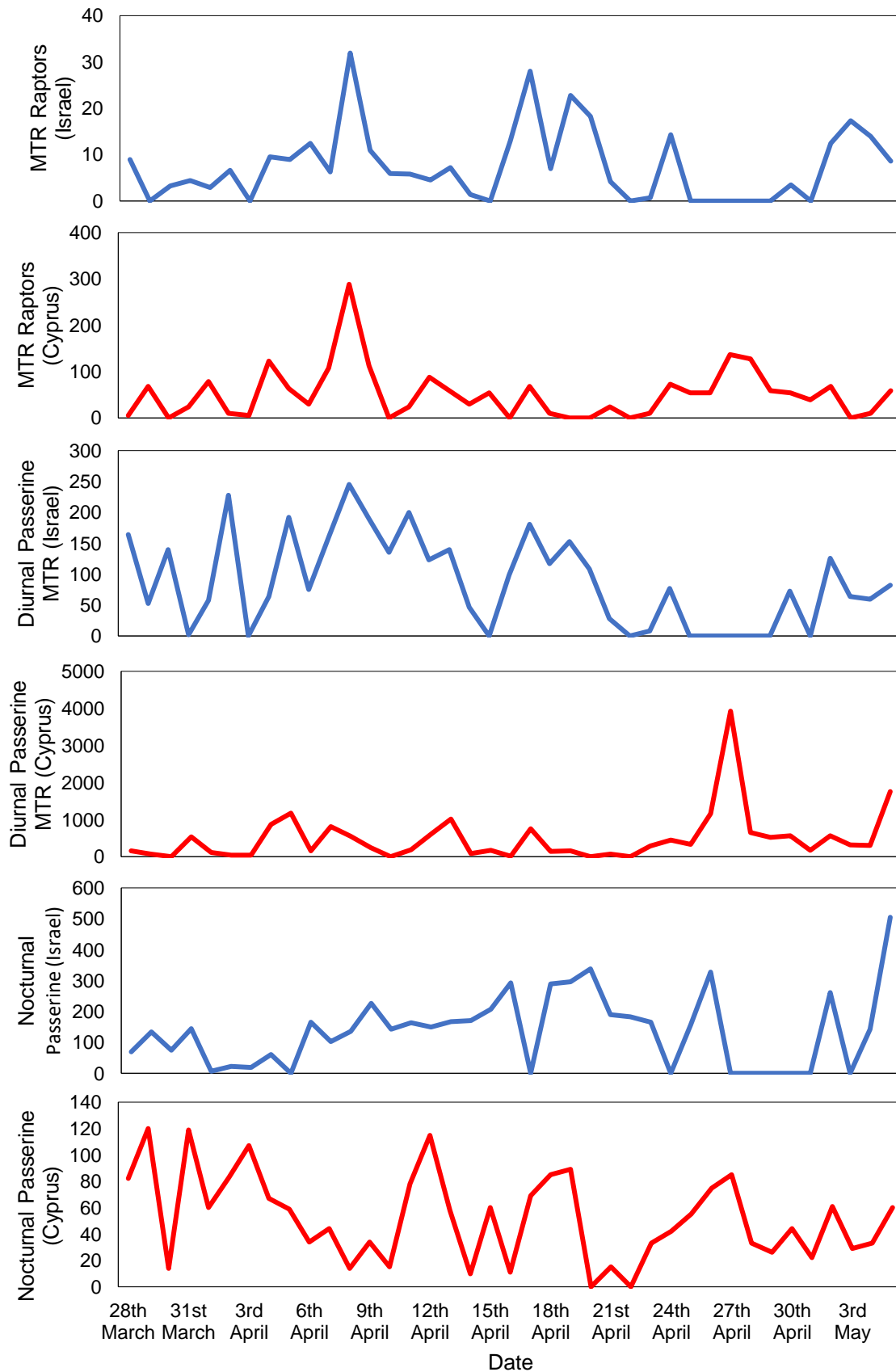
altitudes (>200 m) rendering them too high to spot, and therefore lower total numbers were reported for these days. The altitudinal distribution data from Israel perhaps both agrees with and is partially explained by this theory too because such consistently unfavourable wind directions possibly drove the majority of migrants to lower altitudes during the spring period.



**Figure 4:** Regressions of migration traffic rates and wind direction in Cyprus for (a) raptors (b) diurnally migrating passerines (wind directions of 0 represents tailwinds, a wind direction of 180 represents headwinds)



**Figure 5:** Regression of diurnal passerine migration traffic rates and wind speeds in Israel at each altitude band a) 50-200 m b) 200-400 m c) 400-600 m d) 600-800 m

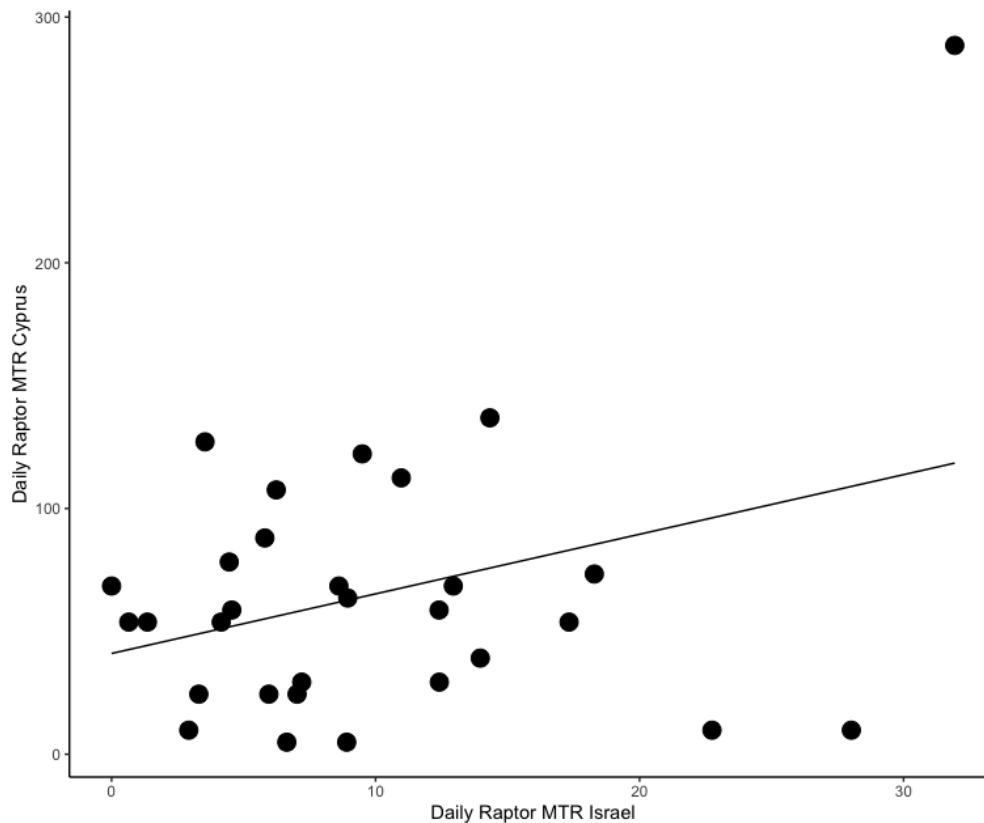


**Figure 6:** Seasonal abundance trends in Israel and Cyprus for raptors, diurnally migrating passerines and nocturnally migrating passerines

Correlation tests were run to compare for similarities in the temporal trends of migration between Israel and Cyprus to elucidate patterns on a regional scale and perhaps ascertain if there is a direct link between migratory birds at the two sites (**Figure 6**). No significant correlation was found to be present between nocturnal or diurnal passerine groups using any temporal comparison. However, there was a statistically significant correlation found between raptor groups for simultaneous days ( $r(21) = 0.62$ ,  $p = 0.002$  (**Figure 7**)). Furthermore, the highest daily raptor MTRs for each site both occurred on 8<sup>th</sup> April (Cyprus: 288.44, Israel: 31.94 (**Figure 6**)). However, when data for 8<sup>th</sup> April were removed, the correlation became insignificant. The mean flight speeds of raptors recorded by the radar was 9.57m/s. From this we can estimate that it would take a minimum of 8 hours 27 minutes to travel the 291 km distance between the Hula valley and site 1 on the Karpaz tip. Moreover, as previously mentioned, we observed raptors working their way along the coastlines towards the Karpaz tip, rather than arriving from the sea to the tip and thus the travel time would certainly be much longer. Consequently, we would expect to observe at least a 1-day lag between patterns at sites if travel between Israel and Cyprus was occurring, but Pearson's test performed under these conditions were not significant (all  $r(21) = <0.15$ ,  $p >0.05$ ). From these findings we can infer that it is highly unlikely that individuals recorded on Cyprus were the same as those recorded in the Hula valley region, and furthermore we can fairly safely assume that they were not from Israel at all. As raptors are the group least affected by climatic conditions during migration, I hypothesise that bird migration occurs in waves fairly consistent across broad, regional fronts, but local weather systems impact on the speed and timings of bird groups differentially. Moreover, this would perhaps explain why unsurprisingly no correlation in migration patterns was found between the more wind-selective passerine groups across such large geographic scales.

Whilst our findings on Cyprus are similar both in patterns and composition to those on the mainland portion of the eastern flyway, aspects such as where the migrants depart land to journey towards Cyprus during the spring and where the island's part in the overall picture of large-scale migration patterns remains largely unclear. Whilst some species such as black stork (*Ciconia nigra*) and





**Figure 7:** Correlation between raptor migration traffic rates in Israel and Cyprus on simultaneous days

great white pelican are known to cross between Europe and Israel via Cyprus, neither species was recorded during our data collection and this does not seem to be the case for our findings. Both species have wintering populations in Israel and have been found to fly across the Karpaz peninsular rather than follow its length and depart northeast at the tip like we observed (Bobek *et al.*, 2008; Izhaki *et al.*, 2002). Furthermore, whilst some instances of seemingly suboptimal migration routes do persist, it would make little sense to migrate northwest towards Cyprus only to turn upon arriving and depart in a northeasterly direction (Sutherland, 1998). This would lengthen the distance of migration and make the risky sea-crossing less justifiable. The uniformity of northeasterly departure found in our observations across all diurnally migrating bird species, combined with our findings of strong same-day similarities in migration intensity across the region suggests that the migrants observed on Cyprus had travelled from elsewhere. Demoiselle cranes (*Grus virgo*), like the majority of migrants we observed have a wintering population in Africa and breed in eastern Europe (and further east). During the spring migration this species has been found to depart land at Egypt

(another migration hotspot), cross Cyprus and then continue towards their breeding grounds to the north of the Black Sea (Hilgerloh, 2009; Meine *et al.*, 1996) (**See Figure 1**). These examples are admittedly of larger species than most recorded during the spring data collection period, however there exists a bias towards larger species in bird tracking studies due to their greater size, flight power and lifespans which increase their viability for their selection to be fitted with heavy and expensive tracking devices (Fiedler, 2009). I propose that these findings for Demoiselle cranes are representative of a broader range of species as this would render both a sea-crossing from Egypt (~360 km SSW of Cyprus) and an eventual northeasterly departure at the Karpaz tip beneficial.

In conclusion, this study has built upon existing research on the effect wind current have on migrating birds. We found that wind had a lower impact on large migrant birds (raptors), whereas songbirds were more selective, choosing to fly in lower wind speeds when wind directions were consistently unfavourable. For the first time this study has compared migration intensity patterns in Cyprus with those of Israel on the mainland, and discovered significant similarities. Furthermore, migration traffic rates through the Karpaz peninsular of Cyprus were found to be proportionally greater than those in an established migratory hotspot, the Hula valley. The Akrotiri peninsular and Cape Greco to the island's south are similarly known to host large levels of migration in the autumn period (Frost, 1994; Roth & Corso, 2005; Roth, 2008; Wilson, 2005). Therefore, Cyprus's other north-pointing peninsulas (Akamas peninsular and Cape Cormakitis) are probably also of great importance during spring when they favourably align with migratory headings. Finally, in order to prove the hypotheses presented, and to quantify vertical bird assemblages over Cyprus, future experimental design should incorporate radar analysis on Cyprus, on-the-ground observations undertaken in Hula valley, and multi-seasonal tracking of birds departing northeast from the tip of the Karpaz peninsular.

## Chapter 2: The phenology of bird and insect migration through the Karpaz peninsular of Cyprus (Spring 2019)

### Abstract

The findings from the first season-long migration survey of the northeast peninsular of Cyprus are presented. Diversity and abundances of diurnally migrating birds, nocturnally migrating birds and diurnal insect migrants were monitored. 7487 diurnal bird migrants, 2644 nocturnal bird migrants and an estimated 50,065,998 diurnal insect migrants were recorded during a 39-day survey period. Migrating crag martins (*Ptyonoprogne rupestris*) and common kestrels (*Falco tinnunculus*) were recorded in surprisingly high numbers for Cyprus (90 crag martins, 165 common kestrels). If records for pallid harriers (*Circus macrourus*) (n = 60, seasonal estimate = 187) are accurate and representative of other years, the Karpaz peninsular would represent Europe's most significant flyway for the species. This is of particular importance because pallid harriers are currently listed as globally near threatened on the IUCN Redlist. In addition, the first African migrant butterfly (*Catopsilia florella*) on Cyprus since 1986 and the first ever Cyprus record of the ladybird *Harmonia quadripunctata* were recorded. Furthermore, evidence of migratory behaviour in agricultural pest species *Delia platura* and *Stomoxys calcitrans* is presented, both of which were not previously considered migratory. Observations of illegal songbird trapping at the study sites is discussed anecdotally. As the first dedicated spring survey in the region, the findings from this survey considerably augment knowledge of spring bird and insect migration through the Karpaz peninsular of Cyprus.

## Introduction

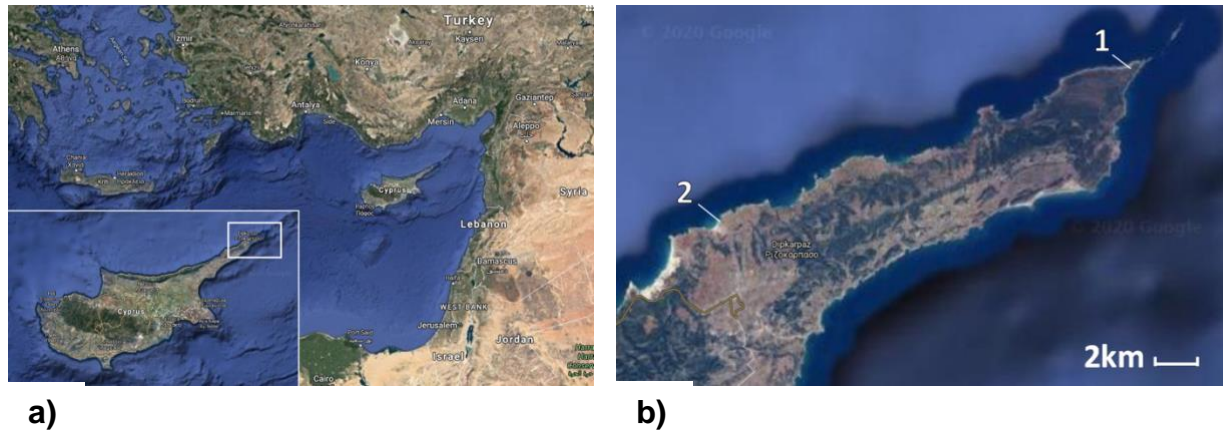
Birds and diurnal insects have been found to migrate across seas via routes involving the least travel across open water (Alerstam, 2001). In the Mediterranean, the most extensively studied of these routes taken by many bird species are the western Flyway across the Gibraltar strait, the central or Adriatic flyway across the Sicilian Channel and Messina strait from Tunisia to Italy, and the Rift Valley/Red sea flyway in the east. Insects adhere to less pre-defined migration routes. Large insects are selective of favourable wind currents and achieve great distances by migrating at times when wind directions aligning with their preferred direction of flight, while smaller species are completely non-selective (Chapman *et al.*, 2012; Chapman *et al.*, 2015; Hu *et al.*, 2016). It is believed that the vast majority of birds travelling by the eastern flyway bypass the Mediterranean Sea and instead travel northwards over land via Lebanon and Syria, however a great number may migrate via Cyprus. This may also be the case with insects.

Cyprus is the only large Mediterranean island to the east and a known migratory hotspot, providing an important stopover point for an estimated 150 million birds every year (Hellicar *et al.* 2014). Over 400 bird species are recorded on Cyprus annually, however only approximately 60 are resident year-round (BirdLife Cyprus, 2019). Of these ~85% of non-resident bird species recorded in Cyprus, some breed on the island, however many pass through en route to more distant destinations. It is now believed that Cyprus is used as a stepping-stone between Turkey and Africa by a significant number of birds (Flint & Stewart, 1992). Birds arrive in broad fronts but traverse to and concentrate at peninsulas favourable to their migratory heading. However, extensive observational research on bird migration in Cyprus is incomplete. All extensive migration data is from southern Cyprus, primarily from Akrotiri, except for two surveys carried out on the eastern coast at Cape Greco (Frost, 1994; Roth & Corso, 2005; Wilson, 2005, Roth, 2008). Furthermore, no dedicated observational studies have been carried out during the spring migration period. Even less is known about insect migration on Cyprus. Most insect migrant studies conducted in the eastern Mediterranean have been focused on agricultural pest species (Campion *et al.*, 1977; Zhou *et al.*, 2000). However, anecdotal

observations of hoverfly migration have suggested Cyprus may host extensive insect migration that has gone largely unreported (Chapman pers.comm. 2018). No systematic, season-long assessment on the scale and diversity of insect migrants has been carried out in Cyprus.

Broadly speaking, birds and insects migrate via two strategies, diurnally or nocturnally (however some birds migrate during both day and night, and diurnal insects will continue sea-crossings into the night until they reach land) (Chapman *et al.*, 2015). Diurnal bird migration is undergone by larger migrant species belonging to the Cinconiiformes (herons and storks), Accipitriformes (raptors) and Gruiformes (cranes). These species are able to use efficient soaring flight (in combination with flapping in some cases/if necessary) to take advantage of thermals which occur over land to migrate at altitudes of hundreds or even thousands of metres at low energetic costs (Leshem & Yom-Tov, 1996; Mateos-Rodríguez & Liechti, 2012). However, some smaller species, including members of the families: Apodidae (swifts), Meropidae (bee-eaters) and Hirundinidae (swallows and martins) also migrate diurnally, however this is due to their supreme flight abilities and highly aerial lifestyle (Lockley, 1969). Most smaller birds, particularly Passeriformes ('songbirds') migrate nocturnally to maximize possible foraging time during the day, reduce predation risk and avoid overheating and dehydration in the cooler and moister conditions at night (Alerstam, 2009). These songbirds typically travel at altitudes between 400-1600 m (however they can fly at altitudes higher than 3500 m) (Alerstam *et al.* 2011). Daylight hours are spent resting and refuelling for the next migratory flight (Alerstam, 2009). Examples of diurnal insect migrant groups include (but are certainly not limited to) Lepidoptera (butterflies and moths), Odonata (dragonflies), Diptera (flies) and Coleoptera (beetles). In migratory insects, cues such as light intensity thresholds, temperature, atmospheric pressure and winds can trigger the decision to depart in a genetically predetermined direction (e.g. north or south) (Chapman *et al.*, 2015; Drake & Reynolds, 2012). Insect migrants close to the ground (this study's focus) are less affected by wind currents and the risk of being drifted off course, as wind speeds are usually lower, however ability to combat drift varies greatly between taxa (Srygley & Dudley, 2008).

The aim of this study was to assess the migratory flow and composition at the Karpaz peninsular in the north-east of Cyprus. In this we examine both diurnally and nocturnally migrating birds, as well as diurnal insect migrants in three separate sections.



**Figure 8: (a)** Location of study area **(b)** Location of two study sites **(1)** Karpaz tip site **(2)** Oasis hotel site (Google Maps, 2020)

## Study Site

The primary field site was located on the tip of the Karpaz peninsular or 'pan-handle'. The site is surrounded by sea on all sides except the south-west. The nearest landmasses are Syria to the east (108 km), Turkey to the north (110 km) and Israel to the south (465 km) **(Figure 8)**. The habitat around the Karpaz tip is rather varied, composed of rocky cliffs and open areas near the extreme tip, rapidly turning into scrub as you move away from the tip. The secondary field site was just inland from the Oasis Hotel located on the north coast approximately 21 km from the tip. This site composed of dunes, scrub and low-intensity farmland and was only used for surveying nocturnal-migrating species assemblages **(Figure 9)**.

## Section 1: Diurnally migrating birds

### Methods

Diurnal migration counts were carried out atop an elevated section of the Karpaz tip from 28<sup>th</sup> March to 5<sup>th</sup> May 2019. Three 45-minute counts were carried out daily from 10:00am, 12:00am, 14:00pm. Binoculars were used to scan the surroundings

(Swarovski EL 10x42 and Swarovski CL Pockets 8x25). All birds that passed us in the allocated time were counted, identified and their flight direction was noted. The



**9a)** Tip site: Open habitat backing onto extensive scrubland



**9b)** Tip site: Rocky open habitat



**9c)** Tip site: Coastal cliff habitat



**9d)** Oasis Site: Hill Scrubland



**9e)** Oasis site: Low-intensity farmland



**9f)** Oasis site: Open scrub and meadow habitat backing onto dunes

**Figure 9: (a-f)** Photographs of habitats present at each site

many gulls that nest on the islets off the tip were ignored during the counts, as were the Peregrines as nesting pairs were present both at the tip and Oasis site. If species-level identification could not be achieved individuals were identified down to genus level e.g. *Falco* sp. Despite the likelihood that a portion of the swifts observed were pallid swifts, due to speed, aerial traffic and difficulty of identification, both common and pallid swifts were treated as common swifts due to the probability that they made up the overwhelming majority. On a small number of days counts were not made due to very adverse weather or essential administration. Any significant observations made between surveys were also noted as supplementary information. For all species recorded the total heading southwest was subtracted from the total heading northeast to produce a migratory flow value. By using daily values from the three 45 minute surveys, an estimate for seasonal totals of birds passing between 9:00 – 16:00 was made for the more frequently observed species. These timings were decided because as this section looks into trends at species-level, I thought it wise to not make estimates for times falling far outside our survey periods. Pearson's correlation tests were performed to test for similarities in temporal trends between major bird groups recorded (raptors, herons, hirundines and swifts). The study period was divided into thirds (3x13 days) to create effective early, middle and late segments for our spring period. One-way analysis of variance tests were carried out on frequently recorded raptor species ( $n = >20$ ) to test for significant differences in temporal abundance. If significance was found, post hoc tests were carried out to determine which time period(s) differed significantly from others. Seasonal abundance patterns were plotted for species where 10 or more individuals were recorded.

## Results

We recorded 7487 birds of 26 species during 4185 minutes (69 hours, 45 minutes) of surveying, a mean passage rate of 1.79 individuals per minute. Of these 447 were Ciconiiformes of 6 species, and 412 were raptors (Accipitriformes) comprising of 12 species and buzzards (*Buteo* sp.) which were not identified to species level. The remaining birds recorded were 2751 swifts, 149 bee-eaters, and 3728 hirundines. The three most abundant species were common swift (2739), barn swallow (2374) and red-rumped swallow (700) (**Tables 1-4**).



**Table 1:** Totals for all raptor species observed, their migratory flow (northeast - southwest) and percentage which flew northeast

<b>Species</b>	<b>Total Number Observed</b>	<b>Migratory Flow (% Northeast)</b>
Osprey ( <i>Pandion haliaetus</i> )	4	4 (100%)
Lesser Spotted Eagle ( <i>Aquila pomarina</i> )	4	2 (75%)
Short-toed Eagle ( <i>Circaetus gallicus</i> )	1	1 (100%)
Black Kite ( <i>Milvus migrans</i> )	2	0 (50%)
Marsh Harrier ( <i>Circus aeruginosus</i> )	49	11 (66.7%)
Hen Harrier ( <i>Circus cyaneus</i> )	7	5 (85.7%)
Pallid Harrier ( <i>Circus macrourus</i> )	60	56 (96.7%)
<i>Circus sp.</i>	18	8 (72.2%)
Steppe/Long-legged Buzzard ( <i>Buteo sp.</i> )	17	13 (88.2%)
Eurasian Sparrowhawk ( <i>Accipiter nisus</i> )	21	1 (52.4%)
Common Kestrel ( <i>Falco tinnunculus</i> )	165	139 (92.1%)
Lesser Kestrel ( <i>Falco naumanni</i> )	14	2 (57.1%)
Red-footed Falcon ( <i>Falco vespertinus</i> )	8	8 (100%)
Eurasian Hobby ( <i>Falco subbuteo</i> )	42	18 (71.4%)

**Table 2:** Totals for all swifts, bee-eaters and hirundine species observed, their migratory flow (northeast - southwest) and percentage which flew northeast

<b>Species</b>	<b>Total Number Observed</b>	<b>Migratory Flow (% Northeast)</b>
Common Swift ( <i>Apus apus</i> )	2739	1288 (73.3%)
Alpine Swift ( <i>Apus melba</i> )	12	8 (83.3%)
European Bee-eater ( <i>Merops apiaster</i> )	149	145 (98.7%)
Sand Martin ( <i>Riparia riparia</i> )	61	59 (98.4%)
Eurasian Crag Martin ( <i>Ptyonoprogne rupestris</i> )	90	56 (81.1%)
Barn Swallow ( <i>Hirundo rustica</i> )	2374	1992 (92%)
Red-rumped Swallow ( <i>Cecropis daurica</i> )	700	660 (97.1%)

Common House Martin ( <i>Delichon urbicum</i> )	503	461 (95.8%)
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**Table 3:** Totals for all heron and ibis species observed, their migratory flow (northeast - southwest) and percentage which flew northeast

Species	Total Number Observed	Migratory Flow (% Northeast)
Cattle Egret ( <i>Bubulcus ibis</i> )	8	8 (100%)
Little Egret ( <i>Egretta garzetta</i> )	8	6 (87.5%)
Great Egret ( <i>Casmerodius albus</i> )	24	2 (54.2%)
Grey Heron ( <i>Ardea cinerea</i> )	10	6 (80%)
Purple Heron ( <i>Ardea purpurea</i> )	1	-1 (0%)
Glossy Ibis ( <i>Plegadis falcinellus</i> )	396	396 (100%)

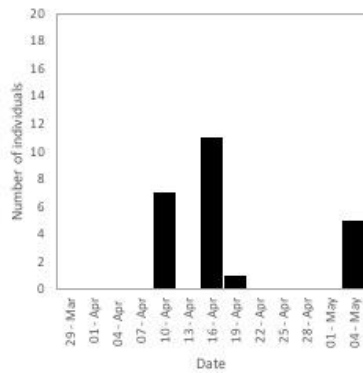
**Table 4:** Seasonal estimates between 9:00 – 16:00

Species	Seasonal Estimate
Pallid Harrier ( <i>Circus macrourus</i> )	187
Common Kestrel ( <i>Falco tinnunculus</i> )	498
Eurasian Hobby ( <i>Falco subbuteo</i> )	131
Common Swift ( <i>Apus apus</i> )	8521
Bee-eaters ( <i>Merops sp.</i> )	464
Barn Swallow ( <i>Hirundo rustica</i> )	7386
Red-rumped Swallow ( <i>Cecropis daurica</i> )	2178
Glossy Ibis ( <i>Plegadis falcinellus</i> )	1232

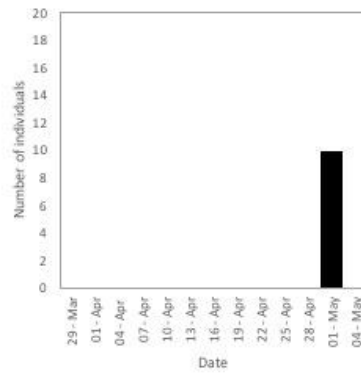
Migration was undergone in a north-easterly direction for all species (except purple heron) following both the north and south coastlines, and centre of the peninsular towards the Klides Islands and out of view. Species predominantly migrated over the land until the tip, the main exception being glossy ibis (*Plegadis falcinellus*) for which 291 were observed migrating out to sea parallel with the peninsular ~200 metres to the south.

Of the raptors, the ring-tailed harriers were the earliest migrants to arrive in numbers and pass through. Pallid harriers (*Circus macrourus*) were recorded in each of the three survey periods, but abundance changed significantly over time (f (2,36) 6.01, p = 0.006) (**Figure 10**). Tukey's Post Hoc tests revealed that the early spring period (first third of study period) differed significantly from the others (p <0.05), and the

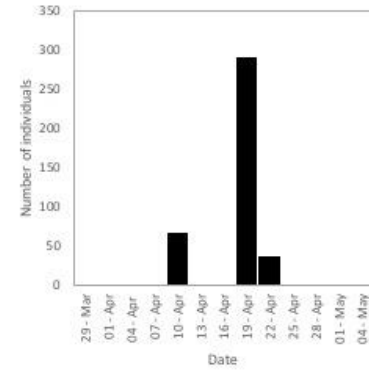
10a) *Casmerodius albus*



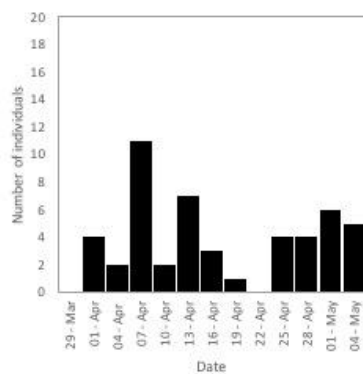
10b) *Ardea cinerea*



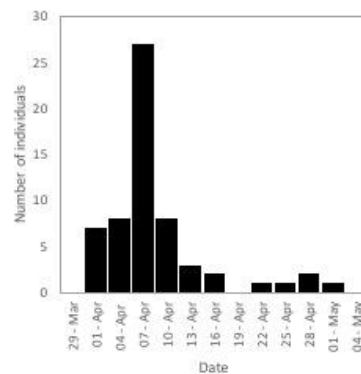
10c) *Plegadis falcinellus*



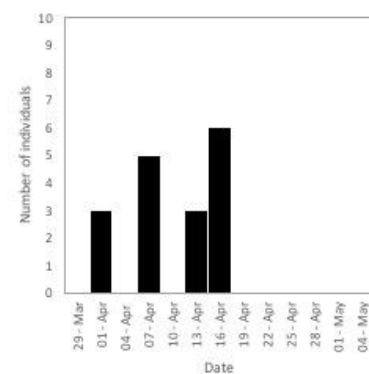
10d) *Circus aeruginosus*



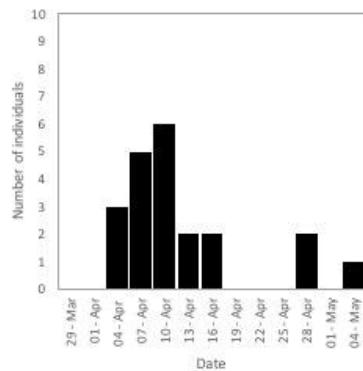
10e) *Circus macrourus*



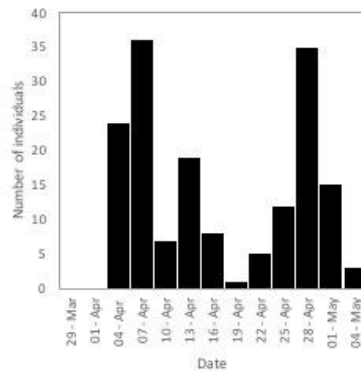
10f) *Buteo sp.*



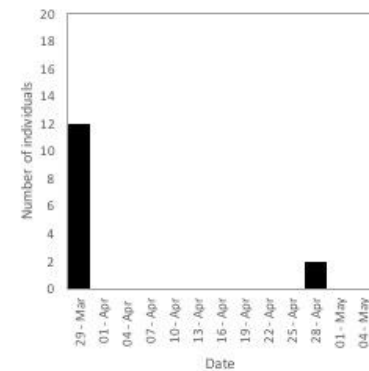
10g) *Accipiter nisus*



10h) *Falco tinnunculus*

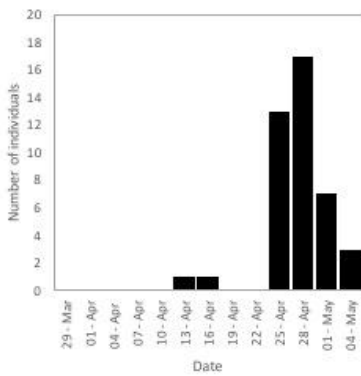


10i) *Falco naumanni*

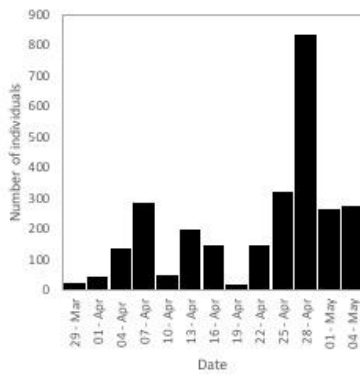


**Figure 10: (a-i)** Spring migration trends for diurnal migrants, depicting total numbers observed against a triad (3-day period, middle date shown) for: **a) Great Egret *Casmerodius albus*** **b) Grey Heron *Ardea cinerea*** **c) Glossy Ibis *Plegadis falcinellus*** **d) Marsh Harrier *Circus aeruginosus*** **e) Pallid Harrier *Circus macrourus*** **f) Long-legged/Steppe Buzzard *Buteo sp.*** **g) Sparrowhawk *Accipiter nisus*** **h) Common Kestrel *Falco tinnunculus*** **i) Lesser Kestrel *Falco naumanni*** (Only species which had 10 or more observations are shown).

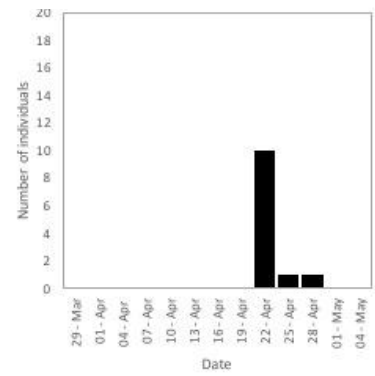
11a) *Falco subbuteo*



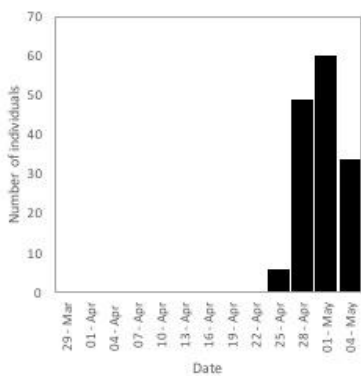
11b) *Apus apus*



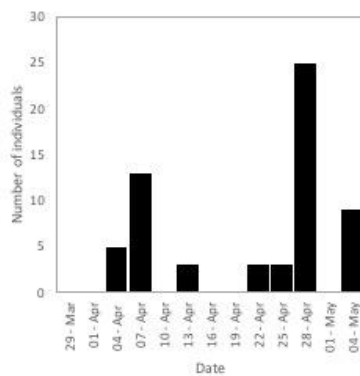
11c) *Apus melba*



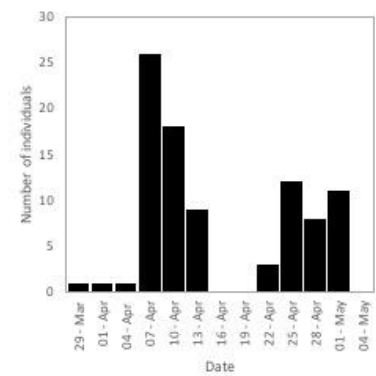
11d) *Merops apiaster*



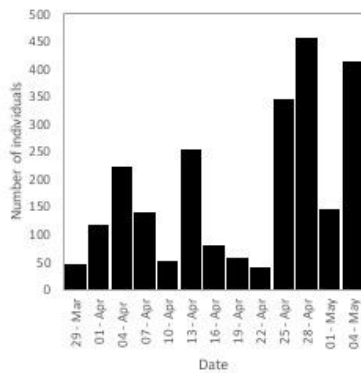
11e) *Riparia riparia*



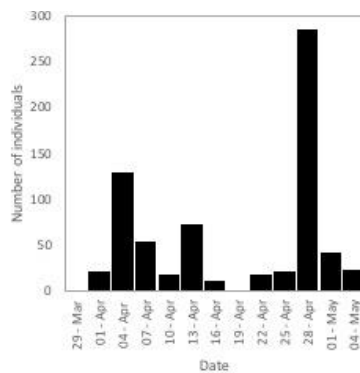
11f) *Ptyonoprogne rupestris*



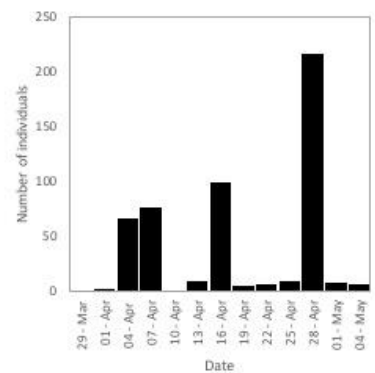
11g) *Hirundo rustica*



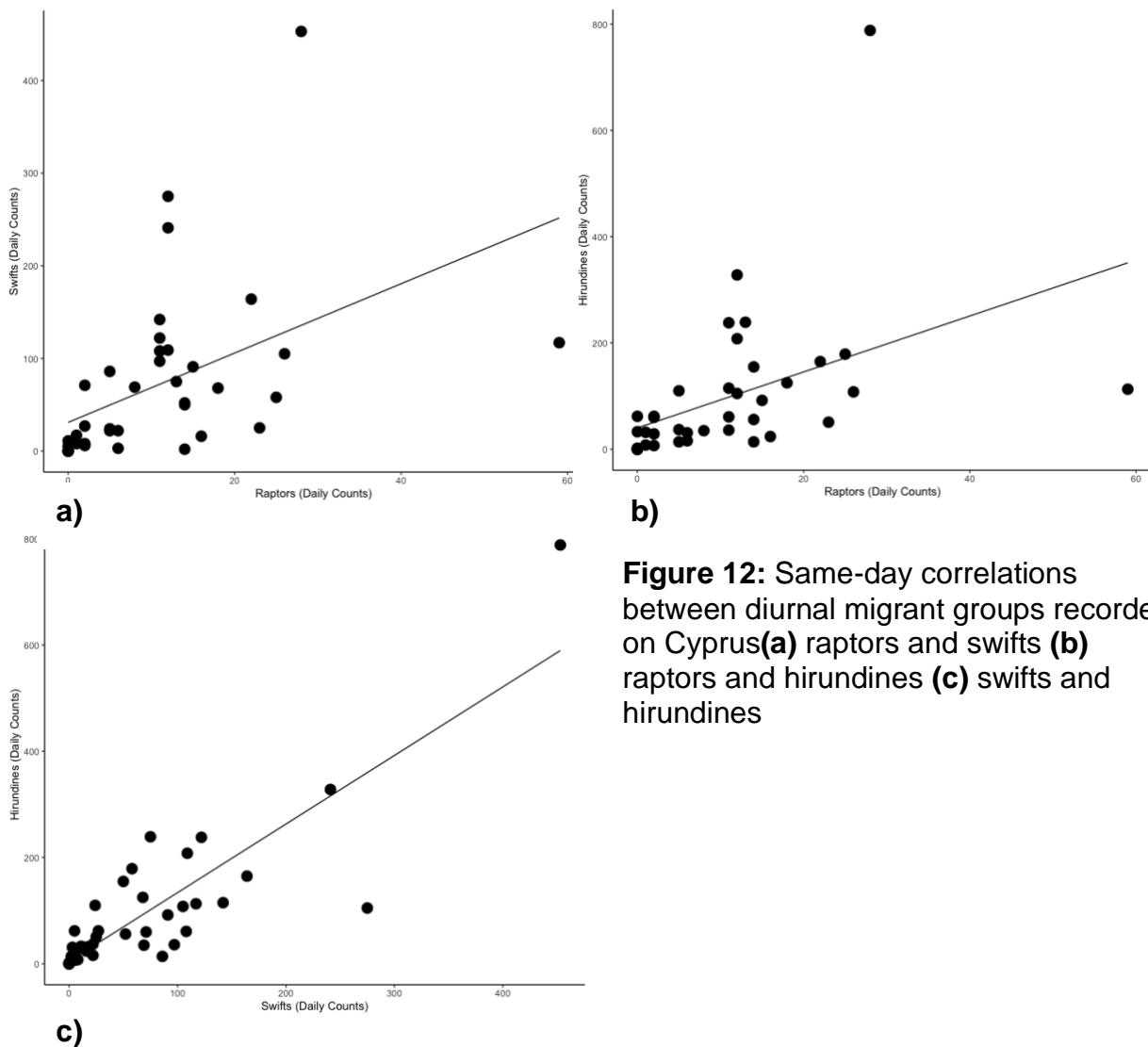
11h) *Cecropis daurica*



11i) *Delichon urbicum*



**Figures 11: (a-i)** Spring migration trends for diurnal migrants, depicting total numbers observed against a triad (3-day period, middle date shown) for: **a) Eurasian Hobby *Falco subbuteo* b) Common Swift *Apus apus* c) Alpine Swift *Apus melba* d) European Bee-eater *Merops apiaster* e) Sand Martin *Riparia riparia* f) Crag Martin *Ptyonoprogne rupestris* g) Barn Swallow *Hirundo rustica* h) Red-rumped Swallow *Cecropis daurica* i) House Martin *Delichon urbicum*** (Only species which had 10 or more observations are shown).



**Figure 12:** Same-day correlations between diurnal migrant groups recorded on Cyprus **(a)** raptors and swifts **(b)** raptors and hirundines **(c)** swifts and hirundines

latter two periods were not significantly different from each other ( $p > 0.05$ ).

Furthermore, their migration had already started by the time the survey had begun (per obs.). Whilst also abundant in the early period, marsh harrier (*Circus aeruginosus*) numbers however did not differ significantly in numbers throughout the survey period ( $f(2,36) < 0.02$ ,  $p > 0.05$ ). The peak day for harrier migration was 08/04/19 during which we observed 9 marsh harriers, 1 hen harrier (*Circus cyaneus*) and 14 pallid harriers (9:00-16:00 estimate: MH: 28, HH: 6, PH: 44). Ring-tailed harrier numbers dropped to mostly singletons after the first 13-day period. Common kestrels (*Falco tinnunculus*) and Eurasian sparrowhawks (*Accipiter nisus*) also showed no significant difference in abundance throughout the spring period (both:  $f(2,36) < 2.0$ ,  $p > 0.05$ ). The latest migrants observed were Eurasian hobby (*Falco subbuteo*), red-footed falcon (*Falco vespertinus*) and European bee-eater (*Merops apiaster*) being first recorded on 13/04, 21/04 and 25/04 respectively (**Figure 11**). Hobby abundance in the last segment of study period differed significantly temporally

( $f(2,36) = 12.72, p < 0.001$ ). Tukey's Post Hoc test found that hobby abundance in the last segment of study period significantly differed from the earlier two periods ( $p < 0.001$ ). Hirundines and common swifts were observed consistently throughout the spring period however with the exception of crag martins, their numbers sharply peaked at the end of April (**Fig.4**).

A significant positive correlation was found between all diurnal migration groups except for Ciconiiformes (herons). Raptors correlated significantly with both swifts ( $r(37) = 0.47, p = 0.003$ ) and hirundines ( $r(37) = 0.43, p = 0.006$ ). A strong significant correlation was found between swifts and hirundines ( $r(37) = 0.85, p < 0.001$ ) (**Figure 12**).

## Discussion

This study is the first systematic survey of diurnal spring bird migration on the Karpaz peninsular, northern Cyprus. Whilst it was previously known to be a migration hotspot, this study is the first to quantify species assemblages and quantities migrating through the peninsular, as well as the direction and timing of these movements. Our findings largely agree with previous theories that diurnally migrating birds arrive at the island on a broad front (south in the spring) and continue along coastlines in a direction aligning with their intended migratory heading, eventually departing northwards towards Turkey. These migrants concentrate at and depart peninsulas so as to minimise the distance spent travelling over open water. We generally observed two strategies; either the individual arrived on the south of the island and immediately follows the coast, or travelled through the island and continued north-eastwards along the north coast. The latter strategy did appear to be more common (pers obs.), however not overwhelmingly so and no strategy appeared to be species-specific. Owing to this theory there are likely at least three major spring migration hotspots on Cyprus: the Karpaz peninsular to the east, the Akamas peninsular to the west, and Cape Cormakitis to the north. Interestingly glossy ibis were the only species observed migrating offshore (~200-300 m south). This appeared to be more commonly observed in an autumn study where birds were seen migrating over water from the peninsular down to Cape Greco (Roth & Corso, 2005). Migration periods were generally not discrete, as was to be expected as

diurnal migrants display less discrete migration windows in spring than autumn (Leshem & Yom-Tov, 1996). Broadly speaking, harriers arrived first, then falcons and then larger birds like lesser-spotted eagle and black kite towards the end of the survey in May. However, there was a large degree of overlap. These observations are in keeping with those observed across the wider region and are believed to be correlated with diet (i.e. in spring, birds with diets of warm-blooded prey or less specialised prey migrate earlier due to emergence-timing at the higher latitudes, and species who feed solely on cold-blooded prey migrate later for the same reasons) (Newton, 2010). Finally, with the exception of the heron family, the seasonal patterns of each main diurnal group correlated significantly. These findings are possibly explained by my findings in Chapter 1, wherein more diurnal migrants (raptors and 'diurnally migrating passerines') were recorded in headwinds probably as a result of being forced to migrate at low altitudes by suboptimal wind current directions, thus resulting in similar seasonal abundance patterns.

The quantity of species totals recorded were not high (only barn swallow and swift >1000), particularly for raptors when compared with other studies in similar areas (Leshem & Yom-Tov, 1996; Corso, 2001; Alon *et al.*, 2004; Roth & Corso, 2007) (**Tables 1-3**). This is possibly due to the low time spent surveying over a probably incomplete spring migration period. The estimates perhaps represent a more accurate total count for some species during the 39-day survey period (between 9:00-16:00) (**Table 4**). A good example of this was that we first recorded European bee-eaters (*Merops apiaster*) from 04/04/19 and consistently saw small numbers between surveys but did not record them during a survey until 25/04/19, therefore, for some species our observations likely only represent their peak in numbers passing. Furthermore, our estimate of 464 bee-eaters passing is probably our largest underestimate as they are also known to migrate nocturnally (Sapir *et al.*, 2011). Some of our most notable raptor sightings also occurred between surveys: 01/04/19 13:30~ 'mixed group of 20 harriers and one *Buteo sp.* passed northeast after bad weather front, of which 4 male pallid harriers and 1 male hen harrier' (Pers.obs). We probably missed many sightings between surveys and thus the estimates are probably conservative. The two most notable findings were for pallid harriers and common kestrels, the two most frequently recorded raptor species. Pallid harriers are listed as near threatened globally and are in decline (IUCN Redlist, 2020). The

numbers we observed during our surveys (N=60) are comparable to spring averages observed over Israel (56) and southern Italy (47.6), the latter being considered Europe's most significant flyway for the species (Leshem & Yom-Tov, 1996; Corso, 2001) (**Table 1**). As mentioned, many were observed between surveys, and so if our estimate of 187 individuals is accurate, it would be of high significance for the species. There is of course the chance however that spring 2019 was a particularly good year or weather conditions funnelled more than average towards the Karpaz peninsular. Common kestrels are well known partial migrants, as such were expected to be primarily resident individuals with a small number exhibiting migratory behaviour, however we observed the opposite. 152 of 165 (92.1%) of common kestrels were observed travelling northeast towards open sea (~110 km from Turkey, the nearest landfall). Again, if the seasonal estimate of 498 is to be believed, it is comparable to seasonal totals observed on the Strait of Messina in southern Italy (mean 642 per spring 1996-2000). Finally, we recorded 90 crag martins (*Ptyonoprogne rupestris*) during our surveys, which is more than would be expected for Cyprus (Gordon, 2002; 2003). On the island they are only known to breed in the west in the Troodos, and thus all of our observations were likely migrating indicating a stronger spring passage to the east of the island than was previously suspected.

During the course of the surveys three species which we expected to see were not recorded: white stork, Montagu's harrier and honey buzzard. On 27/03/19 both a pair of white stork were seen circling and a single Montagu's harrier passed the Oasis Hotel flying northeast, however neither species were observed at the tip during or between surveys. According to Cyprus ornithological society both species are recorded infrequently during spring, but Montagu's harrier are more common during the autumn period (Gordon, 2002; 2003). It is also possible that some of the unidentified *Circus* harriers comprised of Montagu's harriers as juvenile and female ringtail harriers are difficult to identify, particularly from a distance. Furthermore, in Europe most Montagu's harriers appear to migrate via the western and central flyways (Trierweiler *et al.* 2014). Conversely, due to the timing of our sole sightings both species may have migrated predominantly earlier in March and we missed their migratory peak. We did not record a single honey buzzard throughout the season. Honey buzzards are however known to be sighted far less in spring than autumn, however in Israel to the south they are predominantly observed from 10<sup>th</sup> May and so



we could have ended the survey before they reached Cyprus (Leshem & Yom-Tov, 1996).

In conclusion, the Karpaz peninsular is known to be a migratory hotspot, however for the first time we have elucidated the assemblages, abundances and directions of diurnal bird migrants using the region. The Karpaz peninsular may possibly represent Europe's most significant flyway for the globally near threatened pallid harrier, although more observations (in subsequent seasons) are required to verify this. Thankfully, the Karpaz peninsular is currently protected as a SEPA ('Special environment protected area') (Šeffler *et al.* 2010). However, our findings only represent a start to assess the importance of the peninsular for diurnally migrating birds. We would recommend more focused and longer surveys to be carried out in future seasons (both spring and autumn) over multiple years to effectively quantify and monitor temporal changes in species.

## **Section 2: Nocturnally migrating birds**

### **Methods**

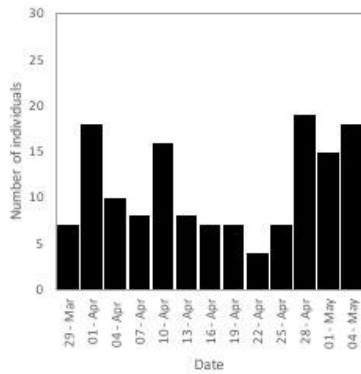
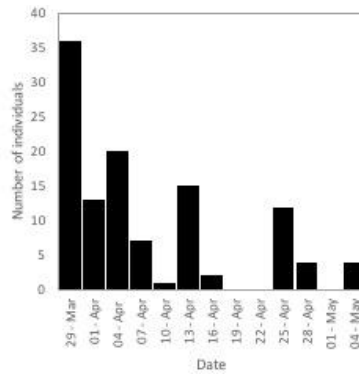
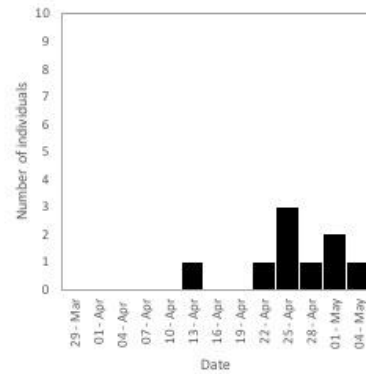
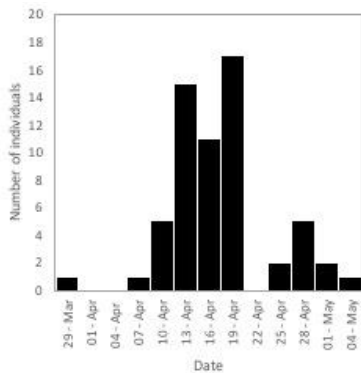
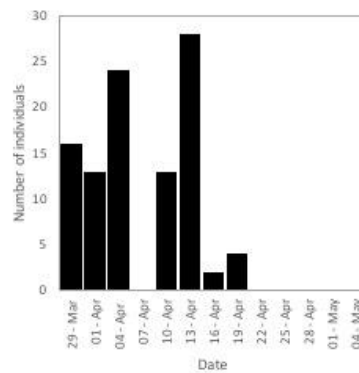
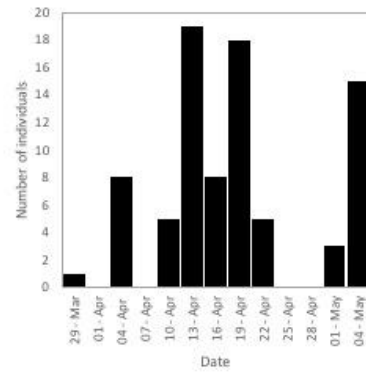
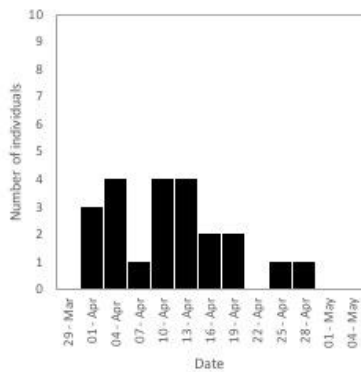
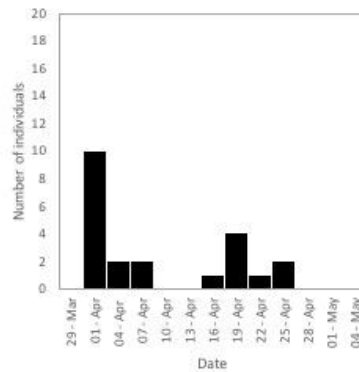
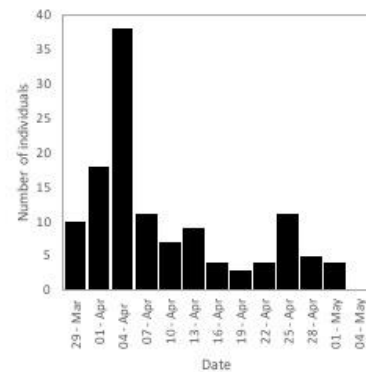
Nocturnal-migrating bird counts were carried out twice daily also from 28<sup>th</sup> March to 5<sup>th</sup> May 2019 and counts were missed due to the same reasons stated in the methods for Section 1. Due to songbirds and other night-time migrants reducing activity during the hottest periods of the day, these counts were carried out for 30 minutes at 7:00am and 5:00pm. The morning surveys were conducted at the Oasis Hotel site, and the evening surveys at Karpaz peninsula tip (**Figure 8**). Both counts were constant effort counts in which the variety and abundance of species observed on an established ~1 km transect during the allotted time was recorded. Both ~1 km transects passed through a diverse array of habitats (**Figure 9**). Only sightings of species were recorded as it was difficult to perceive numbers of some species singing or calling. Some known resident species were recorded because many are partial migrants. All diurnally migrating species (**Section 1**) observed on the transects were omitted except for *M. apiaster* due to it also migrating at night. Once again, binoculars were used by all parties to identify birds down to species level. I also recorded the date for the first sighting of every species encountered and

documented any additional observations. Just as with **Section 1** the findings for the 39-day survey period were split into 3 parts to assess temporal differences in abundance. One-way analysis of variance tests were carried out to test for significant differences in temporal abundances of each major family recorded (except for with Passeridae and Fringillidae because the former mainly comprised of sparrows (*Passer spp.*) which are not considered to be obligate migrants, and representatives of the latter were infrequently recorded).

## Results & Discussion

In total we recorded 2644 birds of 64 species. Nocturnal bird migration occurred on a fairly consistent level throughout the spring period, however earlier abundances were slightly higher, once again suggesting that the survey period should have started earlier (means: 28/03-09/04 = 74, 10/04-22/04 = 61, 23/04-05/05 = 55.3).

Abundance of larks (Alaudidae) was found to vary significantly over the course of the spring period ( $F(2,36) = 4.56$ ,  $p = 0.02$ ). Tukey's Post Hoc tests revealed that lark abundance differed significantly during the middle (13 days) of the study period ( $p < 0.05$ ) (**Figure 13**). Shrike (Laniidae) abundances also significantly differed temporally ( $F(2,36) = 4.4601$ ,  $p = 0.02$ ). Tukey's Post Hoc tests revealed that abundances differed significantly in during the final period of the spring ( $p < 0.05$ ). No significant variance in temporal abundance was found in any other nocturnal migrant group. The findings are split into major families and an 'other' section (for birds from other families from which they were the sole representative or were recorded too infrequently to observe seasonal trends) below. Here seasonal patterns and phenologies are discussed at species level for recorded representatives of each nocturnal migrant family. The seasonal abundance patterns for species where 5 or more individuals were recorded are shown in **Figures 13-16**. Global distribution data for all species were obtained from BirdLife International (BirdLife International, 2020). The migratory status of each species was obtained from BirdLife Cyprus's annual reports (Gordon, 2002; 2003).

**13a) *Galerida cristata*****13b) *Calandrella brachydactyla*****13c) *Anthus campestris*****13d) *Anthus trivialis*****13e) *Motacilla alba*****13f) *Motacilla flava*****13g) *Luscinia megarhynchos*****13h) *Phoenicurus phoenicurus*****13i) *Oenanthe oenanthe***

**Figure 13: (a-i) Spring migration trends for nocturnal migrants, depicting total numbers observed against a triad (3-day period, middle date shown) for: a) Crested Lark *Galerida cristata* (N = 144) b) Short-toed Lark *Calandrella rufescens* (N=114) c) Tawny Pipit *Anthus campestris* (N=9) d) Tree Pipit *Anthus trivialis* (N=60) e) White Wagtail *Motacilla alba* (N=100) f) Yellow Wagtail *Motacilla flava* (N=82) g) Nightingale *Luscinia megarhynchos* (N=22) h) Redstart *Phoenicurus phoenicurus* (N=22) i) Northern Wheatear *Oenanthe oenanthe* (N=124) (Only species which had 5 or more observations are shown).**

## Alaudidae

Three species of lark were recorded during the survey period. The most frequently recorded being crested lark (*Galerida cristata*), of which 144 individuals were recorded. Many of these were likely the same individuals as crested Lark was seen on every day a survey was undergone except one, and the highest daily value between sites was 8. This was unsurprising as Crested Lark are considered a resident species on Cyprus, and we observed no evidence of migration. 114 short-toed larks (*Calandrella brachydactyla*) were recorded and our results showed peak passage between 28/03 – 03/04 (69 records), however two smaller spikes were observed during the middle and end of April (**Figure 13**). Skylark (*Alauda arvensis*), a common winter resident, was observed once on 03/04/2020.

## Motacillidae

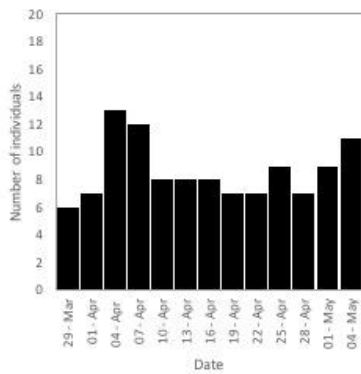
During the survey we had 8 records of tawny pipit (*Anthus campestris*) fairly evenly spread through the spring period and 60 tree pipit peaking in numbers between 12 – 18/04/2020, both considered passage migrants in Cyprus. Both white wagtail (*Motacilla alba*) and yellow wagtail (*Motacilla flava*) were fairly frequently observed having 100 and 82 records respectively. A distinct but expected difference in passage times was seen, white wagtails were not observed after 19<sup>th</sup> April, but yellow wagtails were still recorded at the end of the survey period (**Figure 13**). These differences are likely due to white wagtails being a winter visitor and passage migrant to Cyprus unlike yellow wagtails, which winter much further south and thus migrate later. No systematic count of yellow wagtail races was carried out however the majority appeared to be consistent with the widespread European subspecies *flava* (blue-headed wagtail) and the Balkan subspecies *feldegg* (black-headed wagtail).

## Musciapidae

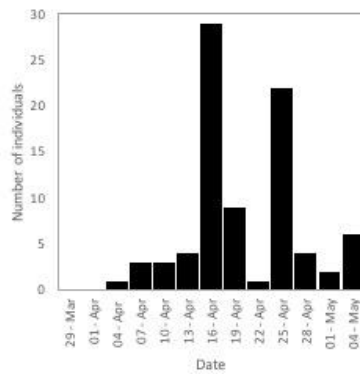
13 species from the *Musciapidae* family were recorded during the spring survey period. Nightingale (*Luscinia megarhynchos*) were recorded in small numbers fairly regularly throughout April, the highest number of individuals during a single survey

was 4. Considering the elusive nature of Nightingales and the abundance of bush and scrub at survey sites, these frequent records suggest a far higher spring-passage abundance. Black redstart (*Phoenicurus ochruros*) were observed far less frequently and earlier than redstart (*P.phoenicurus*), this is likely due to black redstarts wintering in Cyprus and in more northerly regions than redstarts and therefore they leave earlier. Northern (*Oenanthe oenanthe*), Cyprus (*O.cyprica*) and black-eared wheatear (*O.hispanica*) were all recorded, however the latter was far less abundant. Northern wheatear numbers peaked between the 31/03 – 04/04/2019, but continued to arrive in small numbers until May (**Figure 13**). Cyprus wheatear were never recorded more than 10 times on a survey, likely meaning that individuals recorded were breeding and probably the same individuals (**Figure 14**). Stonechat (*Saxicola rubicola*) are wintering visitors on Cyprus, whinchat (*Saxicola rubetra*) are passage migrants which winter across central Africa and so unsurprisingly migratory patterns observed were remarkably similar to those of both observed redstart species. Whinchat numbers did peak comparatively later than Redstart's, 23 individuals were recorded at dusk on 15<sup>th</sup> April (**Figure 14**). Blue rock thrush (*Monticola solitarius*) are another winter visitor and were recorded consistently in low numbers until after 5<sup>th</sup> April when records abruptly ceased (**Figure 14**). Interestingly these consistent numbers and their sex ratios anecdotally staying consistent (2 male 2 females) (pers.obs) suggests that these were likely the same individuals and had stopped over for at least 9 days. 4 flycatcher species were recorded: spotted (*Musciapa striata*), pied (*Ficedula hypoleuca*), semicollared (*F.semitorquata*) and collared (*F.albicollis*), all in low numbers. All species were recorded most between 17-26<sup>th</sup> April, except for semicollared of which 3 individuals were seen during the duration of the study and was recorded twice on 2<sup>nd</sup> April. After 26<sup>th</sup> April only spotted flycatcher was consistently recorded which makes sense as it is also the flycatcher with the most southerly wintering range and small numbers stay and breed in Cyprus during the summer months (**Figure 14**). Finally, two other Musciapid species were observed outside of surveys in the region, the European robin (*Erithacus rubecula*) on 27<sup>th</sup> March (an abundant winter visitor), and more notably two white-throated robins (*Irania gutturalis*) (adult male on 13/04/19, adult female on 28/04/19), a rarely seen spring passage migrant/visitor.

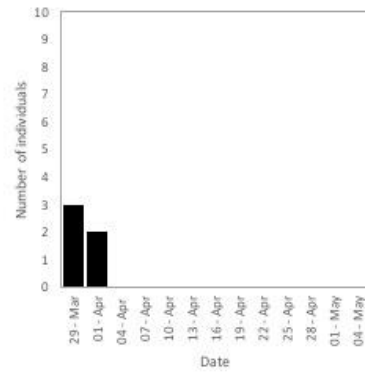
14a) *Oenanthe cypriaca*



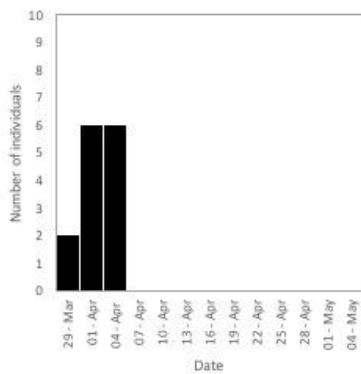
14b) *Saxicola rubetra*



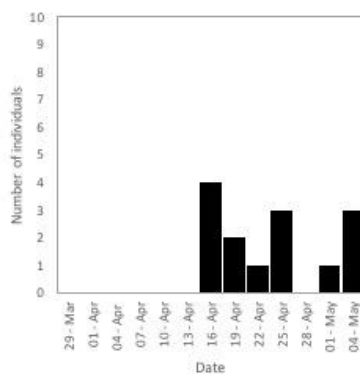
14c) *Saxicola rubicola*



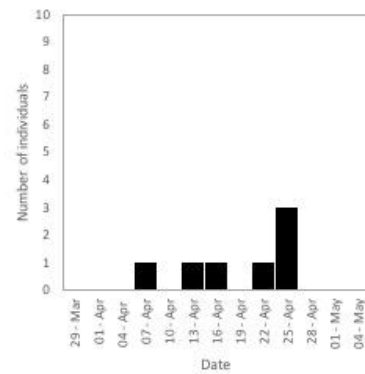
14d) *Monticola solitarius*



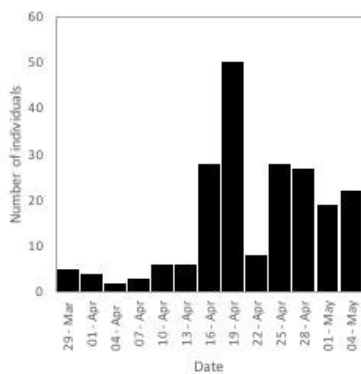
14e) *Muscicapa striata*



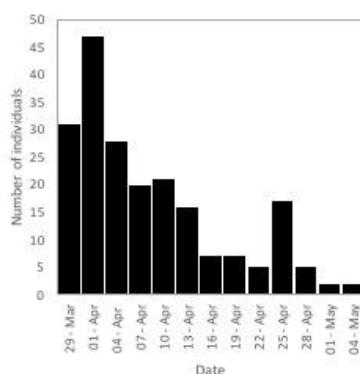
14f) *Ficedula albicollis*



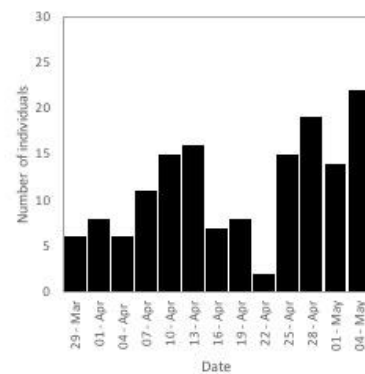
14g) *Sylvia atricapilla*



14h) *Sylvia curruca*



14i) *Sylvia melanocephala*



**Figures 14: (a-i)** Spring migration trends for nocturnal migrants, depicting total numbers observed against a triad (3-day period, middle date shown) for: **a) Cyprus Wheatear** *Oenanthe cypriaca* (N = 112) **b) Whinchat** *Saxicola rubetra* (N=84) **c) Stonechat** *Saxicola rubicola* (N=5) **d) Blue Rock Thrush** *Monticola solitarius* (N=14) **e) Spotted Flycatcher** *Muscicapa striata* (N=14) **f) Collared Flycatcher** *Ficedula albicollis* (N=7) **g) Blackcap** *Sylvia atricapilla* (N=208) **h) Lesser Whitethroat** *Sylvia curruca* (N=208) **i) Sardinian Warbler** *Sylvia melanocephala* (N=149) (Only species which had 5 or more observations are shown).

## **Sylviidae**

Barred warbler (*Sylvia nisoria*), garden warbler (*S. borin*), blackcap (*S. atricapilla*), lesser whitethroat (*S. curruca*), Sardinian warbler (*S. melanocephala*), Rüppell's warbler (*S. ruppeli*), whitethroat (*S. communis*), eastern subalpine warbler (*S. cantillans*), great reed warbler (*Acrocephalus arundinaceus*), icterine warbler (*Hippolais icterina*), olivaceous warbler (*Iduna pallida*), wood warbler (*Phylloscopus sibilatrix*) and eastern Bonelli's warbler (*P. orientalis*) were all recorded during surveys. Due to duller early-spring plumage and the poor conditions of some birds, willow warbler (*P. trochilus*) and chiffchaff (*P. collybita*) were treated as a species pair. Cyprus warbler (*S. melanothorax*) was observed only outside of surveys. Blackcap, lesser whitethroat and chiffchaff/willow warbler were the three highest recorded species during the spring. Sardinian warbler was recorded consistently in fair numbers throughout the study period. Once considered a winter visitor, they have become an increasingly common breeding species and resident in the last 30 years and so a portion were probably there on Cyprus before the survey period, however the low increase in numbers observed suggests that there is passage during the spring (**Figure 14**) (Richardson, 2014). Great numbers of lesser whitethroat and chiffchaff/willow warbler were recorded from late March to early April (as well as a single eastern Bonelli's warbler), however numbers of lesser whitethroat remained high for longer than chiffchaff/willow warbler (**Figure 14 + 15**). During this same period Rüppell's warbler and eastern subalpine warbler also underwent their strongest passage, albeit in significantly lower numbers. Whilst present from the beginning of the survey, blackcap and whitethroat numbers peaked after 16<sup>th</sup> April along with wood warbler in comparatively low numbers. Blackcaps continued to be recorded consistently in smaller number for the remainder of the survey period, and during the end of April/beginning of May small numbers of barred, garden, great reed, olivaceous and icterine warblers were recorded. If distance to migrate and arrival time are correlated, the vast majority (if not all) of the early-spring chiffchaff/willow warblers were probably chiffchaffs. Furthermore, a far smaller second peak for these combined species was observed in late April, perhaps these were willow warblers and their migratory timing is more distinct than expected. Conversely, a portion of the chiffchaffs winter south of the Sahara and would also take longer to migrate. The distance-arrival timing correlation however does not

explain the order of arrival entirely. One would expect that barred warblers would have arrived earlier as they winter in the Horn of Africa similarly to many other species, some of which were the first to pass through Cyprus such as lesser whitethroat and Rüppell's warbler. In these cases, perhaps timing was less due to distance from wintering ground, but instead more predicted by local climate at breeding areas. Rüppell's warblers breed in southern Greece and Turkey where summers quickly become very hot and dry, lesser whitethroats breed in comparatively higher latitudes (and further west) in Europe. Barred warbler breed towards eastern Europe in 'continental climates' which have a wider climatic range than the west due to no Gulf Stream influence. Snow still regularly falls in April in e.g. Ukraine, and perhaps for these reasons early migration is perhaps not just less important, but disadvantageous.

### **Laniidae**

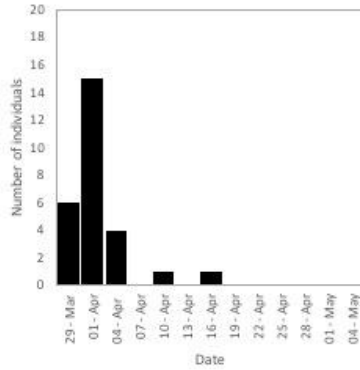
4 shrike species were recorded which arrived in 3 distinct waves. Masked shrike (*Lanius nubicus*) arrived earliest and was first recorded on 29<sup>th</sup> March. Masked shrikes are a common passage migrant and also the only shrike species which commonly breeds on Cyprus. Woodchat shrike (*Lanius senator*) arrived from 11<sup>th</sup> April in small numbers, however these numbers further reduced after 19<sup>th</sup> April. Thirdly from 25<sup>th</sup> April red-backed shrikes (*Lanius collurio*) arrived in high densities as well as two lesser grey shrikes (*Lanius minor*) (**Figure 15**). Once again arrival timings were strongly predicted by distance from wintering grounds, e.g. lesser grey shrike has the most southerly winter distribution and arrived latest. Unlike in a similar study undergone in the autumn, individuals were infrequently observed in similar numbers or in the same location on consecutive days during our surveys suggesting that stopovers in Cyprus during spring may be shorter (Roth, 2008).

### **Passeridae & Fringillidae**

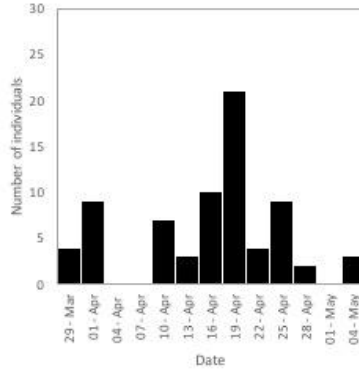
Both house (*Passer domesticus*) and Spanish sparrow (*Passer hispaniolensis*) were seen with some regularity during the course of the survey. Whilst the house sparrow is considered a true resident, the Spanish sparrow is believed to be both resident and a passage migrant. It is difficult to tell the degree to which migration occurred for



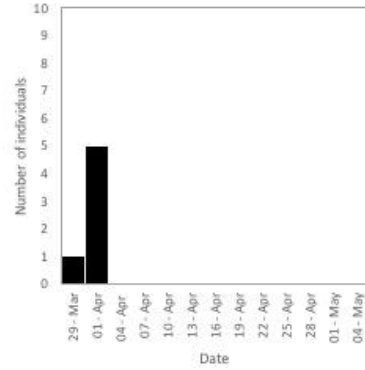
15a) *Sylvia ruppeli*



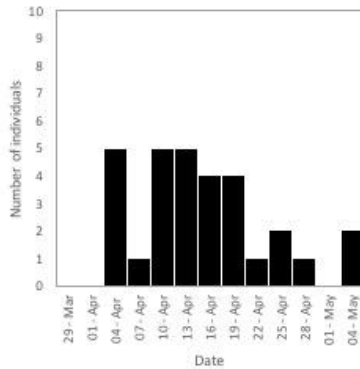
15b) *Sylvia communis*



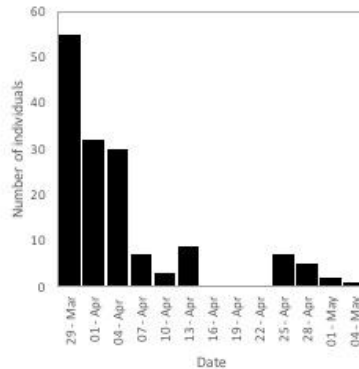
15c) *Sylvia cantillans*



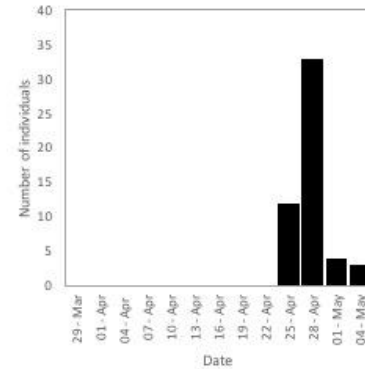
15d) *Phylloscopus sibilatrix*



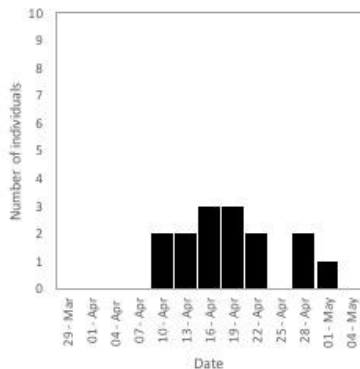
15e) *P.trochilus/collybita*



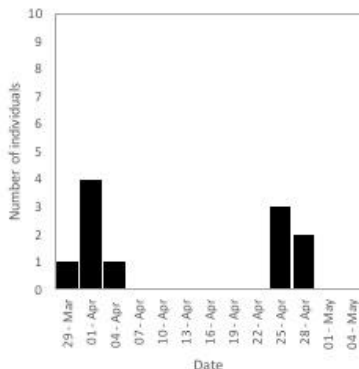
15f) *Lanius collurio*



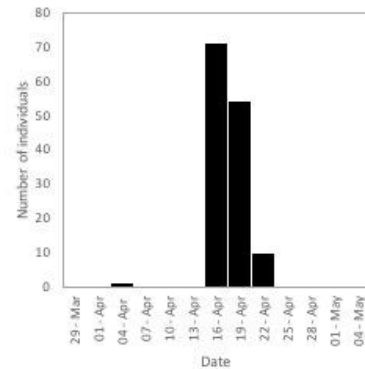
15g) *Lanius senator*



15h) *Lanius nubicus*



15i) *Passer hispaniolensis*



**Figures 15: (a-i)** Spring migration trends for nocturnal migrants, depicting total numbers observed against a triad (3-day period, middle date shown) for: **a) Rüppell’s Warbler *Sylvia ruppeli* (N = 27) b) Whitethroat *Sylvia communis* (N=72) c) Eastern Subalpine Warbler *Sylvia cantillans* (N=6) d) Wood Warbler *Phylloscopus sibilatrix* (N=30) e) Chiffchaff/Willow Warbler *P.trochilus/collybita* (N=151) f) Red-backed Shrike *Lanius collurio* (N=52) g) Woodchat Shrike *Lanius senator* (N=15) h) Masked Shrike *Lanius nubicus* (N=11) i) Spanish Sparrow *Passer hispaniolensis* (N=136)** (Only species which had 5 or more observations are shown).

such a sociable species, however the largest flocks were observed during mid-April (**Figure 15**). These could have been resident flocks with a degree of transience however. Chaffinches (*Fringilla coelebs*) are winter visitors to the study area, only three sightings were made on the 28<sup>th</sup> & 29<sup>th</sup> March. Linnet (*Carduelis cannabina*) and goldfinch (*Carduelis carduelis*) were observed in small numbers, both considered resident with small degrees of passage, however linnet was observed more frequently earlier in the study period. One vagrant trumpeter finch (*Bucanetes githagineus*) was recorded at dusk on 5<sup>th</sup> May.

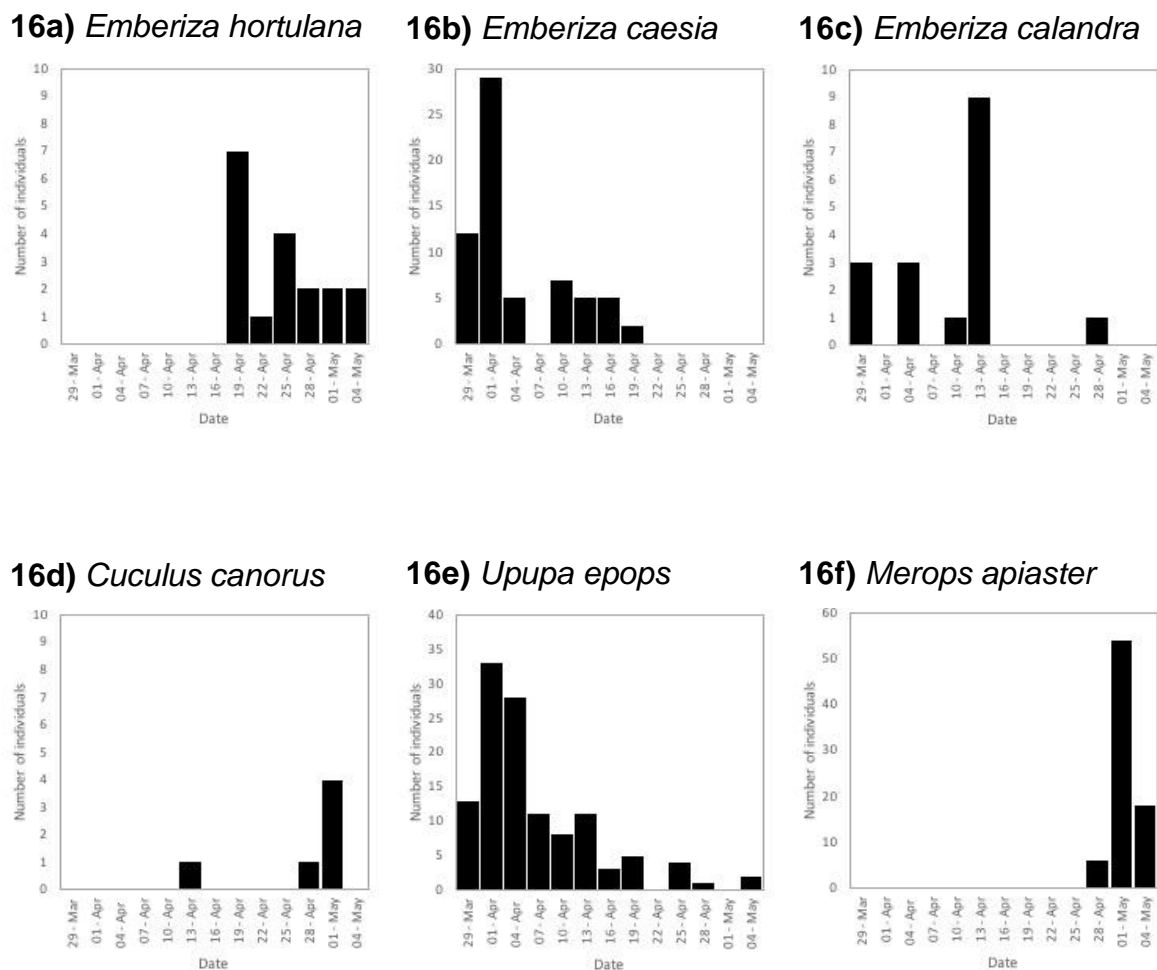
### **Emberizidae**

We recorded 4 bunting species and observed a clear difference in timing between them. Between late-March and mid-April corn bunting (*Emberiza calandra*) and Cretzschmar's bunting (*E.caesia*) were the only species recorded. Corn bunting is a winter visitor, passage migrant and resident breeder on Cyprus and was frequently heard singing during late March and only recorded once after 13<sup>th</sup> April. The largest number of Cretzschmar's bunting were seen at the beginning of April, but continued to persist in smaller numbers until mid-April (**Figure 16**). Whilst they are known to breed on Cyprus, these Cretzschmar's buntings were probably migrants due to the observation site's geography and unfavourable breeding habitats and their persistence for multiple days. Ortolan bunting (*E.hortulana*) were recorded after mid-April in fairly low numbers until the end of the survey. 2 black-headed buntings (*E.melanocephala*) were recorded on 28<sup>th</sup> April.

### **Other**

5 species of *Columbidae* were recorded either during and outside of survey periods, feral pigeon (*Columba livia*) unsurprisingly was the most frequently and consistently recorded species. All other representatives were recorded in very low numbers. During surveys only singles of wood pigeon (*Columba palumbus*) and collared dove (*Streptopelia decaocto*) were recorded, however outside of surveys both species were more abundant in other habitats. Laughing dove (*Streptopelia senegalensis*) was seen frequently in urban areas and once during a count, this species has rapidly increased in abundance over recent years. The origin of this laughing dove's spread

is not certain, nonetheless small numbers would be expected from surrounding mainland countries where they are an established species, however it is more likely due to intentional human releases for hunting. A single turtle dove (*Streptopelia turur*) (a once very abundant passage migrant) was seen during a diurnal migrant survey on 15<sup>th</sup> April (Browne & Aebischer, 2005). A vagrant Namaqua dove (*Oena capensis*) was also seen out of survey on 26<sup>th</sup> April.



**Figures 16: (a-f)** Spring migration trends for nocturnal migrants, depicting total numbers observed against a triad (3-day period, middle date shown) for: **a) Ortolan Bunting *Emberiza hortulana*** (N = 18) **b) Cretzschmar's Bunting *Emberiza caesia*** (N=65) **c) Corn Bunting *Emberiza calandra*** (N=17) **d) Common Cuckoo *Cuculus canorus*** (N=6) **e) Eurasian Hoopoe *Upupa epops*** (N=119) **f) European Bee-eater *Merops apiaster*** (N=78) (Only species which had 5 or more observations are shown).

frequently in late April. Eurasian hoopoe (*Upupa epops*) were seen in good numbers throughout the study period. Hoopoe numbers observed two peaks, first on 31<sup>st</sup> March when 21 individuals were recorded, and on 05<sup>th</sup> April when 14 were observed (**Figure 16**). The majority of passage had ceased by 14<sup>th</sup> April and the low numbers recorded after were possibly the same individuals as some remain on Cyprus throughout the summer. Whilst some are resident, most kingfishers (*Alcedo atthis*) records on Cyprus are likely migratory, we made several coastal observations outside of surveys and one during the survey at dusk on 2<sup>nd</sup> April. As with the diurnal migrant surveys, European bee-eaters (*Merops apiaster*) were frequently seen before they were recorded during a survey, however from 27<sup>th</sup> April they were recorded consistently until the end of the study period (**Figure 16**). Wryneck (*Jynx torquilla*) were recorded 3 times on surveys during the study period, due to their shyness were likely more abundant. Two juvenile golden orioles (*Oriolus oriolus*) were seen on 29<sup>th</sup> April and 1<sup>st</sup> of May. Migration of golden orioles certainly started far earlier however as a group of individuals (including adults) was seen in a section of woodland on 10<sup>th</sup> April. Due to their forest-dwelling habits, they probably avoid the scrub habitats we surveyed, and instead refuelled in woodland.

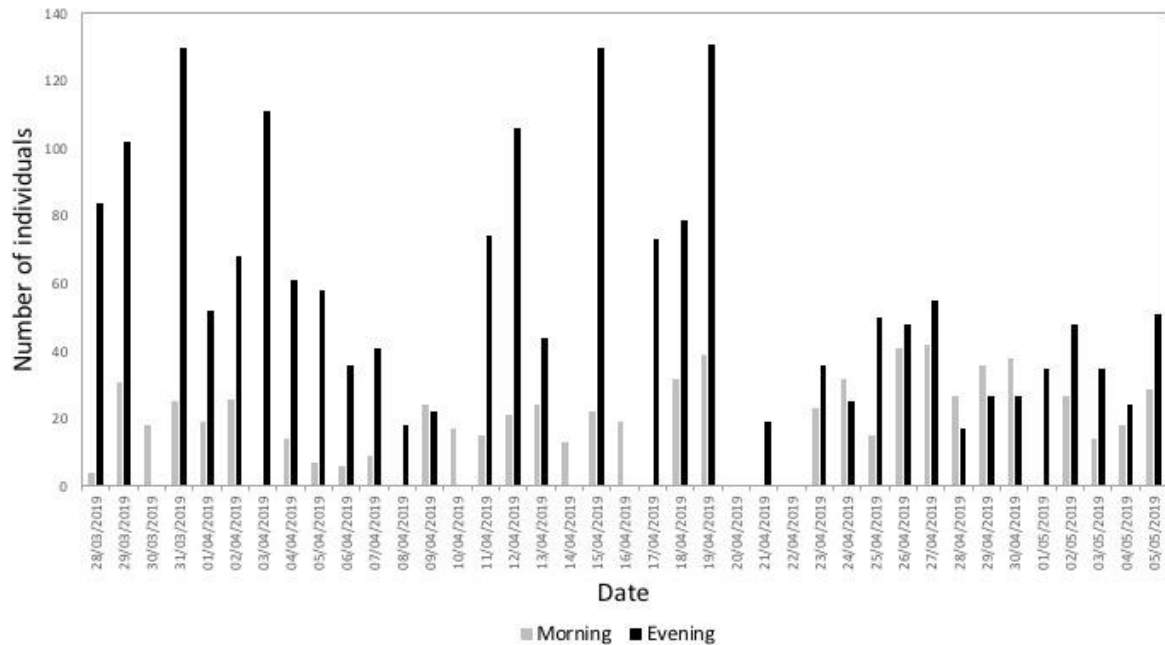
Despite not surveying in any wetland environments we did record some wetland-associated species as after heavy rains the open area of the tip site would flood in areas. Here we recorded individuals of ringed plover (*Charadrius hiaticula*) and little stint (*Calidris minuta*) (both common passage migrants in the region). Further unexpected sightings include: in late March several stone curlew (*Burhinus oedicephalus*) and a corncrake (*Crex crex*) were seen on the dunes behind the Oasis Hotel, on 4<sup>th</sup> April a raven (*Corvus corax*) (a species facing extinction in Cyprus) was observed at the Karpaz tip, and finally on 13<sup>th</sup> April during a diurnal migrant count a single collared pratincole (*Glareola pratincola*) passed heading southwest.

### **Differences Between Sites**

A total of 65 nocturnal migrant surveys were carried out during the spring, 32 in the morning and 33 in the evening. On occasion surveys were not carried out due to the same reasons as for the diurnal migrant surveys. Despite geographic closeness and fairly similar habitats, findings differed in a number of ways between sites. Firstly,

overall numbers differed substantially. Of the 2644 individual birds recorded on all surveys 727 were recorded on the dawn surveys and 1917 were recorded during the dusk surveys. Throughout the spring the mean number of birds recorded on morning surveys was 22.7 and 58.1 for evening surveys. However, the volume of birds at the tip sharply dropped after 20<sup>th</sup> April and the average numbers for each site per survey become more similar (morning: 28.5, evening: 35.5) (**Figure 17**). Variety and numbers of species also varied between sites as 44 total species were recorded at the Oasis site compared to 59 species at the Karpaz tip. 21 species observed during evening surveys were not recorded at the Oasis site. The only obligate migrant species (on Cyprus) recorded at the morning site and not at the tip during surveys were song thrush (*Turdus philomelos*), black-eared wheatear (*O.hispanica*) and great reed Warbler (*A.arundinaceus*). Excluding the 3 previously mentioned species, only 4 migrant species were recorded in higher numbers at the morning site than at the tip: European bee-eater (*M.apiaster*), tree pipit (*A.trivialis*), Sardinian warbler (*S.melanocephala*), eastern subalpine warbler (*S.cantillans*) and red-backed shrike (*L.collurio*). However as previously stated, it is highly likely that Sardinian warbler observations were duplicated due to the high probability that breeding was occurring (Richardson, 2014). Differences in timings for some species was observed between sites. No lag in arrival times was recorded, peaks for species were temporally shared between sites for most species. This is unsurprising as the distance between sites was 21 km and songbirds commonly migrate distances of 200 km or more in a single night (Hall-Karlsson & Fransson, 2008). However, for species which had passed through during our spring period, we noted that they continued to be recorded at the tip site for longer than the Oasis site. Some examples include: northern wheatear was not recorded after 9<sup>th</sup> April at the Oasis site, but continued to be frequently recorded until 1<sup>st</sup> May at the tip, white wagtail observations ceased after 29<sup>th</sup> March and 19<sup>th</sup> April for the dawn and dusk surveys respectively, whinchat arrived at both sites in early April and was not recorded at the Oasis after 24<sup>th</sup> April but persisted at the tip for until the end of the study period, Rüppell's warbler was last recorded on 4<sup>th</sup> April in the morning, and 17<sup>th</sup> April in the evening. I theorise that these differences are due to the Karpaz tip being used as a staging site for many nocturnally migrating birds (Warnock, 2010). Whilst the difference in timings observed may be explained partially by the vast difference in numbers of birds observed between sites, we argue that the higher numbers at the tip are partially because of the longer persistence of

birds which are refuelling to cross the sea which is clearly visible around the site. In conjunction with this, the disparity in numbers is once again likely caused by the funnelling effect of the island's geography.



**Figure 17:** Total number of nocturnally migrating birds recorded per day for morning and evening surveys throughout the spring period.

### Conservation Observations & Conclusions

Many Mediterranean islands have become infamous for their conservation measures and killing of birds, and Cyprus is no exception. A 2014 BirdLife Cyprus publication estimated that more than 2 million songbirds birds are illegally caught and killed on the island annually (BirdLife Cyprus, 2019). Promisingly, during our study period we saw very little evidence of hunting. During our surveys we observed many used shotgun cartridges (likely for use on doves and pigeons) but heard no gunfire. We also observed a small number of warblers (blackcap and olivaceous) which had escaped limesticks and resultingly had very poor feather condition. No limesticks or illegal mist nets were seen, however we were not actively searching for them. Our findings, or lack thereof corresponded with those of BirdLife Cyprus who did not find a single mist net during the period (BirdLife Cyprus, 2019). Whilst positive, these findings must be contextualised by the fact that spring trapping levels are historically lower than those in Autumn.

Increased awareness of the illegal trapping of songbirds in Cyprus has also negatively affected its tourism industry, an increasing number of people choose alternate destinations due to the bad reputation. The losses due to this are estimated to be between 40 – 100 million Euros every year (Terra Cypria, 2019). During our study period the Karpaz tip received a steady flow of tourists, mostly for sightseeing purposes, but also for wildlife. A combination of organised wildlife tours or photographers visited on a near daily basis, particularly in the latter half of Spring. Some photographers were locals, which despite using frowned upon methods (audio call playback, driving over habitats and approaching birds in 4x4 vehicles very closely), indicates a more positive view of birds in Cyprus.

In conclusion, Cyprus is of incredible importance to nocturnal migrating birds. It plays host to vast numbers and a staggering array of species during the spring and autumn windows. The spring phenologies of these species on Cyprus are still not fully understood, however this study provides a strong starting point from which future assessments should derive. A key difficulty of conserving migratory species is that protection of breeding and wintering grounds is not enough, species must be safeguarded throughout their migration route (Kirby *et al.* 2008). Whilst the evidence for illegal trapping of songbirds was low in 2019, counter-efforts must continue. The Karpaz tip is clearly of great importance to many nocturnal migrant species and therefore its status as a SEPA must be maintained and enforced (Šeffer *et al.* 2010).

### **Section 3: Diurnal Insect Migration**

#### **Methods**

Due to the variety in size and flight power of insects, multiple techniques were used to quantify abundance and assemblages of insect migrants. Smaller insects were surveyed via a combination of sweeping a butterfly net and video recordings. Butterfly net sweeping was undergone continuously for two minutes every two hours (10:00 – 16:00) atop gulleys close to shore. All insects caught during the two-minute sweeping were transferred to insect cages for identification. At least family-level identification was achieved for nearly all insects caught. Every insect recorded using

this survey method could safely be considered migratory as they were caught arriving from the sea. Video recordings were taken every day across the (5m) width of a set section of dirt track at site 1. Recordings were taken at 30fps 1080p resolution using a smartphone set to record for 1 minute every 30 minutes between 10:00-16:00. Larger insects (i.e. butterflies and dragonflies) were surveyed in flight by eye both because their larger size makes identification achievable from a distance and their greater flight speeds and agility enables them to avoid capture in the butterfly net sweeping surveys. For butterflies and dragonflies, a 15-minute count was undergone once every two hours (10:00-16:00), during which every individual was counted and identified as it crossed a pre-established 15m line.

For analysis all video files were converted to AVI files using FFMPEG software (<https://ffmpeg.org>) and each frame was viewed individually with ImageJ (<https://imagej.nih.gov/ij/>). Insects were counted as they cross the halfway point of the screen and identified at least to order. Occasional second counts were undertaken further inland at the tip to compare with numbers observed at the point of arrival, and to estimate the number joining our sampled assemblages. Inland samples were found to be 5-times higher than those counted on the dirt track near the peninsular's very tip. Due to these findings our counts were multiplied and then extrapolated further to become representative of the width of the peninsular that insects were actively observed migrating through (40 m across) for a set length of time (10:00-16:00). Pearson's correlation tests were carried out to compare insect migration trends with those of diurnal bird migrants.

Due to the often irruptive nature of insect migration, timing and location of surveys occasionally were required to be slightly more flexible than those for birds. The primary example of this occurred on 05/04/19 when extreme levels of butterfly migration took place early in the morning at site 2. A 15-minute count was undertaken using the same methods as stated previously. Furthermore, a similar method was used to extrapolate the count for the width of the peninsular at site 2 (5 km) over a set time (6:00-9:30). Nocturnal insect migrants are not covered in this report due to theft of our light trap early in the study period.



The briefness of my focus on insects is because a student who collected data with me is focusing on the insect data for his thesis and so I simply present a broad synopsis of our findings, particularly as a counterpoint in relation to the bird data.

## Results

**Table 5:** Seasonal totals for every insect order recorded

<b>Insect Order</b>	<b>Percentage of Total</b>	<b>Estimated Total Number</b>
Diptera	84.05	42,078,205
Hymenoptera	5.61	2,810,411
Coleoptera	1.12	562,843
Hemiptera	2.65	1,325,343
Lepidoptera	5.64	2,822,267
Neuroptera	0.08	38,030
Psocoptera	0.08	39,931
Odonata	0.78	388,958

**Table 6:** Totals for each insect family recorded during sweep surveys and video recordings

<b>Insect Family</b>	<b>Percentage of Total</b>	<b>Estimated Total Number</b>
Acroceridae	0.04	19015
Anthomyiidae	43.72	20783351
Apidae	2.274	1081000
Calliphoridae	1.844	876590
Cantharidae	0.26	123597
Carabidae	0.24	114090
Chalcidae	1.044	496290
Chloropidae	3.91	1858712
Coccinelidae	0.132	62749
Crambidae	0.13	61799
Culicidae (mosquitoe)	0.04	19015
Dermeestidae	0.036	17113
Drosophilidae	1.67	793875
Ichneumonidae	3.23	1535458
Lycaenidae	0.04	19015
Micro moth	0.22	104582
Muscidae	0.94	446852
Mycetophilidae	0.06	28522
Nitidulidae	0.02	9507
Nymphaliidae	0.254	120745
Palloppteridae	1.28	608479

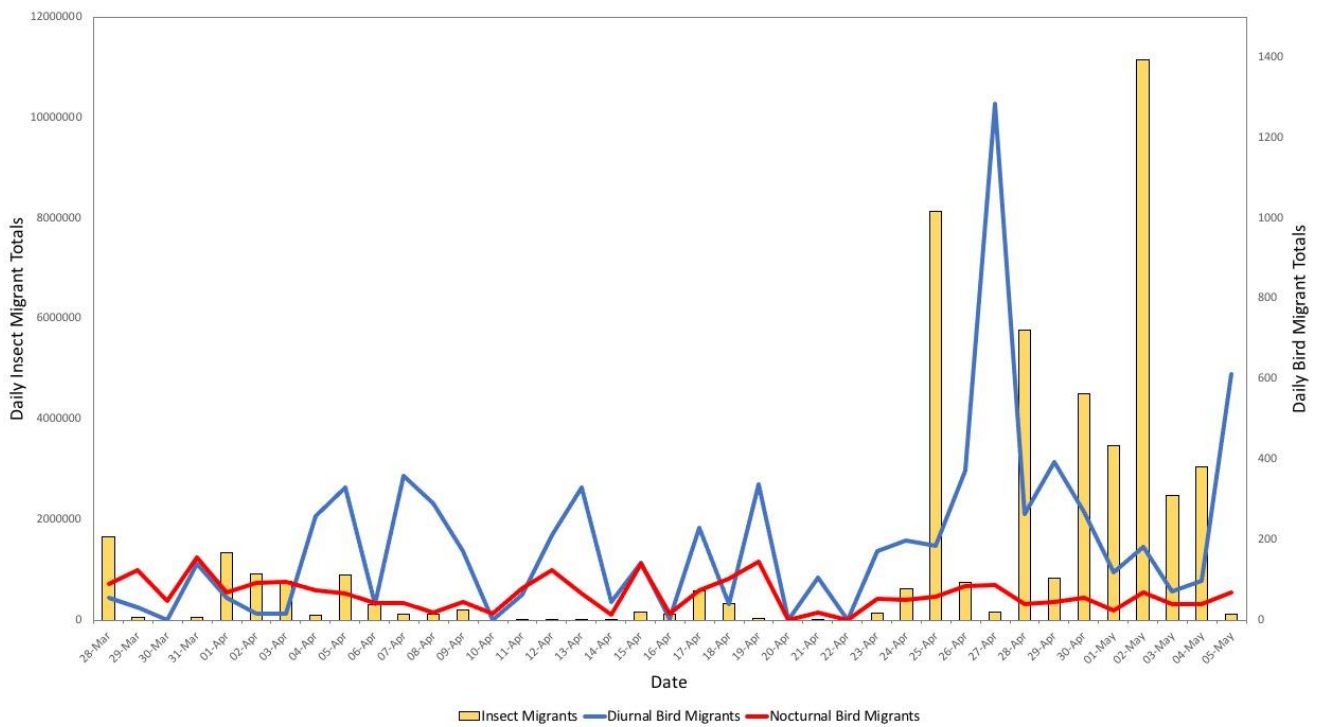
Phoriidae	5.156	2451028
Plutellidae	0.22	104582
Scarabeidae	0.1	47537
Sciaridae	0.16	76060
Sepsidae	11.2	5324189
Staphylinidae	0.624	296633
Syrphidae	18.98	9022599
Tephritidae	0.328	155923
Vespidae	0.214	101730

**Table 7:** Days on which insect migration was estimated to exceed 1 million individuals

Date	Estimated Total Number
28/03/2019	1,663,800
01/04/2019	1,110,600
25/04/2019	8,123,400
28/04/2019	5,746,800
30/04/2019	4,474,800
01/05/2019	3,452,400
02/05/2019	11,118,000
03/05/2019	2,485,200
04/05/2019	3,055,200

From our combined survey counts an estimated total of 50,065,988 insects migrated through the Karpaz peninular of Cyprus between 28/03/19-05/05/19 (**Table 5**). This consisted of 8 different insect orders. By far the most abundant order was Diptera which made up 84.05% of the total insect abundance (est. = 42078205). The three most abundant fly families were Anthomyiidae (est. = 20,783,351), Syrphidae (hoverflies) (est. = 9,022,599) and Sepsidae (est. = 5,324,189) (**Table 6**). Of the estimated 2,822,267 *Lepidoptera* recorded, 1,596,849 were butterflies, 99% of which were painted ladies (*Vanessa cardui*). An estimated 905,967 of the remaining *Lepidoptera* were the pyralid moth rush veneer (*Nomophila noctuella*). Almost all of the 388,958 *Odonata* estimated comprised of vagrant emperors (*Anax ephippiger*). 82.4% of the seasonal total is represented by just 9 days of extreme migration (determined as days on which insect estimates exceeded 1 million), clustered in two peaks at one at the beginning of the survey period, and one at the end (**Table 7 + Figure 18**). From large insect active migration counts, 83.53% of all butterflies and dragonflies were found to be travelling southwest and arriving from the sea. No significant correlation was found between the seasonal patterns of diurnal bird

migrants and insects ( $r(37) > 0, p > 0.05$ ). Finally, we recorded the first spring arrivals of the African migrant butterfly *Catopsilia florella* and the ladybird *Harmonia quadripunctata* in Cyprus (a known migrant and probable migrant species respectively), and additionally found strong supporting evidence for migratory behaviour in not previously considered migratory species such as *Delia platura* and *Stomoxys calcitrans*.



**Figure 18:** Temporal abundance trends of insect migrants, diurnal bird migrants and nocturnal bird migrants across the spring season

## Discussion

This study was the first systematic survey of day-flying insect migrants in the northeast of Cyprus. Our findings not only demonstrate the vast volume of insect biomass that passes through the peninsular but also indicates the taxonomic variety and composition of these movements. By far the most abundant insect order observed were flies (Diptera), which have been largely neglected in the field of insect migration.

Due to the lack of historical surveys from the region it is difficult to tell whether or not our findings from spring 2019 are representative of prior or subsequent seasons. It is unlikely that adjacent seasons would exhibit similar trends for painted lady butterflies

in particular because 2019 produced unusually high numbers of the species. This is because in most years populations are greatly limited by climatic conditions in the arid regions where they spend the winter (Hu, *et al.*, 2021). Years on which huge numbers are observed are caused by significantly higher than average rainfall in these areas; most notably for Cyprus, the Arabian desert (Benyamini, 2017). Furthermore but to a lesser extent, when sequential waves pass through and breed in the same regions parasitoids and pathogens greatly increase in prevalence, we observed this at Site 1 many caterpillars at almost every instar stage simultaneously feed on the same plants. This could limit subsequent northward journeys and by extension the quantity that eventually return south (Stefanescu, *et al.*, 2012). However, parasitoid prevalence is far more impactful on populations of resident species (Altizer *et al.*, 2011; Chapman *et al.*, 2015). There is the possibility that some species that weren't abundant during our data collection period would be more abundant in other years such as red admirals (*Vanessa atalanta*) and hummingbird hawk-moth (*Macroglossum stellatarum*), but not to such an extreme extent as *V.cardui* due to their less obligate migrant lifescycles and less historically fluctuating populations (Cuadrado, 2017; Stefanescu, 2001). As mentioned, extensive hoverfly migration was also observed the spring before, perhaps flies or some fly groups exhibit less year-to-year variation (Chapman pers.comm., 2019). Also due to the short migration windows observed it could also be possible that (for example vagrant emperor (*A. ephippiger*)) migration occurs in high volumes annually but due to lack of historical study it has gone unnoticed on the peninsular. The most feasible conclusion is that spring 2019 was a particularly strong year for insect migration in most cases, however Diptera undoubtedly are the most numerous migrants each year.

Substantial differences were observed between the migration of insects and diurnal avian migrants and no similarities in seasonal patterns were found (**Figure 18**). Insects were observed to migrate in the opposite direction to birds and concentrate in numbers further inland. These findings seem to completely oppose a preference for heading northwards in spring. However, this may be partially explained by a combination of insect's lower ability to combat climatic conditions and their less established migration routes (Chapman *et al.*, 2015). Insects, like birds have been shown to reduce the distance of sea-crossings, however have a less fixed

destination (Brattström *et al.*, 2008; Wikelski *et al.*, 2006). Therefore, insects observed in Cyprus were possibly travelling up through the Middle East and were either already over sea, or chose to cross from Israel or Lebanon (visible from the peninsular) and arrived at the closest point, the Karpaz tip. This theory is further supported by a message received from Nir Sapir in Haifa on 04/04/19, which stated that Israel was experiencing vast levels of painted lady migration; the next day in Cyprus we observed the highest levels of painted lady migration of the season (Sapir pers.comm., 2019). Upon arrival at the Karpaz tip, there is no other over-land direction to fly except southwest, and numbers likely concentrated further inland because the points at which the insects arrived were probably indiscrete due to increased drift in flight and thus became more funnelled inland. Furthermore, for painted lady butterflies and larger hoverflies reproduction was observed on Cyprus, perhaps the next generation moved northwards as mainland Turkey is viewable from the north of the island. Insects also exhibited far more discrete migration windows than birds, heavy migration for a species seldom lasted longer than 2-3 days. It is possible that similarly to birds, high altitudes were attained on some days and thus much insect migration went undetected, however I doubt this to be the case. A 2018 radar study by Bruderer *et al.* has shown that birds arrive at lower altitudes after sea-crossings, and therefore it is unlikely that less powerful insects regularly attain greater altitudes upon arriving from the sea. The spikes observed broadly fell at the beginning and end of the 39-day study period, particularly for Dipterans. This temporally correlates with the length of time for flies to complete development from egg to adult. Therefore, these windows may be truly discrete generational waves similarly enabled by plentiful rains further south, however as northward migration persists (and if resources remain plentiful) I would expect waves to become less discrete due to oviposition occurring over months for some species of hoverflies (Howlett & Gee, 2019).

Mass movements of insects carry out a number of essential ecosystem services. Influxes of insects represent plentiful prey items for resident and migrant carnivores alike. We frequently witnessed various species of warbler (*Sylvia* & *Phylloscopus* spp.) continuously feeding on days of vast fly migration (Pers.obs.). Such plentiful and temporary opportunities for easier prey can also lead to 'prey switching' in some species (Terry *et al.*, 2017). On days when thousands of vagrant emperors were

present, we observed common kestrels (a species which usually preys exclusively on warm-blooded vertebrates (Orihuela-Torres *et al.*, 2017)) hawking for dragonflies for long spells, frequently catching and devouring multiple dragonflies within a minute (Pers.obs.). On a broader scale, most insect migrations involve the death of multiple generations in the completion of a migratory cycle (Satterfield *et al.*, 2020). This results in transport of biomass to regions which would not otherwise receive it (Bauer & Hoye, 2014). Insect bodies are composed of 10% Nitrogen and 1% Phosphorus by dry weight, both are important limiting nutrients in soil (Elser *et al.*, 2000). Mass movements and the resulting mass deaths lead to transfer of these important nutrients, greatly benefiting local plant ecosystems (Landry & Parrott, 2016). In Cyprus we observed the start of this process, exacerbated by migratory culling via entomophaga fungi, thousands of *Eristalis sp.* hoverflies had succumbed and littered the ground, many of which will decompose and eventually improve soil health (Pers.obs.). Thirdly, many of the orders recorded on Cyprus use flowers as a food source and thus are pollinators. Individuals of medium-sized hoverfly genera *Eupeodes* and *Episyrphus* have been found to carry an average of ten pollen grains each on their bodies during migratory flights (Wotton *et al.*, 2019) . Theoretically this could mean that our estimate of over 9,022,599 hoverflies could pollinate over 90 million flowers (if the same species of plant are revisited). Long-distance transport of pollen further assists the genetic diversity of plant populations across great distances (Paschke *et al.*, 2002). This has been shown to be the case for species with fragmented distributions such as an endangered violet (*Viola cazortensis*) in Spain, which benefits from high gene flow due to pollination from migratory hummingbird hawkmoths (*M.stellatarum*) (Herrera & Bazaga, 2008).

Many of the insect migrants recorded on Cyprus are of socioeconomic importance to humans, including some of the most frequently recorded species. Cross pollination from migratory families such as hoverflies has been shown to positively impact on agriculture by increasing crop genetic diversity leading to healthier plants and higher yields (Doyle *et al.*, 2020). Furthermore, ladybirds (e.g. *Coccinella septempunctata*) and larvae of some hoverflies (e.g. *Episyrphus balteatus*) are aphid predators, and therefore are an effective biological control for reducing aphid numbers in crops (Wotton *et al.*, 2019; Schmidt *et al.*, 2003; Hindayana *et al.*, 2001; Dixon & Dixon, 2000; Dixon *et al.*, 1997). Conversely, many species recorded are known agricultural

pests, including the most numerous insect we recorded, the *Anthomyiid* fly *Delia platura* or the 'bean seed fly' (est. = 20,783,351). This species is a pest of a wide range of crops (such as potato, alfalfa, beans, cotton, onion, wheat and peas) which are attacked at germination and can result in a loss of up to 60% of seedlings (Guerra *et al.*, 2017; Kessing & Mau, 1991). Our study presents the first evidence of this species exhibiting migratory behaviour. We also recorded high numbers of *Stomoxys* flies (52% of est. 446852 *Muscidae*), also known as 'stable flies'. These are a hematophagous pest of livestock and in high enough concentrations can cause anaemia in cattle and reduce milk yields (Catangui *et al.*, 1997). Like many blood-feeding insects stable flies are also a vector for disease and carry the potential to spread Surra, brucellosis, equine infectious anaemia, African horse sickness, fowlpox and anthrax (Baldacchino *et al.*, 2013; Turell & Knudson, 1987). When combined with migratory behaviour, vectors of disease have an increased potential for spreading pathogens over a wider geographic range.

In conclusion, we found that insect migration occurring in the northeast of Cyprus is many magnitudes greater than that of birds and accounts for the greatest biomass of animal movement in the region. Furthermore, we have not only proven that the taxonomic diversity of insect migration is greater than was previously known in Cyprus (John *et al.*, 2019), but also put forward evidence of migratory behaviour in insect species not previously thought to undergo such movements. In light of their profound socioeconomic importance to humans and growing evidence that insect populations are on the decline (Dirzo *et al.*, 2014; Sánchez-Bayo & Wyckhuys, 2019), it is of great importance that more research should look into understanding annual cycles and anthropogenic impacts if we seek to effectively coexist with "the little things that run the world" (Satterfield *et al.*, 2020; Wilson, 1987).

## General Conclusion

It is perhaps ironic that we are discovering the levels of decline in migration almost simultaneously to uncovering its importance (Wilcove & Wikelski, 2008). Indeed, there is still much left unstudied and understudied in the field of migration. In this thesis I presented the findings from the first dedicated spring migration survey of northeast Cyprus. We discovered a new ladybird species for Cyprus (*H. quadripunctata*) and rediscovered a butterfly (*C. florella*) not seen on the island since 1968. The latter of these two species is a known migrant species and the former is a suspected migrant. Moreover, we presented evidence of migrational behaviour in two fly species (*D. platura* and *S. calcitrans*) not previously considered migratory, both of which are agricultural pests. As well as for crag martins (*P. rupestris*) and common kestrels (*F. tinnunculus*), we recorded high numbers of globally near threatened pallid harriers (*C. macrourus*). If our pallid harrier records (and resulting estimate) are accurate, northeast Cyprus would provisionally represent Europe's most important flyway for the species. On a broader scale, I contextualised bird migration traffic rates on Cyprus by comparing them with those simultaneously occurring over Israel. I found that due to a bottleneck effect, the Karpaz peninsular hosts proportionally higher rates of migration than over the Hula valley of Israel (per equivalent area), and furthermore propose that Cyprus's other northern peninsulars experience similar trends in the spring (and so too do the southern peninsulars in the autumn). Furthermore, it was encouraging that we observed very few signs of illegal bird trapping and killing at our study sites. Considering the findings I have presented in this thesis, Cyprus's Karpaz peninsular can irrefutably be considered a migration hotspot. Due to a lack of historical records, only surveys in subsequent years will reveal whether or not the abundance of migratory birds and insects it hosts are under threat.



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