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Monitoring Avian Migration with Dedicated Vertical-looking Radar

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signed: …………………………………………………..

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Summary

Bird migration is a long-studied phenomena. Geographical challenges faced on route coupled with changing climate and anthropogenic pressures has made migratory species one of the most threatened groups of birds. As migration is an integral part of their life cycle it is important that we understand these movements to make informed conservation decisions.

However quantifying migration itself is challenging, made even harder as approximately two thirds of migrants travel at night and at altitudes out of the range of the human eye. Ultimately assistance is needed from appropriate technology to view and record migration. In this thesis, I investigate the effective application of a new innovative vertical-looking radar (VLR) with nutating beam, uniquely dedicated to monitoring migratory birds.

Firstly, (chapter 1) I discuss our current understanding of migration and the development of radar systems for detecting animal movements. In chapter 2, I discuss the operation of the VLR and evaluate its capabilities; illustrating with case studies from data collected at the University of Exeter's Cornwall campus during the autumn of 2015 and spring 2016. Recorded bird echoes are compared and organised into classes to monitor the composition of bird migration. I find the radar to be an effective and non-biased tool for monitoring migration rates, direction and flight heights over varying time frames. Chapter 3 explores the seasonal variation and composition of avian migration as revealed by the radar. Here I find that the classes differ in their flight height, speed and migration rate, though have the same preferred direction of travel within each season. Additionally, there appears to be differences in these characteristics when comparing spring and autumn. Finally, I conclude (chapter 4) my findings and propose areas for refinement and further research.

Overall, the aim of this work is to review the suitability of this new radar system for monitoring bird movements and help contribute to our understanding of how wild birds migrate.

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Author's declaration

All chapters were written by Gregory V. Wills with comments provided by Dr. Stephen Votier. Additional comments were given on Chapter 2 provided by Dr. Baptiste Schmid (Swiss Ornithological Institute, Sempach) and chapter 3 by Professor Stuart Bearhop. All data collection was conducted by Gregory V. Wills.

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Publications

There are to be no publications from this thesis.

Chapter 1: General introduction

Animal migration is the movement of organisms between two or more habitats, frequently linked to the rotation of the seasons (Aidley, 1981; Nebel, 2010). Migration is found across a wide variety of diverse taxa, including: insects, fish, crustaceans, amphibians, reptiles, birds and mammals (Bowlin et al., 2010). It is an adaptive response to the seasonal or geographic variation of resources (Gauthreaux, Jr., 1982), produced by differences in the duration and intensity of solar energy. In turn, this often creates a short window of opportunity for migrants to take advantage of an abundance of food and favourable weather conditions (Nebel, 2010; Pulido, 2007). It is these changes in resources and optimal conditions that have likely lead to the evolution of bird migration, with selection acting favourably upon birds that can exploit them.

Migration in ornithology can be defined as a regular seasonal movement of birds between breeding and non-breeding grounds (Salewski & Bruderer, 2007). This leads to a two-way journey that has a cyclic outbound and return journey. This helps separate migration from dispersal that consists of a single movement and has no fixed direction and can change in response to environmental factors (Salewski & Bruderer, 2007). Researchers are gaining information on all levels of migration: from the physiological, behavioural and genetics of individuals to the ecology and evolution of populations expanding our understanding of avian movements on all scales (Dingle & Drake, 2007). These findings have wider implications for the conservation of all migrating taxa as well as our understanding of how selection has shaped the evolution of migration.

In this thesis, I review migration behaviour and discuss the history and development of radar and how it can be used to monitor and quantify avian movements. I discuss previous findings on the evolution of migration and how birds utilise conditions and alter their behaviour to travel more efficiently. Later I explain the operation of the new Birdscan MR1 system currently in operation at the University of Exeter and the role it has to play in the study of migration.

1.1 Why study Migration?

Humans have long been intrigued by migration even before they understood what it was. Migratory birds have cultural significance with their presence heralding the

changing seasons and there are biblical references to movements of common quail *Coturnix coturnix* in Egypt's Sinai Peninsula (Lunn, 2001). With such traditional interest and scientific curiosity; observers have hypothesised numerous explanations to disappearance and reappearance of avian diversity. Theories such as barn swallows *Hirundo rustica rustica* hibernating on lake floors (Bosewell, 1791) have been superseded by contemporary evidence of hemisphere spanning migratory flights, such as the 9 day, 11,680km non-stop journey of bar-tailed godwits *Limosa lapponica* (Gill et al., 2009), revealed by the deployment of satellite tags.

Migratory birds make up an estimated 19% (1,855) of all extant bird species (Birdlife International, 2008a,b). Moreover, migration can involve very large numbers of individuals. For example, an estimated 2.1 billion birds migrate from Europe to Africa each year (Hahn, Bauer & Liechti, 2009) and it is estimated that as many as 5 billion birds annually migrate south from North America to the Neotropics (Cox, 1985). Although these movements are still small in comparison to insect migration - upwards of 3 billion insects migrate over any given 1km stretch of countryside in southern England for a typical summer month (Chapman, Drake, & Reynolds, 2011; Chapman, Reynolds, & Smith, 2003). Studying where and how birds migrate is fundamental in answering behavioural and evolutionary questions on bird weather-dependence for movement as well as what systems drive rates of migration. On a grander scale knowing how birds interact during these movements and respond to environmental changes can give insight to the spread of pest species (Basili & Temple, 1999), disease (Muzaffar et al., 2010) and parasites (Waldenstrom et al., 2002) as well as the consumption and movement of nutrients in preparation to migratory flights (Sánchez, Green & Castellanos, 2006). The quantification of birds and recording of traffic rates may also be of use for the detection of flyways and habitats important for birds on stop-overs. However, migratory birds are under threat. For example, Intercontinental Palearctic–African migrant birds have declined by 40% between 1970-2000 (Kirby et al., 2008; Sandersonet al., 2006). Indeed, many migratory species are declining faster than many non-migratory species (Bairlein, 2016; Vickery et al., 2014). They encompass a sizable proportion of avian taxa and highlights the need to monitor and understand the ecology of migrating species for effective conservation.

1.2 Evolution of bird migration

There is a large amount of evidence to suggest that dispersal rate is dependent on local population size (Travis, Murrell & Dytham, 1999), which in turn can act as a driver for migration as competition for territories and food sources increase. In birds a positive relationship in population size and dispersal has been observed in marsh tit *Poecile palustris* (Nilsson, 1989), house finch *Haemorhous mexicanus* (Veit & Lewis., 1996) and red grouse *Lagopus lagopus scotica* (Watson et al., 1984).

The processes that have led to evolution of bird migration has been much disputed. Two theories have been used to explain the phenomena though they both strongly contradict each other: (1) the "northern-home-theory", where birds have shifted their non-breeding activities away from high latitude breeding grounds in response to favourable changes in climate (Bell, 2000; Salewski & Bruderer, 2007; Wallace, 1874), and (2) the "southern-home-theory", that alternatively proposes bird migration evolved in tropical species that started to breed at higher latitudes (Cox, 1968; Levey & Stiles, 1992; Rappole & Jones, 2002; Salewski & Bruderer, 2007). Despite the disagreement over the exact method that birds have taken to alter their range, consensus seems to be that birds have expanded their range due to climatic changes that provided an alternative environment to colonise. The changing seasons create variations in the suitability of habitat and by following the most favourable habitat create the movements we refer to as migration.

1.3 How migration is triggered

The mechanisms initiating migration are not completely understood. Caged birds show migratory restlessness during the spring and autumn, termed Zugunruhe showing that something was making birds want to start the migratory process (Rappole, 2013).

Spring departure in birds shows a clear association with photoperiod (day length) and the onset of migratory flights. Experimental manipulation of light levels during autumn showed that increased light periods caused Dark-eyed juncos *Junco hyemalis* and American crows *Corvus brachyrhynchos* to head north when

released, while controls, kept under natural light conditions, moved south (Dingle, 1996).

Hormones are also known to play a role in controlling migration and are thought to depend on gonadal condition in spring, but not in autumn. Corticosterone from the adrenal gland has been linked to alteration in migratory physiology of passerines (Holberton, Parrish & Wingfield, 1996). Autumn departure may also be initiated by day length though birds also start to feel added pressures form resources becoming scarce through intraspecific competition and environmental conditions becoming less favourable (Rappole, 2013).

1.4 Preparing for migration

Species that do not forage on migration need to store fuel in preparation for their journey in a process known as hyperphagia, triggered by the internal circannual rhythm - this process is also known as zugdispostion. Fat stores are the main source of energy in migration and produce up to 10 times more energy than carbohydrate or protein in equivalent mass (Jenni & Jenni-eiermann, 1998). If individuals are in poor condition they may resort to catabolizing muscle to release energy (Pennycuick, 1998).

To save weight and maximise migration efficiency some migrants reduce the size of internal organs used for feeding and reproduction (e.g., stomach, gut, liver, kidneys and genitals) returning to normal size once at their destination (Piersma & Gill, 1998). Organs such as the heart or pectoral muscle may increase ahead of migration to aid cost effective flight (Piersma, 1998; Ramenofsky & Wingfield, 2007).

1.5 Orientation and navigation

There have been a number of proposed mechanisms of how birds use environmental cues to orientate during migration. Migrants can use a range of senses to aid in navigation, notably: sight, olfaction, hearing and additional senses that can detect the earth's magnetic field and wind direction.

Migrating birds have been hypothesised to use the earth's magnetic field for orientation analogous to the use of a compass. This has been shown through numerous experimental studies with the use of Kramer cages (circular or octagonal cages that restrict the visual cues of birds. The positioning of the bird

is recorded by registration machines or inking the birds feet (Wiltschko & Wiltschko, 1972; Yeagley & Whitmore, 1947). Birds appear to sense wind direction, using the information to make departure decisions and how to orientate (Larkin, 1980). The mechanism that allows birds to do this still remains unclear.

The visual identification of landmarks can allow birds to learn routes whilst flying and memorise features to orientate in the future (Mettke-Hofmann & Gwinner, 2003). Birds can use the location of the sun as a means to orientation, such as the direction of sunset (Åkesson et al., 2001; Kramer, 1956; Moore & Philips, 1992). Similarly star patterns are also an important cue for migrants (Emlen, 1975; Cochran et al., 2004; Kramer, 1952; Mouritsen & Larsen, 2001). Birds have also been shown to use topographical features such as mountains and coastlines as leading lines and for wind compensation (Akesson, 1993; Bingman et al., 1982; Bruderer & Liechti, 1998).

It has been hypothesised that birds may use olfactory navigation; however this is under much review. Every site on Earth appears to have a unique odour produced by trace molecules in the air and water, which could provide information on location. Pacific salmon *Oncorhynchus spp.* have been shown to use these molecules to find their breeding destinations (Dittman & Quinn, 1996). It is not yet understood the extent at which birds use olfactory cues to navigate but there is evidence that some species or even groups do (Schmidt-koenig, 1987).

The use of hearing in navigation has been shown in rock pigeons *Columba livia* (Beason & Wiltschko, 2015) which could also be present in other birds. The theory is built upon the idea that geographical features such as the wind blowing through valleys and waves colliding with cliffs produce infrasound signatures (low-frequency sound that is lower in frequency than 20 Hz, the "normal" limit of human hearing) that could be specific to an area and therefore used by birds to find their way on migration (Hagstrum, 2000).

1.6 Migration theories and minimising energetic cost

In 1990 Thomas Alerstam and Åke Lindström coined the idea of "Optimal Migration" where by birds will cover the greatest distance for the least amount of energy. Individuals will strive to behave optimally even during changing conditions. They predicted optimal migration by building upon flight theory (FT) (Pennycuick, 1969) and optimal foraging theory (OFT) (Stephens & Krebs, 1986).

Flight theory predicts the energetic cost of bird flight from various physiological and metabolic components (Pennycuick, 1969; Tucker, 1973). It takes into account the induced power of the bird and the force needed to overcome drag caused by the birds body and wings (Pennycuick, 1969; Tucker, 1973). The theory has been shown to be accurate for budgerigars *Melopsittacus undulatus* (Tucker, 1968) and laughing gulls *Leucophaeus atricilla* flying in a wind tunnels but little has been done to test the theory for free flying birds (Tucker, 1972, 1973). The accuracy of the prediction also diminish with birds that have a mass less than 0.1kg and for birds 0.5kg and above (Tucker, 1973). Recommendations made by Tucker (1973) have helped to theoretical predictions become closer to that which is observed in birds and bats in the wild.

Optimal foraging theory helps to predict how an animal will behave whilst obtaining nutrition during fuelling stages of migration. Despite the goal of gaining energy from feeding it is still costly to actively search and capture food (Charnov, 1976; Schoener, 1971; Stephens & Krebs, 1986). Animals want to benefit from the highest returns of energy for they least cost when foraging (Charnov, 1976; Schoener, 1971; Stephens & Krebs, 1986). This is of particular interest to optimal migration theory when birds use stop over sites to refuel. This however could be difficult to incorporate for species that forage on the wing. Optimal foraging theory has come under scrutiny, with some suggesting that optimal strategies may not exist in nature and no studies encountered unequivocally support for the model (Pierce & Ollason, 1987).

By incorporating the role feeding to gain energy stores (OFT) and how this energy is used during flights (FT) it possible to start thinking about what the best migration strategies for birds may be and how weather conditions may be utilised. Fundamental to this approach is the relationship between: flight power and speed, flight range and fuel, total migration duration and flight speed, energy deposition from stop over and energy expenditure from flight and stop over site use (Alerstam, 2011; Alerstam, T & Lindström, 1990). Since the initial hypothesis of flight theory, the number of aspects that are analysed to find optimal migration has increased. This now includes: transition migration/breeding, routes and detours, daily timing, "fly-and-forage migration", wind selectivity, wind drift, phenotypic flexibility, arrival times and moult schedules (Alerstam, 2011).

One possible way to minimise metabolic costs of flight is to utilise favourable winds. This involves selecting the right wind direction, wind strength and altitude. The effective use of these conditions can reduce energy expenditure, reduce the time needed to refuel and in turn may reduce the risk of predation. Favourable wind conditions also vary in different regions (Erni, Liechti & Bruderer, 2005). Despite tailwinds being identified as advantageous for cost effective flight and therefore most favourable there is evidence to counter this idea, with no selectivity or reliance to wind being more beneficial (Thorup, 2006). For example in birds that use thermal soaring and for those that cannot efficiently store fuel during stop over time (Thorup, 2006).

1.7 Methods of studying Migration

Monitoring the vast scale of migration requires new protocols and equipment. There are a wide variety of techniques for studying migration, that vary in terms of cost, impacts upon the study organism and what data the observer wishes to obtain. The most applicable methods are discussed below.

1.7.1 Visual counts, migration watchpoints and bird observatories

The simplest way of monitoring migration is to count the number of birds seen at a given location (Davis, 1967; Russell et al., 1991). Unlike other census techniques such as mist netting, visual counts can be conducted in most conditions apart from when visibility is greatly reduced (Davis, 1967). Visual counts can record first arrival and departure dates, direction of travel and how long the birds are present for. Additionally, if there is a network of sites conducting visual counts such as bird observatories the temporal abundance of bird populations moving north and south during the spring and autumn respectively, can be documented. Over many years Temporal changes in the migration phenology of birds can be deduced (Browne & Aebischer, 2003).

There are also various projects and coordinated counts that are run by volunteers to monitor visible migration. For example the movement of migratory seabirds in SW England (SeaWatch SouthWest); the Batumi Raptor count in Georgia, Eastern Europe that works to monitor and conserve the 950,000+ birds of prey that migrate every autumn through the Batumi Bottleneck (Verhelst, Jansen, & Vansteelant, 2011). Hawk mountain in Pennsylvania, United states uses visual counts to monitor the health of migrating bird populations on the East coast of the

United States of America, since 1934 (Bednarz, et al., 1990). Similarly, observations of raptor, seabird and passerine migration are made at Europa Point on the Strait of Gibraltar.

There is a network of bird observatories in Europe and North America (North American Banding Council), which conducts long-term monitoring of bird populations and migration at prime migration points. Data is collected through daily census counts in a defined recording area and bird ringing/ banding is also typically run in parallel to this.

1.7.2 Bird ringing/banding

Bird ringing (or banding) can be traced back to 1899 when Hans Christian Mortensen ringed European starling (*Sturnus vulgaris*) nestlings with aluminium leg ring or band engraved with a return address and a unique serial number. If recovered in the future, information regarding location and date of where it was found could be relayed back to him (Nebel, 2010).

Birds are typically caught for ringing using fine mist nets and other traps. This technique is highly skilled and licenced. Ringing is perhaps the cheapest capture mark recapture technique but recovery rates of birds recovered elsewhere is typically low. However even an average recovery rate of small bird species of 1 in 300 still provides valuable insights into the routes that migrants take (Nebel, 2010).

There are several variations on bird ringing, which allow individual identification when seen in new areas and particularly at a distance, such as; colour ringing (Hockey, Leseberg, & Loewenthal, 2003), leg flags (Clark et al., 2005), wing tags (Wallace, parker & Temple, 1980; Kinkel, 1989) and neck collars (Johnson & Sibly, 1989). These techniques can in turn provide information on longevity; survival and dispersion that could help understand the health of populations and identify priority habitat and flight paths birds may use.

1.7.3 Biologging and Telemetry

Recent development of devices small enough to attach to animals with little impact on behaviour has revealed complete migratory movements in greater detail than ever before. These devices range from geolocators that take longitude and latitude reading from the position of the sun to more sophisticated (but larger

and more expensive) satellite tags that utilise satellites orbiting the earth to relay updates on the position of the tagged animal.

For example, geolocators shed light on the migratory routes of: Arctic tern *Sterna paradisaea* (Egevang et al., 2010), blackpoll warbler *Setophaga striata* (Deluca et al., 2015) and red-necked phalarope *Phalaropus lobatus* (Smith et al., 2014). The data from the phalarope geolocators revealed that birds did not fly directly south as expected but rather northwest to Greenland and followed the eastern seaboard of North America before passing over the Caribbean and Central America to winter off the coast of Peru and Ecuador. Typically the information can only be obtained by re-catching the bird and downloading the coordinates from the device (Costantini & Møller, 2013; Hahn et al., 2010).

Satellite transmitters (falling under the category telemetry) have been used to reveal the extreme south bound flight of the bar-tailed godwit that in 9 days complete an 11,680km non-stop oceanic journey to New Zealand (Gill et al., 2009). This discovery would have been virtually impossible with just ringing alone, and made more difficult by geolocators that would require retrieval. Radio telemetry has advanced considerably and continues to play a large role in the study of migration. The Motus Wildlife Tracking System (Motus, latin for 'movement') is an international collaborative research network that uses a coordinated automated radio telemetry array to track the movement and behaviour of small flying organisms, such as birds (Cochran, Montgomery & Graber, 1967) and large insects (Wikelski et al., 2010). This tracking system can locate biological targets affixed with digitally-encoded radio transmitters termed "nano-tags" that broadcast signals several times each minute. These signals are detected by multiple automated radio telemetry stations that can span Continents (Motus Wildlife Tracking System, 2017).

All devices attached to a bird need to adhere to a strict weight limit policy, approximately 3-6% of the bird's body mass (Kenward, 2001). Exceeding this limit could prove detrimental to the bird's health. Further consideration should be given to shape, attachment method (harness or glue) and positioning on the bird (Kenward, 2001) as all could impede activities the bird usually performs, such as hunting or preening (Kenwood, 2001).

1.7.4 Stable isotopes

All chemical elements exist in more than one form. These isotopes differ in mass due to their varying number of neutrons, despite having the same number of protons. The lighter form is generally the more common (Hobson & Wassenaar, 2008). This variation in the relative abundance of stable isotopes results from tiny mass differences that cause the isotopes to act differently in chemical reactions and physical processes (Zimmo, Blanco & Nebel, 2012). Stable isotopes vary geographically and can be identified by predictable isotopic signatures (West et al., 2006). By measuring the levels of stable isotopes of hydrogen, oxygen, carbon, nitrogen and sulphur present in a tissue sample of a bird, it is possible to match that to the location in where that sample was formed (Hobson, 1999). This works on the principle that "You Are What You Eat" as stable isotope ratios vary among food webs and are assimilated into an animal's tissue after ingestion (Hobson, 1999; Zimmo, Blanco & Nebel, 2012). There for it is possible to locate a birds breeding or wintering ground from isotope levels providing you know when the sample was produced (Hobson, 2005; Hobson & Wassenaar, 1997). This technique therefore illustrates origins of birds rather than explains migration routes or quantifies migration. Stable isotopes are also beneficial as every capture can be thought as a recapture, with the organisms origin already being held in the tissue sample.

1.7.5 Radar

RADAR (RAdio Detection And Ranging), here after "radar" technology has a long ornithological history although after a number of decades where the technique was not widely used, has experienced a renaissance in recent years and offers an exciting possibility to quantify, movements and gain information on altitude and direction of birds. This coupled with weather data can give vital insights to optimal migration strategies and flyway use.

1.8 The development of radar in ornithology

Birds were first detected using military radar systems inadvertently in 1941, revealing that birds were capable of reflecting radio waves that were strong enough for detection (Lack & Varley, 1945). In 1956, Ernst Sutter completed the first systematic study of nocturnal migration with radar using technology based at

Zurich airport (Sutter, 1957) and from the 1960s radar firmly established itself as a tool to monitor avian movements (Bruderer, 1997b).

Radars can be difficult to classify since individual radars can mix and match different types of technology eg Pulse, Doppler, Harmonic etc. For example, most weather surveillance radars are a form of pulsed-Doppler radar. The general radar types applicable to biological purposes include: tracking radars (following a single target) (Bruderer et al., 2010), surveillance radars (these include weather radars, harmonic radars, and track-while-scan radars which rotate to produce a track from multiple point locations) (Mein & Nebel, 2012), stationary beam radars (passively detecting animals passing through a non-moving beam). Vertical-Looking Radars mix the benefits of stationary beam and surveillance radars.

In the late 1940s radar meteorologists used pulse radar systems to investigate clear air echoes (Gage & Balsley, 1978). These systems looked vertically into the sky using a fixed beam and thus the first Vertical looking radars (VLRs) were born. In 1949 it was concluded that the most point targets that were detected by the radar were insects. In 1975 the first vertical-looking radar was used specifically for studying insects.

The next major development in entomological VLRs was the addition of beam nutation, a periodic variation in the inclination of the axis of a rotation (chapman, Reynolds & smith, 2003). This upgrade allowed the calculation of target speed and direction of travel and together with polarisation, the orientation, size and shape of the target can also be acquired (chapman, Reynolds & smith, 2003).

The Birdscan MR1 is similar to the VLR used by Chapman, Reynolds & Smith (2003) in its protocol using a nutating beam. However it differs by using a smaller antenna with considerably less gain, reducing its sensitivity to weak echoes. It therefore is the first dedicated VLR to the study of birds. Currently operating at the University of Exeter, it has the potential to further develop our understanding of how migrating birds utilise weather conditions and wind strata and what factors drive these moments. Additionally the coastal location of this radar could give insight into the arrival and departure of migrants when crossing geographical obstacles, such as the sea. Other similar radars (without beam nutation) have been used in the past to assess aerial landscapes for potential effects of wind

farms and tall buildings on migrating birds (Bruno Bruderer, 1997a, 1997b; Gauthreaux-Jr. & Belser, 2003).

1.9 Quantification

1.9.1 Continuous monitoring

The majority of birds undertake nocturnal migratory movements though there are birds that migrate during the day (Alerstam, 2009). There are a variety of theories that have been put forward to explain this apparent preference to migrate through the night as well we as explain alternative strategy of day time migration.

It has been suggested that birds migrate through the night as it allows uninterrupted feeding throughout the day, when birds can refuel for the subsequent flight. This has been supported by studies in feeding waders (Lank, 1989). Other possibilities include the avoidance of strong winds and reduced water loss, particular over arid regions (Heiko Schmaljohann, Liechti, & Bruderer, 2009), as lower night time temperatures reduce thermal occurrence, wind strength and water lost during respiration. It has been suggested that birds migrate at night to avoid predation, however there are birds of prey that do migrate at night (Stark & Liechti, 1993) and also evidence of birds of prey hunting by streetlight and moonlight (DeCandido & Allen, 2006; Roth & Lima, 2007). Alternatively birds may migrate at night due to visual cues used for orientation such as the direction of sunset and stars which are used to determine departure direction (Åkesson et al. , 2001).

Diurnal migration may be beneficial to birds that utilise thermals (an upward current of air) to soar, such as birds of prey, storks and cranes which can harness this energy to reduce their own self-propelled flight cost (Leshem, Yossi & Yom-Tov, 1996; Spaar, 1995). There are still diurnal migrants that carry out their journeys using self-powered flight at this time, with the reasons for this unclear. For some birds that use a strategy of "fly and forage" self-powered flight could be beneficial as they can combine the two activities of migration and refuelling but can only be accomplished during the day (Åkesson et al., 2012; Strandberg & Alerstam, 2007). Day time movements may also allow birds to locate and assess suitable staging sites and foraging flocks, which could reduce searching costs when settling post migratory flight (Beauchamp, 2011). Birds may also be able to

change their travel schedule if they travel through or settle in an area that is poor for foraging and refuelling (Alerstam, 2009).

Therefore it is crucial to have a method that can record movements at all hours during the day and night. Radar is advantageous since it can monitor bird migration continuously and systematically, potentially yielding information on the direction and orientation of both diurnal and nocturnal migrants depending on radar type (Richardson, 1978; Cooper et al., 1991). By recording all hours that migration can occur and at different points along the migratory route, inferences can also be made about different migratory strategies (i.e, time of day) and more consistently estimate the total number of birds moving at all hours of the day compared to moonwatching, acoustic monitoring and thermal imaging. Even when visibility is reduced due to mist or clouds radar systems can still detect targets (Cooper et al., 1991). However radar systems may have its signal completely absorbed or reflected by even light rain which in turn causes the radar to operate "blind" as targets behind this can no longer be detected and for this reason cannot function in these conditions.

High flying or distant birds can be detected by radar, and are often missed by visual observation (Cooper et al., 1991). In a study that quantified marbled murrelets *Brachyramphus marmoratus* using high frequency surveillance radar it was found that the system made 5-10 times more detections than human observations (Burger, 1997).

The technique is also a less intrusive method of tracking birds than the fitting of biologging devices (GPS tags, Geolocators, accelerometers etc.) which often require harnesses or leg attachment and are carried by the animal for long periods, in contrast birds only momentarily pass through the radar keeping subject interaction to a minimum (Bruderer, 2003). It has been shown that radar pulses does not affect the flight behaviour of migrating birds (Bruderer et al., 1999). However the technology is not appropriate for tracking individual birds over the entirety of their migration, an area where bio-logging devices are most effective.

The most successful alternative methods of quantifying bird migration include moonwatching, whereby the number of bird silhouettes that cross the face of the moon are counted. With additional light sources targets can be identified through

a telescope (Lowery, 1951). Alternatively the use of a ceilometer in conjunction with an image intensifier or light (again with a telescope for target identification) may also be effective (Gauthreaux & Livingston, 2006; Gauthreaux, 1969). It has however been shown that light beams can alter the flight behaviour of a bird, which is not desirable if focusing on this aspect of migration (Bruderer et al., 1999).

1.9.2 Migration traffic rates

Migration rates and densies vary throughout the migration period. There have been a range of observations and theories involving conditions encountered prior departure as well as conditions experienced on passage that may go some way to explaining this variability. Precipitation, temperature and food security lay the foundation for such theories and these unpredictable conditions may also affect different groups of migrants in different ways. As radar can be run continuously and if the operator knows the survey volume of the emitted cone it is possible to convert the returning echoes into biologically meaningful metric.

The standard metric of bird migration studies is known as the migration traffic rate (MTR) (Gauthreaux & Livingston, 2006). It is crucial to determine the sensed volume of the emitted radar beam as the absolute sensed volume of a radar beam varies with target radar cross section. In its simplistic form, large targets are more easily detected at the outer reaches of the beam and at higher altitude than smaller ones. The absolute sensed volume can be calculated from the maximum detection range for a given radar cross section and the antenna diagram. The misuse of radar by its operators can lead to the wrong quantification of echoes as target size needs to be taken into account within the cone area and weighted accordingly (Schmaljohann et al., 2008).

Using a known sensed volume migration traffic rates (MTRs) of the detection area can be calculated. The intended outcome is to match an echo with an MTR factor and standardise the weight of the echo per 1km per hour. This must be done for all target classifications with the assumption that all objects within the class are the same size, though size between classes (e.g. passerine, swift, wader) can differ. Using the class and the distance interval you assign to each eco an MTR factor, which is the weight to the echo e.g. how much the echo contributes to the MTR. For example 1 echo in the beam at 200m would have an MTR of 5 (as

calculated per km). The weighted echoes are divided by the desired time frame, typically 1 hour to give rate of migration. The sum of all echoes at each elevation within your chosen survey height will equal the MTR. By dividing the migration traffic rate by ground speed it is possible to calculate bird density per km^3 (Gauthreaux & Livingston, 2006; Schmaljohann et al., 2008).

Migration traffic rates can also be calculated using the moonwatching or ceilometer techniques (Kenneth et al., 1975), however they're may be issues detecting targets at distance, between observer differences and are typically very labour intensive as requires manual operation (Liechti, Bruderer, & Paproth, 1995).

Migratory birds can be split into two sub groups, those that are obligate (calendar) migrants whose migratory patterns remain similar year on year operating within fairly strict time frames and destinations and facultative migrants that can settle in the same or widely different areas that are not constricted by timing (Strong et al, 2015). The latter are usually driven by the weather or resource shortages which can lead to a larger number of birds than normal occurring outside of their usual range, in events known as "eruptions"(Strong et al., 2015). Facultative migrants therefore can have sporadic seasonal movements.

The most common irruptions are related to food shortages. For example northern bullfinch *Pyrrhula pyrrhula* dispersion outside of its normal range has been liked back to rowan berry failures (Fox et al., 2009). Pine siskin *Carduelis pinus* too have shown to erupt and expand in to areas when seed crops are masting (Strong et al., 2015). It should perhaps be considered that ultimately these avian movements are affected by prolonged weather conditions during seed and berry development. Pine siskins *Carduelis pinus* in North America moving from North-South and West-East in response to Climate variability (Strong et al., 2015). Climatic Dipoles, defined as climatic anomalies of opposite polarity appearing at two different locations at the same time (Nigam & Baxter, 2015) produce contrasting favourable and unfavourable conditions creating a push-pull effect of bird movement (Strong et al., 2015). An abundance of food may also lead to increased survival of birds or improved breeding success which in turn could go some way to explaining observed fluctuations of migrant population size.

Birds can be halted on departure or during migration that could also go some way to explaining the fluctuating nature of bird passage. Birds will wait for favourable tailwinds to depart on migratory flights (Åkesson & Hedenström, 2000). An example of a sudden cold snap in Central Europe during 1931 caused mortality among a selection of hirundines with many unable to travel from being under provisioned (Alexander, 1933). Other weather conditions such as precipitation can also affect birds during migration with many choosing to avoid flight in such adverse weather (Richardson, 1978). Rain has also been shown to reduce migration densities (Erni et al., 2002) with precipitation potentially weakening birds in flight forcing them to ground (Newton, 2007).

Birds using different routes during north and southward migration could explain differences in migration traffic between spring and autumn movements. For example bar tailed godwits *Limos lapponica baueri* have an innate migration following the East Asian coast on northern journeys but fly directly over the pacific on southbound migration (Gill et al., 2009). Another example of this loop migration this time over land has been observed in Eleonora's falcon *Falco eleonorae* that fly south through Central Africa in the autumn and north along the east African coast in spring (Mellone et al., 2013). Facultative migrants are flexible in their movements and choice of direction. There are also examples of calendar migrants altering their migrations routes, particularly to avoid adverse weather conditions which could force birds into unfavourable environments (e.g. long oceanic crossings) (Mellone et al., 2011).

Automated radar systems could lend themselves particularly well to recording fluctuations in migration mentioned above, due to their ability to operate continuously without a user, so therefore can offer more complete coverage of both migratory and non-migratory periods . When analysed alongside weather and geographical data it may go some way to explain fluctuations in MTR.

1.10 Flight behaviour

1.10.1 Orientation and direction

Whilst travelling to their chosen location in cross winds, birds may encounter orientation problems whereby the birds track (speed and direction relative to ground) is no longer the matching its heading (speed and direction relative to air), this is known as drift (Richardson, 1990). The degree to which birds are affected

by drift is reported to vary depending on the study (Green & Alerstam, 2002). Birds use 7 out of 8 possible orientation stratagies proposed in response to wind flow (Chapman et al., 2011):

(i)   Passive downstream transport is used when animals cannot or do not use self-powered flight (Chapman, Klaassen, et al., 2011). This only seems to occur when birds are disorientated in poor weather conditions with low levels of visibility, however birds will avoid flights in such circumstances preferring to remain grounded (Chapman et al., 2011; Lack, 1944).

(ii) Active downstream orientation where by the organism flies with the wind. The strategy is used by migratory birds when wanting to leave difficult environments and conditions e.g. deserts using "escape flights" (Chapman et al., 2011; Richardson, 1991).

(iii) Full drift can be identified when a bird maintains a constant heading towards to its target goal destination but experience displacement by wind flow that does not match its intended direction (Chapman et al., 2011; Green & Alerstam, 2002). This arises when animals cannot detect the flow direction. At high altitudes nocturnal migrating passerines seem to fall into this category (Liechti, 2006). Full drift may in some cases be optimal. This includes when cross winds counteract themselves along a migration route (Stoddard et al., 1983) or during early stages of migration where compensation can be postponed as drift in the opposite direction may be experienced later in the route (Klaassen et al., 2011). Another scenario would be when destination goals of young birds will only be learned after first migration (Thorup et al., 2003).

(iv) Partial compensation occurs when the bird alters its heading to fly into crosswind so that its track is closer to its preferred direction of travel and ultimately destination (Chapman et al., 2011; Green & Alerstam, 2002; Richardson, 1990). This response is perhaps the most common but the extent of the compensation varies greatly (Chapman et al., 2011; Green et al., 2004; Klaassen et al., 2011; Liechti, 2006; Thorup et al., 2003). It is likely that birds use visual cues from ground features to assess wind strength (Chapman et al., 2011); Klaassen, et al.,

2011), which could go some way to explain why high altitude, nocturnal migrants that cross the sea (Alerstam, 1976; Liechti, 2006), appear to compensate less than birds that migrate during the day and at lower altitudes (Klaassen et al., 2011; Thorup et al., 2003).

(v)   Complete compensation occurs when a bird alters its heading into the cross flow so much that its tract matches its preferred direction of travel (Chapman et al., 2011; Klaassen, et al., 2011; Green & Alerstam, 2002). This would be the optimal method of travel for birds but requires the ability to sense wind flow and an understanding of how it would affect your track (Chapman et al., 2011; Klaassen, et al., 2011). Complete compensation is rare in birds and has only been shown in migration over short distances in specific areas, at low altitudes during the night (Bingman et al., 1982) and during the day over land (Alerstam, 1976). The most notable case of complete compensation in birds was show in common swift migration (Karlsson et al., 2010). The majority of cases of animal complete compensation is observed in insects travelling short distances that are non-migratory movements (Riley et al., 2003; Riley et al, 1999).

(vi)   Overcompensation occurs when a bird alters its heading into the flow so much that its track falls short of its preferred goal direction. The response has been best documented in diurnal migrants at low altitudes, whereby they combine with nocturnal flights that are subject to drift (Alerstam, 1979).

(vii)   The final strategy used by birds is upstream orientation whereby birds fly head on into the flow (Chapman et al., 2011; Klaassen, et al., 2011). This strategy is not commonly seen in birds but has been observed in roosting swifts which position themselves upwind, which is believed to help the birds stay within their home range (Backman & Alerstam, 2001). I have yet to find an example of this strategy for migration, with most examples being in other taxa for foraging and mate searching flights.

Whilst birds show both drift and compensation strategies, insects for comparison expose themselves to much higher degrees of drift when trying to obtain the assistance of strong wind (Chapman et al., 2015). In turn insects reach higher

ground speeds (speed relative to ground) in comparison to birds but are less precise in their arrival destination (Chapman et al., 2015).

It needs to be considered that if a bird moves in the same direction as the wind it may not necessarily be drift. Instead birds may be selecting to depart along preferred tracks in changed wind conditions (Alerstam, 1978). This phenomena has been termed pseudodrift (Evans, 1966). In order to correctly assess the extent of pseudodrift the relative density of migration along different track directions during migratory flights and the association between these movements must be known (Alerstam, 1978). However in most cases accurate information on these criteria are not recorded.

Radar has been used to investigate how migrants react and orientate to a range of geographical and weather factors (Bruderer, 1997b). Orientation and flight direction can be recorded with more sophisticated tracking radar, allowing observers to investigate drift versus compensation scenarios as well as departure decisions and how migrants orientate to the coast. When passerines are preparing to depart land to start migratory flights they do so on days with tailwinds (wind blowing in the same direction as travel). There is a significant correlation between departure direction and wind, highlighting that birds take current wind conditions into consideration (Åkesson & Hedenström, 2000). Birds will leave at a later date regardless of wind direction if they do not encounter favourable winds (Åkesson & Hedenström, 2000).

Tracking radar was used to investigate wind compensation of common crane *Grus grus* over both sea and land. It was found that they compensated completely for drift over land, whereas they only partially compensate over the sea (Alerstam, 1975). Further studies have also shown migrant birds are able to compensate for wind drift but only under certain conditions (Evans, 1966). Arctic waders have been shown to compensate for drift, which is in line with adaptive drift theory that predicts initial drift during migratory flight followed by compensation in the latter stages where birds are reaching their destination (Green et al., 2004). This conflicts with what has been found in other radar tracking studies, where birds were found to not compensate for drift at all (Lack, 1958, 1959).

The Tracking radar system has been used to observer wood pigeon orientation behaviour where by birds were tracked flying parallel to the coast (Alerstam &

Ulfstrand, 1973). Birds were shown to be more dependent on tail winds for sea crossings. In contrast swifts consistently orientate into a head wind (Backman & Alerstam, 2001; Karlsson et al., 2010). With the developments from Swiss-birdradar and the production of the BirdScan MR1 it offers a less labour intensive way of gathering flight direction which can be used to answer various orientation questions.

1.10.2 Speed

Using radar it is possible to record ground speed (currently tracking systems are best but also possible with birdscan MR1) which often can give insights to two what the observed target might be and what the target is doing.

Radars are often used to see how targets respond in varying weather conditions. It has been shown than migratory birds increase their airspeed (the speed of the bird relative to the air that it is moving in) in headwinds (wind travelling in the opposite direction of travel) and reduce speed in tailwinds (Bloch & Bruderer, 1982). In contrast other research has shown passerines to be more reliant on self-powered flight during migration periods to travel in their chosen direction and less selective of wind conditions at times without tailwinds (Alerstam et al., 2011).

Tracking radar can show differences in flight speeds in certain situations, for example common cranes *Grus grus* fly at 67 km/h over the sea but reduced their speed to 44km/h (Alerstam, 1975) whilst nocturnally migrating birds in coastal areas have a higher average flight speed over islands than when leaving the mainland (Bruno Bruderer & Liechti, 1998), both examples showing different behavioural responses to changes in geographical barriers. Tracking radar systems have also uncovered that common wood pigeons *Columba palumbus* use tail winds to maximise their ground speed to greater than 80km/h (Alerstam & Ulfstrand, 1973) and Steppe Buzzards *Buteo buteo vulpinus* have also been shown to use tail winds to increase their average cross country speed (Spaar, 1995). Radar is not just limited to migration studies but has also been used to show flight behaviour differences of marbled murrelets *Brachyramphus marmoratus* departing and returning to the colony. Birds leaving the forest flew faster with a mean speed 119km/h compared to 74km/h to arriving (Burger, 1997). This was also slower than birds that were simply circling the colony at 81 km/h (Burger, 1997). This was likely linked to topography, with birds entering the

colony dropping down between tall trees, whereas birds leaving the site flew over a low lying valley so had a direct unimpeded flight. The song flight speeds of skylarks *Alauda arvensis* have been measured for comparison to both predicted speeds and actual migration flight speeds (Hedenstrom & Alerstam, 1996).

1.10.3 Altitude

Tracking and stationary radar systems are commonly used to record the flight altitude of birds (Backman & Alerstam, 2001; Liechti & Scaller, 1999; Schmaljohann et al., 2009; Spaar, 1995). The altitude at which a bird flies has been shown to be an important factor in determining its travelling efficiency (Liechti, 2006; Schmaljohann, Liechti, & Bruderer, 2009). Radars studies inform us that most bird migration takes place below 1km but in some situations can be between 5–9km (Liechti & Scaller, 1999).

Birds fly at altitudes that minimise the cost of transport and when migration occurs at altitudes much higher than usual, a significant correlation exists between the altitude of densest migration and altitude of most favourable wind (Gauthreaux, Jr., 1991). It has been shown that birds select for wind strata with favourable tail winds and that true airspeed increases with increased altitude and decreased air density (Bruderer et al., 1989; Kranstauber et al., 2015; Schmaljohann & Liechti, 2009). Insects too have been shown to travel at altitudes that match with the fastest air streams (Alerstam et al., 2011).

Selection of flight altitude could also be to avoid turbulence which is supressed in thermal stratification (Rennie, 2013). Altitude selection could also vary in response to climatic conditions. Tracking radar in the Sahara Desert has shown the majority of passerines fly below 1,000 m above ground, which is optimal for gaining tailwind assistance and minimizing energetic costs of flight during travel but optimal for minimising water loss (Schmaljohann et al., 2009). Therefore in warm conditions it could be more beneficial to fly at higher altitudes where the air is cooler and more humid. By optimising altitude it would be possible to shorten travel time depending upon the presence of strong and predictable winds. Higher altitudes tend to have stronger winds but are less predictable (Kranstauber et al., 2015).

Radar can be used to investigate altitudinal behaviour questions such as seen in Bäckman and Alerstam's common swift study. Birds did not select for altitude

and speed regulation with a potential explanation being that head wind orientation was sufficient enough to keep nocturnal displacement from their home range with in the territory (Backman & Alerstam, 2001). Other radar studies have looked at how the altitude of birds very over time. For example steppe buzzard *Buteo buteo vulpinus* flight height was dependant on time of day, with birds utilising thermals at the warmer times of day (Spaar, 1995). The tracking radar also allowed the thermal climbing rates of birds to be recorded, with these rates being found to be the decisive trait when it came to explaining the chosen flight behaviour of the birds (Spaar, 1995).

1.10.4 Wing-beat characteristics

The radiowave energy reflected by a bird and subsequently the echo recorded by the radar closely resembles its wing beat pattern (Schmaljohann et al., 2008). This has been further supported by video footage showing echo signatures closely reflecting wingbeat patterns (Bruderer & Popa-Lisseanu, 2005). The ability to record frequency ranges and wing-beat patterns allow comparison between variation of species, taxonomic groups and types of flight (Bruderer et al., 2010). Wing-beat frequency has been described as a function of body mass, wingspan, wing area, gravity and air density (the power fraction has to also be considered for birds with passerine type flight) (Pennycuick, 2001). These parameters can help aid in target discrimination and identification.

Radar technology has its limitations. It is unable to identify individual species due to the large intraspecific echo variation, it can however identify groups of birds with reasonable accuracy by the way they fly (wader type, passerine, swift type etc) (Bruderer et al., 2010). There can be issues when detecting and successfully classifying flocks of birds as they produce an insufficient echo and birds within flocks could cause a layering effect of said echoes (Schmaljohann et al., 2008). Radars are also limited to detected within a set range and anything above and below these heights will not be detected (Russell et al., 2011).

1.11 General introduction summary and thesis topic

As our desire to understand bird migration in all its facets grows so does our requirement for suitable technologies. Radar has been used for both migration quantification and also understanding the movement behaviour of birds. It is now

possibly to use the BirdscanMR1 to answer behavioural questions of bird movements and quantify them to a much finer resolution than ever before.

In his thesis I investigate the proof of concept of the BirdscanMR1 vertical-looking radar system investigating both its capability and suitability as a tool to monitor bird migration with goal of producing a methods paper for the technology (chapter 2). Using the classification feature I investigate if these classes alter in their preferences of flight height and direction, as well as their flight speed and rates of migration (chapter 3).

The investigation will determine how effective this remote technology can be at: detecting differences in target characteristics, how useful this technology can be in the future at both monitoring migration and understanding its composition and suggesting avenues for development and exploration in the future.

Chapter 2: New developments in vertical-looking radar to study bird migration

Abstract

Bird migrations occurs on an intercontinental scale. An estimated 2.1 billion birds move between Europe and Africa annually but recording this migration can be extremely difficult. Much of this migration is nocturnal and takes place at high altitudes making it difficult to quantify migration by observation and understand fully the flight characteristics of migratory birds.

Here we describe a new application of vertical-looking radar technology dedicated to ornithology. The novel system is the first dedicated bird radar to utilise a nutating beam to continuously record: height, speed, direction, size and wingbeat frequency of targets. This system can then automatically record and classify the flight types of targets to a relatively low taxonomic level, in detail without the need for constant operator supervision. We discuss what the user can achieve with the system's features as well as its limitations and suggest how this can be applied to the study of avian movements.

Introduction

Migratory birds make up an estimated 19% (1,855) of all extant bird species (Birdlife International, 2008a,b). An estimated 2.1 billion birds migrate from Europe to Africa each year (Hahn, Bauer & Liechti, 2009) and it is estimated that as many as 5 billion birds annually migrate south from North America to the Neotropics (Cox, 1985). Studying where and how birds migrate is fundamental in answering behavioural questions on bird weather-dependence for movement as well as what systems drive rates of migration. On a larger scale knowing how birds interact from these movements can give insight to the spread of disease (Muzaffar et al., 2010) and parasites (Waldenstrom et al., 2002) as well as the consumption and movement of nutrients in preparation to migratory flights (Sánchez, Green & Castellanos, 2006). The quantification of birds and recording of traffic rates may also be of use for the detection of flyways and habitats important for birds during stopovers. However, migratory birds are under threat. For instance, Intercontinental Palearctic–African migrant birds have declined by 40% between 1970-2000 (Kirby et al., 2008; Sandersonet al.,

2006). Indeed, many migratory species are declining faster than many non-migratory species (Bairlein, 2016; Vickery et al., 2014). They encompass a sizable proportion of avian taxa and highlights the need to monitor and understand the ecology of migrating species for effective conservation.

Many birds migrate through the night (Alerstam, 2009) in order to use celestial cues for navigation (Åkesson et al., 2001; Kramer, 1956), as well as to take advantage of the cooler air temperatures to reduce water loss (Schmaljohann et al., 2009), avoid turbulence (Rennie, 2013) and keep the day free for feeding and depositing fat that fuels migratory flights ((Lank, 1989; Schaub et al, 2001). These migrants also travel at altitudes up to several kilometres (Able, 1970) when searching for favourable winds to travel efficiently (Liechti, 2006; Schmaljohann et al., 2009). Diurnal migration may be beneficial to birds that utilise thermals to soar, such as birds of prey, storks and cranes. Thermals (an upward current of warm air) form during the day, birds can thus harness this energy to reduce their own self-propelled flight cost (Leshem, Yossi & Yom-Tov, 1996; Spaar, 1995). There are still diurnal migrants that carry out their journeys using self-powered at this time. By flying during the day, it is easier for birds to keep in sight of other individuals to learn migration routes through social interaction (Mueller et al., 2013). For some birds that use a strategy of "fly and forage" self-powered flight could be beneficial as they can combine the two activities of migration and refuelling but can only be accomplished during the day (Åkesson et al., 2012; Strandberg & Alerstam, 2007). Day time movements may also allow birds to locate and assess suitable staging sites and foraging flocks which could reduce the cost of search and settling post migratory flight (Beauchamp, 2011). Birds may also be able to change their travel schedule if they travel through or settle in an area that is poor for foraging and refuelling (Alerstam, 2009).

Avian migration has been studied using a wide variety of techniques. Biologging has been at the heart of a revolution in studying animal movement (Cooke, 2008; Rutz & Hays, 2009) and include GPS tags, geolocators, accelerometers. However these devices are attached to animals, with the potential for deleterious impacts or behavioural alterations, and with limits on the size of species that can be studied. The alternative is recording behavioural by human observations, such as moon watching, which is hugely labour intensive. Animal

logging is limited to recording individual or small population movement behaviour, which makes it very difficult to generalise a species movement behaviour. Radar (Radio Detection And Ranging) can be used to investigate mass of movements. The use of radar has been shown to have no effect on flight behaviour of birds and offers a non-invasive method of remote sensing that can be used to gather 3D temporal, spatial and directional data on study organisms.

Radars generate radio waves that are emitted by a transmitter and if these signals come into contact with an object, some of the energy will be reflected back in the form of an echo. This echo is then detected by a receiver and a target is identified by the radar from the recorded wingbeat frequency and pattern. Development of radar technology was driven by its need for use in the Second World War, where birds were inadvertently detected for the first time on military radar systems in 1941 (Lack & Varley, 1945). It was discovered that birds were capable of reflecting radio waves that were strong enough for detection (Lack & Varley, 1945) and following that in 1956, Ernst Sutter completed the first systematic study of nocturnal migration with radar using technology based at Zurich airport (Sutter, 1957). From the 1960s radar firmly established itself as a tool to monitor avian movements (Bruderer, 1997b) due to the technique not being limited to daylight hours or desirable celestial. The five most commonly used radar systems are: Pulse (that determines the distance to the target by using the time between emitting and receiving the radio energy), Doppler (a form of pulse radar but analyses the shift in wavelength within the pulse or "Doppler shift" caused by the target moving relative to the radar), continuous wave (also using the Doppler shits but using separate transmitters and receivers), harmonic (that detect individual animals that wear a tag that can be tracked) and weather radars. (Mein & Nebel, 2012). Radars can come in both Tracking (Bruderer et al., 2010) where targets can be followed and fixed beam forms (Gauthreaux & Livingston, 2006), which allow survey a restricted patch of sky to be surveyed with constant effort. Both allow the user to collect very different types of data. Fixed beams are used for the quantification of birds but provide little information on flight behaviour with only vertical distributions recorded with accuracy, whereas only rough approximation of speed and direction are given. Track while scan radars come in 2D (range and

azimuth) and 3D (elevation information with range and azimuth) forms and do not quantify migration easily their primary function is to record information on flight behaviour. Both tracking radars accurately record flight direction, with 2D tracking radars able to roughly give speed but not the height of an object. 3D tracking radars can provide information on velocity and altitude as well as direction but requires manual operation. Vertical-looking radars (VLRs) are a hybrid system that utilises the benefits of fixed-beam and surveillance radars that focuses on a fixed section of air space and have been used previously in entomology. A device of particular interest was the first VLR to operate with a nutating beam, whereby the beam wobbles on a tilted axis allowing the calculation of target speed and direction of travel. This information was not formerly obtainable with a standard fixed beam radar. Birdscan MR1 is fully automated VLR and can record altitude, direction of flight, speed and quantify migrants making this system unique. Here we outline the first ornithological vertical-looking radar with a nutating beam, built by Swiss Birdradar Solution AG. First, we describe the hardware and the method of beam nutation. Second we explore technical details relating to the sensitivity time control, survey volume of the radar beam and methods for monitoring migration traffic rates. Third we discuss the identification algorithm and the features that are used for this. Forth, we look at the interface of the radar. Finally, using data obtained from the first year of the radars deployment at The University of Exeter, Cornwall Campus located at the base of the Lizard Peninsula (50°10'15.2"N 5°07'39.9"W), we provide four examples of applications of the device: (1) temporal activity, (2) directional, (3) target identification and (4) flight height. In addition to this we also discuss some of the results and future prospects of how this technology can be best utilised.

Birdscan MR1 Specifications

The BirdScan MR1 radar (Swiss Bird Radar Solutions) uses technology that for the first time has been dedicated to the study of bird migration. The quantification of animal movement aloft requires precise knowledge on the detection probabilities of the objects and technical understanding of the radar system's features and settings. Here we describe the main characteristics and their contribution to the detection probabilities. We then describe the procedure for a proper quantification of the aerial animal movements.

Figure 1. The Birdscan MR1 system on the roof of the Environment and sustainability Institute building at the University of Exeter. The device is compact and can be sited in any location provided its line of sight is not blocked by other structures or vegetation. Photograph: Greg Wills, University of Exeter.

Hardware

The Birdscan MR1 VLR is compact system [90kg, Fig. 1] and consists of a marine X-band pulse-radar (9.4 GHz; Bridgemaster©). Antenna type: a conical, corrugated Horn Antenna with dimensions approximately 30 cm in length and 20 cm diameter. The half-power width of non-nutating beam and nutating survey volume for both settings is "conical". The maximal range and width is dependent on several hard-ware parameters e.g. transmitted power, antenna shape and size, detection threshold and sensitivity time control (STC), together with the size of the illuminated animal. Transmitter power at 25 kW. The antenna (Antenna gain = 20dBi) projects electromagnetic waves vertically from a nutated vertical axis that can rotate (rotation frequency: 0.8 Hz) . BirdScan's vertical antenna reduces detection of ground clutter (e.g. buildings, trees, sea waves) yet still retains coverage at low altitudes. In addition, the system also comprises of a server that uses a digitizer, which converts the analogue input signals into digital data.

Display

The VLR consists of its own 19" Racksystem (System: Dell PowerEdge R220 Rack Server, CPU: Intel Xeon E-1270, 3.3GHz, 8M Cache, Memory: 16GB) that can be accessed via the external network connector (category 3), network cable inside the locker or the use of a remote PC programme for wireless access. Once accessed the visual display of the radar should appear [Fig. 2] with a live view window showing what has passed through the radar from current time to 5 minutes previous. Other features visible include a control box for the A scope and sensitivity time control (STC) settings and button to access the data of detected echoes. Once set up, continuous connection to the radar is not required as measurements are taken automatically. Raw data is retained and high quality offline-analytics/ non real time post processing is possible.
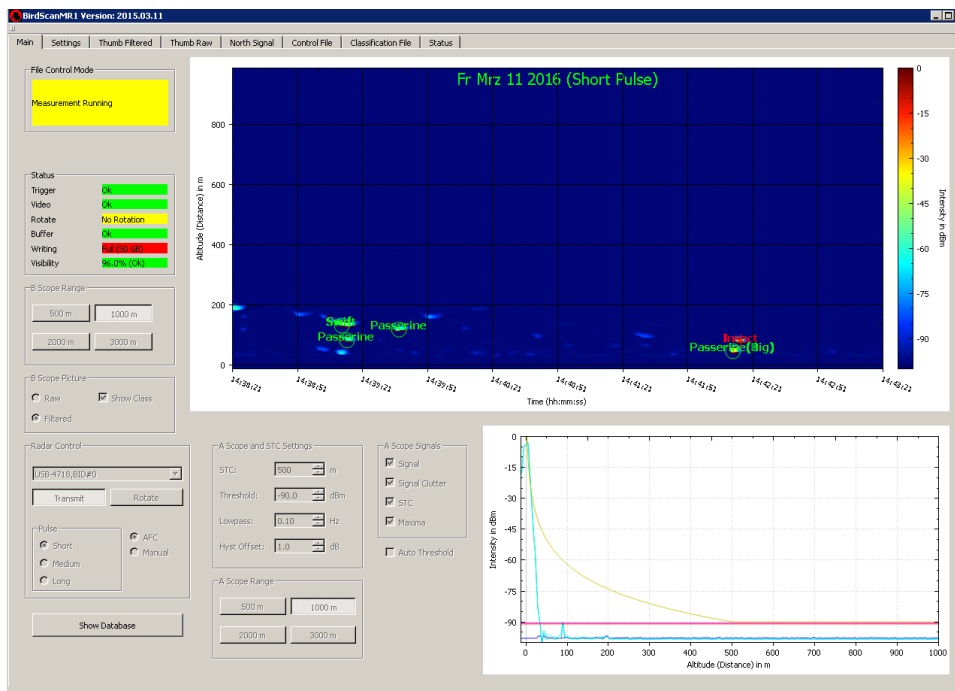
Figure 2. Main Birdscan MR1 display showing the live view window with echoes (Temporal variation of energy reflected by the target) as they are being detected and classified in real time. Also shown is the control panel and scope and STC settings.

Pulse length and detection ranges

The electromagnetic waves are generated by the transmit unit in three pulse modes: short pulse (50 ns, pulse repetition frequency (PRF) 1800 Hz), medium

pulse (250 ns, PRF 1800 Hz), and long pulse (750 ns, PRF 785 Hz). The pulse length determines the range resolution of the radar, defined by the distance covered by half the of pulse length. The range resolution describes the minimal distance between two objects required to record two separated echoes. Therefore, the minimal distance between object is of 7.5 m for short pulse, 37.5 m for medium pulse, and 112.5 m for long pulse. Whilst transmitting the system cannot record echoes so is temporarily blind. Therefore, the pulse length and pulse repetition frequency determine the minimal measuring range (blind range), i.e. the minimum distance before which an object can be detected. For example, the blind ranges extend to 50 m for short pulse but increase to 150m when using long pulse mode. If a bird flies through a range which is blind to the radar, the bird will not be detected.

If these pulses meet a passing target the antenna will receive the back-scattered signal. The time it takes for the pulse to return depends on the distance of the target from the radar. The received signal is converted into a digital signal by the digitizer and processed by specialist software. The software extracts the relevant information from the data. Each object generates its own echo, which can be analysed and classified.

The pulse length also influences the maximal detection ranges. A small passerine (e.g. chaffinches) can be detected up to ca. 800 m agl using short-pulse, and to 1200 m agl using long pulse. The detection ranges indicate the maximal distance of detection (maximal height for a vertical looking antenna), and the "width of the beam" for a given height (horizontal range for a vertical looking antenna). In order to make the echoes biologically meaningful it is crucial to understand and estimate the detection ranges of a system with best accuracy, which is essential for a proper quantification of animal movements by radar.

The detection ranges of targets depend on both object size and several characteristics of the radar system. We can estimate the detection ranges for a given object size, knowing the antenna diagram (as provided by the antenna manufacturer), the power of the electromagnetic waves sent (25 kW), the antenna gain (20 dBi), and pulse length. In its simplistic form, large targets are more easily detected at the outer reaches of the beam and at higher altitude

than smaller ones [Fig. 3]. The mean surveyed volume is the weighted mean of the radar cross-sections detected.

Object size

The object size is estimated by the radar cross section (RCS). Radar cross-sections (A measure of target size as seen by a particular radar that has the dimension of an area (cm^2). The RCS is linked to echo intensity and corrected for the height at which the target passes through the beam. RCS also assumes that the object has a spherical shape and is uniform in surface. The impression of a bird differs when seen from underneath, side or head on and when seen by a radar the shape detected would hugely vary and alter the radar cross section (Mirkovic et al., 2016). A vertical looking antenna as used by BirdScan reduces the number of possible ways a bird can be detected by simply detecting birds that only fly overhead. However, RCS can also change with its position in the horizontal plane in the beam. The RCS is maximal for objects flying in the middle of the beam and decreases with increasing distance from the centre of the beam. This means a large bird (e.g. kite) flying in the periphery of the beam could show a similar RCS as a small bird (e.g. finch) that flies through the centre of the beam [Fig. 3]. How an object scatters the returned radio wave energy can affect the way a target is discriminated and classified. Mie scattering (or resonant scattering) is caused by pollen, dust, and water droplets in the lower atmosphere. It occurs when the particles causing the scattering are larger than the radiation contacting them. If Mie scattering is occurring, you will not obtain the correct radar reflectivity value and consequently radar cross section. Therefore discrimination between more than one class of birds or birds and insects could prove problematic. To avoid these issues it is possible to bypass the problematic lower levels of atmosphere where larger particles are present (i.e start detecting >50m above the radar) or to set a detection threshold where by only echo values that are deemed strong enough are classified.
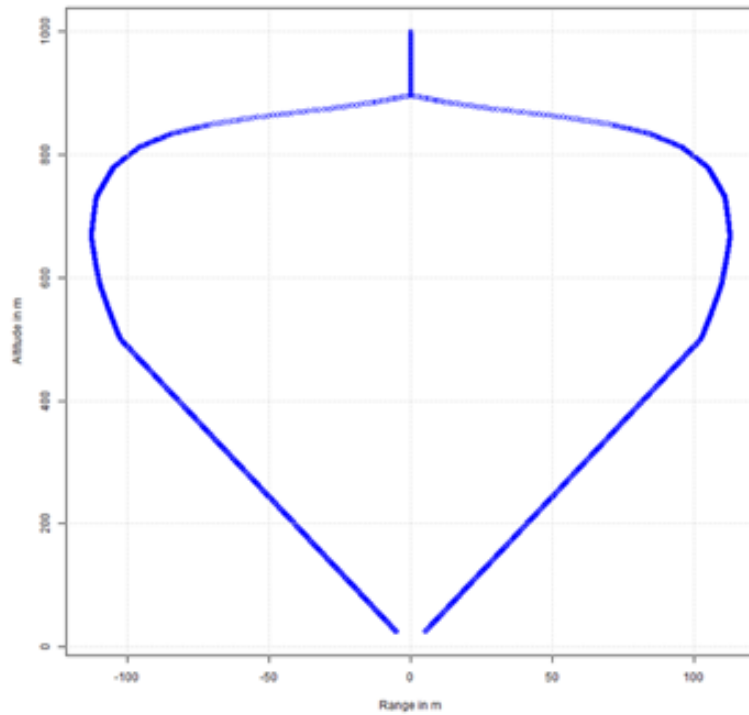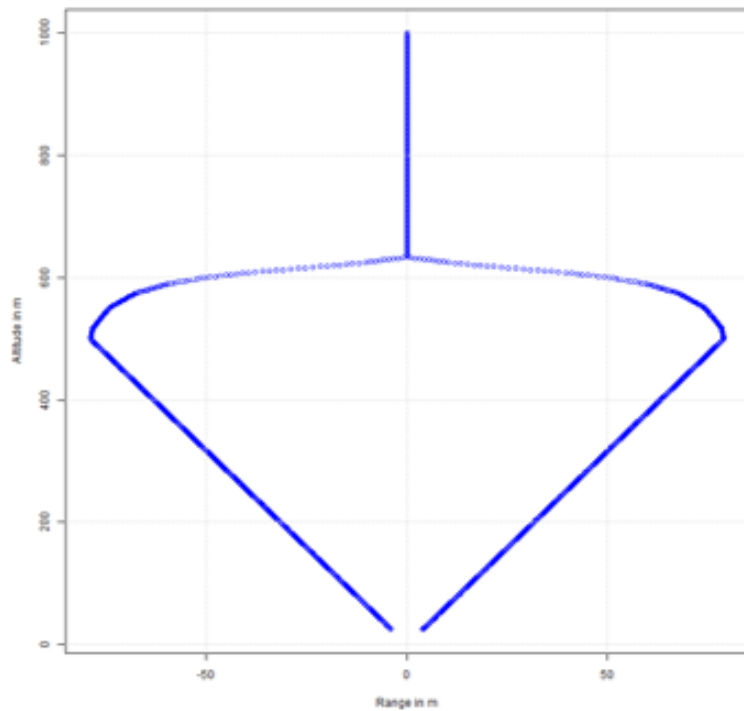
Figure 3. The effect radar cross section has on survey volume. (a) Shows a target with a diameter of 8cm is detectable for approximately 900m vertically and just over 100m radius from the centre of the radar beam. (b) Shows a target with 4cm have a reduced detection range to an altitude of just over 600m and approximately a 75m radius from the beam centre. Settings used: 1000m altitude limit, 50m bin width, Detection/class threshold and STC threshold of -90dBm, STC range of 500m, transmission power of 25000 W.

Sensitivity time control

Objects that are near to the radar can reflect large amount of pulse energy, resulting in an increased sensitivity at close ranges. To reduce the amount of small scattering objects such as insects or ground clutter (Schmaljohann et al., 2008), it is possible to set a minimal detection threshold (echoes that do not reach this intensity threshold are not detected), and a sensitivity time control (STC) filters low reflecting objects.

The STC is a distance-dependent threshold (Bruderer, Steuri & Baumgartner, 1995) that limits the distance at which a minimal object size will be detected (according to the threshold value, power sent and antenna gain); at the same time reducing the survey volume of the radar at a rate known to the observer [Fig. 4] (Schmaljohann et al., 2008). Objects below this size cannot be detected past this distance. Altering the STC value will in turn modify the surveyed volume below the STC range. The threshold and STC values will need to be selected to the need of the study and documented in order to properly estimate the detection ranges (Schmaljohann et al., 2008).
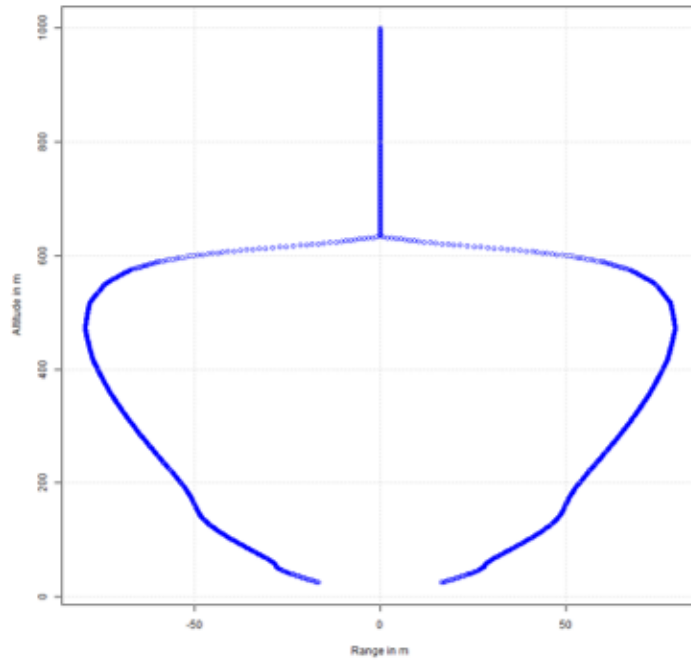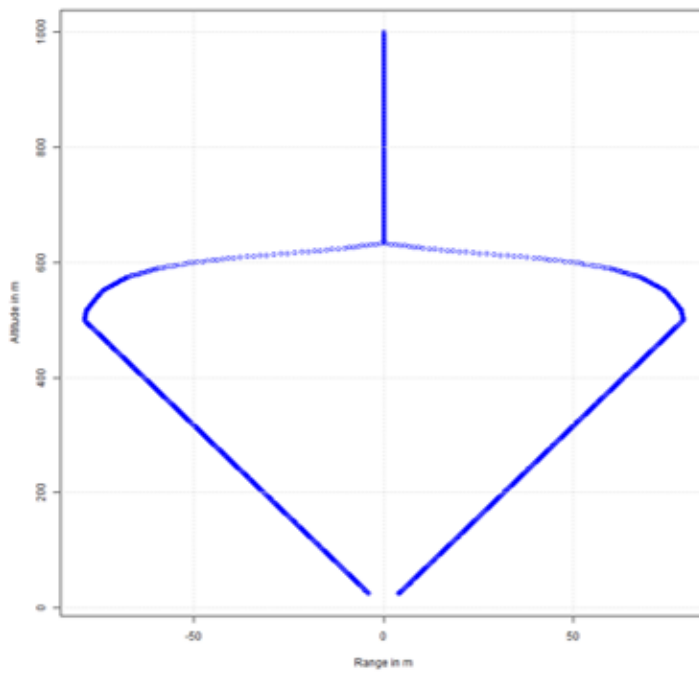
Figure 4. Comparison of standard radar beam survey area without STC (a) and with STC (b). The STC is a post-processing filter which removes emitted energy escaping outside the desired survey area and detecting ground clutter. It also reduces the survey volume of the radar at a rate known to the observer. STC threshold of -90dBm with a range of 500m.

Speed and direction

This is the first ornithological radar to use a nutating beam (meaning the beam rotates 2° elliptically around its vertical axis) in order to calculate velocity and direction of travel. This is a feature already in use in entomological radars (Chapman et al., 2003) This additional information can only be obtained when the radar operates in its rotation protocol.

The Birdscan system can calculate basic information on orientation. The rotation of the antenna creates circular-polarised electromagnetic waves, which can provide information as to whether the object is spherical or elongated in shape. For elongated objects information can also be obtained on heading orientation when combined with information on track direction.

The slight nutation of the antenna (Rotating at approximately 0.8 rotations per second and by tilting the antenna by 2°) enables the estimation of the object's track direction and ground speed. The angle formed by the object as it enters and exits the beam in relation to the beam centre is used to calculate flight direction. Therefore, the first and the last of the signal is taken (α_{start} and α_{end}). Out of these values the direction of the object can be estimated. Because small differences in entry and exit angles can lead to big errors, directions are only calculated if the radar is rotating and the alpha-angle is bigger than 60° or smaller than 270°.

The angle formed by the targets entry and exit point from the beam also provides information on flight distance. When this distance is divided by the echo duration (recorded time of the object) it gives the user the groundspeed of the target. The radar can continually nutate, run as a standard fixed beam or can alternate between a fixed and nutating beam at regular intervals.

Quantifying migration

Migration Traffic Rates

Migratory traffic rates (MTR) provide a standardised measure of movement intensities, defined as the number of animal per km and hour ($N*km^{-1}*h^{-1}$). MTR are computed for a given height interval (50m to maximal detection range) and illustrate the number of birds crossing a virtual line of fixed length

perpendicular to the flight direction within a given time frame (5 min, to one hour, day or season). In order to compute MTR we must first classify targets and consider radar cross section (body size) to understand detection probabilities. We can then estimate the horizontal range of the echo according to its class and height (vertical range). The horizontal range relates to the detection probability and is used to compute the MTR at the desired height and time interval.

Echo detection and classification

The BirdScan MR1 software automatically detects and registers echoes. The echo intensity varies within the recoding time of an echo (2 to 20 seconds) and it's this temporal variation in in echo intensity that is called the echo signature (Fig. 5). Having a sufficiently long dwell time of animals passing through the beam is critical to obtaining wingbeat data and estimating target type. A build-in algorithm automatically extracts characteristics from the echo signature, such as the RCS and the wing flapping frequency. A Naïve Bayesian Classifier uses the features extracted from the echo signature which can be classified and consolidated into 3 main bird groups: passerine, wader and swift type flights [Fig. 5]. Currently the Birdscan MR1 uses 14 classification types; including unidentified bird, large single birds, non-bird (Zaugg et., 2008) .
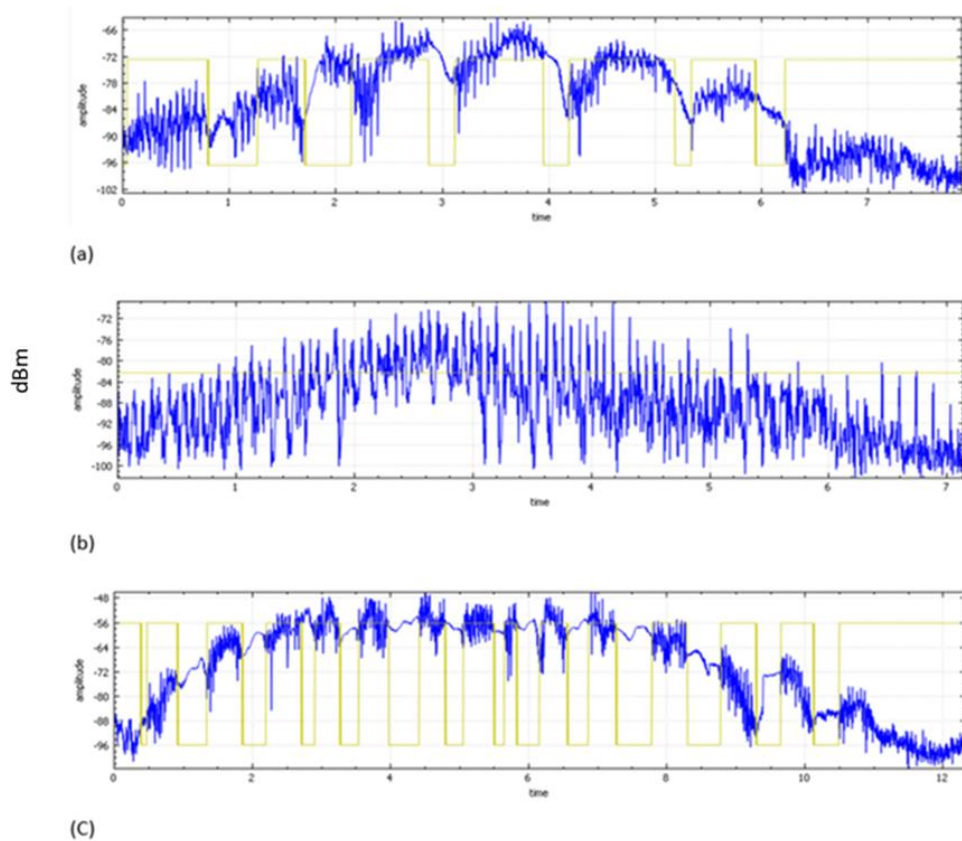
Figure 5. Three examples of returned echo-signatures collected by birdscanMR1. From this 3 major classifications have been produced all with characteristic wing-beat patterns types. (a) Passerine type flight, (b) wader type flight and (c) swift flight type. The blue line shows the signal and the yellow line shows the pulse-pause signal. Amplitude is measured in dBm and time in seconds.

Birds and insects are discriminated by radar cross-section, echo signature (variation in radar cross section over time) and air speed. Radar cross-section and echo signatures tend to vary less in insects than birds, likely down to the difficulty of detecting the wings of insects and small body size. The wingbeat patterns of birds closely resemble the echo signature that is produced by the target and subsequently recorded by the radar. The echo signature of birds tend to be well defined whereas the signature of insects are more complicated as they are made up by body movements as well as small wingbeats (Schmaljohann et al., 2008). Ground speed is used for discrimination as most insects fly slower than 5 m/s (Larkin, 1980) whilst the majority of birds fly faster 10 m/s (Bloch & Bruderer, 1982; Bruno Bruderer & Boldt, 2001). Issues can arise though as some insects can achieve high air speeds up to 11 m/s and some birds can much slower than the norm.

The classification is based on the wing flaps of and ground speeds of birds that are extracted from the echoes. These are visible as intensity modulations in the signal. This in turn means wing flapping frequency can be determined and used for classifications based upon their Fast Fourier Transformation (FFT). The FFT takes the signal received by the radar, which in this form measures the phase and amplitude over time and converts it into a frequency spectrum. FFT analysis also allows echoes to be stored as only few data, which is of particular use when detecting large migration movement over long periods of time. In addition to this, features like the bursts of wing flapping and intermittent pauses (pulse-pause behaviour) or the size of the object derived from the radar cross-section is also evaluated and can be used to aid classification.

The wing flapping frequency (WFF) can also give insight to the size of the bird, with WFF dependent on size, flight type, condition and morphology (Pennycuick, 2001). WFF can give a good indication of size for birds of similar flight types, with small birds showing higher WFF (>13Hz) than large birds (<13) (Bruderer et al., 2010). Using this information BirdScan's software can further classify to lower taxonomic levels, for example passerine can be refined to small or large passerine. It is important to be aware that the actual size of each bird cannot be determined (as the RCS decreases as the target passes further from the centre of the beam) and the WFF can vary greatly within individual birds (Bruderer et al., 2010). Therefore we must assume with best of our knowledge that the bird sizes with in a class are similar (Schmaljohann et al., 2008). We use a reference body size calculated for each class using the 0.95 quartile of the RCS to estimate detection probabilities and to accurately calculate migration traffic rates.

Echo detection probability and migration traffic rates

The detection probability of birds varies in relation to the bird's position within the beam. Using the calculated sensed volumes MTRs of the area can be assessed. These are a representation of the migration frequency. The intended outcome is to match an echo with an MTR factor (standardised weight echo per 1km). This has to be done for all classifications with the assumption that all objects within the class are the same size. Using the class and the distance interval you assign to each eco an MTR factor, which is the weight to the echo

e.g. how much the echo contributes to the MTR. For example, 1 echo in the beam at 200m would have an MTR of 5 (as calculated per km). The weighted echoes are divided by the desired time frame (1 hour, day, night) to give rate of migration. The sum of all echoes at each elevation within your chosen survey height will equal the MTR. By dividing the migration traffic rate by ground speed it is possible to calculate bird density per km^3.

Historically migration traffic rates have also be calculated using the moonwatching or ceilometer techniques (Kenneth et al., 1975), however there are issues detecting targets at distance, between observer differences and are very labour intensive as requires manual operation (Liechti, Bruderer, & Paproth, 1995). Birdscan MR1 removes such issues from MTR calculation and introduces a standardised method of monitoring migration.

Case study: Monitoring avian movements over The Lizard Peninsula, Cornwall

In the following section, I use data recorded at the University of Exeter, Cornwall campus located at the base of The Lizard Peninsula, Cornwall as a case study to illustrate the capabilities and specific features of the BirdScan MR1 radar system as a tool to quantitatively monitor avian migration and flight behaviour.

Temporal activity

Radar can be left for long periods of months or even entire seasons to see if migration events are made up of continuous traffic or perhaps large movements of individuals over just one or two nights [fig. 6].
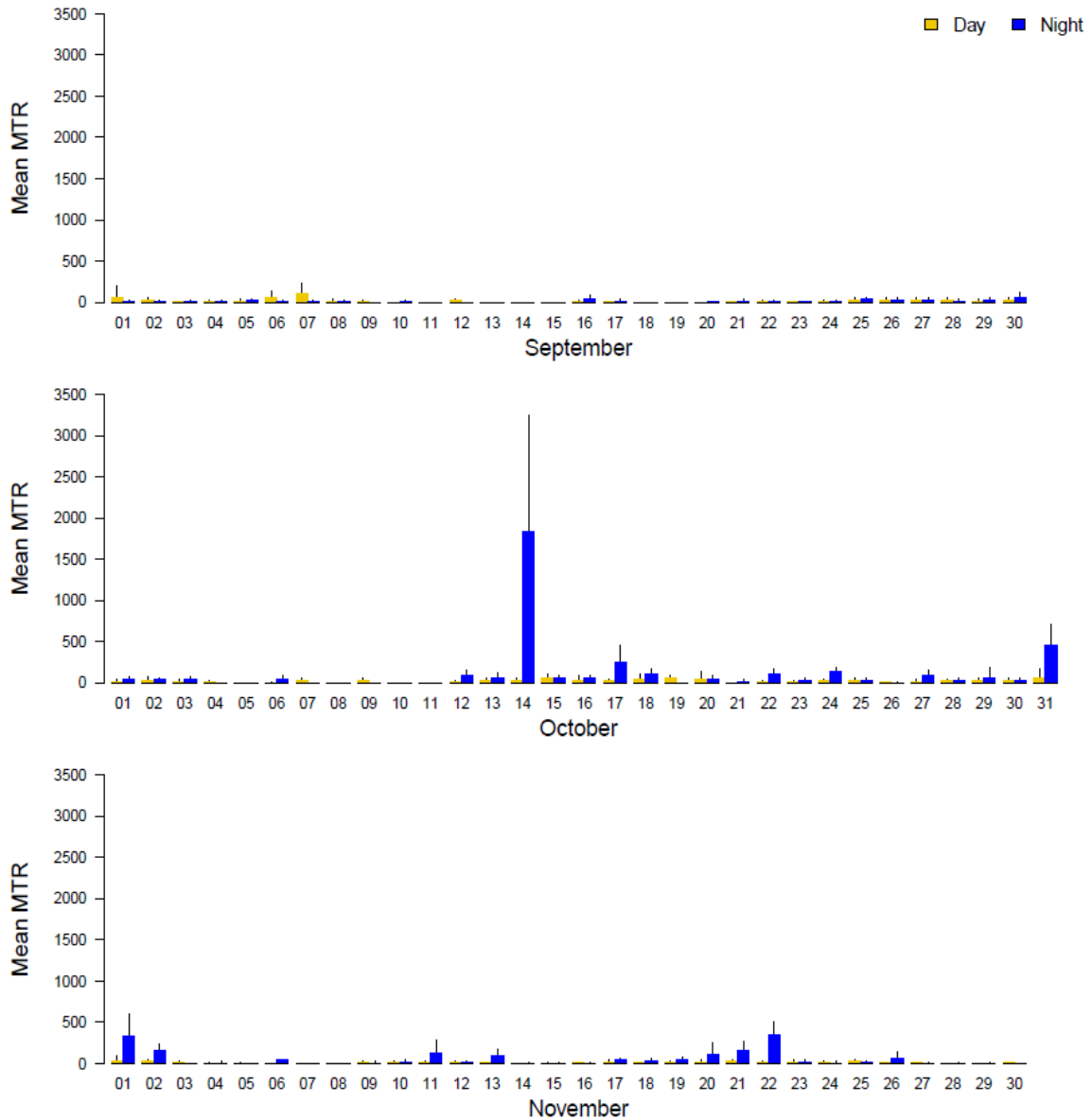
Figure 6. The daily migration traffic rates of nocturnal bird echoes (blue) and diurnal bird echoes (yellow) across the autumn of 2015. Error bars show 1 standard deviation of the MTR.

One of the greatest advantages of radar is its ability to observe nocturnal bird movements, even during the day an unaided observer can only detect birds at a distance of approximately 100m. There are a number of theories that have been put forward to explain this apparent preference to migrate through the night as well we as explain alternative strategy of day time migration. With birds difficult to observe outside the moon watching technique (counting silhouettes as they cross the moons face) (Liechti et al., 1995) and with the methods validity varying with experience of the observer and at larger distances, many birds are missed.
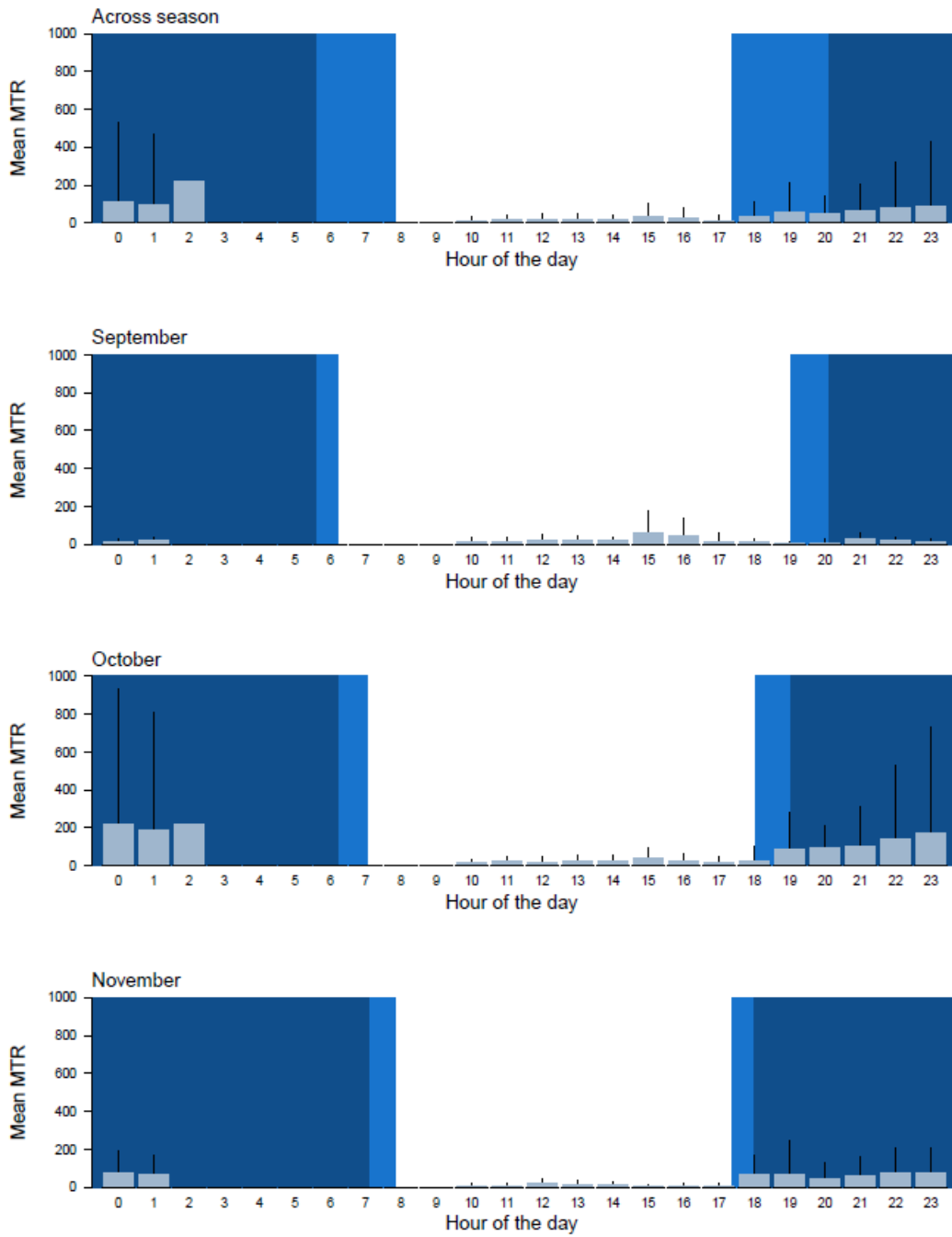
Figure 7. The migration traffic rate (MTR) shows standardised weight echo per 1km per hour of all bird echoes through 24 hours across the 2015 Autumn season (all three autumn months combined) and individual months. Night (dark blue), twilight (light blue) and day (white) are shown. Error bars show 1 standard deviation of the MTR.

Radar could potentially be used to identify the periods when migrating birds are most active and have practical application such as switching off wind turbines during high migration traffic or forecasting the composition of migration to minimise the risk of bird strikes at airports if used with traditional surveillance radars. From our observations, we find that the number of birds flying during autumn migration is low between the hours of 2am and 7am [Fig. 7]. During these times birds may have landed in order to rest after making transoceanic journeys across the Celtic Sea.

Direction and speed of targets

Direction and speed are two parameters that are often crucial in flight performance and spatial studies. Radar has been used to investigate how migrants react and orientate to a range of geographical and weather factors (Bruderer, 1997b). Orientation and flight direction can be recorded with more sophisticated tracking radar when the winds aloft are also known, allowing observers to investigate drift versus compensation scenarios as well as departure decisions and how migrants orientate to the coast. Previous studies have shown passerines preparing to depart land at the start of migratory flights do so on days with tailwinds (wind blowing in the same direction as travel) and there is a significant correlation between departure direction and wind, highlighting that birds take current wind conditions into consideration (Åkesson & Hedenström, 2000). Birds will wait for favoured winds but if these do not occur they are forced to leave at a later day regardless of wind direction.. (Åkesson & Hedenström, 2000).

Similar investigations into behavioural and orientation would hopefully be possible with this more compact and automated radar system but it could also be the precursor for numerous directional studies with large numbers of tracks able to be detected without the need for human assistance. Currently Birdscan MR1 t is the only radar dedicated to birds that can record direction in this way.
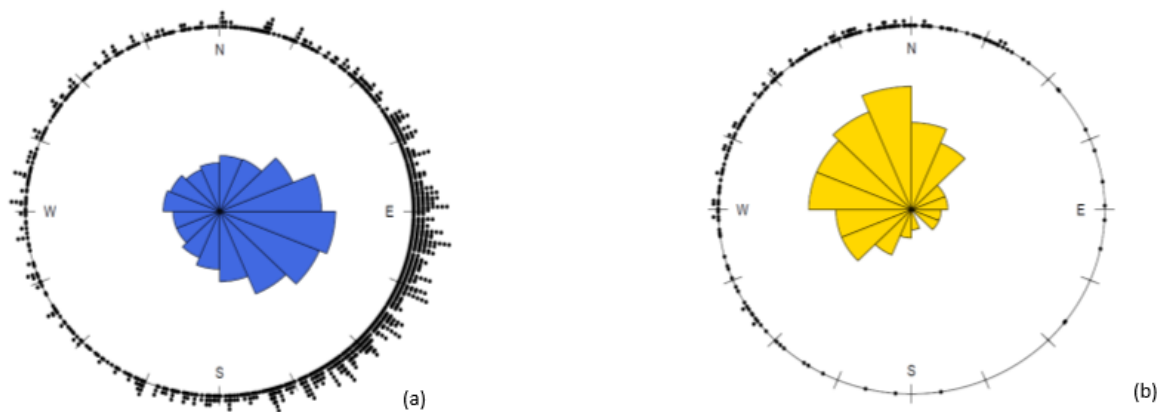
Figure 8. The relative frequency of flight directions of nocturnal passerines (a) October 2015 (blue) and (b) March 2016 (yellow). Black dots show raw data for each individual flight direction.

The clearest directional example is the different preferred direction of travel for spring and autumn migration [Fig. 8]. Nocturnal echoes that were recorded in March in Cornwall and classified as passerines show a strong preference to travel in North Westerly direction. This could be a species like redwing *Turdus iliacus* which are migrating to Iceland on spring migration and using Ireland as a staging site. In October nocturnal passerine echoes are focused in an Easterly/South Easterly quarter with birds seemingly looking to progress across to continental Europe.

Altitude distribution

Tracking and static radar systems are commonly used to record the flight altitude of birds (Backman & Alerstam, 2001; Liechti & Scaller, 1999; Schmaljohann et al., 2009; Spaar, 1995). The altitude at which a bird flies has been shown to be an important factor in determining its travelling efficiency (Liechti, 2006; Schmaljohann, Liechti, & Bruderer, 2009). However tracking systems can only follow single targets with the altitude distribution very much dependent on the sampling bias of the targets. Therefore tracking radars on standard target selection protocols do not provide proper quantitative height distributions. Fixed beam radars such as our described system can give valuable information on the altitude of migrating birds [Fig. 9] and have informed

us that most migration takes place below 1km but in some situations can be between 5–9km (Liechti & Scaller, 1999).
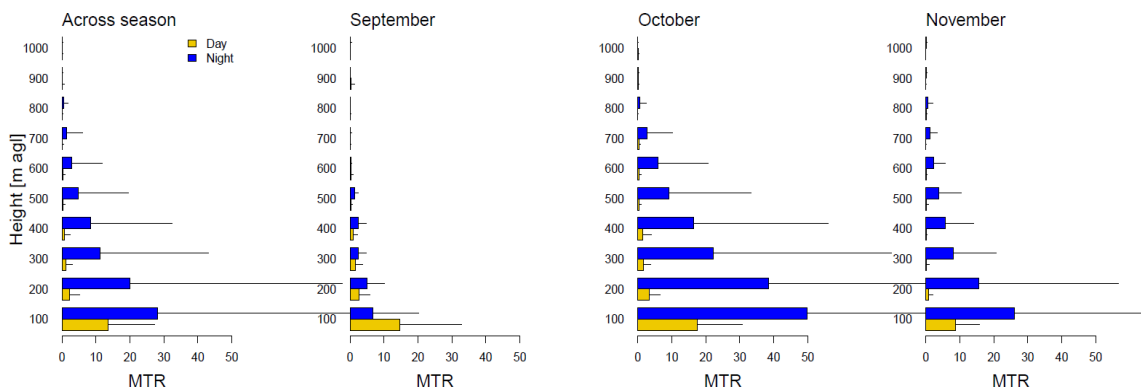
Figure 9. The altitude of migration traffic rates (MTRs) in metres above ground level (m agl), bounded by 100m and 1000m, at 100m intervals. Nocturnal migration (blue) and diurnal migration (yellow) indication that nocturnal passage occurs at higher altitudes. Error bars show standard deviation. MTRs are given for 3 months in the Autumn of 2015 and combined to give an across season overview.

Radar can be used to investigate altitudinal behaviour questions such as seen in Bäckman and Alerstam's common swift study. Birds did not select for altitude and speed regulation with a potential explanation being that head wind orientation being sufficient enough to keep nocturnal displacement from their home range with in the territory (Backman & Alerstam, 2001). Other radar studies have looked at how the altitude of birds vary over time. For example steppe buzzard *Buteo buteo vulpinus* flight height was dependant on time of day, with birds utilising thermals at the warmer times of day (Spaar, 1995). The tracking radar also allowed the thermal climbing rates of birds to be recorded, with these rates being found to be the decisive trait when it came to explaining the chosen flight behaviour of the birds (Spaar, 1995).

Where next and further applications?

Perhaps the most ambitious development would be to strive towards species level identification, with at least further refinement of taxonomic groups or flight behaviours. To do this would require an extensive database of multiple echo signatures for different species in order to see if there is clear distinction between any of the recorded parameters. For example, radar cross section could be used to distinguish the size of targets and wing flapping frequency can

determine the flight type of a target. Together there is the possibility to obtain a more refined idea of what targets may be and in some instances possibly to species level. Species level identification is highly difficult and may only be used where species diversity is low or for monitoring a colony of birds consisting of one species (Burger, 1997). The greatest challenges for low level classification remains high species diversity, the flight similarity of different species, collecting reference echoes and atmospheric distortion (Mie scattering) (Gauthreaux & Belser, 2003; O'Neal, Stafford & Larkin, 2010; Larkin, 1991), Schmaljohann et al., 2008).

A current feature under development is that of a means to record when the radar is operating blind. During data collection for this thesis these time frames were not recorded and were simple treated as periods of no migration. This scenario could be caused by a reduction in visibility from rain that hinders the transmission and detection of radio waves. In turn by knowing when the radar is not recording echoes a more accurate account of migration traffic rates can be determined as periods of no migration and "blindness" will not be confused.

In previous entomological radars, nutation and polarisation was used to derive body shape and alignment. By developing how the Birdscan MR1 utilises polarisation it could be possible to gather the same information for avian targets and in turn use it to calculate heading, which could be compared with direction of travel to examine displacement.

it is important to make clear that a current limitation is that speed, direction and ability to record wing beat frequency cannot be obtained simultaneously on the same bird. This highlights that there will perhaps always be a trade-off between settings and what the operators wants to record at any one time. Though, different settings can be alternate through on a chosen cycle which can at least provide a broader range of data recorded during field deployment.

On a much wider scale this radar system could be used in conjunction with radars throughout Europe to enhance the work of groups such as OPERA (Operational Programme for the Exchange of weather RAdar information). In addition to this the European Network for the Radar surveillance of Animal Movement (ENRAM) has been established to automatically retrieve bird densities from this European weather radar systems and can be used to record

animal movements on a continental scale similar to the NEXRAD (Next-Generation Radar) network of 160 high-resolution S-band Doppler weather radars operating in North America. The highly specialised nature of the Birdscan MR1 could help feed in valuable information to more generic systems and validate their findings and better understand much larger patterns of migration.

Conclusions

The unique features of this VLR allow the monitoring of both diurnal and nocturnal migration in greater detail of any automated ornithological system. Not only can the device quantify the number of targets at high altitudes (1km in this study but has the potential to operate at 3km) but also give insight to the mechanics of flight, providing another avenue to explore theoretical framework.

The radar is an ideal addition for migration watch points and observatories and similarly can be deployed to survey areas where the skyline may be disturbed by development in order to see what impact new structures may have on flyways. Similar systems by Birdscan are used to turn off wind turbines once migration levels reach a certain threshold illustrating how beneficial the system can be in conservation of avian flyways. Perhaps the more exciting avenue is the scientific findings that could be achieved. How do migrants respond to weather conditions or physical barriers? How do birds leave their roosts to forage? Can birds be identified to species level by wingbeat frequency? Can we forecast bird migration? When used creatively there are a wealth of opportunities for discovery and hopefully contribute significantly to ornithology.

Chapter 3: Seasonal variation in avian migration revealed using vertical looking radar

Abstract

Bird migration takes place on an enormous scale with typically billions of birds crossing continents each spring and autumn. Quantifying and monitoring migratory flight behaviours still proves a challenging task that often requires the development and refinement of new technology. Over 5,500 echoes of nocturnally migrating birds were recorded using an innovative automated vertical-looking radar on a non-traditional flyway at the base of the Lizard Peninsula, Cornwall (close to the southernmost point in mainland United Kingdom). This study investigates the composition of migration and how flight characteristics vary with bird class. Echoes were separated into 3 classes based on the similarities of their echo signature: passerine type flight, swift type flight and wader type. We then compared the flight altitude, direction, speed and rates of migration over the autumn 2015 (September, October and November inclusive) and spring 2016 (March, April and May inclusive) periods. We address seasonal differences in fundamental flight behaviour (altitude, speed and direction, and traffic rate) for three classes of migrants: (i) does the flight height of migrants vary between season and flight type? (ii) does the flight speed of migrants vary between season and flight type? (iii) does the migration traffic rates of migrants vary between season and flight type? (iv) does the flight direction of migrants vary between season and flight type? We found, swifts flew at the lowest heights in both seasons and wader was consistently the highest. Swifts reached the highest ground speeds, where as in the autumn waders flew the slowest and were replaced in the spring by passerines. To our knowledge there is no evidence from published material of a migration traffic rate (MTR) ever being calculated in the UK, meaning our MTRs could represent the first calculated at the fringe of a flyway. Passerines had the highest MTR in both seasons, with the lowest being found in Swifts. There was no difference in spring (304.12°- 316.04°) or autumn (99.62°- 104.35°) directions between all 3 classes. This suggests that all classes within each season travelled in the same direction. There was a difference between each classes spring and autumn direction.

Introduction

Animal migration is the movement of organisms between two or more habitats, frequently linked to the rotation of the seasons (Aidley, 1981; Nebel, 2010). It is an adaptive response to the seasonal or geographic variation of resources (Gauthreaux, Jr., 1982).

The factors that regulate the timing and rate of migration is not fully understood (Marra et al., 2005). These aspects of migration may be constrained and inflexible which means migrants may arrive at habitat that has yet to be reach or has passed their optimum condition, as seen in pied flycatchers *Ficedula hypoleuca* (Both & Visser, 2001).

In contrast, rates of migration may be flexible and change in response to food and weather conditions (Marra et al., 2005). Stop over time varies with habitat quality (Lindstrom, 1991).This could introduce differences in flight strategies within and between species as individuals are delayed by lack of resources or missed their availability entirely. Alternative explanations for delayed stop over times and reduced migration rates could be adverse weather conditions. Extreme weather events in the form of late winter storms, cold fronts, and waiting for unfavourable winds to pass could all halt or slow bird movements (Huin & Sparks, 1998, 2000; Liechti, 2006; Richardson, 1978; Schmaljohann et al., 2009). Departure, arrival and peak migration dates can also be species specific differences in migratory behaviour, with certain species showing preference for migrating early or late in migration period (Davis, 1967; Mason, 1995). Arrival dates within species can also be influenced by sex (Gunnarsson et al., 2006).

It may be possible that birds have to alter their altitude, speed and direction to achieve optimal flight in these changing conditions and that this may in fact also vary with taxa. Previous studies have focused on explaining the variation of these flight characterises treating all migrants as one large group. Very few studies have investigated the composition of migration (Liechti & Bruderer, 1995). Mass migrating flocks can be formed from a variety of taxonomic groups and although they share the same flyways, they might occupy the air space at different times, flight levels, have different preferred directions of travel, migrating in their own unique way (Liechti & Bruderer, 1995).

Birds will select winds at favourable altitudes, usually tailwinds (Akesson & Hedenstrom, 2000; Gauthreaux, 1991). In southern Israel, autumn migrants make use of the northerly tail winds at low altitude despite high temperatures, while northbound spring migrants tend to reach south-westerly tailwinds at higher levels (Bruderer et al., 1989). This is most likely a site-specific phenomenon and varies with geographic barriers and prevailing winds. How birds of different size and flight type utilise altitude remains unclear, while there also seems to be little work done on how flight height differs with season.

Previous studies have shown birds fly at faster speeds in the spring in comparison to the autumn (Fransson, 1995; Yohannes et al., 2009). It has been suggested that these pre-breeding flights are under greater time constraints than autumnal flights due to competition for territories in breeding locations (Kokko, 1999). The limited compositional studies have also shown differences in the groundspeeds in different bird flight types i.e. continuously flapping (wader type) and intermittent flapping (passerine type flight) (Liechti & Bruderer, 1995).

The rate at which migration takes place fluctuates on a nightly basis and appears to be strongly linked to weather conditions. Weak tailwinds appear to be associated with heavy migratory movements (Richardson, 1978). Larger migration levels can be expected in the autumn due to the recruitment of young birds to the population. Comparisons of migrating flight type rates appears to be under studied, however the proportion of classes that make up total migration have been compared with passerine type flight appearing to be the dominant class (Liechti & Bruderer, 1995).

From a northern temperate perspective, there is of course an obvious north and south bound difference due to the spring and autumn migration respectively. In directional studies attention is given to how birds react to wind conditions and whether birds experience drift or compensate for such conditions. A simple yet valuable component of directional work is determining migrants preferred direction of travel and there has been no evidence to suggest that different bird classes travel in different flight directions in the same flyway (Liechti & Bruderer, 1995).

Here I use vertical looking radar to investigate how migratory flight characteristics and migration rates vary between seasons and whether this is affected by taxonomic class (flight type). I aim to answer the research questions: (i) does the flight height of migrants vary between season and flight type? (ii) does flight speed of migrants vary between season and flight type? (iii) does migration traffic rates of migrants vary between season and flight type? and (iv) does the flight direction of migrants vary between season and flight type?

Methods

Radar deployment

The Birdscan MR1 vertical-looking radar system (VLR) was deployed during autumn 2015 (September, October and November inclusive) and spring 2016 (March, April and May inclusive) at the base of the Lizard Peninsula, UK (50°10'15.2"N 5°07'39.9"W). For all Hardware details see: "*New developments in vertical-looking radar to study bird migration*", this section also discusses settings, which are the same as used in this investigation unless stated otherwise below. The radar was set to a 1500m altitude limit, 50m bin width, Detection/class threshold and STC threshold of -90dBm, STC range of 500m, with a transmission power of 25000 W.

Classes were created by the Birdscan MR1 software which are separated on echo signatures that had be transformed via a fast fourier transform (FFT). These classifications have been based on previous class ground truthing (Schmaljohann et al., 2008; Bruderer et al., 2010). The classes created were based on similarities of the flap glide components within the wingbeat pattern and differences in groundspeed, which can be sorted into 3 distinct groups. These consisted of: passerine type flight (flap-pause), wader type flight (continuous) and swift type flight (sporadic flap and glides) (As shown in Fig 1, Chapter 2). These classifications are also simply referred to as passerine, wader and swift.

The radar operated at a short pulse length and alternated between fixed beam and rotation setting every 15 minutes continuously for the 24 hours a day throughout the survey period. By switching between the two functions, speed, azimuth, altitude and wingbeat frequency can be collected for all class samples but not for all individual echo signatures. Only nocturnal echoes were included in the analysis. This is to exclude daytime traffic created by local resident birds.

To analyse rates of migration, echoes for each class were weighted to consider the changing sensitivity of the beam; converted into migratory traffic rates (MTR). MTRs provide a standardised measure of movement intensity, defined as the number of objects per km of sky and hour ($N*km^{-1}*h^{-1}$). MTRs where computed for 1 hour intervals and a given height interval (50m to the 1500km maximal detection range).

Directional data was collected by calculating the entry and exit point of the target as it passes through the beam. All directions are in degrees from North. Speed was recorded as birds passed through the beam and recorded in meters per second (ms^{-1}) and is a ground speed. Altitude (in meters) was calculated by recording how long it took for the emitted pulse to be reflected to the receiver. The detection range was from 50-1500m.

Statistical analysis

Only echoes recorded between evening civil twilight and morning civil twilight were used in the analysis. This allowed echoes that were most likely to belong to nocturnal migrants to be included and exclude any non-migratory day time bird traffic.

Flight height data was not normally distributed and strongly right-skewed (see appendix, Fig. S1; Kolmogorov–Smirnov test: Height, D=1, P=<0.0001).

Flight speed histograms was not normally distributed and right skewed (see appendix, Fig. S2; Kolmogorov–Smirnov test: Height, D=0.98, P=<0.0001).

Migration traffic rates (MTR) were very heavily right skewed (see appendix, Fig. S3) due to lots of 0 values and for so for analysis each data point was +1 was added to be able to run GLMs. When tested data was still found to be non-normally distributed. (Kolmogorov–Smirnov test: MTR, D=0.85, P=<0.0001).

When calculating Mean MTRs the raw data was used rather than the MTR+1 values.

Directional data for spring (Shapiro-Wilk test: Azimuth, W=0.95, P=<0.0001) and autumn (Shapiro-Wilk test: Azimuth, W=0.93, P=<0.0001) where both not normally distributed necessitating the use of non-parametric Watson-wheeler tests which compares the for homogeneity of two or more samples of circular data.

Altitude, direction, speed and rates of migration were analysed using Gamma GLMs using an inverse function taking into account season and classification. Gamma glms were used as the data was positively skewed i.e. non-normal with a long tail to the right as identified in (Crawley, 2012). Models with the lowest Akaike information criterion (AIC) values where used for analysis. For flight height, the model with the lowest AIC and therefor the best fit for my data was a model that excluded interaction and used only season and class (see appendix, Table S1) to avoid over fitting. GLMs for speed (see appendix, Table S2) and MTR (see appendix, Table S3) were fully saturated. Interaction between direction and other variables was not examined due to the difficulty in mixing circular and linear variables in the same GLM.

To test differences in flight height, speed and MTR between classes I used a Kruskal Wallis test and if there was a significant difference these interactions were investigated further with a post hoc Dunn's test.

All analyses were carried out in R version 3.0.2 (R Core Team, 2013).

Results

Flight height

Overall, flight height varied by class [Fig. 10]. Swift-type birds flew the lowest (Gamma GLM: Swift, t = 9.01, N=228, P= <0.0001), wader was highest (Gamma GLM: Wader, t=-19.97, N=1442, P=<0.0001) and passerines were intermediate (Gamma GLM: Passerine, t = 139.73, N=5786, P= <0.0001). This pattern of class flight heights was maintained within each season (Fig. 10, Table 1). In general there was also a seasonal difference in flight height with, spring birds flying at a higher altitude in comparison to autumn (Gamma GLM: Spring,

t=-12.07, N=1302, P=<0.0001). Flight height differed significantly with bird class and season (Kruskal–Wallis test: H=616.96, 5 d.f., P= <0.0001) [Fig. 10].
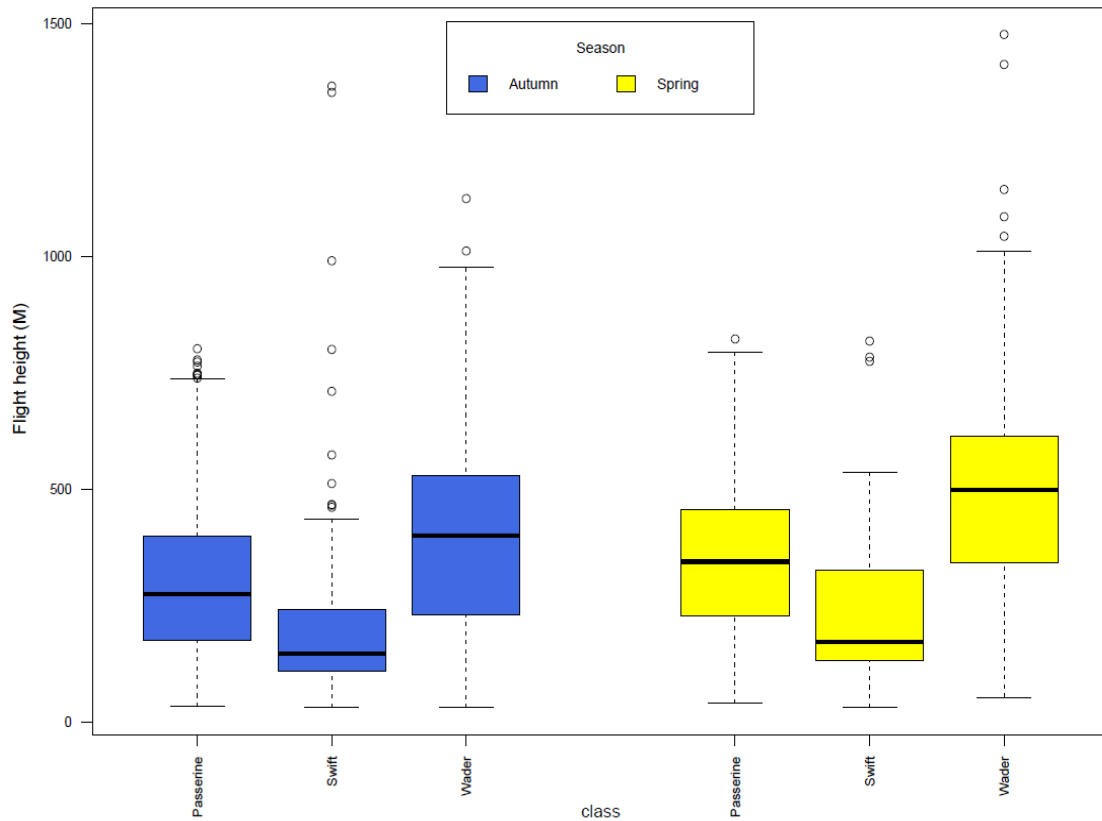
Figure 10. Avian flight height (m) by class and season. Shown here are flight heights (median, interquartile range, minimum and maximum values) for autumn 2015 (Blue) and Spring 2016 (Yellow). Height measurements collected for Autumn classes consist: Passerine (n=4890), Swift (n=192) and Wader (n=1072). Heights recorded for Spring consisted of: Passerine (n=896), Swift (n=36) and Wader (n=370). Migration levels shown here are lower than elsewhere in Europe due our study site being located outside the Western flyway.

Table 1. Flight height of bird classes. The pairwise comparison of each class for autumn and spring using post-hoc Dunn's test. Z statistic shows how the first class compares to the second.

Flight height

Season	Comparison	Z	P value
Autumn	Passerine - Swift	9.58	<0.0001
	Passerine -Wader	-14.28	<0.0001
	Swift- Wader	-15.14	<0.0001
Spring	Passerine - Swift	4.03	<0.0001
	Passerine -Wader	-9.56	<0.0001
	Swift- Wader	-7.30	<0.0001

Flight height compared between spring and autumn

Passerines flew significantly lower in autumn than in spring (Dunn's test: Z= -8.86, P=<0.0001). Waders also flew significantly lower in autumn than in spring (Dunn's test: Z= -7.15, P=<0.0001). There was no significant difference in the flight heights of swift in spring and autumn (Dunn's test: Z= -1.88, P=0.06).

Flight speed

Flight speed differed significantly with bird class and season (Kruskal–Wallis test: H=136.46, 5 d.f., P= <0.0001) [Fig. 11].

Flight speed in autumn

Swift-type birds flew the fastest in Autumn (Gamma GLM: Swift Autumn, t = -7.03, N=182, P= <0.0001), wader-type were the slowest (Gamma GLM: Wader t = 2.93, N=345, P= <0.01) and passerines were intermediate (Gamma GLM: Passerine, t = 104.90, N=1720, P= <0.0001). The 3 classes all significantly differed in their autumn flight speed [table 2]

Flight speed in spring

In spring, swift-type birds were again the fastest group (Gamma GLM: Swift Spring, t = -4.14, N=33, P= <0.0001), passerine-type was the slowest (Gamma GLM: Passerine Spring, t = 7.14, N=346, P= <0.0001) and wader was intermediate (Gamma GLM: Wader Spring, t = -5.28, N=117, P= <0.0001). Pairwise comparisons showed spring flight speed significantly varied between each flight type [table 2].

Table 2. Flight speed of bird classes. The pairwise comparison of each class for autumn and spring using post-hoc Dunn's test. Z statistic shows how the first class compares to the second.

Flight speed			
Season	Comparison	Z	P value
Autumn	Passerine - Swift	-6.67	<0.0001
	Passerine -Wader	3.35	<0.01
	Swift- Wader	7.84	<0.0001
Spring	Passerine - Swift	-6.09	<0.001
	Passerine -Wader	-3.42	<0.001
	Swift- Wader	3.77	<0.0001
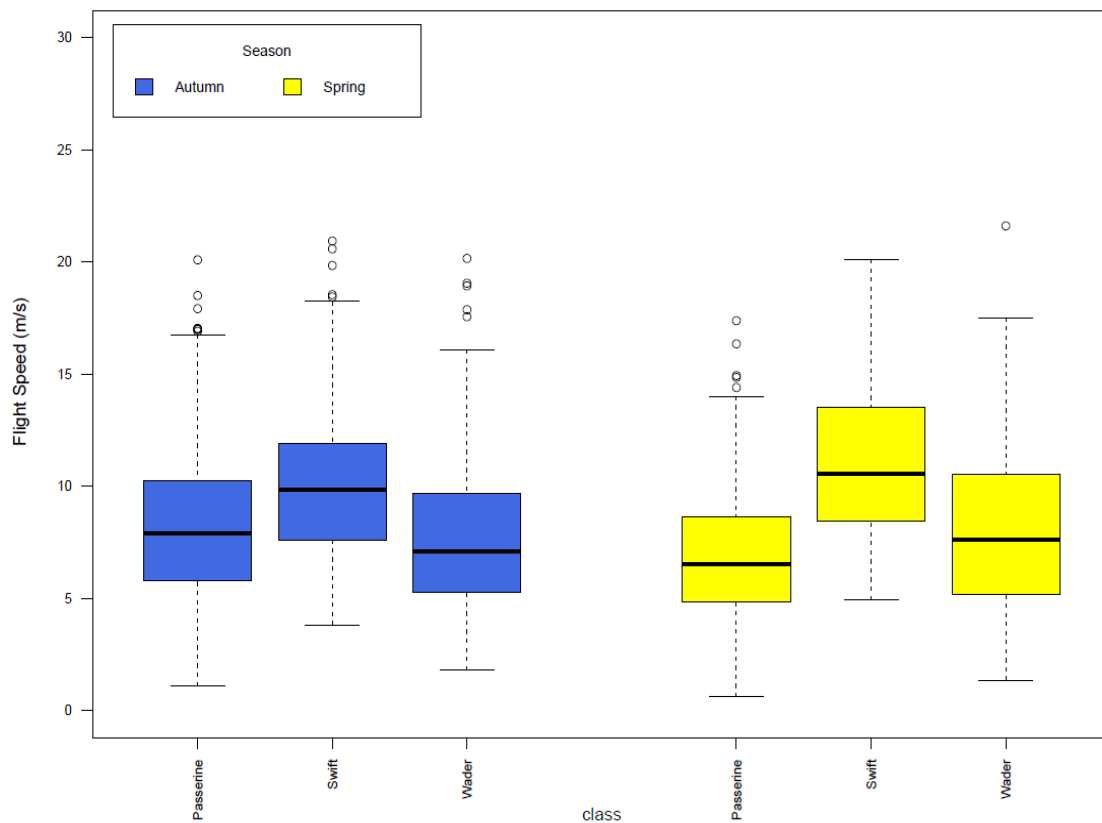
Figure 11. The flight speed of bird classes across season. The raw data is plotted in meters per second (median, interquartile range, minimum and maximum values) for autumn 2015 (Blue) and Spring 2016 (Yellow). Speed measurements collected for Autumn classes consist: Passerine (n=1720), Swift (n=182) and Wader (n=345). Speeds recorded for Spring consisted of: Passerine (n=346), Swift (n=33) and Wader (n=117). Error bars show the slowest and highest recorded flight speed for each class. Note: Sample sizes are lower than those for height as Birdscan can only record speed when nutating where as height can be recorded in all protocols.

Class flight speed compared between Spring and Autumn

Passerines flew significantly faster during the autumn than in the spring (Dunn's test: 7.17, P=<0.001). However, there was no significant difference in autumn and spring flight speed of waders (Dunn's test: Z= -1.32, P=0.215) or swifts (Dunn's test: Z= -0.88, P=0.41).

MTR

Overall, MTR differed significantly with bird class and season (Kruskal–Wallis test: H=273.78, 5 d.f., P= <0.0001) [Fig. 12].

MTR in autumn

Autumn passerines had the highest migration traffic rates (Gamma GLM: Passerine Autumn, t = -9.61, N=730, P= <0.0001), autumn swift the lowest

(Gamma GLM: Swift Autumn, t = 2.95, N=730, P= <0.01) and autumn wader was the intermediate (Gamma GLM: Wader Autumn, t = 3.57, N=117, P= <0.001). All 3 classes differed significantly in their autumn MTRs [Table 3].

MTR in spring

Passerines-type had the highest MTR in spring (Gamma GLM: Passerine Spring, t = 9.62, N=680, P= <0.0001), swift-type the lowest (Gamma GLM: Swift Spring, t = -2.95, N=680, P= <0.01) and wader-type was the intermediate group (Gamma GLM: Wader Spring, t = -3.57, N=680, P= <0.001). All 3 classes differed significantly in their spring MTRs [table 3].

Table 3. Migration traffic rates of bird classes (MTR). The pairwise comparison of each class for autumn and spring using post-hoc Dunn's test. Z statistic shows how the first class compares to the second.

MTR

Season	Comparison	Z	P value
Autumn	Passerine - Swift	11.60	<0.0001
	Passerine -Wader	7.92	<0.0001
	Swift- Wader	-3.68	<0.001
Spring	Passerine - Swift	9.07	<0.0001
	Passerine -Wader	5.77	<0.0001
	Swift- Wader	-3.30	<0.01
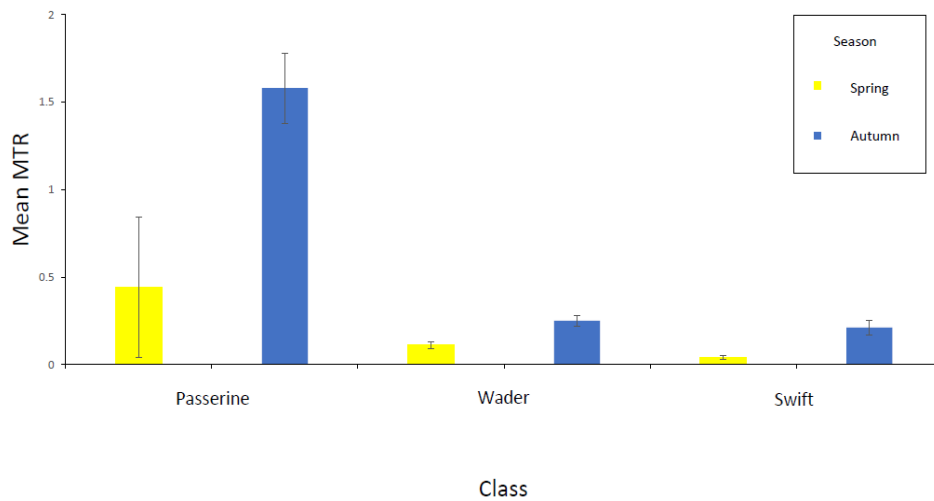
Figure 12. The mean migration traffic rate (MTR) of bird classes across season. The raw data is plotted in per hour per km for Autumn 2015 (Blue) and Spring 2016 (Yellow). Spring MTR factors n=680 and Autumn MTR factors n=730. Error bars shows the standard error.

Class MTR compared between Spring and Autumn

All MTRs were higher in autumn than spring. Passerine MTR was significantly higher in the autumn compared to the spring (Dunn's test: Z= 5.40, P=<0.0001), waders had higher MTR in autumn than the spring (Dunn's test: Z= 3.50, P=<0.001) as did swifts (Dunn's test: Z= 3.24, P=<0.01).

Flight direction

The average flight direction for each class was calculated in degrees from North. The flight direction of all classes in Spring all followed a North Westerly pattern and are as follows: Passerine 304.12°, SD = 109.50°, wader 316.04°, SD = 101.32° and swift 304.14°, SD = 109.97°. There was no significant difference between the direction of travel of the three classes in Spring (Watson Wheeler test: W= 8.73, d.f. = 4, P=0.07).

The flight direction of all classes in Autumn all followed a South Easterly heading, with average direction for each class being: Passerine 99.62°, SD = 94.69° Wader 101.54°, SD= 95.68° and Swift 104.35°, SD = 92.54°. Again,

there was no significant difference between the direction of travel of these classes (Watson Wheeler test: W= 1.18, d.f. = 4, P=0.88).

All classes showed a difference between preferred direction of travel between the spring and the autumn. The direction of autumn and spring passerine were significantly different (Watson Wheeler test: W= 263.14, d.f. = 2, P=<0.0001) [Fig. 13], as was the difference between spring and autumn waders (Watson Wheeler test: W= 93.62 d.f. = 2, P=<0.0001) [Fig. 13] and swift between the two seasons (Watson Wheeler test: W= 23.71, d.f. = 2, P=0.0001) [Fig. 13].
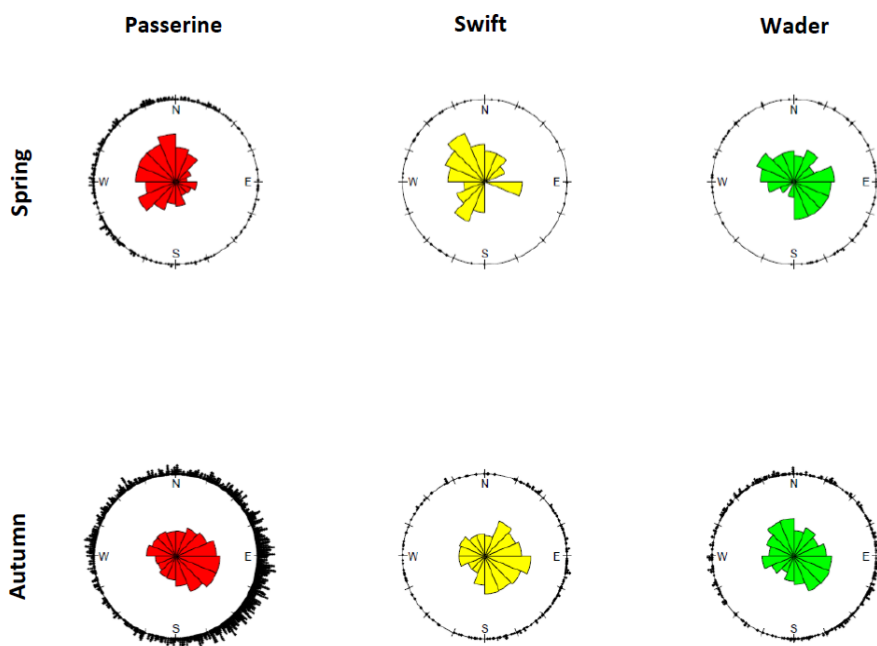
Figure 13. The flight direction of bird classes across season. The raw data is plotted in degrees from North for Spring 2016 (Above) and Autumn 2015 (Below). Tracks are illustrated in red (Passerine), yellow (swift) and green (Wader). Direction measurements collected for Autumn classes consist: Passerine (n=1720), Swift (n=182) and Wader (n=345). Speeds recorded for Spring consisted of: Passerine (n=346), Swift (n=33) and Wader (n=117).

Discussion

The aim of this study was to compare the flight height, speed, migration rate and direction of travel, of three difference groups of birds (passerine, wader and swift), identified on the basis of shared features in terms of wing-beat frequency. The passerine class in autumn is likely to be made up of predominantly winter

thrushes, particularly redwing *Turdus iliacus*, song thrush *Turdus philomelos* and fieldfare *Turdus pilaris* (Personal, Obs, 2015). In spring the passerine class may still comprise of a few remaining winter thrushes (particularly in march), though is much more likely to be returning warblers and chats. The wader class is made up of continuously flapping birds, with waders such as snipe *Gallinago gallinago* and woodcock *Scolopax rusticola* commonly passing through and wintering the study site. Wildfowl such as mallard *Anas platyrhynchos*, teal *Anas crecca* and wigeon *Anas penelope* also winters locally and pass further south to France and Spain. Swift type birds pose more of an identification question. Spring echoes could be made by common swift *Apus apus* in April and May but seems unlikely for autumn echoes as most birds typical depart the United Kingdom by the end of August. Alternative species could be birds with a large glide component to their wing beat patter, such as gulls and terns.

Passerine were the most frequent class (n=5786), followed by wader (n=1442) and then swift (n=228). This is in line with findings from Southern Israel where passerine type echoes where also the most dominant class (Liechti & Bruderer, 1995). Passerine type birds are also likely to make up the majority of biomass, however quantifying this could be difficult. We found significant differences in flight height, speed and MTR between all classes and in some cases differences between season. All groups travelled in similar directions within each season with all classes showing obvious differences in flight direction when comparing spring and autumn. Waders showed the high variance in flight direction for both seasons, which suggests that they could in fact be non-migratory birds.

Altitude

In this study, I found that swift type birds flew at the lowest altitudes, waders were highest and passerines were intermediate (Fig. 10). These differences in class flight height could be related to physiology of the birds and their tolerance to certain conditions. Wader type birds are perhaps more robust and can pioneer these higher altitudes, which are associated with higher wind speeds (Alerstam et al., 2011; Chapman et al., 2010; Chapman, Reynolds, & Smith, 2003). Wader-type birds could typically be larger than passerine and swift-type birds and be less vulnerable to the cooler temperatures found out higher altitudes (Alerstam et al., 2011). In addition, their constant wing flapping

behaviour could mean they are less susceptible to displacement from these winds (Chapman, Klaassen, et al., 2011; Green & Alerstam, 2002). In contrast swifts (or at least species with wing beat frequencies most akin to swifts) have the largest glide component in their flight which could make them vulnerable to drift (Chapman, Klaassen, et al., 2011; Green & Alerstam, 2002). However there is a paucity of work examining how and why different types of birds utilise different altitudes therefore there is little previous research to draw upon to explain the observed patterns.

Flight height could also be linked to the overall migratory distance. For example, reaching higher altitudes could be energetically costly and birds that perform short bouts of migration will be landing on a more regular basis. This in turn means birds must also climb to their preferred height of travel more often and they may therefore be constrained by the cost of reaching higher altitudes. Birds that travel for long periods can remain at higher altitudes. This all could ultimately be linked to the bird's build, ability to store and respire energy. Alternatively, birds increase flight altitudes to seek out more supportive winds when wind conditions near the surface are prohibitive. Therefore, birds may not select flight altitudes only to optimise wind support but instead prefer to fly at low altitudes unless wind conditions there were unsupportive of migration (Kemp et al, 2013).

The flight height of birds seems to be predominantly linked to birds selecting for the most favourable winds to travel in (Liechti, 2006; Schmaljohann, Liechti, & Bruderer, 2009). This could explain the increased height in autumn compared to spring, where potentially the wind speeds in the different strata alter and wind direction shifts. However, we were unable to access information on wind speeds at different altitudes at this site – wind conditions at ground level were available but do not necessarily correlate with winds at higher altitudes (Alerstam et al., 2011).

Speed

Swifts were the fastest class recorded with the other two classes showing similar, slower, flight speeds (Fig. 11). These results are in contrast to studies from the Middle East which have shown waders to be the faster class in comparison to passerines (Liechti & Bruderer, 1995). This could in part be

explained by the low taxonomic resolution achieved by the radar identification algorithms.

All birds were faster in the autumn but only passerines were significantly so (Fig. 11). These findings are inconsistent with the current paradigm that birds fly faster during spring migration to aid early arrival and therefore obtain access to the best breeding territories (Fransson, 1995; Kokko, 1999; Nilsson, Klaassen, & Alerstam, 2013).

Visual observations reveal that a large proportion of the birds encountered in the autumn were winter thrushes (predominantly redwing *Turdus iliacus*). These large thrushes have higher flight speeds than smaller passerines and differences in species composition could go some way to explaining the higher autumn flight speed (Liechti & Bruderer, 1995). This highlights that the paradigm that flight speeds in spring are higher than autumn may only be relevant when the same species are considered. Previous studies have also shown selection for faster flights under opposing winds and birds increase their airspeed in response to increasing air density, which could be an alternative explanation. This also further highlights the importance of monitoring the wind strata and weather conditions to help explain migration behaviours. The region is very susceptible to autumn storms as the South West of England protrudes into the Atlantic. These weather events could not be taken into consideration for analysis due to the lack of suitable weather data. If favourable, birds could potentially utilise these faster winds.

A more refined approach to splitting classes, for example, having small and large passerines, may be beneficial for future work. Previous studies have done and as discussed with regards to large thrushes it could help control for size of the target. As discussed previously, this approach remains very difficult due to the considerable overlap in wing beat rate and pattern among species as well as atmospheric distortion (Mie scattering). Splitting the seasons into early and late categories could help to identify different species of migrant and help to address the competition hypothesis.

MTR

Migration traffic rates for all classes were higher during autumn than the spring [Fig. 12]. This is not surprising as likely reflects the recruitment of birds into the population post breeding season.

Simply comparing seasons might not provide enough resolution to investigate MTR patterns. Large amounts of migration over a few days are lost when averaged with days containing no migration. Providing that the radar system can be kept running, continuously monthly or potentially daily comparison in MTR could be made and provide further insight into taxa specific migration behaviours. Previous studies have shown that weather conditions explain 2/3 of the variation in migration intensity (Zehnder et al., 2001). This highlights the importance of collecting suitable weather data to help describe why MTRs fluctuate. As show in previously literature winter storms, cold fronts, and unfavourable winds could all halt bird movements (Huin & Sparks, 1998, 2000; Liechti, 2006; Richardson, 1978; Schmaljohann et al., 2009).

Direction

There was no significant difference in flight direction between the classes when compared within the spring and autumn seasons, suggesting all birds were heading in a similar direction for the next stage of their journey [Fig. 13]. Alternatively, birds may simply have no option but to travel in these recorded directions with the south west peninsula of the United Kingdom surrounded by oceanic barriers, birds simply have to reorientate to find the most direct route to cross these obstacles. All classes in the spring were traveling in a north westerly direction suggesting birds were arriving from the continent, likely Brittany on the North-West tip of France or continuing to the southern coast of Ireland. In the autumn all classes travelled in a South Easterly direction, heading for North-West France. During the autumn period much of the migration witnessed over the study site was comprised of winter thrushes most notable the redwing *Turdus iliacus* (personal observation, 2015). It is possible that these redwings *Turdus iliacus* from the Icelandic population have been travelling in a south westerly direction via Ireland before being detected by the radar system. This however is speculative. Unsurprisingly the flight direction of each class was significantly different between spring and autumn, due to the north/south nature of bird migration from a northern temperate perspective.

Recommendations for further study

There are two main areas to alter when conducting further studies on the migration behaviour of birds with radar. The first is to include weather data in analysis. This is no easy task as the conditions within an air column are constantly changing, therefor to acquire accurate data on wind direction, speed and air pressure is challenging. Ground weather stations cannot provide the desired data, so equipment or procedures that can record at different strata offer the best solution. This can be done by launching small weather balloons to generate wind profiles. By collecting accurate weather data that the birds experience we can begin to understand their reasoning for selecting these flight heights.

The second major improvement it is to refine methods of classifying birds and splitting data for analysis. To improve classification, assigning echo signatures with species or class determined from visually identifying targets will help build up a comprehensive database in which to start looking for differences echo characteristics. Even by refining to a lower taxonomic level or by identifying new classes on the same level it will help assign the signature to the most accurate class. In addition to separating into more accurate classes, breaking the seasonal data into monthly or ideally daily time frames could possibly help identify more fine scale patterns in migration. For example, MTRs could vary greatly on a daily basis with a large night or week of movements being lost in seasonal scale analysis, if there are many nights when no migration takes place. This could be true for all other response variables investigated in this project.

Conclusion

Quantification of nocturnal migration is notoriously difficult. Even harder still is breaking down migration into taxonomic groups. Moon watching has proved useful for quantifying migration and simply involves watching birds cross the face of the moon with a telescope (Liechti, Bruderer & Paproth, 1995). The method is highly labour intensive and restricted to clear nights with a full moon (Bulyuk & Chernetsov, 2005; Liechti et al., 1995). The technique is useful until about 1km in altitude before the observer is limited by distance (Liechti et al.,

1995) and though most bird migration takes place below 1km radar has informed us in some situations can be between 5–9km (Liechti & Scaller, 1999) suggesting migration could be missed. Therefore the current Birdscan MR1 system offers constant coverage with little labour to quantify bird migration. The vertical looking radar can also allow the user to break down migration into lower taxonomic levels based on the wing flapping frequency of the bird, and could lead to more in depth compositional migration studies in the future.

This project differs from the majority of migration studies by being conducted at a non-conventional migration watchpoint, contrasting to work conductedat the Alps or Negev. It does however still shed light on the composition and variation of migration across the seasons. To my knowledge no calculated migration traffic rate has been publish for the United Kingdom so the calculated MTRs could be the first calculated for the country. With further refinement of technology and methodology, radar can continue to reveal migration in ever greater detail.

Chapter 4: General discussion

The movements and migration of birds has long been studied. There are however still many facets of migration that that are not fully understood. With these questions comes the development of technology and theories to explain them. Avian migration is hugely complex with numerous examples of migrant types, which have a vast array of migration strategies and responses to the challenges faced on passage.

In this thesis I have used vertical-looking radar to study the migration of birds in south west United Kingdom. The introductory chapter covers the theory behind migration, how it has been studied and how radar has been developed for monitoring avian movements. Chapter 2 describes the how BirdscanMR1 works, the data it is capable of collecting and how this can be presented. The chapter also covers how to determine detection ranges and calculate migration traffic rates, which are important aspects to consider for comparable and biologically meaningful radar studies. Chapter 3 further explores how the classifications based on flight type differ in their flight characteristics and rates of migration. In this chapter, the conclusions of my work are presented and I suggest areas for further investigation.

4.1 Conclusions of BirdscanMR1

Radar technology can provide insights to the flight behaviour and decision making of migrants and the vertical looking radar at the Lizard Peninsula, Cornwall offers the exciting opportunity to study the movement of birds with technology that is unique. The system can record the speed and direction the only dedicated ornithological VLR of its kind to do so, as well as gather information of the targets altitude and wingbeat frequency.

4.1.1 Wingbeat

The wingbeat frequency of birds can be retrieved from the echo signature by many radar systems. It is then up to the user how if at all these echoes are categorised, though common categories of passerine, wader and swift are usually settled upon. Birdscan MR1 can refine classification of echoes to a lower taxonomic level than ever before and do so autonomously. There is still

issues with classification which can only be addressed with further target validation and by comparing echoes to see if classes have discernible differences. For my thesis, I combined these lower level classifications e.g. small swift, large swift and huge swift in to one category to have sufficient sample sizes. With these classifications based on wing flapping pattern ,which is heavily influence by air density, weather mass, wing physiology) (Pennycuick, 1996) and ground speed, we can begin to hypothesise on species that comprise these classifications. The majority of passerine echoes in autumn are in all likelihood winter thrushes from Iceland and Fenno Scandinavia, which are abundant in the southwest of England from October when the bulk of passerine echoes occur. These birds also likely make up a large proportion of spring echoes when they make their return journey but could also be joined by other nocturnal migrants such as chat species chat species (wheatear *Oenanthe oenanthe*, robin *Erithacus rubecula* etc.). The continuous flapping wader type echoes are likely to be made up from various wader species as well as ducks that also share this continuous wingbeat pattern. Swift echoes could be more problematic as they may relate to birds such as the swift *Apus apus*, however diurnal ground truthing data (not discussed in this thesis) found that gulls typically herring gull *Larus argentatus* and common buzzard *Buteo buteo* all produced swift type echoes due to their flap glide component. The ability to classify echoes into distinct groups (passerine, wader and swift) formed the corner stone of my investigation, allowing the comparison of flight characteristics between groups and between seasons. However, further studies are needed to confirm which species might make up these classifications.

4.1.2 Altitude

The birdscan MR1 system can record quantitative height distributions of migrating birds without the sampling bias found in tracking radars that are not used with a carefully executed target selection protocol, which result from following single targets. Therefore, accurate altitude profiles of where migration occurs can be determined. I found that there were class differences in flight height with wader flight type birds consistently flying the highest of the three classifications and swifts the lowest. These differences between classes could be linked to physiology and flight pattern. Larger birds may be able to reach

higher altitudes where winds can be much stronger and therefore tolerate these conditions. Additionally, bird classes like swift type that have large glide components may choose to stay at lower altitudes as they could be more susceptible to wind displacement as they use less powered flight. The altitude at which a bird flies can have an important impact in determining its travelling efficiency (Liechti, 2006; Schmaljohann, Liechti, & Bruderer, 2009). Flight height seems to be predominantly linked to birds selecting for the most favourable winds to travel in (Liechti, 2006; Schmaljohann, Liechti, & Bruderer, 2009).

4.1.3 Speed
Our system is currently the only dedicated bird vertical looking radar to be able to record the speed of targets. Measuring the speed of targets can first aid in discriminating and classifying targets. After this it is possible to answer behavioural questions of flight speed like how birds alter flight speed in relation to geographical barriers or in response to climatic conditions. I compared the flight speed of the three classes in both spring and autumn. Swifts were consistently the fastest fliers in the two seasons whereas waders flew the slowest in the autumn and passerines slowest in the spring. The change in slowest class for each season suggest that different species are being recorded in autumn compared to spring. Winter thrushes that are recorded in higher numbers in the autumn are some of the fastest flying passerines and could explain why the class flew faster than the wader type birds. The slower speed of passerines in spring which goes against theories that birds are under increased pressure to fly faster in spring to avoid competition at breeding sites, but this could be down to change in species being recorded.

4.1.4 Direction
Direction can be calculated using the phase differences of entry and exit angles of objects in the radar beam, a unique feature to birdscanMR1. I found that all classes flew in opposite directions when comparing season with spring all classes in spring flying in a north westerly direction compared to a south easterly direction in autumn. There was no significant difference in flight direction between classes in any given season. The chosen flight direction of birds is likely going to be affected by geographically barriers and dominant winds encountered on passage. It could be very likely that all classes are re-

orientating once reaching the tip of the South West Peninsula, in order to avoid flying in the wrong direction over large stretches of ocean.

4.1.5 Migration traffic rate

Migration traffic rates are the standard metric of quantitative migration studies. The number of birds crossing a virtual line of fixed length perpendicular to the flight direction can be calculated for a given period. There for MTRs can be calculated for simply an hour or more usefully over a night month or season (Chapter 1). As the birdscan system could be left unattended to record birds passing through the beam seasonal MTRs were calculated. In my study differences were found between spring and autumn as well as differences between the classes. Autumn MTRs were higher with passerines having the highest MTR of any class.

Mean MTRs are much lower in Cornwall than when compared to MTRs calculated in other radar locations (Zehnder et al., 2001). However these sites are typically in known migration hotspots. For example, the Falsterbo peninsula, Sweden (55° 23' N, 12° 50' E) geographically is sparse with a few small stand of bushes and trees in otherwise open country (Zehnder et al., 2001). This coupled with the spit protruding into the Baltic sea makes it perfect for funnelling migrants (Zehnder et al., 2001). With Cornwall being at the far edge of the continent and leading into the Atlantic birds have very few options or reasons to travel over the peninsula. This suggests that Cornwall itself is not a prime migration location.

4.2 Where next?

There is a conservation role for radar, understanding the numbers and occurrence of migration for effective protection, as well as being a tool to understanding the behaviours of bird migration (which in turn may have conservation value).

Radar can be used to identify priority areas for conservation. Such as flyways that would be sensitive to developments or staging sites that experience high traffic of migrants coming to use them. Similar Birdscan systems are currently being used to protect bird populations in through windfarm sites. BirdScan MV1

is specifically designed to monitor air space around turbines using a fixed-beam vertical radar. It records bird and bat movements in real time so that if a pre-set migration threshold is passed, the device holts the operation of the wind turbines. As soon as the biological traffic decreases, MV1 allows the turbines to continue generating power.

Birds are expected to behave optimally when migrating by minimising the energetic cost of travel and maximise the distance travelled, an idea that has been encompassed in "optimal migration theory". Optimal flight can be achieved by utilising the flow of wind both for favourable tail winds and to counteract drift effects. To be able to compensate for flows birds are required to know how to orientate themselves and so sense then wind, as well as use the earth's magnetic field and visual land marks to navigate. To answer these and similar questions, information on a birds flight direction alignment, speed, flight altitude and radar systems offer the most complete solution to monitor these behavioural question in situ.

4.2.3 Future investigations

Given the Birdscan MR1's ability to record highly detailed data it is hoped it can be used to validate other less precise weather radar in the OPERA network (Operational Programme for the Exchange of weather RAdar information), which are currently try and retrieve biological data from these systems for the European Network for the Radar surveillance of Animal Movement (ENRAM). Therefor this single radar system may have major implications for understanding the much larger patterns of migration across the continent.

Of particular interest would be to see how weather conditions affect the flight performance of birds. This is no easy feat due to how variable air conditions can be at difference strata. But by being able to record weather at these altitudes, which have active bird migration it can possibly provide information to best explain movements. Also, due to the coastal location of the radar at the base of the lizard peninsula it may be possible in the future to see how birds arrive and depart over the physical barrier of the English Channel and potentially use the geography of the land to orientate.

The University of Exeter now has two highly dedicated radar systems for two different taxa in place at the same location, which is unique with no other

institution in the world currently in possession of similar equipment. Therefor a comparative study of insect and birds using the two systems seems like a natural progression for future investigations. Possibly avenues for exploration could be investigating if birds follow the movement of insect biomass on migration to utilise them as a food source. Alternative you could compare insect and avian movement strategies to see if they are susceptible to displacement from the wind and how they may compensate for this, if at all.

In conclusion, radar systems can monitor migration in a way not possible by other practices, with the subject of radar itself being diverse. Recorded target characteristics can vary with different radar systems used and at this time the Birdscan MR1 VLR offers the most complete set of functions to log a broad range of data. Information collected by radar equipment can be applied for conservation purposes or to help answer fundamental questions in bird movement behaviour. With a strong foundation of research already in place and with the constant refinement of technology it will be possible to further our comprehension of avian movement ecology and how they may be affected in the future.

Appendix
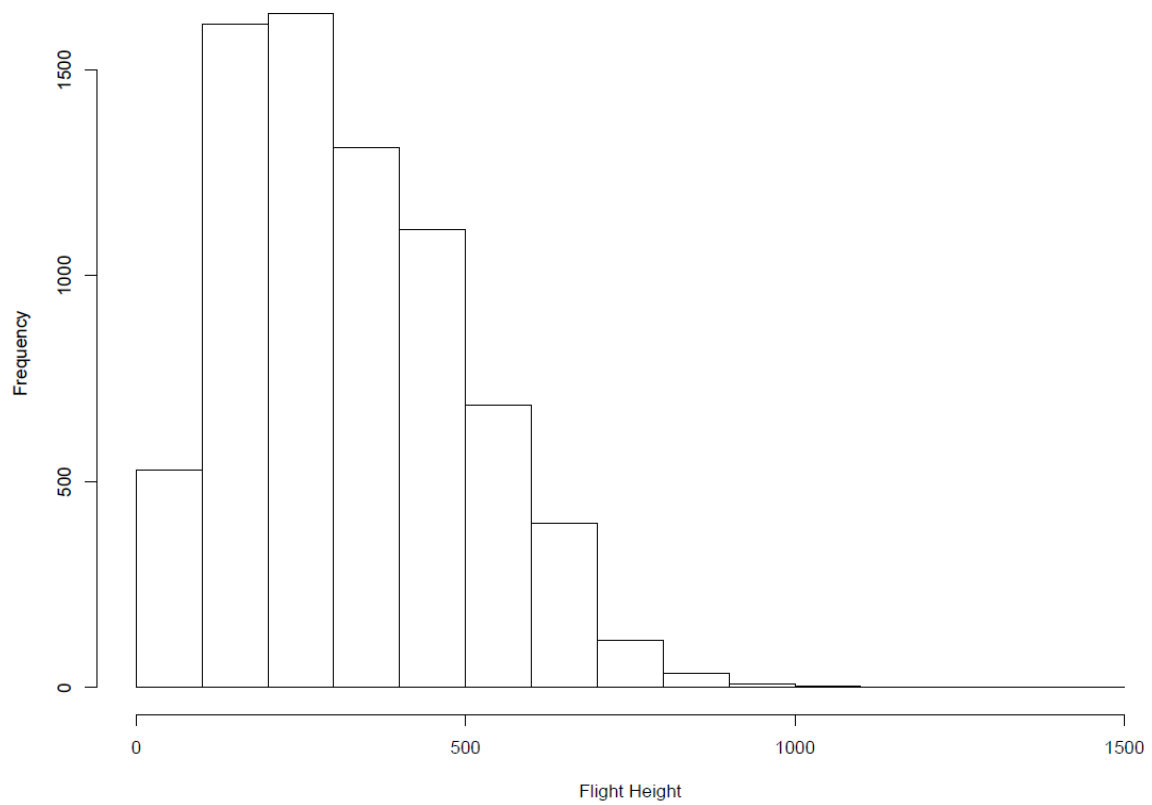
Figure S1: Flight height frequency histogram of all bird echoes from autumn 2015 and spring 2016
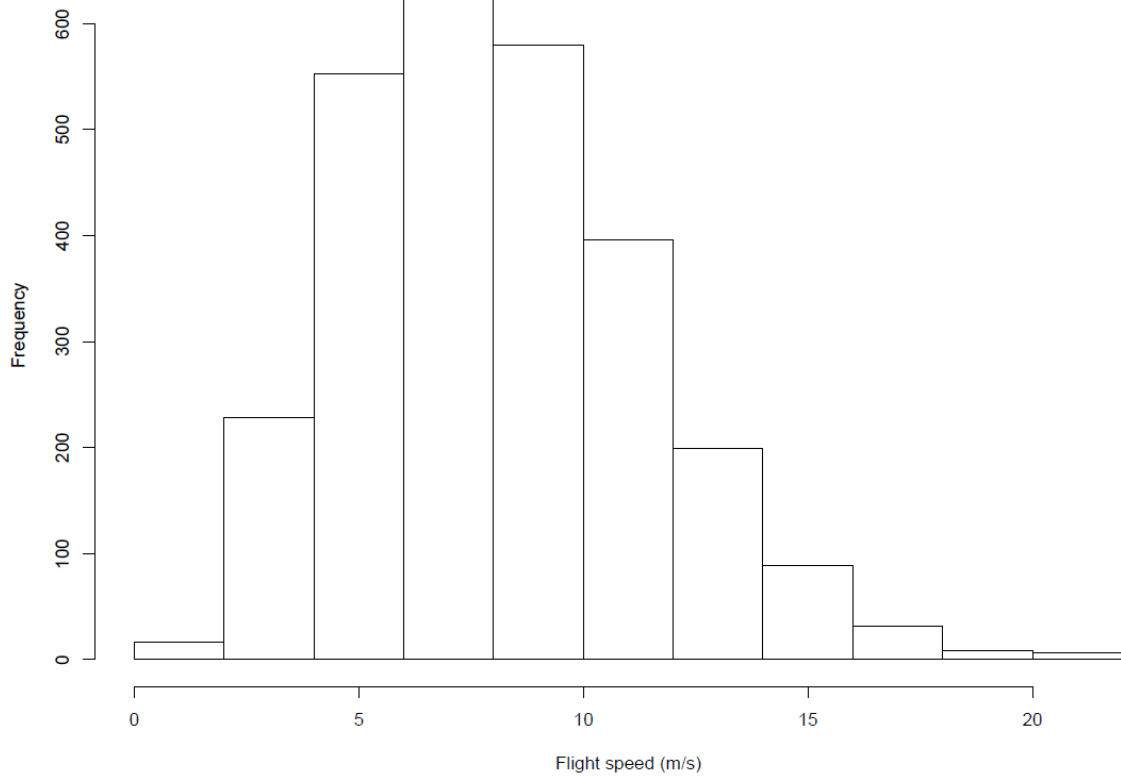
Figure S2: Flight speed frequency histogram of all bird echoes from autumn 2015 and spring 2016
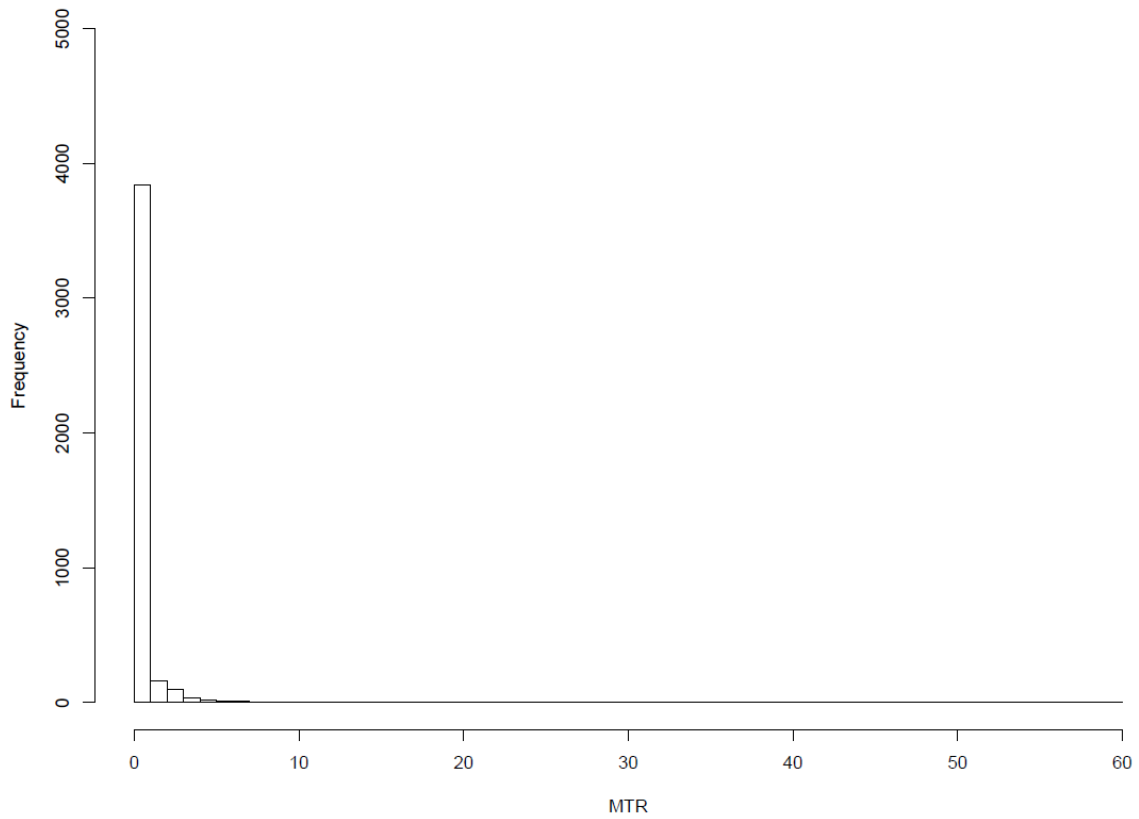
Figure S3: Migration traffic rate (MTR)+1 frequency histogram of all bird echoes from autumn 2015 and spring 2016

Table S1: AIC values for flight height models

Response	Model	AIC	Δ AIC	df.
Flight height	Intercept	98212	1709	7455
	Class	96626	123	7453
	Season	96952	449	7454
	Season + Class	96503	0	7452
	Fully Saturated	96505	2	7450

Table S2: AIC values for flight speed models

Response	Model	AIC	Δ AIC	df.
Flight speed	Intercept	14290	291	2742
	Class	14049	50	2740
	Season	14100	101	2741
	Season + Class	14029	30	2739
	Fully Saturated	13999	0	2737

Table S3: AIC values for MTR +1 models

Response	Model	AIC	Δ AIC	df.
MTR	Intercept	19570	10897.9	4229
	Class	9081.1	409	4227
	Season	9651.1	979	4228
	Season + Class	8730.5	58.4	4226
	Fully Saturated	8672.1	0	4224

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