ECOLOGY OF THE ENDEMIC MIGRATORY PASSERINE CYPRUS WHEATEAR *OENANTHE CYPRIACA*: THE EFFECTS OF CLIMATE CHANGE ON A RESTRICTED RANGE SPECIES

Marina Xenophontos

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ECOLOGY OF THE ENDEMIC MIGRATORY PASSERINE CYPRUS WHEATEAR *OENANTHE CYPRIACA*,

THE EFFECTS OF CLIMATE CHANGE ON A RESTRICTED RANGE SPECIES

By

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Submitted for the Degree of Doctor of Philosophy
to the University of St Andrews

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March 2015

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In the memory of my loving parents

Andreas and Ellie Xenophontos

ABSTRACT

Migrant birds may be vulnerable to climate change at different stages of their annual cycles especially on the breeding grounds, where changes in phenology may affect their ability to synchronise breeding with the peak of resources availability. Understanding how phenology of breeding, survival and productivity varies between and within years is therefore crucial to understand migrant population dynamics. This thesis describes this variation in the Cyprus Wheatear *Oenanthe cypriaca*, with particular emphasis on a colour-ringed population at Troodos, Cyprus, 2010 - 2012. Our results suggest that the phenology of breeding of Cyprus Wheatear is variable with breeding onset and number of breeding attempts probably varying with annual temperature variation. Minimum true survival rates were very high for a small passerine migrant, although they were probably sufficiently annually variable to profoundly affect annual population dynamics. For productivity, nest survival was very high and did not vary between years, or nesting attempts, or with clutch initiation date but it was significantly higher in the chick stage versus the egg stage. Post-fledging survival in the first 4 weeks was very high. Renesting probability was significantly different in all years, yet total productivity per pair was the same in each of three years. Cyprus Wheatears at Troodos showed such high productivity and survival that the population must be a major source population and this was reflected in the very high density of breeding pairs at the study site. Finally we used altitude as a proxy for variation in temperature and investigated how abundance, productivity and phenology in Cyprus Wheatears varied between and within years, from sea level to 1952 m, using transect surveys to record breeding birds across Cyprus. Cyprus Wheatears were common in all habitats and altitudes; altitudinal temperature variation probably affected the occurrence of double brooding and so the timing of chick production, but not the onset of breeding. The results suggest that Cyprus Wheatears are already very well adapted to high variation in temperature within and between seasons, changing investment accordingly.

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TABLE OF CONTENTS:

CHAPTER 1. INTRODUCTION: ECOLOGY AND POPULATION DYNAMICS OF MIGRATORY PASSERINES IN CHANGING WORLD

This thesis will explore the ecology of the endemic migratory species the Cyprus Wheatear, focusing on its breeding cycle in an area with the highest breeding density on the island and the phenology of its breeding with respect to seasonal variation and altitude. Islands have high levels of endemism but our knowledge of island endemics is limited. We thus know little of how pressures like life-cycle events, can act towards population declines and extinction. Studies on the Cyprus wheatear have been sporadic and limited, thus this thesis highlights the ecological aspects of a little studied species which may provide an interesting model of how island endemic birds adapt and deal with climate change.

This thesis examines the breeding ecology and survival of a migrant passerine species – aspects in common with all bird species such as clutch size, nest survival and annual survival, but from the point of view of how such aspects might be particularly affected by climate change that is more likely to affect a migrant species because of their timing and time constraints.

First, to serve as a general introduction and justification for the intense study of the phenology, productivity and survival of a passerine migrant, I will discuss the issue of anthropogenic climate change and the current observed decline of Afro-Palearctic migrants. I will then discuss how population dynamics arise, in the general case and in the specific case of a migrant. I will then introduce the study species and system and the specific aims of the thesis within the context of understanding the population dynamics of Cyprus wheatears as a consequence of environmental variation.

1.1 The problem of climate change

Climate change has profound effects on birds leading to a shift in timing or phenology of their reproduction. The environmental factors most important in determining the time window for breeding are those that determine the phenology of the prey of the bird species of interest (Visser et al. 2006), which may consequently determine whether the species is in optimal condition for reproduction and the availability of resources for offspring. This relationship between when young are produced and the peak of resources to feed these young is therefore a crucial determinant of fitness (Thomas et al. 2001, Visser et al. 2006). Therefore one main way to assess the consequence of these shifts is a comparison of the rates of phenological change in the reproduction of birds with that of the food for their offspring (Visser et al. 2012). In some areas birds show such a phenological mismatch. This is hypothesised to arise by two mechanisms: either the cues used no longer accurately predict the peak in food abundance (the cues hypothesis), or the fitness costs of egg production and/or incubation of laying early enough to match reproduction are substantial in early spring and are not compensated by the fitness benefits of a better timed reproduction (constraint hypothesis) (Visser et al. 2012). Ideally the mismatch between resources and reproduction is measured, but in practice many studies have identified mismatch by correlating productivity to environmental variation, and this is the approach adopted in this thesis.

The increase in the Earth's temperature reported during the last few decades (Houghton 2002) in response to climate change is clearly influencing ecological processes (Walther et al. 2002b), where responses to global warming results in plant phenology advancing and birds exhibiting earlier arrival and breeding in warmer springs. Shifts are unequal across the trophic chain, thus changes are different across the globe with increasing temperature in southerly latitudes and increasing rainfall in the north (Easterling et al. 2000, 2003). The annual cycle of migratory birds has to coincide with seasonality changes and environmental fluctuations, hence individuals use the tropics for wintering and the temperate region for breeding. Spring weather changes may impose asynchrony on the phase relation between predictive daylength information and food peak which consequently reflects energetic and fitness costs on, for example, tits (Visser et al. 1998). For example, Both and Visser (2001), showed that the timing of breeding for Pied Flycatcher *Ficedula hypoleuca* in the Netherlands, was mismatched with optimal breeding time of the species, suggested an arrival time constraint – i.e. phenology mismatch.

Phenology mismatch may be a major problem for some species, as with the pied flycatcher mentioned above. Short-distance migrants show greater advances in arrival date than do long-distance migrants (Forchhammer et al. 2002). Thus warmer springs may lead to greater survival of short-distance migrants and residents and an earlier onset of breeding, whereas the resulting increased competition may disadvantage long-distance migrants (Lemoine and Bohning-Gaese 2003). For insectivorous Afro-Palaearctic migrants breeding in the Netherlands, species that used forests declined most strongly; a habitat that is characterized by a short spring food peak; whereas species that live in marshes where food is less seasonal the declines were less (Both

2010, Vickery et al. 2014). Food peak mismatch was documented to be one of the possible causes of the relationship between timing of migrant declines in the UK and wintering latitude, with species wintering further south tending to exhibit more recent declines (Thaxter et al. 2010). Thaxter *et al.* (2010), used bird population trends to test the importance of breeding habitat, predation risk to nest sites, species climatic niche, migration strategy and over-wintering bioclimatic zones of migrants. They found that farmland birds declined more, reflecting agriculture intensification. Birds with towards with northerly European distributions showed larger declines than did southerly-distributed species. Larger population declines were recorded for Afro-tropical migrants than for species wintering in Europe or in UK, and species over-wintering in both arid savannah and in humid bioclimatic zones in Africa showed the strongest decreases in population. Furthermore, Sanderson *et al.* (2006) found that long-distance migrants are more susceptible to agricultural intensification on their European breeding grounds than short-distance migrants and residents, again suggesting some sort of phenological mismatch.

Temporal and spatial variation of global warming trends is considerable however, differentially affecting migratory birds' annual cycles from the tropics to the temperate areas. Thus warming temperatures may advance, retard or cancel out effects on a particular species' spring phenology. Marra (2005) suggested that the relationship between the timing and the rate of spring migration of long-distance migratory birds and variables such as temperature, the North Atlantic Oscillation (NAO) and plant phenology and the timing of migration, is flexible and can be adjusted in response to variation in weather and/or phenology along migration routes. Thus, these results suggest that long-distance Nearctic-Neotropical migratory birds adjust their timing by adjusting their rate of migration to match annual variations in ambient temperatures or associated factors such as leaf emergence and resource availability. Although there may be cases where migrants are affected by climate change and phenology mismatch, many migrants are flexible and indeed migrants are likely to be pre-adapted to climate change (Cresswell 2014).

1.2 The problem of migrant declines

In recent decades Afro-Palaearctic migrant birds' populations have declined. Vickery *et al.* (2014), review evidence of different factors that are responsible for driving declines of Afro-Palaearctic migrants, with focus on European-breeding species, and they provide a synthesis of the potential causes according to season (breeding and non-breeding), factor (habitat loss, nest predation) and parameter affected. Their review suggests that human-related habitat change is the most important factor affecting Afro-Palaearctic declines across both breeding and non-breeding areas, with predation and climate change also being important factors in breeding areas, and hunting during the non-breeding season for some species. Additionally, they stated that threats for long-distance migrants during the breeding season were associated with farmland and forest practices, as well as agricultural abandonment. Regarding the non-breeding season, the wintering and staging areas, declines of Afro-Palaearctic migrants are related to ecological conditions which are strongly associated with rainfall; thus the Sahel drought has been frequently linked to declines of many species. Drought conditions and thus deteriorating ecological status of wintering habitats causes density-dependent overwinter mortality due to reduction in the carrying capacity of habitats and consequently food limitation, competition and disease. A widespread deterioration of the habitats in wooded savannah, climate changes and the drought are associated with species decline (Wilson and Cresswell 2006).

Declines of European migratory bird populations that winter in arid savannahs of tropical Africa may arise from the same cause, from the effects of drought and increasing desertification, whereas declining in North America migratory bird populations have been attributed to the anthropogenic land use changes in their breeding range and, in particular, forest fragmentation which increase both predation and parasitism. Migrant populations can be influenced by factors operating on both wintering and breeding grounds, and population size may even be regulated at restricted stopover sites due to high densities and limited food supplies (Newton 2004). Overall, the cause of migrant declines are likely to be species specific, related to the location of breeding areas and passage routes, with an over-arching effect of habitat reduction on the wintering grounds causing declines for all populations (due to only very large scale connectivity) (Cresswell 2014).

There is growing evidence to suggest that migratory birds' declines are caused throughout the annual cycle by changes in winter and breeding season conditions and stopover areas. Conditions on the breeding ground are likely to dominate however (Cresswell 2014). For example, Willow Warblers *Phylloscopus trochilus* that breed in Scotland are increasing and those that breed a few hundred kilometres away in England are declining, and both probably winter in the same areas (Morrison et al. 2013). General patterns can however be found to link declines of Palearctic migrants to conditions on the wintering grounds if studies are conducted on a suitably large scale (Schaub et al. 2005, Cresswell 2014). Thus migrants wintering in arid rather than humid zones right across West Africa were identified to have declined much more, identifying historical drought as a possible large scale cause (Sanderson et al. 2006), while more recently the reverse has occurred: that humid zone migrants are declining faster, implicating habitat destruction as a possible large scale cause (Ockendon et al. 2012).

1.3 How population dynamics arise

Declines or changes in bird populations arise because of individuals not matching offspring production to compensate for their inevitable mortality (discussed in detail below), but there are other processes that act on a larger scale to determine population dynamics. A key issue is density-dependent mortality. For example, Arcese *et al.* (1992) studied the population dynamics of the Song Sparrow *Melospiza melodia* on Mandarte Island and found that reproductive output was strongly dependent on nest failure due to parasitism and predation. Furthermore, the rate of juvenile recruitment was inversely related to the density of adults because of interference competition for breeding territories between adults and yearlings. Thus, models of the population indicated that density-dependent reproductive success or density-dependent recruitment of locally hatched juveniles regulated population size. Thus a population at carrying capacity may have substantial mortality, which is then compensated for by density-dependent increases in productivity.

Another key issue in population dynamics is the meta-population idea (Levins 1969). Populations exist as source and sink subpopulations, where sources are demographically viable with juvenile production exceeding adult mortality, whereas sinks are demographically inviable where juvenile production does not compensate for adult mortality and ultimately disappear unless immigrants become established (Pulliam 1988). Thus alteration of source habitats may affect the structure, function and size of the overall population. Sink populations in sites with poor quality habitats are maintained by immigrants from source populations on a large scale and so alteration to these habitats may make little difference. For example, Holmes *et al.* (1996) assessed habitat-specific demography of long-distance migratory Black-throated Blue Warblers *Dendroica caerulescens*, and showed how the species selects between habitats in density, reproductive performance, and local survival consistent with a sink and source metapopulation model. Similarly, studies on migratory Oven-bird *Seiurus aurocapillus*, Red-eyed Vireo *Vireo olivaceus* and Wood Thrush *Hylocichla mustelina* in the Neotropics showed that when the species bred in fragmented forest their populations appeared to be sinks, whereas in contiguous forest, they were sources because of increased nest predation and parasitism in fragmented habitats (Donovan et al. 1995b). The effects of habitat fragmentation on source/sink demography of Neotropical migratory birds was then modelled, and findings emphasized the need to identify and protect large intact source habitats throughout a species' breeding range to ensure long-term metapopulation survival (Donovan et al. 1995a). Therefore, population size and growth rate may vary as functions of the relative proportion of different habitat types available (Pulliam and Danielson 1991). For many populations, a large proportion of the individuals may occur regularly in 'sink' habitats, where within-habitat reproduction is insufficient to balance local mortality. Nevertheless, the population may persist in such habitats, being locally maintained by continued immigration from more productive 'source' areas nearby (Pulliam 1988). It is therefore important to consider source/sink dynamics when determining the factors that influence population dynamics.

Another key issue to population dynamics and indeed declines of migrants is site fidelity (Cresswell 2014). The population dynamics of species inhabiting complex habitat mosaics involve two components: the distribution of individuals among habitats, and habitat specific demographic rates (Pulliam and Danielson 1991). Thus the distribution of individuals between habitat types depends on the selective abilities of the species. Since reproductive and mortality rates can vary between suitable and less suitable habitats, populations may be determined by movement and subsequent distribution across available habitats. Animals may not be free to move however. This may depended on the availability of alternative habitats, competition for these habitats, and information on whether these are available and their location. Natal philopatry and site fidelity to breeding and wintering areas is therefore very important, as is determining the factors that might influence this.

1.4 Migratory passerines, like all birds, have population dynamics dependent on the trade-offs between breeding output and mortality rate which in turn depends on environmental variation

Birds survive from one breeding season to another, grow to maturity and reproduce: the process of balancing these energetic conflicting demands under the different ecological conditions that occur in different environments results in a distinct diversity of life history traits evolving amongst populations or species (Bennett and Owens 2002). For example, in arid ecosystems there is a fluctuation in primary production due to scarce and unpredictable rains, which results in variation between years on biological processes such as the reproduction of birds. Illera and Diaz (2006), analysed between year variation in the reproductive output of the narrow range endemic Stonechat *Saxicola dacotiae* of the semiarid island of Fuerteventura (Canary Islands Spain) with respect to the effects of rainfall, temperature, food availability and nest predation. They found that the onset of breeding and reproductive investment (number of clutches and clutch size) was strongly related to rainfall which consequently was correlated with arthropod availability which forms the species main food resource. Their findings indicated that pairs bred once in dry year where clutch size found to be smaller and twice in wet years when clutch size was larger. Such trade-offs cause variation in the fitness of individuals within the population and thus lead to population dynamics (Caughley 1994). For example, Clark and Martin (2007), showed that variation in population dynamics is inherently related to the life history characteristics of species. They showed nest success and juvenile survival exert the largest effects on population growth in species of birds breeding in northern Arizona with moderate to high reproductive output, thus variation in clutch size or fledgling production – and also for any other life history trait - provides a gradient for understanding constraints on population growth.

Natural selection favours those life history traits which allow the individuals possessing them to maximize their overall genetic contribution to subsequent breeding populations and these should depend on environmental conditions. Thus nidicolous birds living in temperate areas should decrease clutch size as the season progresses in order to fledge chicks in time for winter (Stearns 1976). The evolution of life history tactics is influenced by spatial and temporal variations of relevant environmental variables, where the most relevant to life-histories are food, temperature, breeding sites, refugia, competitors and predators (Stearns 1976). But with any level of environmental conditions there are many possible trade-offs because breeding output will have a cost on parental survival, future reproduction and offspring conditions. For example, conflicts between energy use for reproduction and fat storage cause a trade-off between reproduction and parental survival, especially in passerines where energy storage reserves tend to be limited (Zera and Harshman 2001), thus although increasing fat storage could support reproduction, there are survival costs in terms of energetics or reduced flight agility (Gosler et al. 1995).

There is therefore an evolutionary ‘trade-off’ between annual fecundity and survival such that high investment in reproduction reduces the chances of surviving to breed again. Bennett *et al.* (2002), stated, in common with Lack (Lack 1947, Lack 1948, 1968), that there is much evidence that some avian families have evolved slow development, delayed breeding, reduced reproduction effort and increased adult survival rate, whereas others have evolved the opposite pattern, thus, resulting in the ‘slow-fast’ life-history continuum. For example, Martin (1995), examined variation and covariation of life history traits of North American Passeriformes in relation to nest sites, nest predation, and foraging sites to examine the possible roles of these ecological factors in life history evolution of birds. He found that interspecific differences in nest predation were correlated with much of the variation in the life history traits, thus, increased nest predation was associated with a shortened nestling period and both were associated with more broods per year. Additionally he found that the numbers of broods was associated with adult survival, although ultimately food limitation probably caused the trade-offs between annual fecundity and adult survival.

Greater nest predation may favour smaller clutch sizes, allowing more energy for renesting attempts following failure (Bulmer 1984), whereas, saved energy can also be used for additional broods following any success (Martin 1987).

Although food limitation underlies much of the variation in life history traits for birds, annual fecundity is strongly inversely related to adult survival (Martin 1995): thus all things being equal in terms of food supply, one species might invest heavily in a large clutch and pay high survival costs whereas a second might lay a smaller clutch offset against a higher adult survival probability allowing it to breed again in another year (Bennett and Harvey 1988, Saether 1988). Generally, parents should value their own survival over their offspring in species with higher probability of adult survival and fewer offspring. For example, Southern Hemisphere birds have higher adult survival and smaller clutch sizes than Northern Hemisphere species and they respond to nest-predation risk by reducing mortality risk to themselves, whereas northern parents respond more to reduce risk to their offspring with greater risk to themselves (Ghalambor and Martin 2001). Such trade-offs can vary at the level of individuals within a population, populations within species and, of course, between species and are fundamental to understanding to how a population will be affected by environmental change.

1.5 Migratory passerines can also move to more favourable environments to reduce environmental variation therefore changing trade-offs between breeding output and mortality rate

Migratory birds, however, also adopt a strategy of moving between environments, and thus have a further trade-off between the costs of moving set against the homogenisation of environmental conditions. Thus migratory bird population dynamics can be regulated by different habitats in both summer and winter, and connecting habitats in between (Holmes et al. 1996, Sherry and Holmes 1996). For example, the important consequence for population dynamics that may arise from the seasonal change in the distribution of migrant individuals among habitats and their relative success in those habitats was examined for the long-distance migratory Black-throated Blue Warblers, and population structure and reproductive output was found to be regulated by the availability, distribution and extent of high quality breeding habitat (Holmes et al. 1996). However, in another long distance migrant the American Redstart *Setophaga ruticilla*, it was the quality of the winter habitat affecting juvenile survival and so losses of tropical habitats that were most likely to have negative effects on population in the following breeding season and so overall declines (Norris et al. 2004).

Migration is a dynamic response of birds to changing environmental conditions through which many species track seasonal productivity outputs across large environmental gradients (Baker 1978), and show great diversity of migratory strategies among and within species due to differences in habitat seasonality which in turn is associated with latitude and elevation (Herrera 1978, Newton and Dale 1996). The strategy of migration enables species to exploit seasonal habitats for both breeding and wintering and thus to benefit from resources and therefore increased productivity. However migration may also involve important costs related to energy consumption during travel, exposure to predators and weather hazards and foraging unpredictability, all of which are associated with mortality costs (Berthold 1998, Perez-Tris and Telleria 2002). For example, migrating birds must travel through unfamiliar areas and alien habitats, making it more difficult to find food and avoid predators (Newton 1998). Newton (2007), provided a review of weather-related mass-mortality events in migrants, such as in-flight losses caused by storms and other adverse weather on route, unseasonable cold weather soon after arrival in breeding areas, and unseasonable cold weather before departure, and found that local breeding densities could change from previous years by 25-90%, depending on species and area.

Thus the evolution of different migratory strategies must involve changes in behaviour, ecological and life history traits to compensate for the costs of migration (Berthold 2001), but also particularly migratory birds need to adjust their life cycles to complete their breeding and moult outwith the migration period (Gwinner 1996). Migratory birds like long-distance migratory passerines are constrained by reproduction time and moult which need to be completed before migration, hence breeding and post-nuptial moult may overlap (Hemborg et al. 2001). Thus, studies on Wood Thrushes showed that late nesting thrushes postponed feather moult and individuals in poor energetic condition migrated to the tropics significantly later (Stutchbury et al. 2011). Although birds may migrate and so breed and winter in seasonal habitats to maximise fitness, they show increased vulnerability to change that can act on both the breeding and wintering ground and along the migratory routes, and so vulnerability to anthropogenic threats such as habitat losses and degradation, increase of predators and competition and global scale climate change (Berthold and Terrill 1991).

1.6 Migrant population dynamics

Migrant population dynamics thus arise from productivity and survival, with key aspects of productivity particularly associated with migrants being timing of breeding, and key aspects of survival being survival during a juvenile’s first migration and migrant survival being dependent on a chain of suitable habitats. Here I review productivity and survival as they affect all birds and in the special case of migrants. I then explain how I will investigate productivity and survival in the special case of Cyprus Wheatears.

1.6.1 Productivity

General Timing

The timing of seasonal life-cycle events, or phenology, is considered to be a major structural force in ecology and evolution of the biological processes of organisms (Forrest and Miller-Rushing 2010). The timing of breeding is a crucial component to productivity (Lack 1968, Perrins 1970). Empirical evidence suggest that breeding conditions generally decline over the course of the breeding season in songbirds (Verhulst et al. 1995). For example, Verhulst and Nilsson (2008), studied the extent of seasonal variation in fitness components due to timing and individual quality and the combination of the two. They found that seasonal variation in reproductive success was dependent on both, with better birds tending to be early breeders with both of these effects contributing to higher breeding success.

Timing of breeding is associated with food availability for females to be in sufficient body condition to produce eggs and for rearing offspring during the optimal food peak. Perrins (1970) found in Great Tits *Parus major* that the date at which the female actually lays is a result of an interaction between the evolutionary advantages of early breeding where more surviving young can be raised and the physiological state of the female. Thus there is a selection for early breeding which is prevented until a certain amount of food is available. In tropical areas, for example, insectivorous species show a peak of breeding during the wet season, likely coinciding with the large increase in invertebrate numbers (Poulin et al. 1993). Cox *et al.* (2013) showed that tropical savannah birds concentrated their breeding around predicted periods of increased food availability coincident with rainfall.

Phenology mismatch

Migrants must also time their annual migrations to be able to breed at the right time to maximise fitness (Perrins 1970, Newton 2008), with early arrival at the breeding ground generally being associated with quality of the territory, mates, an increase in breeding attempts and higher survival rates of offspring (Dunn 2004). But environmental conditions and migratory strategies throughout the different annual cycle stages of migratory birds, in different geographical areas will also affect their breeding output. Migratory passerines must adjust life cycle events – migration, breeding, moult – in a temporally and spatially variable environment, involving a suite of physiological mechanisms and environmental cues to ensure correct timing. Unavoidable overlaps in the timing of life-cycle events may result in further trade-offs.

Breeding output is particularly affected by constraints caused by migration such as late arrival for the breeding season and/or poor condition delaying breeding (discussed in detail with respect to effects on clutch size and timing below). For example, early arriving American Redstarts select higher quality territories, initiate earlier breeding, and consequently may experience greater reproductive success (Smith and Moore 2005). Barn Swallows *Hirundo rustica* return to their breeding grounds earlier in Italy when there are favourable ecological conditions on their wintering grounds in Africa as measured by higher values of the Normalized Difference Vegetation Index (NDVI) (Saino et al. 2004). Late arrivals can result in a mismatch with the food peak for chicks, resulting in changes to the occurrence of second broods and even delayed moult at the end of breeding. For example, Ogden and Stutchbury (1996), examined the constraints on double brooding Hooded Warblers *Wilsonia citrina*, and found that individuals were usually feeding fledglings while undergoing moult or they delay moult, imposing high energetic costs due to overlap with fledgling care or a delay to migration, with survival consequences for both adults and offspring through limitations in acquisition of a winter territory. Thus conditions on the wintering ground may determine breeding timing and further constraints during breeding.

Arrival times and so timing of breeding of migrants, often shown to be a consequence of climatic conditions on the wintering grounds, or on passage are crucial to population dynamics (Brown and Brown 2000, Jonzen et al. 2007). For example Both and Visser (2001) showed that in Pied Flycatchers migration is probably triggered by day length change on the wintering grounds, but climate change on the breeding grounds has advanced their food peak so that a significant part of the population arrives and lays too late to exploit the peak of optimal food resources.

Robson and Barriocanal (2011), however, examined the effect of changes in the environmental conditions on wintering and passage area of 13 trans-Saharan passerines during their spring migration, and found that annual variation in the mean date of passage was positively correlated with vegetation growth (the NDVI) and most species advanced the timing of their passing, thus ecological conditions in both winter quarters and *en route* were the major influencing factors of spring arrival at breeding ground.

Furthermore, Gordo (2007) reviewed the potential climatic and weather mechanisms underlying the detected shifts in migratory dates of spring arrivals at the breeding ground. He documented the effects of climate and weather in departure areas on the plasticity of migration onset, showing generally that there is phenotypic plasticity in migratory phenology, in response to variable ecological conditions in the wintering quarters allowing individuals to improve body condition and depart earlier for the breeding grounds. An important variable that was documented in his review was the physiological condition of individuals in the departure area during the days/weeks preceding migration onset. Pre-migratory body condition (fuel stores) can depend mostly on occupied winter habitats, and therefore food resource availability on the wintering grounds: these, as above, may be determined themselves by breeding timing the previous year however.

Long distance-migrants may be particularly constrained in their adjustment of arrival date to climate changes on breeding ground compare with short-distance migrants (Both and Visser 2001). In long distance migrant birds the potential for phenological mismatch is particularly pronounced because species must coincide their movements and life history to seasonal conditions 5,000 km or more away (Parmesan and Yohe

2003). In their review, Both *et al.* (2010), argued that long-distance migrant flycatchers, at their wintering grounds cannot therefore predict when spring starts at their distant breeding grounds. Thus, what cues may trigger migration to the breeding ground (which takes them at least 3 weeks) is not well known, however laboratory studies indicated that they probably use photoperiod (Gwinner 1996), which will, of course, not change with climate.

Clutch size

Clutch size and its variation is fundamental to productivity in birds, and provides one of the best examples of how life history trade-offs arise, and also how the timing of breeding is crucial. Clutch size varies interspecifically as a reflection of life history evolution in response to limits to food supply (Lack's hypothesis). Clutch size also varies intraspecifically in response to climate and competition for food on a large spatial scale (Ashmole's hypothesis) and on a temporal scale through a season (Perrin's hypothesis).

First, clutch size varies because of life history. In avian populations clutch size is a fundamental life-history trait because it reflects both fecundity and reproductive effort (Lack 1947, Bennett and Owens 2002). Lack's food-limitation hypothesis suggests that parents raise the maximum number of young allowed by food resources (Lack 1948), thus food availability determines whether birds tend to lay large clutches or reduce clutch size. Lack (1947, 1948) hypothesized that natural selection has caused clutch size in birds to evolve towards the size which produces the most surviving offspring and argued that the mechanism determining the upper limit to clutch size is parental ability to provide food for nestlings (Lack 1954, 1966). He hypothesised that food availability was the primary ecological constraint for population regulation and interspecific differences in all major life-history traits.

Second, clutch size varies because of spatial variation in food supply because of environmental conditions and competition. Ashmole’s clutch size hypothesis (Ashmole 1961) refers to the relationship between clutch size and latitude, where he outlined a simple hypothesis based upon seasonality of resources. He suggests that reproductive rate should depend upon both resource level and population density during the breeding season. He stated that if populations were limited by resources during the nonbreeding season, the level of resources available in the breeding season relative to population density would depend upon the seasonality of resources, and accordingly clutch size would increase in direct proportion to seasonality, irrespective of the average resource level. According to Ashmole’s hypothesis, resources limit population size during the period of greatest scarcity, usually between breeding seasons, therefore, the number of young that each adult can feed, and hence clutch size, is related directly to resource availability during the breeding season and inversely to the density of the population. Furthermore increasing seasonality causes greater overwinter mortality from resource scarcity at higher latitudes and provides more per capita resources for breeding that allows larger clutch size (Ashmole 1961).

Cody (1966) expanded on Ashmole’s hypothesis with a more general theory of clutch size. He stated that the more stable an environment is for a species, the greater the incidence of selection for *K* selection in population of that species, and the more interand intraspecific competition will occur and consequently reduction in clutch size: this would then be associated with environments in the tropics and oceanic islands, with climatic stability. On the other hand temperate regions where there are unstable climatic conditions will favour *r* natural selection. This also includes mountainous areas that are more unstable and unpredictable in their climate, which accounts for the general trend for species nesting at high altitudes to lay larger clutches, as with increases observed from the coast to inland (Lack 1947). Therefore Cody (1966) concluded that whereas in the temperate zones most energy is used to increase the reproductive rate *r*, in the tropics, the carrying capacity of the habitat is more important, resulting in smaller clutch size thus resulting in different phenotypes or genotypes correlated with different environments. For example, Drury (1961), in his studies on the breeding biology of four Arctic passerines on Bylot Island, Northwest Canada, suggested that the larger clutch size observed for the species could be explained as adaptation to increase *r* selection, due to climatic extremes and as a result of concentrating the annual production of young into one large clutch.

Third, clutch size varies because of temporal variation in food supply. Perrins (1965) stated that the reduction in clutch-size with date is an adaptation to a steadily worsening food supply for the young which consequently reduces the chances of raising many well-nourished young. He also hypothesised that birds that lay larger clutches would, on average, breed fewer times and thus, selection would favour genotypes of parents which laid slightly smaller clutches, but survive to breed again.

Data from a long term study of the population fluctuation and clutch-size in Great Tits showed that there was a great advantage in being an early breeder but not too early, due to constraints of sufficient food to produce eggs earlier in the season, thus, the species showed a delay in starting breeding early due to cold weather and so shortage of food. Although there was selective pressure towards breeding at the best time in relation to caterpillar availability (the main food resource for feeding Great Tit chicks), the time that they actually start to breed is related to the availability of spring food for females (Perrins 1965), and so clutch size in turn may show a quadratic function: initially low, peaking as the caterpillar food supply peaks and then declining as this food availability declines through the spring. Hence, he contended that many other species vary their clutch-size in the same way as the Great Tit, with the first clutches being largest and a steady decrease in clutch-size occurring throughout the season.

An example of this is Oberg *et al.* (2014), where long-term data (17 years) on the breeding phenology of Northern Wheatears *Oenanthe oenanthe* were used to investigate seasonal reproductive patterns. They found that the overall reproductive components - nest success (reflecting nest predation rate), clutch size, fledging success and recruitment success - showed a clear decline with season whereas subsequent adult survival did not. Their results indicated overall fitness declined with season, suggesting strong selection for early breeding, in their population of wheatears, due to the overall action of increasing nest predation rates and the deterioration of other environmental conditions (e.g. declining food availability, post-fledging predation) on the production and recruitment of young. They then argued, that the observed seasonal decline in clutch size was therefore likely to be an adaptive response (Rowe et al. 1994) to the deteriorating conditions. Here we have a clear example of individuals maximising their breeding output to environmental conditions, while maintaining a threshold adult survival rate: such trade-offs apply to all bird species but determining at which life-stage they occur (clutch size vs multiple brooding vs juvenile survival vs adult survival) is necessary to understand how, when and where changing environmental conditions will impact on populations.

Overall, clutch size is determined by the availability of food and so the environmental conditions that determine this. This is shown most clearly by inter-annual variation in clutch size, with years that have poor resource conditions for the survival of young affecting individuals laying larger clutches more than those laying smaller clutches, hence it is more advantageous to lay smaller clutches (Boyce and Perrins 1987). For example, clutch size in Great Tits is affected by resource abundance for both laying females and during brood rearing, caused by environmental variability, with severe consequences for young in large clutches in poor years. Selection for smaller clutch size is thus correlated with selection for reduced variance in clutch size among years (Boyce and Perrins 1987).

Factors that can determine clutch size in birds are thus any environmental variable that affect food supply. These include climatic variables, latitudinal gradients, density and predation, competition and parasitism (Klomp 1970). Rainfall in arid, semi-arid and subtropical areas, is the key determinant of clutch size (Boag and Grant 1984). For example Lloyd (1999) showed that there was evidence of an increase in clutch size in the Grey-backed Finchlark *Eremopterix verticalis* breeding in the arid zone in South Africa following heavy rainfall.

Nest survival rates

Clutch size predominantly determines breeding output as long as nests escape predation or accident. Nest predation is however an important cause of nest failure in birds and is the primary source of nesting mortality and can potentially affect life history traits in several ways, while also acting together with food limitation (Martin 1995). For example, Lack (1968), argued that the absence of selective pressures of predation on cavity-nesting parrots has resulted in low growth rates in comparison with growth rates of open-nesting altricial birds. Predation is the major cause of egg or chick losses in most birds (Newton 1998), and can be the greatest source of mortality for small landbirds (Ricklefs 1973). Accordingly, nest predation risk has been shown to be an important factor in shaping avian breeding habitat preferences and life history strategies that reduce predator impacts on nestling survival (Martin 1995, Roos and Part 2004). Nest predation risk may select for reduced clutch size and parental nest activity (Martin et al. 2000a). Nest predation is thought to fundamentally affect structure and function of bird communities (Martin 1993a, Martin 1993b, Martin and Wright 1993, Martin 1995, Martin et al. 1995). Because nest predation is a crucial source of the reproductive failure in passerines it therefore also has significant consequences for population persistence (Donovan and Thompson 2001).

Nest predation rates will depend crucially on the predator community and their behaviour. Predators on birds’ nests in the temperate regions mainly are mammals (rodents, mustelids and foxes), reptiles (snakes and lizards) and other birds (corvids and raptors). Most of these predators of birds are generalists, and take a wide variety of prey, switching from one prey species to another as opportunities and needs arise, and others are specialist, concentrating on one or a few main prey species (Newton

1998). Predation on a particular prey species also varies through time, in response to changes in the vulnerability of the prey, in the availability of alternative prey, or in the prey-predator ratio (Erlinge et al. 1983, Newton 1986). Rates of nest predation can vary widely between species within a habitat (Martin 1993a), between nest stages (Peak et al. 2004, Cottam et al. 2009), and intra-seasonally within a species (Weidinger 2009, Benson et al. 2010, Shustack and Rodewald 2010). Much of the variation is probably due to differences in the abundance and/ or activity of nest predators (Cox et al. 2012), with breeding birds and their nests facing different predation risk, depending on their nest site (e.g. on the ground vs. in a tree cavity), habitat (forest vs. grassland), and geographic location (Thompson 2007).

Seasonal variation in passerine nest predation is relatively common (Wilson and Cooper 1998, Post van der Burg et al. 2010) because predators' activity patterns or diet (Sieving and Willson 1999) shift across the breeding season. For example, Thomas *et al.* (2010) studied the predation of the Swainson's Warblers *Limnothlypis swainsonii*, to identify dominant nest predators. They found that predation by Rat Snakes *Elaphe obsolete* and raptors were more common during the nesting period, whereas predation by Brown-headed Cowbirds *Molothrus ater* occurred more during incubation. Additionally, they found that the risk of predation by raptors and cowbirds decreased throughout the breeding season, whereas, rat snake predation risk increased. Specifically they found that rat snakes and raptors cause higher predation risk during nestling period using parental activity as a cue, because nestlings are more profitable prey. In another example, Cox *et al.* (2012) investigated whether temperature influenced predator-specific rates of nest predation by analysing data from Golden-cheeked Warblers *Setophaga chrysoparia*, Black Capped Vireos *Vireo* *atricapilla*, Indigo Buntings *Passerina cyanea* and Acadian Flycatchers *Empidonax virescens*. They found that rates of nest predation by snakes and birds increased as daily maximum temperature increased (i.e. as the season progressed), whereas predation by mammals was essentially invariant in response to temperature. Changes in the timing of nesting and phenology mismatch effects due to coincidence of nesting with a particular activity pattern of an important nest predator may then be very important in the population dynamics of a species.

Nest predation risk varies crucially with nest stage because eggs are much less conspicuous than nestlings which may be noisy and which require regular visits from the parents so revealing the nest location. Thompson (2007) found that temporal factors affecting nest predation can include year, time of season (date) and stage of nest cycle (laying, incubating, nestling). Specifically, he found that timing of risk within the nest cycle can be related to variation in cues provided by prey (eggs or nestling) or parents, where eggs may be more exposed during laying than incubation, nestlings may provide more cues than eggs and older nestlings may provide more cues than younger nestlings. Additionally, he argued that parental behaviour, such as the amount of time spent on the nest or number of trips to the nest, may vary the cues provided to predators. In view of that, several studies have found lower nest success during the nestling stage (Young 1963, Robertso 1972, Schaub et al. 1992, Burhans et al. 2002), due to increased cues provided by parents' feeding trips to the nest. For example, Northern Wheatear's nests as found by Schneider *et al.* (2012), like the nests of other ground breeding bird species, are very cryptic throughout the incubation period and can have only few cues for active nest detection. They found that nest predation during incubation was mainly caused by predators like mustelids which found nests incidentally while hunting for their primary prey (i.e. voles), and therefore predation patterns during the incubation stage mainly reflect spatial predator activity patterns. However during nestling feeding, predation risk was related to nest activity and led to direct mammal predation.

A final important factor affecting nest survival rates is parental care quality: yearling females have lower fledging success than older females (Saether 1990), and high parental quality and the total feeding rate to nestlings is associated with higher productivity, and brood reduction with lower quality and feeding rates (Newton 1998). For example, in Barn Swallows, the care of young before fledging influences juvenile survival and this varies annually dependent on environmental conditions (Gruebler and Naef-Daenzer 2008a).

Desertion

Productivity may be substantially reduced by desertion of the nest by one or more adults. Desertion of nests has been observed mainly due to trade-off between adult/offspring survival (i.e. in response to food shortages), to human disturbances and parasitism. For example, Graveland *et al.* (1993) found that in the Netherlands there were high incidences of clutch desertion due to calcium limitation in wild birds because of acidification of the forest ecosystems they inhabited. Parental care is also costly and energetic, thus conflicts can arise in multiple-brooded species and within pairs of a species, for example the Penduline Tit *Remiz pendulinus*, in which male and female may sequentially mate with several mates, about 30% of clutches were deserted (Bleeker et al. 2005). They also found that because nest building in this species with elaborate nests was energetically more demanding than incubation, birds in good condition would desert their clutch more often. Where renesting opportunities are low, such as at the end of a season, or when environmental conditions are unpredictable then brood desertion rates may be low (Wingfield and Sapolsky 2003).

Brood parasitism

Brood parasites can reduce the fitness of birds, either by lowering the body condition of the adults as they incubate or feed non-related offspring, or by lowering the body condition and survival of their own offspring through competition or direct predation from the parasitic chicks (Newton 1998). For example, Payne and Payne (1998) observed brood parasitism by Brown-beaded Cowbirds *Molothrus ater* on Indigo Buntings and estimated impact of parasitism on the success of the individual buntings in their nests and in their future survival and reproduction. They found that the rates of parasitism over 8 years were 26.6% in 1040 nests and 19.8% in 693 nests in two areas in southern Michigan, illustrating the potentially high population effects of brood parasitism. Most species of brood-parasites remove host eggs when they deposit their own eggs in the host nest, and in some cases the resulting nestlings evict host young from the nest or grow more rapidly, diminishing the growth and survival of the host young (Rothstein 1990, Payne 1997).

Renesting probability

A final very crucial component to productivity is renesting probability. One way for birds to increase their reproductive outputs is by producing more than one brood per season (Lack 1954). The number of reproductive events in one breeding season for a multi-brooded avian species is therefore a major determinant of the individual's fitness and the frequency of laying a second clutch is an important parameter for population growth. Interspecific differences are related to life history in the same way as with variation in clutch size (Lack 1947b, Bennett and Owens 2002). Changes in environmental conditions can consequently change a multi-brood occurrence and substantially impact on breeding patterns of the avian species (e.g. the Stonechat example described earlier of Illera and Diaz (2006)).

In the temperate zone many passerines have been documented to double-brood, however the frequency of pairs double brooding may be strongly affected by environmental factors. Food resource availability is usually seasonally dependent, and so the timing of reproduction relative to the peak in food abundance, and the duration of this peak has been demonstrated to affect double brooding rates (Verboven et al. 2001). For example, Lambrechts *et al*. (2008) compared first and second broods in double-brooded Great Tits in southern France in order to investigate the relative importance of mismatched reproduction and breeding time and success. They found that second clutches of Great Tits were favoured in the evergreen habitats (coniferous, holm oak) where the optimal breeding period occurs later in the season and/or for a longer duration. They also hypothesised that double brooded great tits show better adaptation than single-brooded blue tits in a heterogeneous Mediterranean habitat mosaic in mainland southern France, because great tits were more opportunistic in their foraging habits than blue tits, as reflected in their larger size range of prey and their greater diet breadth (Massa et al. 2004). Such seasonal variation in food supply will also lead to differences between the first and second breeding attempts in clutch size, egg size and fledging success (Ojanen et al. 1979, Orell and Ojanen 1983, Mägi and Mänd 2004). Similarly the effect of food availability on renesting probability within a season was shown in Black-throated Blue Warblers by increased food supplementation increasing the probability that females initiated second broods, which in turn affected annual recruitment rates and population size (Nagy and Holmes 2005a).

Passerines may be single brooded or multi-brooded but many species show a cline in this over their range in response to climate, suggesting this is a flexible trait. For example, Husby *et al.* (2009) examined temporal trends of Great Tits double-brooding in four long-term populations in the Netherlands. Their results showed that the relative frequency of double-brooding females declined in all populations and the decline was related to the timing of first clutch relative to the peak in caterpillar abundance, and that the probability of double brooding declined throughout the season. Additionally, they showed that the numbers of recruits from second clutches decreased significantly over the period of 30 years in all four populations, showing a likely directional selection response to changing climate conditions and so ultimately life-history traits. Similarly, Pimentel and Nilsson (2007) studied the breeding biology of Great Tits, in north and south of Portugal, where the two sites are located in the transition zone between Atlantic climate in the north and Mediterranean in the south. Their results showed variation in timing of breeding and different allocation of reproductive investment between successive breeding attempts (first and second brood) in the two different climatic zones. They found that the southern population bred earlier than the northern and produced a larger first clutch and number of first brood fledglings.

Age may affect the probability of renesting. Studies on Wrentit *Chamaea fasciata* documented 20% of breeding pairs during a four year period attempting a second brood after successfully fledging young from an earlier brood, with double brooded pairs being older, with adults that reduced the amount of post-fledging care and with first clutches earlier in the season (Geupel and Desante 1990).

1.6.2 Survival

The factors affecting survival during breeding are in common with all of the birds including migrants, and these have already been discussed above with respect to life-history trade-offs such the trade-off between parental condition (and so survival probability) and clutch size. In many bird species, parental care is crucial for the development of offspring (Gubernick and Teferi 2000), however the costs of parental care may weaken the overall reproductive output and survival of the parents (Van Dijk et al. 2010), creating a conflict between current investment in care and future reproduction (Williams 1966). The optimal amount of care provided is different between offspring and parents and between male- and female-parents (Trivers 1974, Parker and Macnair 1979), for example, with parents often trying to shift the workload towards each other (Van Dijk et al. 2007). This consequently may lead to one of the parents deserting both the mate and offspring (Houston and Davies 1985, McNamara et al. 1999).

Different parental roles during breeding may then lead to differential survival for adults by sex during breeding. Adult birds themselves, of course, are at risk from predators and this may increase due to nesting, for both hole or ground and open nesters during incubation when predator exposure may be increased and escape options may be reduced. If one sex incubates preferentially then they may be at risk and have lower survival. Nest failure may then also result because of lack of or reduction in parental care. Females usually have lower survival rate if they are the sole incubator (Low et al. 2010).

Post fledging survival

Newly fledged chicks have no experience of foraging or of predation and are often not fully developed in their physical ability to thermoregulate, forage or escape from predators. The survival rate of chicks just after fledging is a very important component of productivity because post-fledging survival, particularly in the first month, is invariably low. Newton (1998) stated that food shortage might increase the risk of predation, or predators might increase the risk of starvation. He argued that a comparison with well-fed chicks, hungry ones are known to be more vulnerable to predation as they become more visible when searching for food. For example, Naef-Daenzer *et al*. (2001), studied the post-fledging survival of Great and Coal Tits *Parus ater* in relation to chick body condition and timing of breeding: chicks with higher fledging mass had higher survival rates and produced most recruits into the breeding population. Food-shortages can also enhance chick predation, because adults spend more time foraging rather than guarding their chicks. The first few weeks of post-fledging are crucial for chicks to survive, find resources and escape predators and hence this can affect population dynamics. Studies on post-fledging survival period are scarce although this is an important component for species conservation and their habitats as well as estimation for population growth. In their review of the literature on post-fledging period of passerine birds, Cox *et al.* (2014b) stated that fledging age was a strong predictor of survival, with the highest mortality occurring during the first 3 weeks after birds fledge.

Survival of juveniles on their first migration

In most long-distance migratory birds, juveniles migrate without their parents, have no precise information of where to go and are subject to many factors which affect their trajectory, thus juveniles end up stochastically in Africa on the scale of >1000 km resulting in lower survival (Cresswell 2014). Avian migrants that travel first time lack precise migratory orientation, with orientation of first year birds being genetically determined (Helbig 1996), but with this being variable. Ringing recoveries during autumn migration reveal a significantly larger directional scatter for juveniles than adults (Backman and Alerstam 2003). Juvenile passerine birds are subject to extensive wind drift and deviations on their intended course, whereas adults correct after displacement (Thorup et al. 2003). For example, studies on migration routes and at the wintering areas of Willow Warbles *Phylloscopus trochilus*, indicated that juveniles leave the natal area before adults and migration direction showed a greater variation than adults, with adults accomplishing a greater accuracy by making use of navigational information from earlier migrations along the route (Hedenstrom and Pettersson 1987). Adults return to the same site that allowed them to survive the previous year, and by a faster and more direct route, so reducing much of the uncertainty of the migration process and thus have higher survival (Cresswell 2014). Juveniles traveling for the first time to the wintering grounds are lacking basic information to promote a successful migration, however if they survive migration their survival rate may not differ from adults during their first winter (Sillett and Holmes 2002). Survival of yearling migrant birds is invariably lower compared with adults (Saether 1989, Donovan et al. 1995b, Saether and Bakke 2000, Clark and Martin 2007), but whether this is due to events on the wintering ground, migration there or back is unclear (Newton 2006).

Survival of migrants generally: the multiple jeopardy or the chain-link hypothesis

Migrants use a number of sites or habitats during their annual cycle akin to the links in a chain (Cresswell 2014). If any one of these areas is removed or degraded then the chain breaks with corresponding decrease in survival. If the probability of change of any habitat or area is the same, then species or individuals which use more than one area (migrants) will have a higher probability of encountering an area that has changed compared to those that only use one (residents): this is the multiple-jeopardy hypothesis (Newton 2004a). Migratory species extend over a wide range of geographical gradients and habitats, and so variable environmental conditions may influence survival rates in each area (Schaub et al. 2012). In short, the more areas that individuals used, the more likely that any one will be detrimentally changed, thus migrant populations which use more sites – and migration distance is a likely proxy of this –show greater population declines (Sanderson et al. 2006, Jones and Cresswell 2010).

Survival during migration itself has been shown to be reduced with respect to survival on either the breeding or the wintering ground (e.g. marsh harriers *Circus aeruginosus* (Strandberg et al. 2010)). As mentioned above juveniles once on their wintering ground may have the same survival rate as adults (Sillett and Holmes 2002). It has been suggested in several studies that survival rates during migration decrease, affected by factors such as predation risk (Lindstrom 1989, Sillett and Holmes 2002), and a high metabolic demand (Akesson and Hedenstrom 2007). Weather conditions must be important for the survival of migratory species and most have to cross ecological barriers such as the Mediterranean Sea and the Sahara Desert. But a major problem is partitioning survival between the wintering ground and stage of migration to and from the wintering ground. As the marsh harrier example cited above shows it is necessary to have tags that communicate when a bird is dead to accurately record this during migration, because mark recapture methods at a sufficient scale during migration are impossible. Such tags are not currently small enough to use on almost any passerine migrants.

There is some indication that conditions on the wintering ground and/or during migration are important for migrant survival. For example, Salewski *et al.* (2013) evaluated apparent survival of resident, short- and long- distancemigrant passerines during breeding and non-breeding seasons and consequently modelled in capture-recapture models correlated with weather conditions. Their results suggest that between-year apparent survival may depend on weather during the non-breeding season, thus, rainfall in the Sahel zone was found to be associated with survival, perhaps because it is crucial for fuel accumulation during spring migration. Additionally they found that warmer winters were associated with higher apparent survival of short-distance migrants (e.g. Dunnock *Prunella modularis* and Chiffchaff *Phylloscopus collybita*, Reed Bunting *Emberiza schoeniclus* and Blackcap *Sylvia atricapilla*).

Having discussed the key factors of productivity and survival that will determine the overall population dynamics and their relation to environmental conditions and their variation, I now introduce the study species in which to explore these issues, to inform our understanding of how climate change might affect migrant populations.

1.7 Cyprus wheatear as a case study for studying factors affecting migrants and how climate change might affect them

The Cyprus Wheatear is an endemic species breeding widely in the island of Cyprus, across diverse habitats and altitudinal gradients. The species is common and distributed from sea level up to the highest mountainous area of the island, with highest densities in forest, agriculture and abandoned agricultural areas and rural areas that still maintain small agricultural fields or gardens. They occur in habitats that include open, stony areas, scrub and bush vegetation, open coniferous (pines and junipers) and deciduous (oak) forests, as well as cultivation (vine yards and orchards that still maintain traditional stonewalls).

Climatic conditions on the island are characterised by high temperatures and aridity, where precipitation varies greatly from year to year and droughts are frequent with heat waves also occurring. In short – anywhere you go on Cyprus there will be a breeding Cyprus wheatear, thus making the species common and conspicuous, breeding over a wide altitudinal range and subject to a varying range of environmental conditions.

The Cyprus wheatear is a short-distance migrant, a summer visitor arriving on the breeding grounds in mid-late March with males arriving earlier than females. It is the smallest West Palaearctic wheatear with males averaging 15.9 g during April-May. Its small size and low weight may be an adaptation to the insular climate and ecology of the island and its latitude, enabling the species to function more efficiently at high temperatures (Flint 2011). The species has an extremely wide habitat range found in every type of vegetation from grassland to woodland, and thus has a wide range extent in maquis, motorral, forest, arable land, orchards and vineyards and pastures (Pomeroy 2004). It is most common in the mountains and hills, particularly on areas with open ground with scattered trees or open forest.

The breeding habitat for Cyprus wheatear consists of open stony areas within open forest and areas with scattered trees and bushes (Randler et al. 2010b). The Cyprus wheatear is a hole nesting, multi-brooded, highly territorial species (Collar 2014). The species' breeding season extends from April through July and August and it leaves the island from August throughout October, migrating to Sudan and Ethiopia where they are present from November to March. The breeding population may be more than 12,000 pairs (Birdlife International 2008, http://www.birdlife.org/).

The genus *Oenanthe* consists of more or less generalist insectivorous species, hunting arthropods opportunistically and most have overlapping diets (Panov 2005, Kaboli et al. 2006), thus suggesting that Cyprus Wheatear feeds mainly on a wide range of insect and larvae. The species is sexually dimorphic with the males boldly patterned black and white and the females brown and dirty white (Collar 2014). There are sex-specific differences in foraging behaviour, thus males use aerial sallies and pounce from higher perches while females more often forage on the ground (Randler et al. 2010a). Males are often arboreal using high perches for song posts and they can be seen regularly perching on trees, high bushes, buildings, antennae and wires.

In this study I use Cyprus Wheatears as an example species to test how environmental variation across years, within seasons and across an altitudinal gradient results in variation in productivity and survival and therefore population dynamics. Although Cyprus wheatears are common and not of conservation concern, it is valuable to study successful species because their conditions and adaptations can provide an insight that can be applied in the management of less successful species. The species also allows sufficient sample sizes and ease of gaining data so that a comprehensive and robust study can be made.

1.8 Aims and structure of the thesis

The aim of this thesis was to provide an ecological insight into the breeding biology of the endemic migratory Cyprus Wheatear, looking at the phenology of the species, its reproductive output, and its survival, along with distribution of the species across different habitats and an altitudinal gradient. The ecology of the species and especially its reproductive success and its distribution and abundance was related to environmental variation as a proxy for climatic variation to determine how climate change might be affecting the species, and so other long distance migrant species.

Breeding phenology (Chapter 2)

Migrant birds may be vulnerable to climate change at different stages of their annual cycles especially on the breeding grounds, where changes in phenology may affect their ability to synchronise breeding with the peak of resources for their offspring. Understanding how phenology of breeding varies between and within years in response to temperature is therefore crucial to understand migrant population dynamics. I will first describe variation in the patterns and consequences of breeding phenology between and within years. Results suggest that the phenology of breeding of Cyprus Wheatear may be sensitive to climatic changes, with breeding onset and number of breeding attempts determined by temperature.

Survival and dispersal (Chapter 3)

Many populations of European migrant bird species are declining and this may be driven by survival rates but there are few studies that can estimate true survival rates. I measured apparent survival by recording territory occupation and reoccupation in a colour-ringed population to determine how it varied with sex, age and year. I then estimated true survival by correcting apparent survival for dispersal by recording territory shifts and how this also varied by sex, age and year. The results indicate a very high survival rate for a small passerine migrant, although they are probably sufficiently annually variable to profoundly affect annual population dynamics.

Reproductive success and productivity (Chapter 4)

Population dynamics of annually breeding bird species depend crucially on productivity in any year. Initial clutch size and the survival of eggs, nestlings and fledged young all determine productivity, as does the probability of renesting after success or initial failure. These factors can all vary within and between years, determining whether overall productivity balances first year and adult survival and so whether the population size changes. I investigated variation in annual productivity. Cyprus wheatears at Troodos Mountain showed several unusual breeding parameters including a highly variable renest probability, high nestling and very high fledgling survival, resulting in exceptionally high productivity. This high productivity combined with the high survival rates means that the population of Cyprus Wheatears at National Forest Park (NFP) of Troodos Mountain is a source population.

Variation in abundance, productivity and phenology with altitude (Chapter 5)

The phenology of breeding of Afro-Palearctic migrants may be affected by climate change, leading to breeding success variation both within and between years. Determining such effects requires temperature variation data over many years, or a system where different populations breeding in a similar area are subject to different temperatures that lead to differing phenology. Here I used altitude as a proxy for variation in temperature and investigated how abundance, productivity and phenology in Cyprus Wheatears varied between and within years dependent on altitude, from sea level to 1952 m, over a range of 20 - 30 km. The results suggest that Cyprus

Wheatears are already very well adapted to high variation in temperature within and between seasons, changing investment from a larger single brood to two smaller broods as temperature increases, as also shown by the results of Chapter 2.

General discussion (Chapter 6)

I finish the thesis by attempting to answer some more general questions from all of the different aspects of the study:

1. How typical are Cyprus Wheatears?
2. What are the overall population dynamics of Cyprus Wheatears?
3. How might Cyprus Wheatears be affected by climate variation?
4. What can Cyprus Wheatears tell us about how climate change might affect other migrants and so their declines?

CHAPTER 2. BREEDING PHENOLOGY AT TROODOS MOUNTAIN

2.1 ABSTRACT

Migrant birds may be vulnerable to climate change at different stages of their annual cycles especially on the breeding grounds, where changes in phenology may affect their ability to synchronise breeding with the peak of resources for their offspring. Understanding how phenology of breeding varies between and within years in response to temperature is therefore crucial to understand migrant population dynamics. Here I describe variation in the patterns and consequences of breeding phenology between and within years for the Cyprus Wheatear. I analyzed data collected in three breeding seasons, 2010 - 2012, on seasonal variation in singing activity, clutch initiation date, duration of the egg, nestling and fed fledged chick stage, and renesting probability and then related this to temperature.

There were clear seasonal peaks and patterns in breeding behaviour, with 2010 being a relatively early year for clutch initiation date, but with differences between years disappearing by the fed fledged chick stage. Territorial singing was highest at the start of breeding but declined significantly through May, June and July until there was very little singing heard in August: the decline was significantly steeper in 2011. Clutch initiation date varied between years: first nests were significantly later on average in 2011 (c. 8 days) compared to 2010 and significantly earlier in 2012 (c. 4 days) compared to 2010. Second nests after success were on average initiated 35 days later, whereas second nests after failure were initiated on average 22 days later. Egg stage duration varied significantly with year (16.4 + 0.5 days in 2010, 20.0 + 1.4 days in 2011, 17.2 + 1.1 days in 2012).

Nestling stage duration was on average 14.8 + 0.4 days and did not vary with year. Duration of the fed fledged chick stage declined slightly with date, but was significantly much greater during 2010 (28.7 days) compared to 2011 (11.7 days) or 2012 (15.6 days). The duration of the fed fledged chick stage for second nests was longer than first nests in 2011 and 2012, but shorter in 2010.

Probability of renesting after a successful nest varied significantly with year, with a higher renest probability in 2011 and 2012 compared to 2010. Probability of renesting declined with date, but this decline was similar across years. Maximum daily temperature varied within and between seasons: 2010 was the hottest year, with 2011 and 2012 being cooler years, although all years were similar at the time of peak chick fledging. The year 2010 showed a markedly different phenology to 2011 and 2012, with an early start to breeding, but only one breeding attempt and an extended period (4 weeks) of chick feeding post-fledging for nearly all pairs. The year 2011 and 2012 had later starts, but cooler conditions may have allowed second broods, although with a trade-off of a reduced fledged chick feeding period (2 weeks). Results suggest that the phenology of breeding of Cyprus Wheatear may be sensitive to climatic changes, with breeding onset and number of breeding attempts determined by temperature.

2.2 INTRODUCTION

Phenology is the study of annually repeated life cycle events for organisms, both plants and animals, and the factors that influence these events. The timing of phenological events is influenced by biotic and abiotic factors that are integrated by organisms over time and space (Balbontin et al. 2009b, Both et al. 2009). The adaptation of phenology to the environment is crucial for individuals' fitness and so population dynamics, where failure to adapt to changing conditions has been found to be associated with substantial population declines in passerines (Both et al. 2006a). At the individual level, phenology may be governed by phenotypic plasticity, whereas at the population level it may be governed by evolutionary changes leading to adaptation to changed environmental conditions (Balbontin et al. 2009a, Pulido and Berthold 2010).

Global warming has an impact on bird populations associated with changes in the phenology of life-history events, predominantly in breeding (Crick et al. 1997, Winkel and Hudde 1997, Dunn 2004, Visser et al. 2006), and laying of eggs earlier in years with high temperatures (Both et al. 2009). The timing of reproduction is a life-history trait with important fitness consequences (Perrins 1965, Verhulst et al. 1995), because for many species there is a short time-window in the annual cycle where conditions are sufficiently good that successful reproduction can occur. As the seasonal pattern in environmental conditions varies from year to year, so the optimal time window in the birds' annual cycle for reproduction will vary annually. The environmental factors most important in determining the time window for breeding are those that determine the phenology of the prey of the bird species of interest (Visser et al. 2006), which may consequently determine whether the species is in optimal condition for reproduction and the availability of resources for offspring. This relationship between when young are produced and the peak of resources to feed these young is therefore a crucial determinant of fitness (Thomas 2001, Visser et al. 2006). Seasonal peaks in the food abundance have advanced due to higher spring temperatures (Kuchlein and Ellis 1997), and consequently the synchronization of production of chicks with peak of food availability has changed leading to population effects (Crick et al. 1997, McCleery and Perrins 1998, Cresswell and McCleery 2003). Many bird species have, however, advanced their laying date in response to the increase in spring temperatures over the past three decades (Crick et al. 1997, McCleery and Perrins 1998, Walther et al. 2002a, Dunn and Møller 2014). Therefore, with increasing temperatures, many bird species have shifted their seasonal timing, or phenology of reproduction.

Migrant bird species may be particularly vulnerable to the impacts of climate change, because they may be affected by weather conditions at various locations throughout their life cycle, and by events at both the wintering and breeding grounds (Both 2010). Climate on the wintering grounds has been documented to affect overwinter survival of some species, (Peach et al. 1991). It has also been shown that carry-over effects can occur when the conditions on the wintering grounds influence the condition of birds before their spring migration, thus, potentially altering arrival time on the breeding grounds with consequent effects on the reproductive success of the species (Saino et al. 2004a). Changes in population dynamics of other species have also been attributed to climate change on the breeding grounds. Both et al. (2006b), analysed the effects vegetation growth on the wintering grounds and sites en route on the annual timing of breeding of populations of Pied Flycatchers, and found that timing of breeding was largely correlated with local spring temperatures, supplemented by a striking effect of African vegetation and North Atlantic Oscillation (the NAO – a proxy for annual climatic patterns for much of Europe and Africa). They suggested that Pied Flycatchers bred earlier in years with more vegetation in the northern Sahel zone and North Africa, and late breeding populations advanced their breeding dates when circumstances in Europe were more advanced, thus the timing of breeding depended upon local circumstances and on conditions encountered during traveling.

Advances in spring migration phenology in response to climate change are however site and species specific (Both and te Marvelde 2007). Both and te Marvelde (2007) modelled the trends in laying date of a short-distance migrant, the Common Starling *Sturnus vulgaris,* and a long-distance migrant, the Pied Flycatcher, combining both geographical variation and the effect of temperature. Results from their study indicated that Starlings advanced breeding over most of their range, whereas, Pied Flycatchers have delayed their laying in northern Europe but advanced it in western and central Europe because temperature during migration had changed differently for the populations heading to different breeding areas. Additionally Both *et al.* (2004), found that advancement of laying date across Europe for populations of Pied Flycatchers was stronger in areas where spring temperatures increased more.

The reproductive period is a very critical time for all birds including migrants, where individuals have to decide where, when and how many offspring to produce: parameters such as number of breeding attempts and the number of offspring produced per breeding attempt can have important fitness consequences and are considered primary life history traits (Hochachka 1990, Verhulst et al. 1995, Svensson 1997). The effect of climate change on populations therefore depends on the change in such parameters with variable temperature.

In this study I analysed short-term (2010-2012) variation of the phenology of breeding parameters of Cyprus Wheatear in the context of intra- and inter-annual temperature gradients. Population responses to climate change can really only be elucidated with long term studies, for example on long-distance migrants such as the Pied Flycatcher studied by Both and Visser (2005), and Visser *et al.* (2004) so this study can only suggest possible linkages. Nevertheless, even the suggestion of such linkages will aid our understanding of the population dynamics of migrants, and provide the necessary start of any long term study. The objectives of current thesis were to obtain information on the breeding seasonality of the Cyprus Wheatear within and across years. The current study measures a number of parameters which should be highly responsive to climate change: the onset of breeding behaviour through territorial activity via singing and clutch initiation date, the duration of different nesting stages (egg stage, chick and fed fledged chick stage), and the probability of a second brood.

2.2.1 Singing

Territoriality and singing behaviour by males has been found to vary within and between years in most passerines, with a clear decline in singing through the season. For example, Rubolini *et al.* (2010), assessed temporal change in spring First Singing Date (FSD) to test whether migratory status affected by local temperatures. They found that higher local temperatures were associated with earlier FSD, and multi-brooded species showed a stronger advancement in FSD with higher temperatures than single-brooded species. Responses of singing to temperature changes also depended on whether species were migrants or not.

2.2.2 Clutch initiation date

Clutch initiation date has been found to vary within and between years, dependent on whether it is the first or second brood. Dunn and Møller (2014) analysed extensive data on temporal change in laying date and clutch size of birds from Europe and North America. They found that laying date advanced significantly with warmer temperatures and such advances were most associated with species that had multiple broods per season. Variation in clutch initiation date is again, however, species and context specific. For example, climate change and the timing of the peak of food abundance in relation to breeding dates was studied for the British population of Great tits in Wytham Wood, Oxford, England (Cresswell and McCleery 2003). Here birds advanced their egg laying date more than the timing of their caterpillar prey advanced, thus leading to differential changes in the breeding dates that were compensated for by increases in incubation duration. In contrast, a Dutch Great tit population on the Hoge Veluwe, showed an inverse relationship, where there has been a shift in the peak date of the caterpillar availability but not in the average onset of egg laying (Visser et al. 2003). Comparing phenological shifts of the two populations, there has been an increased selection for early laying in the Hoge Veluwe population, but not in the Wytham Wood population where selection for early laying has declined.

2.2.3 Duration of nest stages

The duration of the egg and nestling stage is likely to vary little in passerines because it should always be minimized to reduce the probability of nest predation, which is dependent on the number of days a nest is exposed. For example, Kleindorfer (2007), studied the ecology of the Galapagos Finch *Geospiza fuliginosa* that breeds in geographically distinct habitats (lowlands and highlands) on Santa Cruz Island. He suggested that the small clutch size of the species was an adaptive response to high predation risk by behavioural conspicuousness at the nest, the duration of stages and to lower the energetic costs of re-nesting. Results of his study indicated that the highland birds that had smaller clutch sizes and shorter re-nesting intervals were characterized by high nest predation, whereas the lowlands were characterized by low nest predation. Additionally the mean duration of incubation bouts was longer in the highlands (with fewer events per hour), which was consistent with the prediction of reduced behavioural conspicuousness at nests, and shorter duration of the incubation period, under conditions of high predation risk. In contrast, a study by Cresswell and Mcleery (2003) found that the duration of the Great Tit's incubation period was variable due to a temperature-mediated incubation scheduling response rather than minimised to reduce predation risk: great tits are however hole nesters and so are subject to lower predation risk which may then give them greater flexibility to increase the duration of the nesting period without greatly increased risk of nest predation.

2.2.4 Duration of the post-fledging period and renesting probability

Renesting probability after failure is not likely to vary between years because renesting rate is important to maintain productivity. In contrast, renesting probability after success is likely to be highly variable because the probability of having time or resources to make a further successful breeding attempt will depend on annually varying factors and timing during the breeding season (e.g. life history trade-offs, Bennett et al. (2002)). For example, Visser *et al.* (2003), using data on 24 populations of Tits (*Parus* spp.), from six European countries, found evidence for a link between rising temperatures and the frequency of second broods because of extended breeding seasons reducing the costs of second broods. Similarly, the duration of parental care of fledged chicks, i.e. continued feeding of chicks after they have fledged, is likely to depend on seasonably variable factors such as clutch initiation date and previous productivity because these influence the relative costs and benefits of investing in continuing to feed the previous brood versus initiating a second one. Time allocation to one brood can entail future reproductive costs in multi-brood species because this may delay the start of the next breeding attempt, whereas in turn, there will be effects on the reproductive value of the next brood because of declining environmental conditions (Martin 1987). In an analytical model Verhulst *et al.* (1997), showed that ending care early can be advantageous for renesting because starting the subsequent brood earlier may result in increased juvenile survival. Gruebler and Naef-Daenzer (2008b), suggested that in seasonal environments, multiple brooders may trade off fitness benefits of the time invested in the care of fledglings of one brood against the benefits of an advanced start of the subsequent clutch. They studied the double-brooded Barn Swallow, in which they found that the duration of post-fledging parental care was shorter for first broods than for single and second broods, thus depended on the pair’s breeding season length. Their results support the hypothesis that multi-brooded birds adjust the duration of post-fledging care in relation to future reproductive attempts because of an intra-seasonal trade-off in the allocation of time between successive broods.

2.2.5 This study

In this study I measured intra- and inter-annual variation in the phenology of breeding in a colour-ringed population of Cyprus Wheatears over three years (2010-2012) from

April – August. I measured occurrence of territoriality via singing rates of males, clutch initiation dates, duration of the different nest stages, and renesting probability. Finally I related this to temperature variation within and between years, with the caveat that we only had 3 years' data and so can only suggest possible relationships for future testing. I tested for variation within and between years in:

2.2.5.1 Male singing (and therefore territorial and breeding activity). I predicted that singing activity would decline as the season progressed as found for most other passerine species.

2.2.5.2 Clutch initiation date, and how this varies with nest type. I predicted that clutch initiation would vary with year and nest type, and variation with nest type was likely to differ between years as found in many other passerine species.

2.2.5.3 Duration of the different nest stages controlling for nest type and clutch initiation date. Nest stages measured were duration of the egg stage, chick in the nest (nestling) stage, and duration of the period of feeding of chicks post fledging. I predicted that duration of the egg and nestling was unlikely to vary with year, clutch initiation date or nest type because the duration of these stages should always be minimized to reduce probability of nest predation.

2.2.5.4 The duration of the post-fledging period and the frequency of renesting probability after a successful first brood, controlling for clutch initiation date and previous productivity. I predicted that the duration of the period of feeding of chicks post fledging might vary because feeding fledged chicks is a trade-off with investment in second brood. I predicted that renesting probability after failure would not vary between years because renesting rate is important to maintain productivity but would vary with clutch initiation date and previous productivity because these would influence the relative costs and benefits of continuing to feed the previous brood versus initiating a second one.

2.2.5.5 Temperature and particularly temperature at clutch initiation date and fledging date for first nests. I used 2011 as a reference year because this was the year with the consistently lowest temperature throughout the breeding season. I predicted that temperature will affect clutch initiation date as has been found for most other passerine species.

2.3 METHODS

This study was carried out during the annual breeding season of the endemic Cyprus Wheatear in the island of Cyprus (Geographic coordinates: 35 00 N, 33 00 E). Cyprus Wheatears breed annually between late April (start of nest building) and early August (last chicks fledge) and the current study was conducted from 2009 to 2013 in a 130 ha area at National Forest Park of Troodos, Cyprus (34°56′11″N 32°51′48″E), at about 1800 m a.s.l. (Figure 2.1 a.).

The National Forest Park (NFP) of the Troodos Mountain range (Appendices: Figure F) consist of high quality habitats for the Cyprus Wheatear. The intensive study was located on the highest peak of Troodos which had natural habitat types of coniferous forest, serpentinophilous grassland and evergreen vegetation, consisting of open rocky/crevices spaces with sparse understory shrubs. The high quality of the habitats across the study area was probably homogenous, because the forest comprises of a mosaic of big openings with sparse low vegetation, presenting a suitable habitat for Cyprus wheatear.

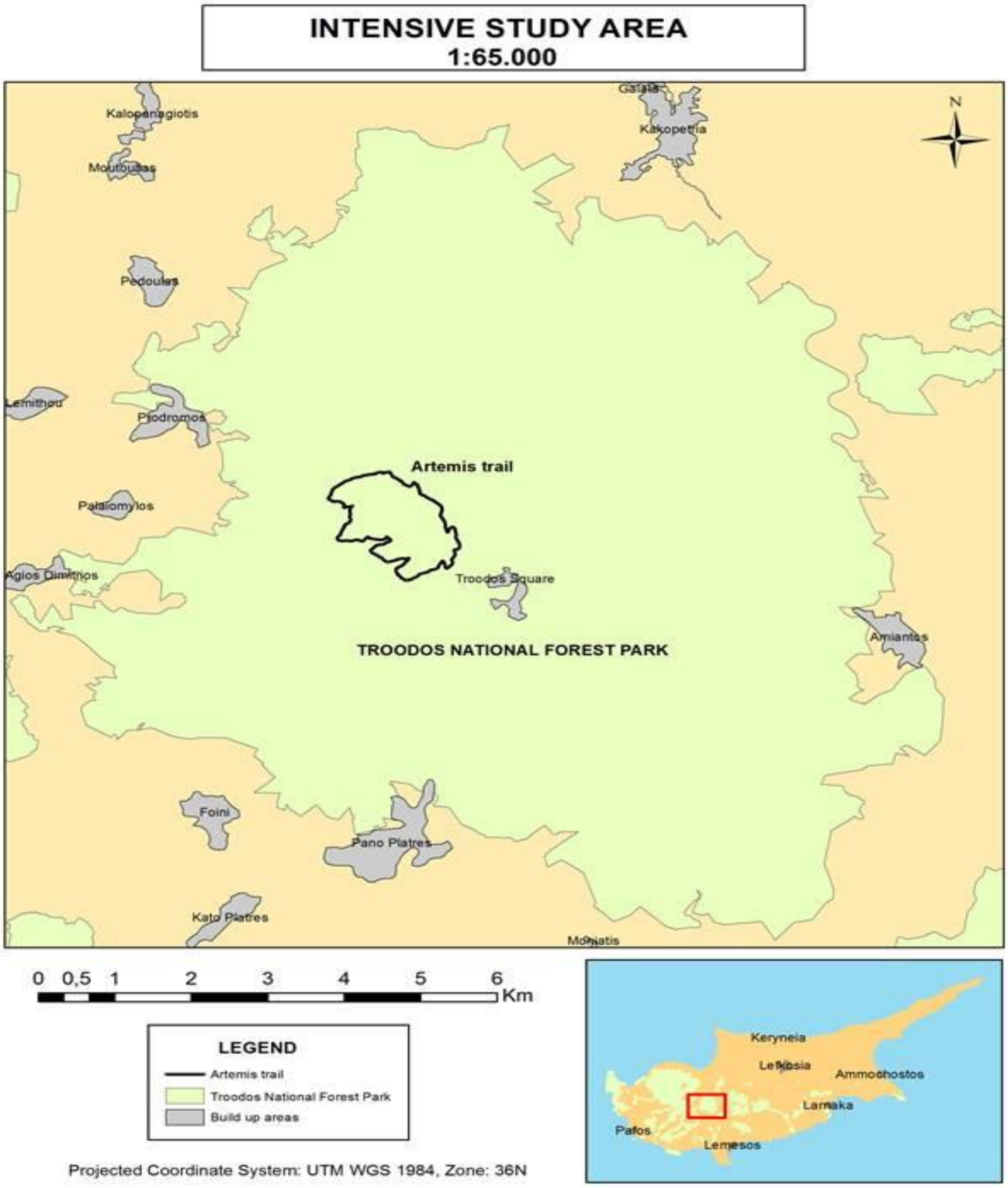

Figure 2.1 a. Map of the intensive study area at the Mountain of Troodos National Forest Park, Cyprus.

The study area was the surroundings of the “Artemis Trail” (east and west facing slopes) with old low density coniferous forest, supporting the one of the densest breeding Cyprus Wheatear populations on the island (Flint and Stewart 1992). The NFP of Troodos is located at the centre of Troodos massif that ranges from the northwest to the southeast part of Cyprus. The NFP of Troodos covers an area of 9,029 ha. with highest peak of Chionistra at 1952 m, situated almost at the centre of an Ophiolite Complex. The main habitats that characterized the study area are those of the endemic *Pinus nigra* ssp. *pallasiana* forest, the Black Pine zone which starts from 1400 m and reaches up to the top of the mountains to 1952 m, the Juniper woodland *Juniperus foetidissima* and Serpentinophilous grasslands that are distributed at the highest parts and that occur in openings of the black pine forest in the form of small, scattered patches. The understorey of Black Pine consists of Golden Oak *Quercus alnifolia*, Prickly Juniper *Juniperus oxycedrus*, Foetid Juniper *Juniperus foetidissima*, Whitebeam *Sorbus aria* ssp. *cretica*, *Berberis cretica*, *Arbutus andrachne*, *Rosa chionistrae*, *Rosa canina*, *Cotoneaster racemiflorus* var. *nummularius* etc.

Figure 2.1 b.: Typical vegetation at NFP of Troodos, Cyprus.

Annual precipitation in the area is very high with more than 1100 mm being recorded and temperature varies through the year from freezing during winter to a maximum of about 35°C during very hot dry summers. We obtained annual daily temperature from the Department of Meteorology, with data used coming from a station in Troodos village square approximately 1.5 km from the nearest edge of the study site.

During 2009 a pilot study identified a study area and monitored and mapped territories but without colour-ringing of birds. In subsequent years 2010-2012, individuals were colour-ringed when they were actively defending a territory and locations of territories were plotted on maps. The study area consisted of 4 parallel transects containing about 80 mapped territory locations over the 4 years, containing 30, 45, 69, and 50 focal territories over the four years of the conducted study. Observation and data recording started around mid-end of March each year when the first individuals arrived at the breeding grounds, and regular monitoring continued until the end of August, with sporadic visits (once a week) until October.

Pairs were marked within their territory and at least one individual of the pair was coloured-ringed. The study contained 324 individuals that were colour ringed over 2010-2013 (110 males, 91 females and 123 chicks). Birds were captured throughout the season (but especially during arrival and territory establishment for the adults) with spring traps that were baited with maggots. Playback using conspecific song was used during trapping. Birds were ringed with individual combinations of colour rings: Individuals were sexed on the basis of standard plumage characters (see Chapter 3).

A licence for ringing was granted to myself and my supervisor Professor Will Cresswell from the Game and Fauna Services, Ministry of Interior, which is the competent authority for the implementation of the Birds Directive 2009/147/EC, in Cyprus. Ringing carried out mainly each spring by myself and my supervisor.

At each territory during 2010-2012, I recorded arrival dates of individuals, resighted colour-ringed birds, mapped territories, monitored territoriality by singing activity (presence or absence during a territory visit) and monitored nesting. Nests were found opportunistically at different nest stages (building-laying, incubation, feeding of chicks within the nest and feeding fledged chicks), were mapped and visited at least twice a week. Laying date was determined by direct observation of the first egg laid in a just completed nest, or by back calculation from the hatch date, or occasionally fledging date based on the mean duration of nestling and egg stage from known nests. Eggs and chicks were examined by direct observation or using an inspection camera on a flexible meter long stalk. A nest failure was defined as when a known nest (nest and eggs or chicks being monitored) lost its eggs or chicks and the parents resumed activities consistent with them renesting or stopping breeding. I recorded nest stage and nest type (first, second after failure and second after success) for each visit. I then calculated duration of the egg stage (clutch initiation date, i.e. first egg to hatch), duration of chick stage (hatch to fledging), and duration of the fed fledged chick stage (fledging to the period when the adults stopped feeding the fledglings). Not all territories could be monitored completely and so complete information is not available for all territories: some nests were not found, and many were found only in the chick stage when they become more conspicuous. Sample sizes vary throughout consequently.

Breeding was defined to be successful when fledglings were observed, or intense warning calls of parents after fledging were heard (at ≥ 15 days after hatching). Fledglings were monitored for at least a month after fledging to record the number of surviving chicks and the period of feeding by the parents. Chicks were reasonably conspicuous and stayed together in the small territories allowing a reasonable assessment of the number: nevertheless any estimates I present may be underestimates of survival because of imperfect detectability. Data on the number of fledglings surviving and feeding was restricted to the central territories of the study area.

2.3.1 Analysis

General phenology was described by calculating the proportion of territories showing a particular nesting stage for each visit and visually exploring how these proportions varied through the breeding season.

The phenology of territorial behaviour was modelled by predicting the probability that singing was heard in each territory visited with respect to Julian date, year and the interaction between Julian date*year. Julian date was also added to the model as a random effect (as well as a fixed effect covariate) to control for the pseudoreplication caused by a variable number of territories being visited on any one day. Probability of singing was a binary response variable (heard or not) and so we used a Generalised Linear Mixed Model (GLMM) with a binomial distribution and a log-link function.

The phenology of clutch initiation date was modelled predicting the Julian date of the first egg laid with respect to the nest type (first, second after failure, second after success) and year and the interaction between Julian date*nest type. A General Linear Model assuming a normal distribution was used.

The duration of the three nest stages were modelled using duration of the egg, nestling and fed fledged chick stage as response variables in three separate models. In the models for duration of egg stage and nestling stage, only year and clutch initiation date were included, without their interaction because sample sizes were small (N = 26 first nests – relatively few nests were found before clutch initiation so that exact egg stage duration could be measured). Nest type was also not included in these models because egg stage duration was only measured in 3 other nests that were not first nests. In the model for fed fledged chick stage duration, clutch initiation date, year and nest type were included as predictors along with the interaction between year*nest type.

Probability of renesting after a successful first brood was modelled with respect to the number of chicks fledged from the first nest (productivity), year and clutch initiation date along with the interaction between clutch initiation date * year. Probability of renesting was a binary response variable (second nest or no second nest) and so I used a Generalised Linear Model with a binomial distribution and a log-link function.

I modelled maximum daily temperature with respect to date, the quadratic of date and year, and their interactions. I included the quadratic of date because temperature is expected to peak during the breeding season and then decline as autumn approaches. I also examined whether temperature at clutch initiation varied significantly with year. The maximum temperature for a 7 day period centred on the day of clutch initiation was calculated for each nest and then a model predicting this with year and controlling for the date of clutch initiation was constructed. The same procedure was used to test whether temperature at fledging varied significantly with year, except maximum temperature for a 7 day period centred on the day of fledging was calculated for each nest. General Linear Models (GLM) assuming a normal distribution were used throughout for the temperature analyses. Analyses were repeated using minimum and mean temperatures but very similar results were obtained and these are not reported further.

Analysis was carried out using R 3.0.2. Interactions were only tested where there was an a priori biological hypothesis to be tested; some interactions could not be tested because of sample sizes and missing information (e.g. duration of nest stages). Quadratic effects of clutch initiation date were considered because breeding activities may have peaked mid-season rather than at the start: there was no strong evidence for quadratic effects unless otherwise reported. Full models were simplified by AIC comparison using the information theoretic approach (Akaike 1974, Burnham and Anderson 2002). Non-significant interactions were removed by default. The top models were then evaluated for both biological and statistical significance. Figures illustrate the results of models and plot the predicted values (parameter estimates) for the variable of interest, with other variable values set to their median (and so typical) values. Means are given +/- 1 standard error unless otherwise stated.

2.4 RESULTS

Initial description of the phenology of breeding

There were clear seasonal peaks and patterns in breeding behaviour (Figure 2.2).

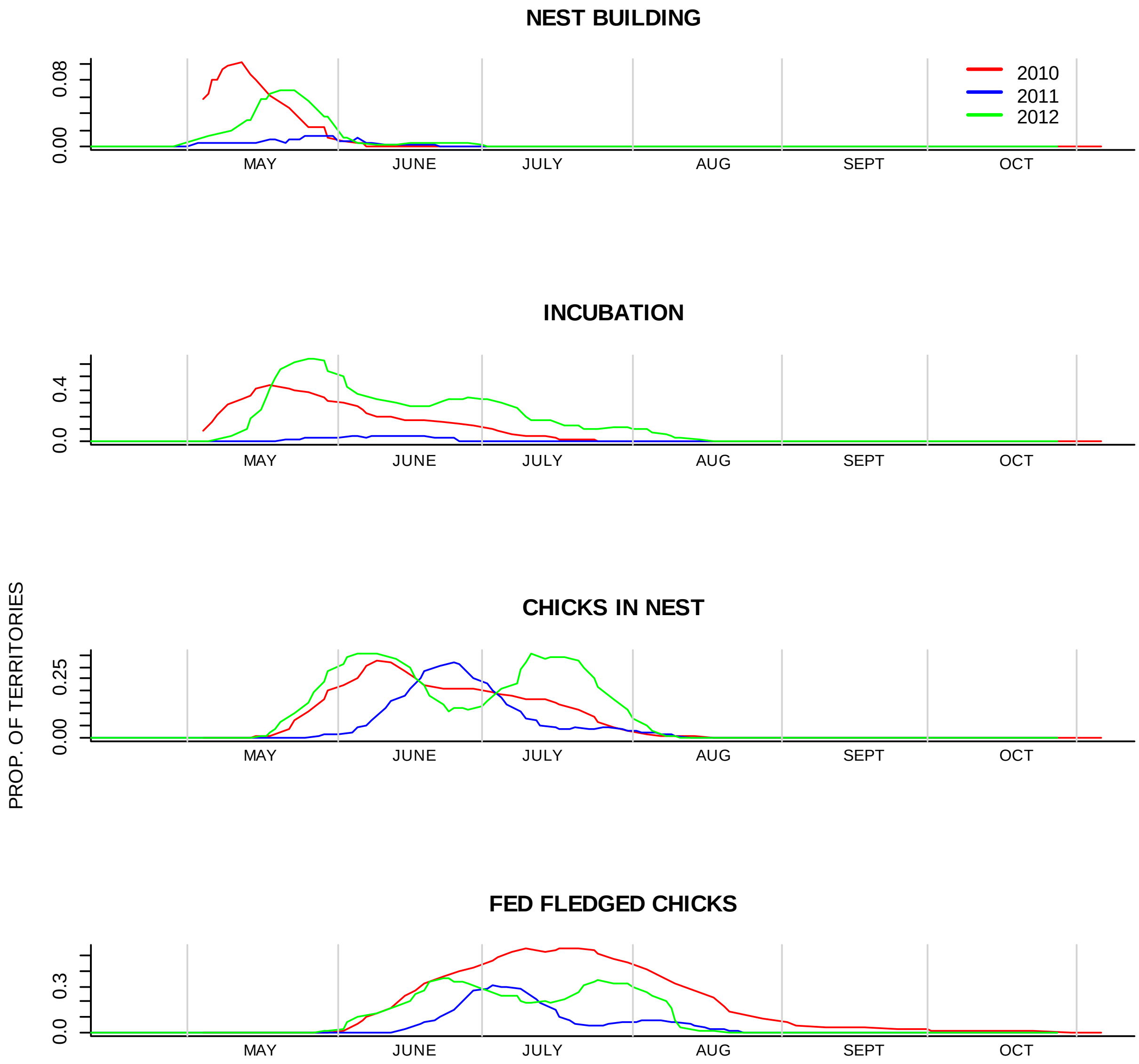

Figure 2.2: The proportion of territories showing the main nesting stages with date to illustrate broad variation in nesting phenology for Cyprus Wheatears at Troodos in Cyprus. Breeding activity of the species started during May, with territories being (re-) established in April, and lasted until August when the last fledged chicks became independent.

Data from the 2010 breeding season showed that the starting dates of nest building and egg laying were the first week of May with a peak in the first days of the 2nd week of May; incubation started in the first week of May with a peak mid-May; chicks hatched in the mid – last week of May with a peak at the end of 1st week of June; and fledging started mid-June with a peak mid-July (2nd to 3rd week) of fledged chicks that were still being fed by their parents (fed fledged chicks): Figure 2.2.

Data from the 2011 breeding season showed a later season than 2010. Starting dates of nest building and egg laying were mid-May with a peak in the 2nd – 3rd week of May; incubation started mid-May with a peak in the 4th week of May; chicks hatched at the beginning of June with a peak in the 3rd week of June; and fed fledged chicks first appeared in the last week of June with a peak in the first week of July.

Data from the 2012 breeding season showed a more similar phenology to 2011, i.e. later than 2010. Starting dates of nest building and egg laying were mid-May with a peak at the 3rd week of May; incubation started at the beginning of the 2nd week of May with a peak beginning the 3rd week of May; chicks hatched in the 4th week of May with a peak in the 1st week of June; and fed fledged chicks first appeared in the 1st week of June with a peak in the 3rd week of June.

Overall the phenology showed a clear seasonal pattern from clutch initiation. Although this varied between years, once nests started then the phenology was similar between years, with the differences between years becoming less pronounced by the fed fledged chick stage. The duration of the fed fledged chick stage was highly variable however, being nearly a month in duration in 2010, but approximately two weeks in duration in 2011 and 2012. On average, females started nest building and egg-laying in the first two weeks of May (approximately the 8th of May), egg stage duration was 17.0 ± 0.4 days (N = 33), hatchling stage duration was 14.4 ± 0.2 days (N = 98) and the fed fledged chick period was 2-4 weeks. Variation in the breeding phenology of the

Cyprus Wheatear was predominantly determined by inter-annual variation in clutch initiation dates, renesting probability and duration of the fed fledged chick stage controlled by year (see below).

2.4.1. Singing

The probability of hearing a male Cyprus Wheatear singing when visiting a territory was high at the beginning of the season (c. 0.8) but declined significantly through May, June and July until there was very little singing heard in August (Table 2.1, Figure 2.3). The strength of the decline varied significantly with year, with a significantly steeper decline in 2011 (Table 2.1, Figure 2.3).

Table 2.1: Results of a GLMM to predict the probability that singing was heard in a territory during a visit in terms of Julian date (jdate) and year, and their interaction. N = 8,617 separate territory visits on N = 291 separate days: visit date was added as a random effect to the model.

Variable	Estimate	SE	z	*p*

[1] (Intercept)	2.04	0.41	4.9	< 0.0001
jdate	-0.03	0.00	-9.8	< 0.0001
2011	0.94	0.59	1.6	0.11
2012	-0.53	0.58	-0.9	0.36
jdate:year2011	-0.02	0.01	-2.8	0.005
jdate:year2012	0.00	0.00	0.6	0.58

[1] (Intercept) = Male singing & 2010

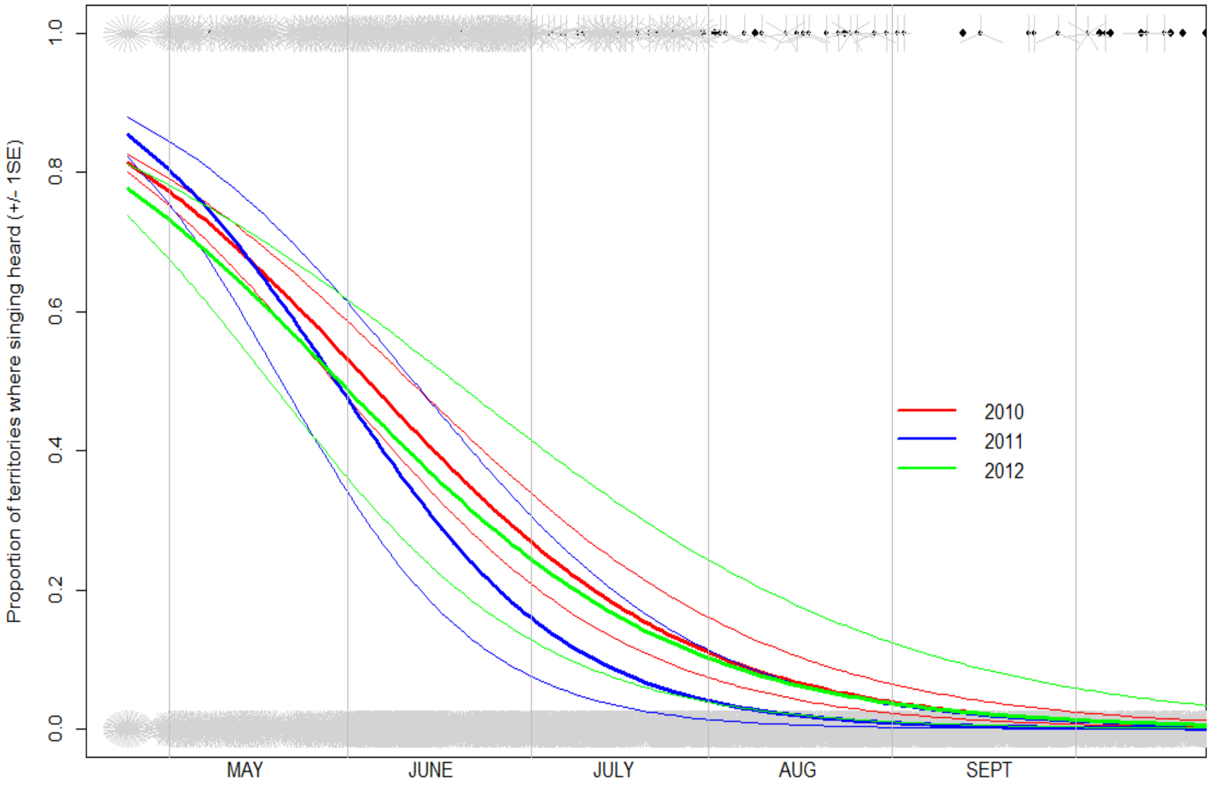

Figure 2.3: Variation in the proportion of territories visited where a male was heard singing within and between years. Predicted lines (± 1 standard error) are plotted using the parameter estimates from the model in Table 2.1: the pattern of decline varied with year, although overall, singing declined markedly as the season progressed. Thick lines show mean predicted values and thin lines predicted means +/- 1 SE.

2.4.2. Clutch initiation date

Clutch initiation date was significantly dependent on nest type and year, but variation in clutch initiation date dependent on nest type did not differ significantly across years (Table 2.2, Figure 2.4). Second nests after success were on average initiated 35 days later, whereas second nests after failure were initiated on average 22 days later

(Table 2.2, Figure 2.4 top). First nests were significantly later on average in 2011 (c. 8 days) compared to 2010 and significantly earlier in 2012 (c. 4 days) compared to 2010 (Table 2.2, Figure 2.4 bottom).

Table 2.2: Results of a GLM to test whether clutch initiation date for Cyprus wheatear varied with nest type (1 = first, 2 = second after success, 3 = second after failure) and year and their interaction.

Variable	Estimate	SE	t	*p*
[1] (Intercept)	15.43	1.48	10.4	<0.0001
Nest Type 2	34.95	2.69	13.0	<0.0001
Nest Type 3	21.52	2.84	7.6	<0.0001
2011	8.36	2.19	3.8	<0.001
2012	-4.81	1.98	-2.4	0.016

[1] (Intercept) = Clutch initiation date & Nest type 1 & 2010.

The interaction nest type * year was not significant $F_{3,,216} = 1.3$, $p = 0.28$ Delta AIC = 2 and was removed from the model.

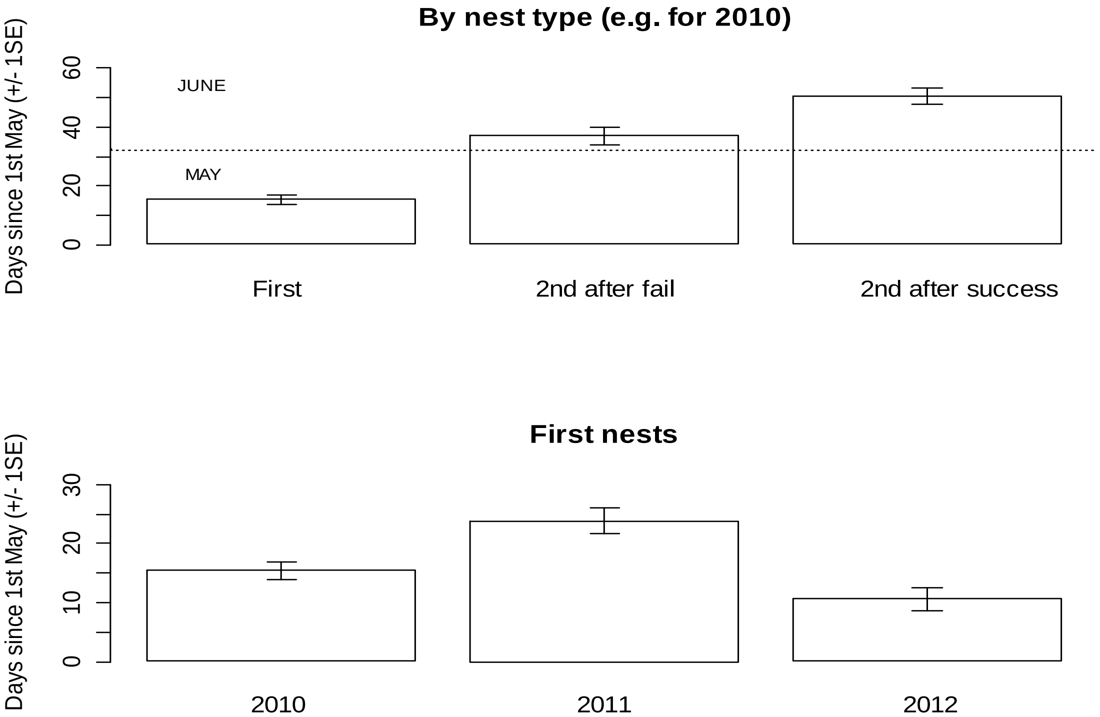

Figure 2.4: Variation in clutch initiation date by nest type (top) and year for first nests (bottom). The intervals between nest types were the same across years (i.e. no interaction of year * nest type – see Table 2.2). Predicted values are plotted from the parameter estimates from the model in Table 2.2.

2.4.3. Duration of nest stages

Egg stage duration varied with year, being significantly longer in 2011 than in 2010 or 2012. Egg stage duration was 16.4 ± 0.5 days in 2010, 20.0 ± 1.4 days in 2011 (t = 2.6, $p = 0.016$) and 17.2 ± 1.1 days in 2012 (t = 0.7, $p = 0.48$): overall model $F_{2,24} = 3.29$, $p = 0.05$ (Figure 2.5). Nestling stage duration did not vary significantly with year ($F_{2,22} = 0.1$, $p = 0.87$) or with clutch initiation date ($F_{1,22} = 0.2$, $p = 0.69$). Nestling stage duration was on average 14.8 ± 0.4 days (N = 26 first nests).

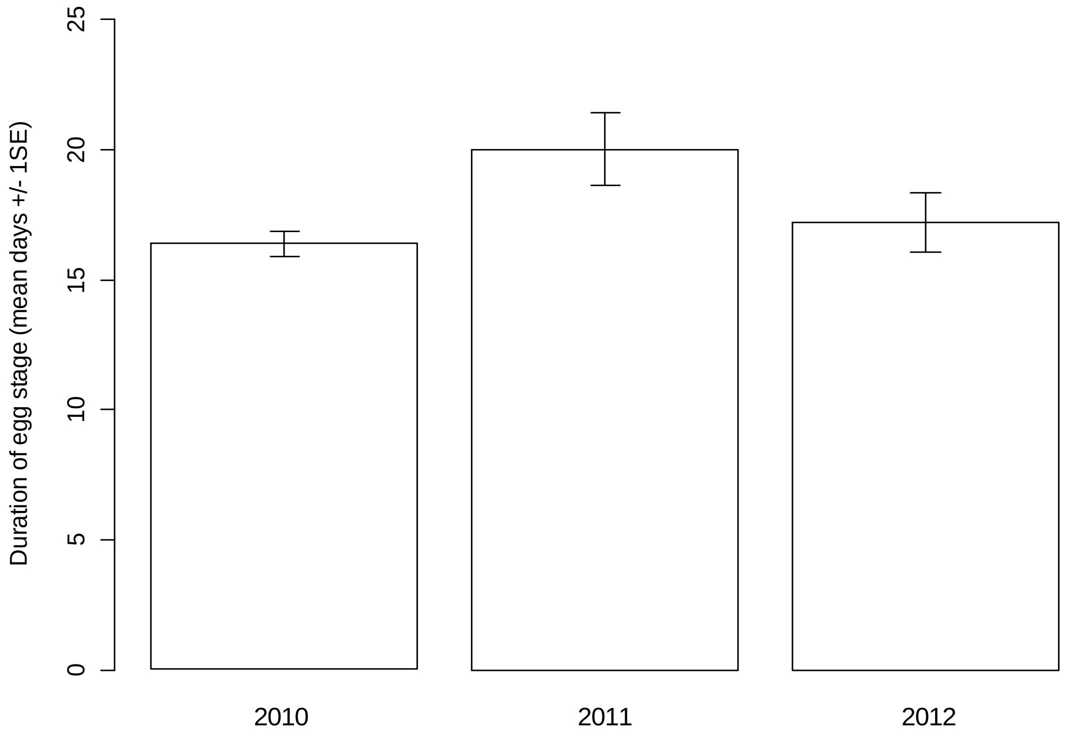

Figure 2.5: The predicted duration of egg stage (mean days +/- 1 SE) for three breeding seasons (2010-2012) from a GLM of duration ~ year, N = 29 nests.

2.4.4. Duration of the post-fledging period and renesting probability

Duration of the fed fledged chick stage varied significantly and depended on year and nest type (Table 2.3, Figure 2.6). Duration of the fed fledged chick stage declined slightly with date, but was significantly much greater during 2010 (28.7 days) than in 2011 (11.7 days) or 2012 (15.6 days): Table 2.3, Fig. 2.6. the difference in duration dependent on nest type also varied significantly between years (i.e. the interaction between nest type * year), with duration of second nests being generally longer than first nests in 2011 and 2012, but shorter in 2010: Table 2.3, Figure 2.7.

Table 2.3: Results of a GLM to predict the duration of the fed fledged chick stage in terms of year, nest type and clutch initiation date, and the interaction between year*nest type. Nest type: 1 = first nest, 2 = second nest after failure, 3 = second nest after success)

Variable	Estimate	SE	t	*p*
[1] (Intercept)	28.74	1.17	24.5	<0.0001
2011	-17.00	1.26	-13.5	<0.0001
2012	-13.14	1.30	-10.1	<0.0001
Clutch initiation date	-0.08	0.04	-2.0	0.04
Nest type 2	-6.99	3.93	-1.8	0.08
Nest type 3	-4.26	2.76	-1.6	0.13
2011: Nest type 2	8.38	4.78	1.8	0.08
2012: Nest type 2	8.09	3.94	2.1	0.04
2011: Nest type 3	10.07	4.55	2.2	0.03
2012: Nest type 3	7.18	3.43	2.1	0.04

[1] (Intercept) = Fed fledged chick & First nest type & Clutch initiation date & 2010

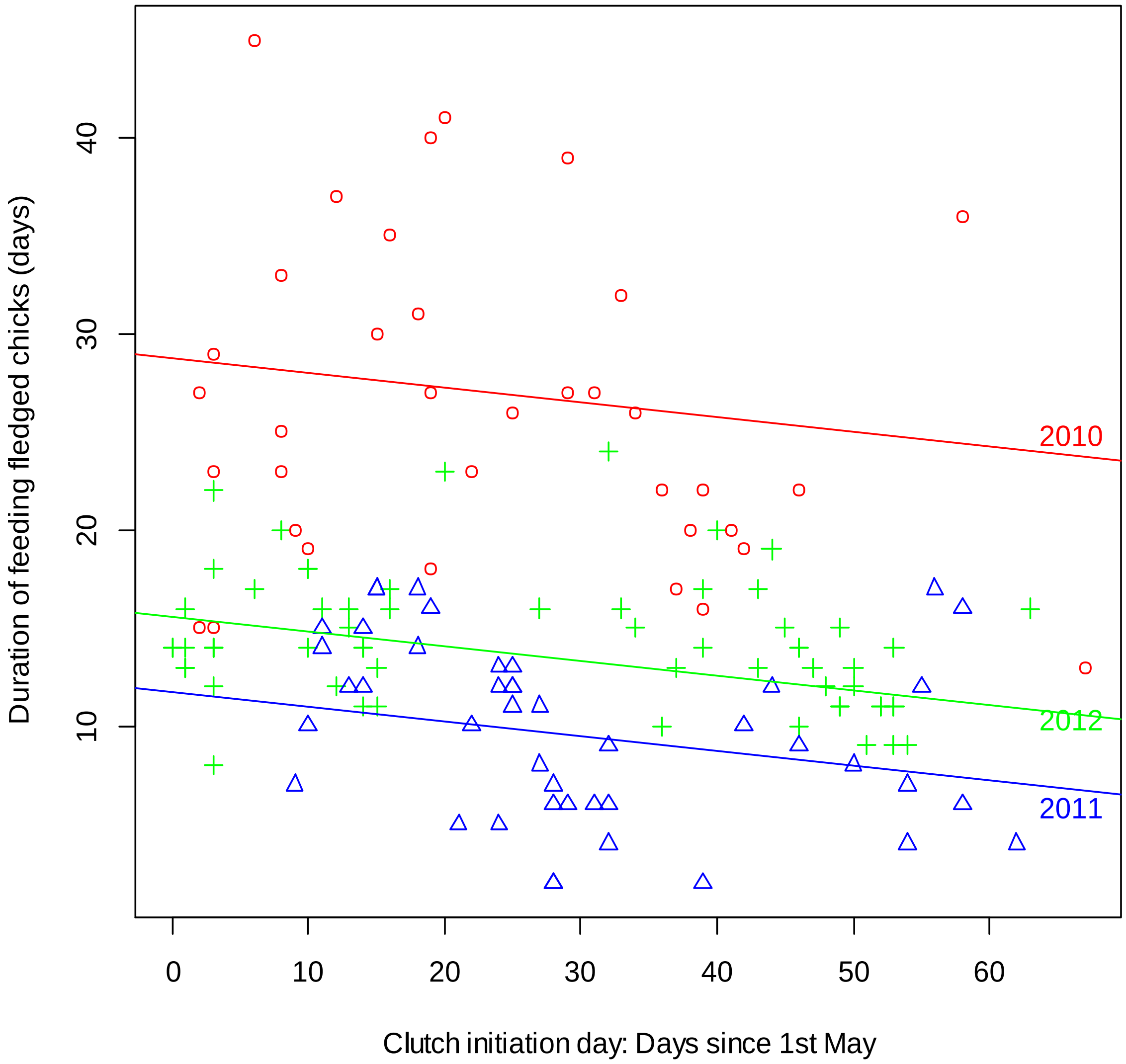

Figure 2.6: Scatter diagram of the variation of the duration of feeding fledged chicks with Julian date since 1st of May for 1st nest types. Predicted lines are plotted from the parameter estimates from the model in Table 2.3.

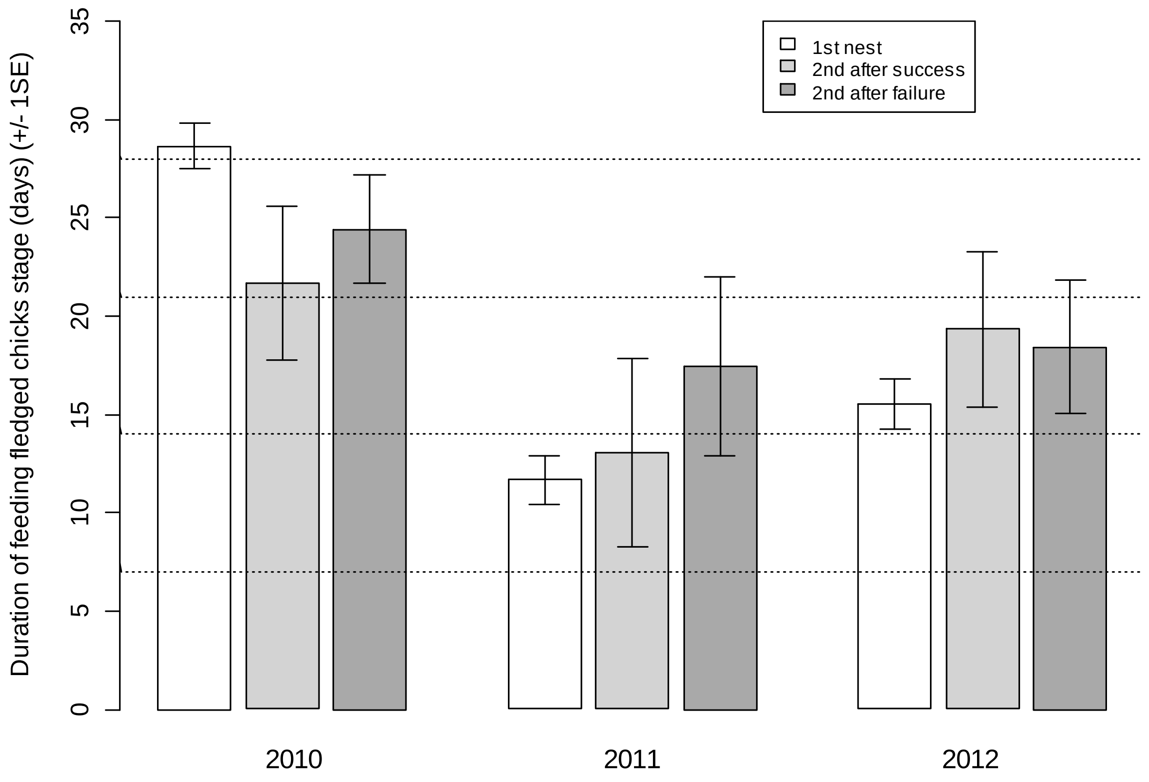

Figure 2.7: Duration of the fed fledged chick stage with respect to year and nest type, illustrating the significant interaction between year and nest type (i.e. broods from second nests were fed longer than first broods in some years, but not others). Predicted values are plotted from the parameter estimates from the model in Table 2.3. Horizontal dashed lines indicate periods of a week.

Renesting probability differed significantly between years (26%, 48% and 78% renesting rate): see Chapter 4. 2010 had a much lower renesting rate after success with very few second broods (29% versus 76% and 73% in 2011 and 2012 respectively). Probability of renesting after a successful nest varied significantly with year, with a higher renest probability in 2011 and 2012 compared to 2010 (Table 2.4,

Figure 2.8). Probability of renesting declined with date, but this decline was similar across years (Table 2.4, Figure 2.9).

Table 2.4: Results of a GLM to predict renesting probability after a successful first nest with number of fledged chicks from the previous nest, year and clutch initiation date, and also testing the interaction between year * clutch initiation date.

Variable	Estimate	SE	z	*p*
[1] (Intercept)	-1.24	2.21	-0.6	0.57
No. fledged chicks	0.09	0.45	0.2	0.85
2011	5.03	1.20	4.2	<0.0001
2012	3.74	1.13	3.3	0.001
Clutch initiation date	0.17	0.04	-3.9	<0.0001

[1] (Intercept) = Renesting after success of Nest type 1 with number of Fledged chicks & 2010

The interaction year*clutch initiation $F_{2,102} = 2.2$, $p = 0.11$ Delta AIC = 0.3 was not significant and removed from the model.

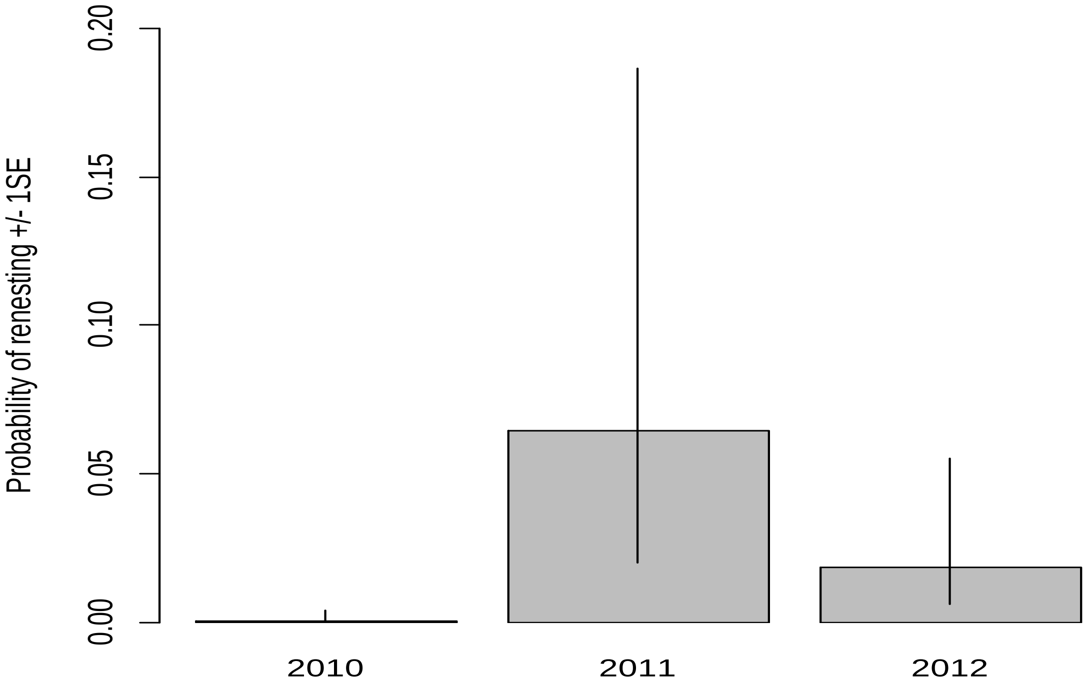

Figure 2.8: The probability of renesting after a successful first nest with year. Predicted values from the parameter estimates from the model in Table 2.4 are plotted, with clutch initiation date set at June 10th, the approximate earliest date for a second brood after a successful first nest. June - first observed renest after success and median number of chicks fledged in previous breeding attempt.

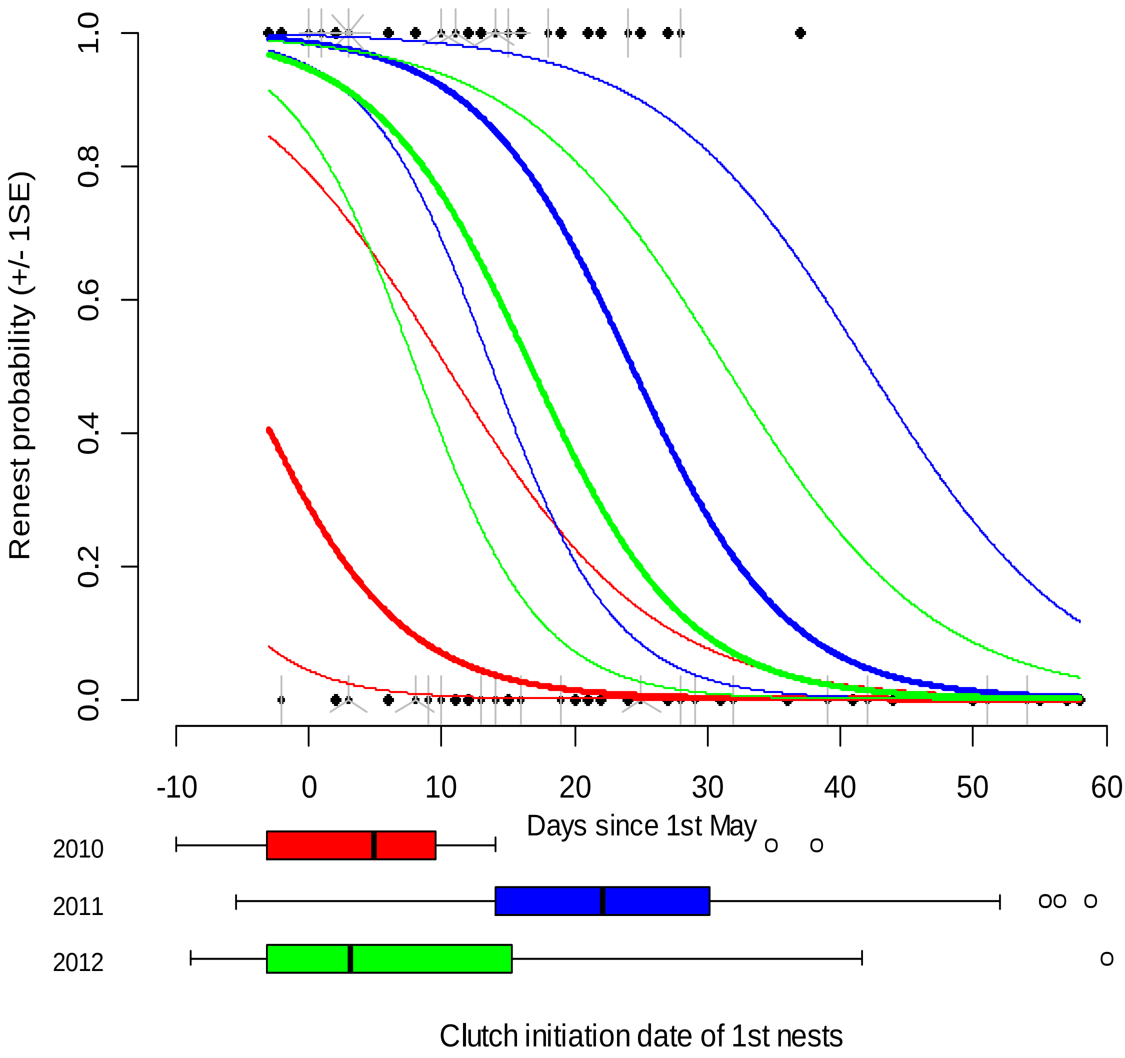

Figure 2.9: The probability of renesting after a successful first nest with clutch initiation date for the three years of the study. Note that there is no interaction between year * clutch initiation date. Predicted values from the parameter estimates from the model in Table 2.4 are plotted. Thick lines show mean predicted values and thin lines predicted means +/- 1 SE.

2.4.5. Temperature variation

Maximum daily temperature varied within and between seasons on the study site (Table 2.5, Figure 2.10). 2010 was the hottest year, with higher temperatures in April, a linear increase in temperature continuing without levelling off until August. 2011 and 2012 were cooler years, starting cooler in April and levelling off in temperature by August, particularly in 2012. Temperature varied significantly at the date of clutch initiation for first breeding attempt (1st nest type) across years: 2011, 9.2 ± 0.6°C (set as reference as the coolest year); 2010 14.4 ± 0.5°C ($t_{1,99}$ = 9.5, $p < 0.0001$); 2011 12.0 ± 0.6°C ($t_{1,99}$ = 5.0, $p < 0.0001$); model including clutch initiation date (0.19 + 0.02 per day, $t_{1,99}$ = 11.3, $p < 0.0001$). Temperature did not, however, vary significantly with year at the date of fledging of chicks after the first breeding attempt ($F_{2,99}$ = 1.9, p = 0.16); model again including clutch initiation date (-0.05 + 0.02 per day, $t_{1,99}$ = -1.9, p = 0.049).

Table 2.5: Results of a GLM the model to test whether maximum daily temperature for three consecutive years was dependent on date, the quadratic of date (i.e. a seasonal peak in temperature would be expected) and year, and their interactions.

Variables	Estimate	SE	t	*p*
[1] (Intercept)	-4.92	2.30	-2.1	0.033
Julian date (JD)	0.23	0.03	6.9	<0.0001
JD^2	0.00	0.00	-3.1	0.002
2011	11.07	3.26	3.4	0.001
2012	-9.69	3.27	-3.0	0.003
JD * 2011	-0.11	0.05	-2.3	0.02
JD * 2012	0.15	0.05	3.3	0.001
JD^2 * 2011	0.00	0.00	1.9	0.06
JD^2 * 2012	0.00	0.00	-3.4	0.001

[1] (Intercept) = Maximum daily temperature & 2010

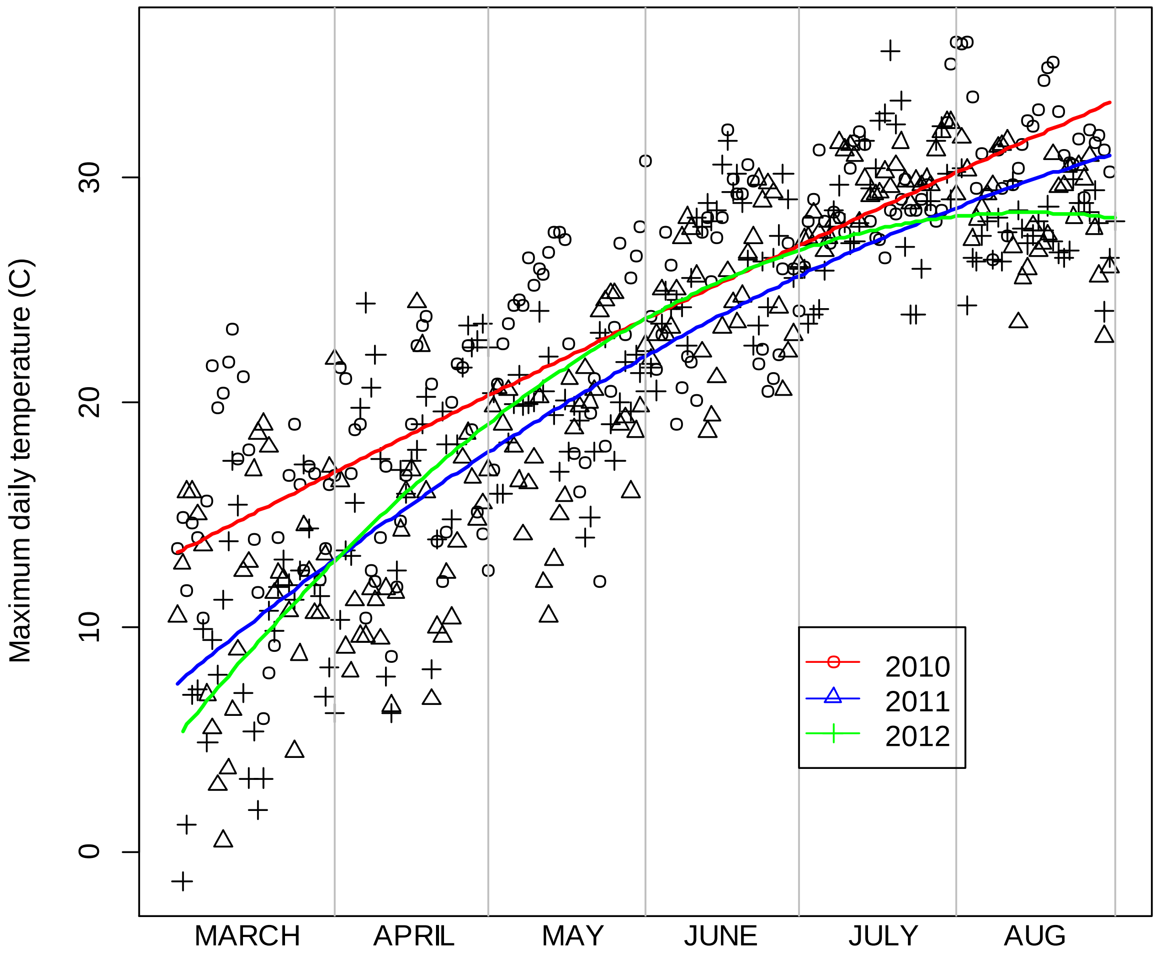

Figure 2.10: Variation in maximum daily temperature with year at the study site. Predicted values from the parameter estimates from the model in Table 2.5 are plotted.

2.5 DISCUSSION

The breeding phenology of Cyprus Wheatear at Troodos Mountain showed clear seasonality patterns varying between years that arose mostly from variation in clutch initiation date at the start of breeding. Although the overall breeding cycle varied between years, once clutch initiation started the phenology was similar between years, although differences were more pronounced for the period of post-fledged parental care. Significant variation between the three years for post fledged parental care were shown: during 2010 the species was found to care for fledglings for approximately one month in comparison to 2011-2012 when the period was for approximately two weeks. After the species started breeding and the first egg was laid, the duration of incubation and hatchling was fairly constant between years. Variation in the breeding phenology of the Cyprus Wheatear was predominantly determined by inter-annual variation in clutch initiation dates, renesting probability and the duration of parental care after chicks fledged.

The results showed that the singing activity of Cyprus Wheatear was high during the beginning of the season, during pair formation and before egg-laying but declined sharply thereafter (Figure 2.3). The seasonal pattern of singing observed in the current study is likely to reflect its function in mate attraction and retention. Singing clearly reflects breeding effort (see Chapter 5) and as such I demonstrated that its occurrence varied with year as we also demonstrated that other aspects of phenology such as clutch initiation date varied by year. Similar observations were made by Merila and Sorjonen (1994) studying the functions of male song in Bluethroat *Luscinia svecica svecica*, by examining seasonal and diurnal patterns of song. They found that seasonal patterns of singing activity peaked shortly after male arrival and before the onset of egg-laying. Similarly Lampe and Espmark (1987) showed when studying the function of song of Redwings *Turdus iliacus* throughout the breeding season, that the singing rate of breeding males decreased significantly when egg-laying started, whereas inter-seasonal variation of song was negligible.

Results indicated that clutch initiation date for Cyprus Wheatear varied across years, probably in response to temperature, and this variation consequently dominated the rest of the breeding phenology. The Cyprus Wheatear breeding phenology showed flexibility in response to warm and cold springs indicating that the species may adjust clutch initiation days to optimum food availability at least at Troodos, where first nest attempts were significantly later in the cold spring of 2011, compared to 2010 and significantly earlier in 2012 in a warm spring. The Cyprus Wheatear is a generalist insectivorous species that is likely to time its breeding to the availability of its insect food that will become more abundant as spring temperatures rise. Many migratory species, and particularly small passerine long-distance migrants such as wheatears use food resources on the breeding grounds for egg production: low temperatures on arrival may limit food availability and delay laying, and in contrast, with warmer springs, migrants may nest earlier (Ockendon et al. 2013). For example, in a long-term study of the migratory Pied Flycatcher, advances in egg-laying day correlated with advances in food availability (Both and Visser 2005). Visser *et al.* (2004) argued that climate change might lead to differential changes in the breeding dates and the time of maximum food abundance. As they showed in their paper Dutch Great Tits responded too weakly to climate change in comparison with a UK population (Cresswell and McCleery 2003), which showed better synchronization with their prey and overall flexibility to advance hatching in warm springs, and consequently to maintain breeding success over the years. Whether Cyprus Wheatears are modifying their clutch initiation date adaptively to their peak of food availability, if indeed such exists, remains to be investigated.

The duration of the egg stage for Cyprus Wheatear varied with year being significantly longer in 2011 than in 2010 a 2012 (Figure 2.5) suggesting that this too is responsive to conditions such as temperature and food availability. Both and Visser (2005) showed that Pied Flycatchers that breed earlier in warmer years reduce intervals between laying and hatching. In contrast, early laying Great Tits increase laying-hatching intervals (Cresswell and McCleery 2003). In both cases the birds were shown to be adaptively adjusting their hatch date to coincide with the peak of food availability for feeding chicks. The duration of the nestling stage showed little variation being about 2 weeks in duration in all cases. Predation pressure accounted for most if not all nest failures in our population and it is likely that fledging chicks as rapidly as possible is the best defence against this risk (see Chapter 4).

The duration of post-fledging parental care varied significantly depending on year and nest type, showing a decline through the season with date but with extended parental care during 2010 compared to 2011-2012 (Figure 2.6). Post-fledging care lasted on average for two weeks during 2011-2012 and for more than three weeks during 2010 (range 12-29 days), the latter being comparable with Northern Wheatears (Moreno 1984a). Such variation may arise through annual variation in food availability as shown with studies on Great Tits where food availability may determine the duration of post-fledging care (Higuchi and Momose 1981). The decision to terminate or extend the period of post-fledging care is unlikely to be independent of the decision to have a second brood. There is a trade-off between successive reproductive attempts, whereas, starting a second clutch reduces the reproductive value of the first clutch because of the effect of second clutches on post-fledging care (Verhulst et al. 1995). Verhulst and Hund (1996), observed that in species that initiate multiple broods in a single season there is usually a trade-off between the number of young in the first brood, and the timing and occurrence of the subsequent broods. They studied the effect of second clutch on the post-fledging care in great tits and found that parental care continued for 20 days (range 10-32 days) after fledging but that second clutches reduced the females' contribution to post fledging care. Husby *et al.* (2009) examined temporal population-level trends in the proportion of female Great Tits double-brooding, and found that the probability that a female produces a second clutch was related to the timing of first clutch relative to the peak in caterpillar abundances, and thus declined over the season. Key in these trade-offs is the length of the breeding season and also the length of the food peak available for the chicks. For example, in the Black Wheatear *Oenanthe leucura*, there were two variables which determined the number of breeding attempts: the date of onset of breeding and the intervals between raising a brood and laying another clutch (Soler et al. 1995). Late first broods and long periods of post fledging care because of low food availability may therefore prevent second broods.

Renesting probability declined through the breeding season in Cyprus Wheatears. This may reflect seasonal declines in the fitness of clutches. For example, Öberg *et al.* (2014) used long-term data on breeding time in Northern Wheatears to investigate seasonal declines in reproductive output. They suggested that degrading environmental conditions (i.e. reduction in food supply to feed chicks) together with effects of nest predation were the main determinants of the seasonal decline in fitness. Renesting probability differed significantly between years, with 2010 having the lowest renesting rate after success attaining very few second broods (Figure 2.8): this effectively resulted in that year being single-brooded and the other two years being double-brooded. The implication is that environmental conditions were substantially different in 2010. As the temperature data showed, this was a particularly warm, early year suggesting that it may be high temperatures that affect availability of food for chicks in second broods.

Local ambient temperature patterns are likely to be the cue for Cyprus Wheatear breeding, and thus timing of their clutch initiation date and occurrence of post-fledging care period and a second brood – crucial life-history and population demographic traits for the species. With only three years' data we can only speculate, but examination of Figures 2.8 and 2.9 suggest that early warm temperatures and later higher temperatures lead to a reduction in the probability of a second brood. Analyses of mean daily ambient temperature for April throughout August for the three years of the current study showed that 2010 was on average much warmer (by several degrees) although this difference was less pronounced later in the season. Studies on, for example, great tits have verified that first egg date (Forchhammer et al. 1998), clutch size (Perrins 1970), incubation date (Van Balen 1973) and hatch date (Winkel and Hudde 1997) all depend on the temperature. And other studies, for example Cresswell and McCleery (2003), have shown how Great Tits can very subtly adapt their schedules to intra- and inter-seasonal variation in temperature. In Cyprus Wheatears we have the likely confirmation of another facultative mechanism of optimising reproductive scheduling to ambient temperature conditions – highly variable periods of post-fledging care versus initiating a second brood.

The great flexibility of the species breeding under fluctuating ambient temperature suggests that they are already adapted to climate change, particularly with a seasonally dependent optimization of clutch initiation date and probability of second broods on the basis of the temperatures being high during a season. There seems already to be an adaptation by the species to variable climate and so climate change. But there is a need for long term studies to test these hypotheses with more than N = 3 years of data. In particular I would predict that in early hot years there will be early initiation of breeding, extended post-fledging care and a low proportion of second broods.

CHAPTER 3. SURVIVAL AND DISPERSAL

3.1 ABSTRACT

Many populations of European migrant bird species are declining and this may be driven by survival rates but there are few studies that can estimate true survival rates. Cyprus Wheatears are an endemic migrant that winters in East Africa: populations are probably not declining but are annually variable. I measured apparent survival in Cyprus Wheatears by recording territory occupation and reoccupation in a colour-ringed population over 4 years (2010-2013) from April – August, to determine how it varied with sex, age and year. I then estimated true survival by correcting apparent survival for dispersal by recording territory shifts and how this also varied by sex, age and year. Apparent annual survival rate varied significantly by sex, age and year (males 2010-2012: 0.70, 0.50, 0.62; females: 0.56, 0.34, 0.47; chicks: 0.35, 0.19, 0.28) but was not affected by the productivity of territory. An average of 1.1% of males and 8.2% of females were lost during breeding, and 71.4% of the 7 lost females were found depredated during incubation. Most losses occurred over-winter, with apparent over-winter survival rates (September to April inclusive) being very similar to annual rates.

The probability that a Cyprus Wheatear changed territory between years was not dependent on sex, productivity or year (87% of adults birds were resident, 12% moved 1-4, and 1% 6 territories away, N = 109), but chicks were significantly more likely to move from their natal territories (mode 3 territories, range 0-7, N = 36) than adults (probability of change = 0.90 chicks versus 0.13 adults), although this was also not

dependent on the sex of the chick. After correcting apparent survival for the probability of not detecting a chick or adult that changed territories (i.e. that any bird moving according to observed dispersal patterns left the study site) and for mean female incubation mortality, minimum true annual survival rates were very similar to apparent survival rates for males and females, but were much higher for chicks due to their higher dispersal rates. Males had the highest true minimum annual survival compared to females which were very similar to chicks (males 2010-2012: 0.77, 0.50, 0.65; females: 0.65, 0.35, 0.50; chicks: 0.64, 0.34, 0.49). The results indicate a very high survival rate for a small passerine migrant, although they are probably sufficiently annually variable to profoundly affect annual population dynamics. Females suffer greater mortality because only they incubate and may also have lower overwinter survival compared to males, suggesting that the sex ratio at birth may be female biased to compensate. Females may, however, have longer range dispersal than measured in our study, particularly if they respond to their mates not returning by moving territories, leading to an underestimate of their true survival.

3.2 INTRODUCTION

Many populations of European migrant bird species are declining, and measuring survival rates at the different stages in their annual cycle is crucial to understand why this is so. Studies on migrant bird species that breed in Europe and winter in sub-Saharan Africa have shown that their rate of decline is greater than residents and short-distance migrants (Sanderson et al. 2006). Populations of Afro-Palearctic migrants declined over large parts of Europe between 1970 and 2000, particularly species wintering in arid open habitats in Africa and long-distance migrants

(Sanderson et al. 2006, Moller 2008, Jones and Cresswell 2010, Van Turnhout et al. 2010). More recent analyses have identified that species wintering in the Guinea savannah may now have greater declines (Thaxter et al. 2010, Ockendon et al. 2012). The causes of these declines are not well known and are likely to be species specific, for example, reduced rainfall and so habitat quality on the wintering grounds (Kanyamibwa et al. 1993), habitat quality of stop-over sites (Saino et al. 2004, Schaub et al. 2005) or phenology mismatch (Forchhammer et al. 2002, Both and te Marvelde 2007, Jones and Cresswell 2010). There is much evidence, however, that survival rates and body condition of temperate-tropical migrants in the non-breeding season may be very important to population dynamics (Rappole and McDonald 1994, Newton 2004, 2008).

Survival rate is an important fitness component, and accurate measurement of this at different life history stages to identify which are most influential for population dynamics is therefore essential to understand and manage any declining population. Environmental conditions such as weather and food availability (Peach et al. 1999, Robinson et al. 2007), as well as density-dependent processes (Saether and Engen 2002), are the important factors shaping survival at any stage. Survival may however, also be related to age (Clobert et al. 1988), sex (Post and Götmark 2006a), or may vary between individuals according to their social status (Schubert et al. 2008). In passerines body condition is also an important determinant of fitness and consequently survival of individuals (Houston and McNamara 1993, Covas et al. 2002), where post-fledging survival and local recruitment rates are often positively correlated with body mass (Naef-Daenzer et al. 2001). Reproductive efforts can also impact adult survival rates (McCleery et al. 1996).

Population declines arise because productivity is less than annual mortality (Newton 1998). Population dynamics may therefore be driven by survival rates of adults and particularly first years (Arlt et al. 2008, Arlt and Part 2008, Low et al. 2010). The annual survival of migratory birds that travel through a diversity of habitats on different continents, may be influenced at many stages of their cycle, at various times and locations during the year. Evidence suggests that the greatest mortality of migrants may occur during migrations (Sillett and Holmes 2002), although events and conditions during the breeding season such as variation in food availability (Arlt et al. 2008) may also affect the cost of reproduction and so survival of adult birds due to the increase of parental workload when food is scarce (Low et al. 2010). There may be mortality specifically associated with breeding and its constraints such as restriction to a fixed site during incubation and chick rearing, and where one sex has a greater role in this then sex-specific mortality may arise.

During the breeding cycle males searching and competing for mates and territories usually have high levels of mobility, signalling and display behaviours, which may entail higher risk of exposure of males to predators (Jakobsson et al. 1995, Zuk and Kolluru 1998). Females need to forage extensively to meet energy requirements during egg production and incubation, which may make them less vigilant (Dukas and Kamil 2000) and may increase significantly in weight when forming eggs, which may impair their flight performance and ability to escape predators (Witter et al. 1994). Post and Gotmark (2006), studied predation by Sparrowhawks *Accipiter nisus* in Pied Flycatchers and found that females during egg-laying, incubation and feeding of offspring had a higher risk of predation. Predation may also be higher during incubation for females which are killed on the nest by mammalian nest predators

(Alatalo and Lundberg 1990). Consequently, if females are the sole incubators they may have an enhanced risk of predation during incubation (Gruebler et al. 2008, Perlut et al. 2008).

The juvenile stage may also represent a time of particularly high mortality during the nestling and early post-fledging stages (Anders et al. 1997) when experience and physical capability is relatively low, and this is likely to also be true during their first migration. Kershner *et al.* (2004), found that mortality of Meadowlarks *Sturnella magna* was greatest during the first week after fledging, when juveniles are flightless and vulnerable to predators. Juvenile survival has been found universally to be lower than adult survival in migrants (Saether 1989, Donovan et al. 1995b, Saether and Bakke 2000) and arises because juveniles initially can have no experience of migration routes or their wintering ground, and their inexperience in foraging ability (Desrochers 1992) or habitat choice (Cresswell 1994). Migration generally reduces survival because of its associated uncertainties (Strandberg et al. 2010), and juveniles that have established territories on the wintering ground tend to have the same survival as adults (Sillett and Holmes 2002) suggesting that much of juvenile mortality reflects uncertainty that is substantially reduced when adults gain experience of a survivable migration route and wintering area.

Although knowledge of survival rates are crucial for understanding population dynamics they are rarely measured properly. Estimating true survival rates for adults and juvenile migrants is difficult because estimates are confounded by site fidelity (apparent survival): birds that have not returned to a study area may have died or may have dispersed (e.g. Doligez and Part 2008). This is particularly a problem for estimating juvenile survival because juveniles tend to disperse away from their natal site to some degree during their first year. For example, Gardali *et al.* (2003), estimated annual rates of survival for adult and juvenile Swainson's Thrushes *Catharus ustulatus* as 56% and 25% respectively, but to what degree either are confounded by dispersal out of the study area is not known. True survival estimates require dispersal to be accounted for and so require large scale studies or species that have only small scale dispersal. For example, in the Northern Wheatear studies of survival rate of adults breeding in Sweden probably reflected true survival (Low et al. 2010), because they minimised the effect of breeding dispersal by surveying a radius of 2-4 km away from central study area between consequent years.

Here I measure survival in a Palearctic migrant, the Cyprus Wheatear. Cyprus Wheatears are a widespread and common migrant endemic to Cyprus that winters in southern Sudan and Ethiopia. They have a broad niche range, breeding from sea level up to the highest mountains in Cyprus, inhabiting diverse habitat types, including open, stony areas, urban areas, as well as shrub, scrub, and bush vegetation and sparse coniferous woodland (Randler et al. 2010b). Populations of Cyprus Wheatear are probably not declining but are probably annually variable. The population size of Cyprus Wheatear is approximately 90,000-180,000 breeding pairs and its population status is regarded as secure (Randler et al. 2010b). The population of Cyprus Wheatear may be stable in the long term, but there are likely to be annual fluctuations in populations due to varying productivity and survival as a consequence of annual environmental and anthropogenic variation. Cyprus Wheatears may therefore provide a tractable model study system in which to study the population dynamics of a migrant.

I measured apparent survival in Cyprus Wheatears by recording territory occupation and reoccupation in a colour-ringed population over 4 years (2010-2013) from April – August, to determine how it varied with sex, age and year. I then estimated true survival by correcting apparent survival for dispersal by recording territory shifts and how this also varied by sex, age and year.

3.3 METHODS

The study was conducted from 2009 to 2013 in a 130 ha area at National Forest Park of Troodos (34°56′11″N 32°51′48″E), at about 1800 m a.s.l. on the Island of Cyprus during the breeding season. The study area was surrounded by the “Artemis Trail” with old low density coniferous forest, supporting the one of the densest breeding Cyprus Wheatear populations on the island (Flint and Stewart 1992). The National Forest Park of Troodos (NFP of Troodos) is located at the centre of Troodos massif that ranges from the northwest to the southeast part of Cyprus. The NFP of Troodos covers an area of 9,029 ha. with the highest peak of Chionistra at 1952 m, situated almost at the centre of an Ophiolite Complex. The main habitats that characterized the study area are those of the endemic *Pinus nigra* ssp. *pallasiana* forest, the Black Pine zone which starts from 1400 m and reaches up to the top of the mountains to 1952 m, and *Juniperus foetidissima* and Serpentinophilous grasslands that are distributed at the highest parts and that occur in openings of the black pine forest in the form of small, scattered patches. The understorey of Black Pine consists of *Quercus alnifolia*, *Juniperus oxycedrus*, *Juniperus foetidissima*, *Sorbus aria* ssp. *cretica*, *Berberis cretica*, *Arbutus andrachne*, *Rosa chionistrae*, *Rosa canina*, *Cotoneaster racemiflorus* var. nummularius etc. Annual precipitation in the area is very high with more than 1100 mm being recorded and temperature varies through the year from freezing during winter to a maximum of about 35 °C during very hot dry summers.

During 2009 a pilot study identified a study area and monitored and mapped territories (Figure A) but without colour-ringing of birds. In subsequent years 2010-2012, individuals were colour-ringed (Appendices: Table A, B and C) when they were actively defending a territory and locations of territories were plotted on maps (Figure B, C and D); territories were intensively monitored to record details of breeding. During April-May, 2013, only territory mapping and resighting was carried out, but in an expanded study area, covering a buffer zone of around 500 meters around the previous study area. The study area consisted of 4 parallels transects containing about 80 mapped territory locations over the 4 years. Pairs were marked within their territory and at least one individual of the pair was coloured-ringed (Territory Maps Figures B, C and D showing territories monitored in each year). All territories were regularly monitored throughout the breeding season (at least every second/third day) and detailed data were collected from a central and intensively studied 130 ha part of the total study area, with the surrounding area monitored for adult and chick dispersal only during 2013.

Cyprus Wheatears were highly site faithful, holding distinct territories and returning to them in the subsequent breeding season, thus they can be relocated easily. Territories were defended by males during the arrival stage and territories were numbered according to the date that individuals were first located or relocated.

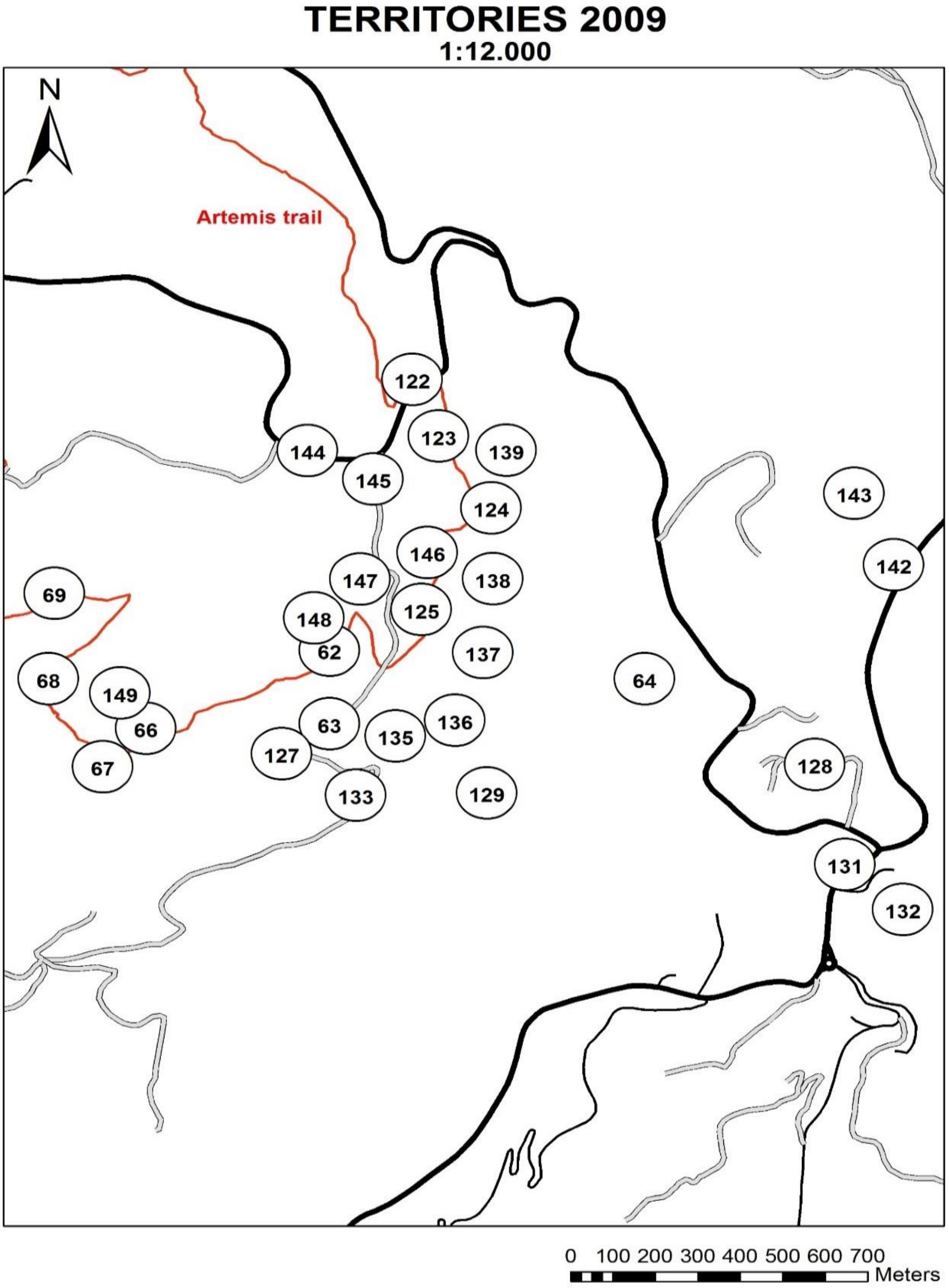

Figure A. Territory locations during the pilot study year (2009) when individuals were not colour ringed.

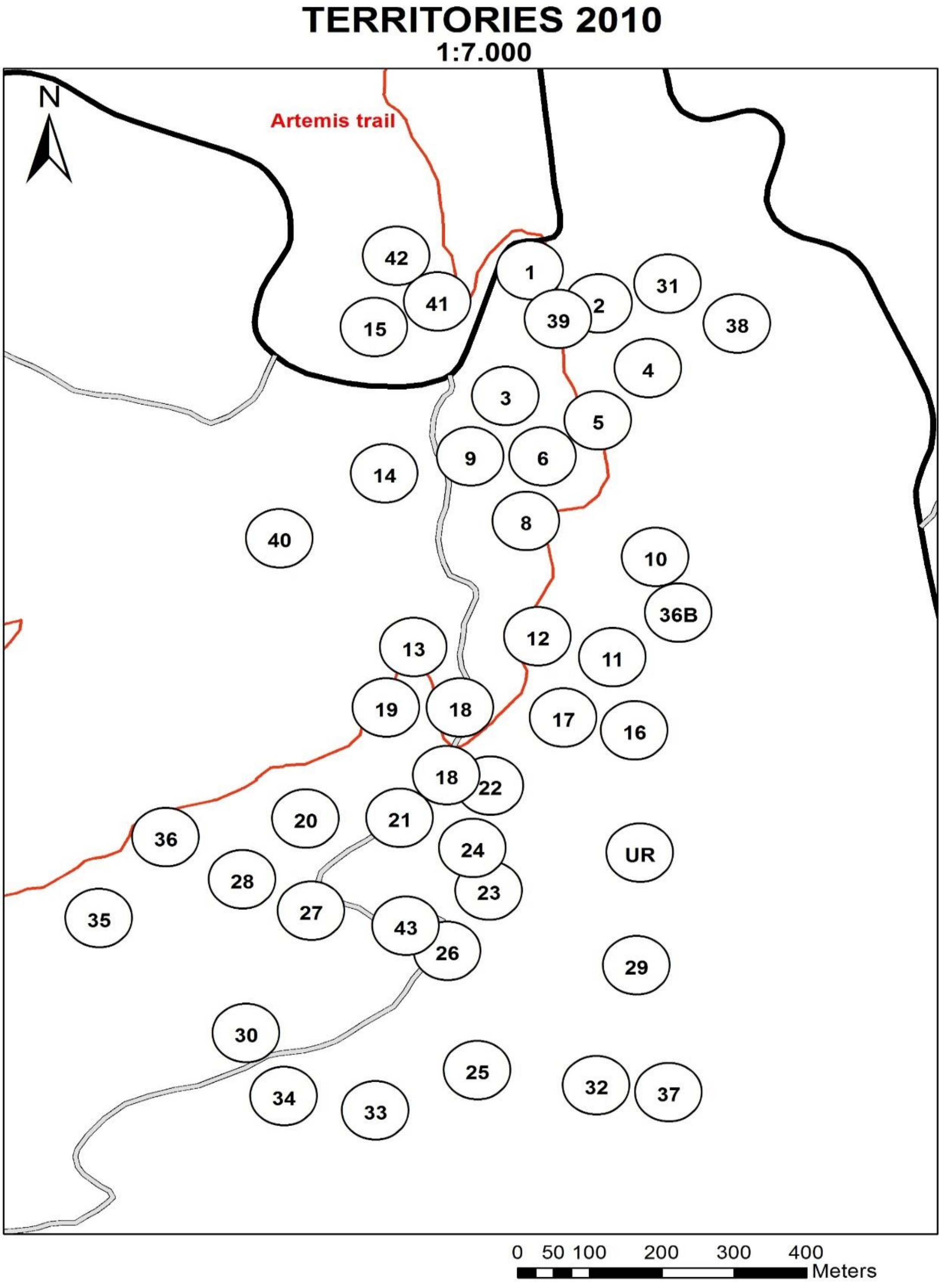

Figure B. Territory locations of Cyprus Wheatears during the breeding season 2010.

Note that new numbers were often given to the same territory in different years.

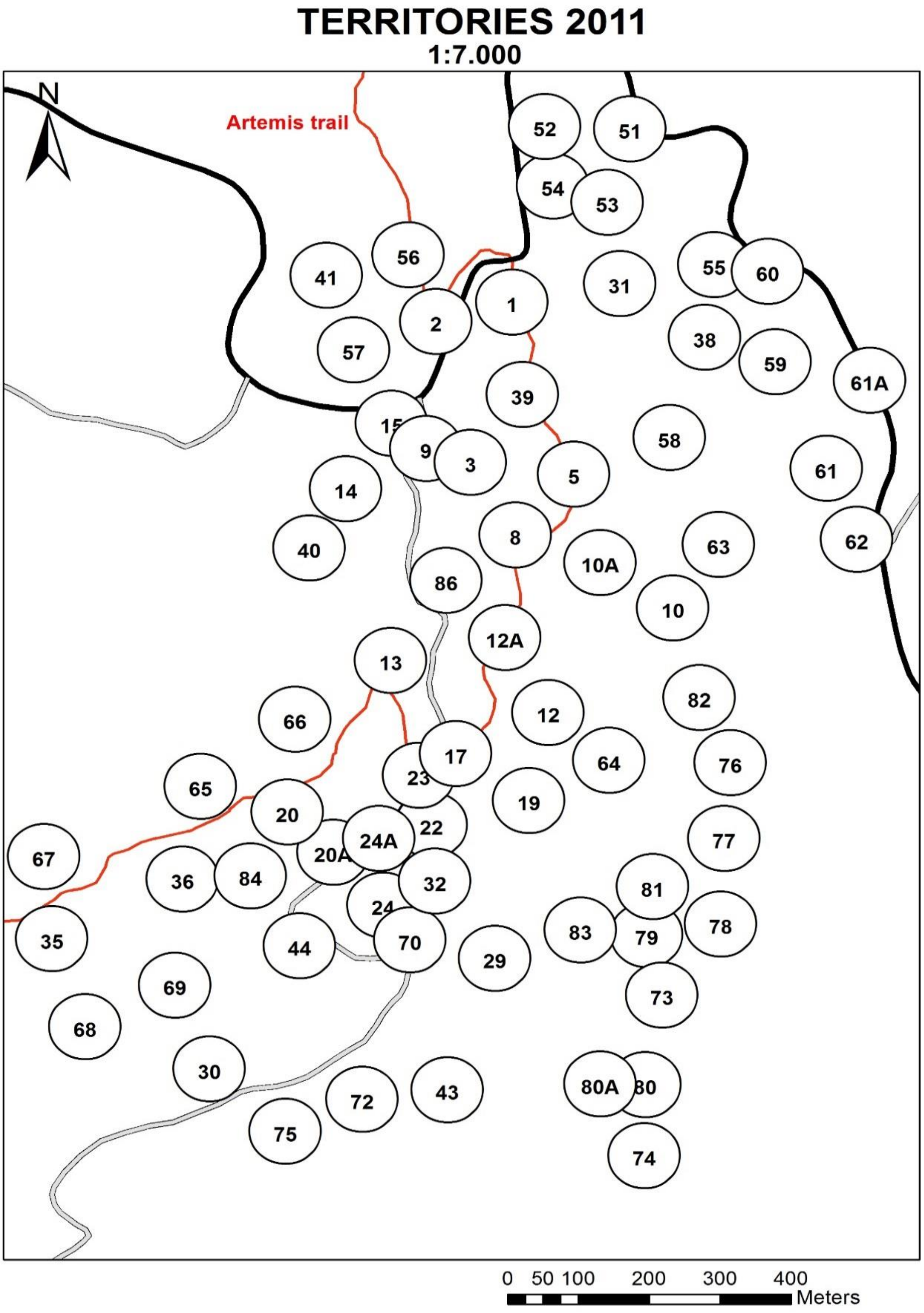

Figure C. Territory locations of Cyprus Wheatears during the breeding season 2011.

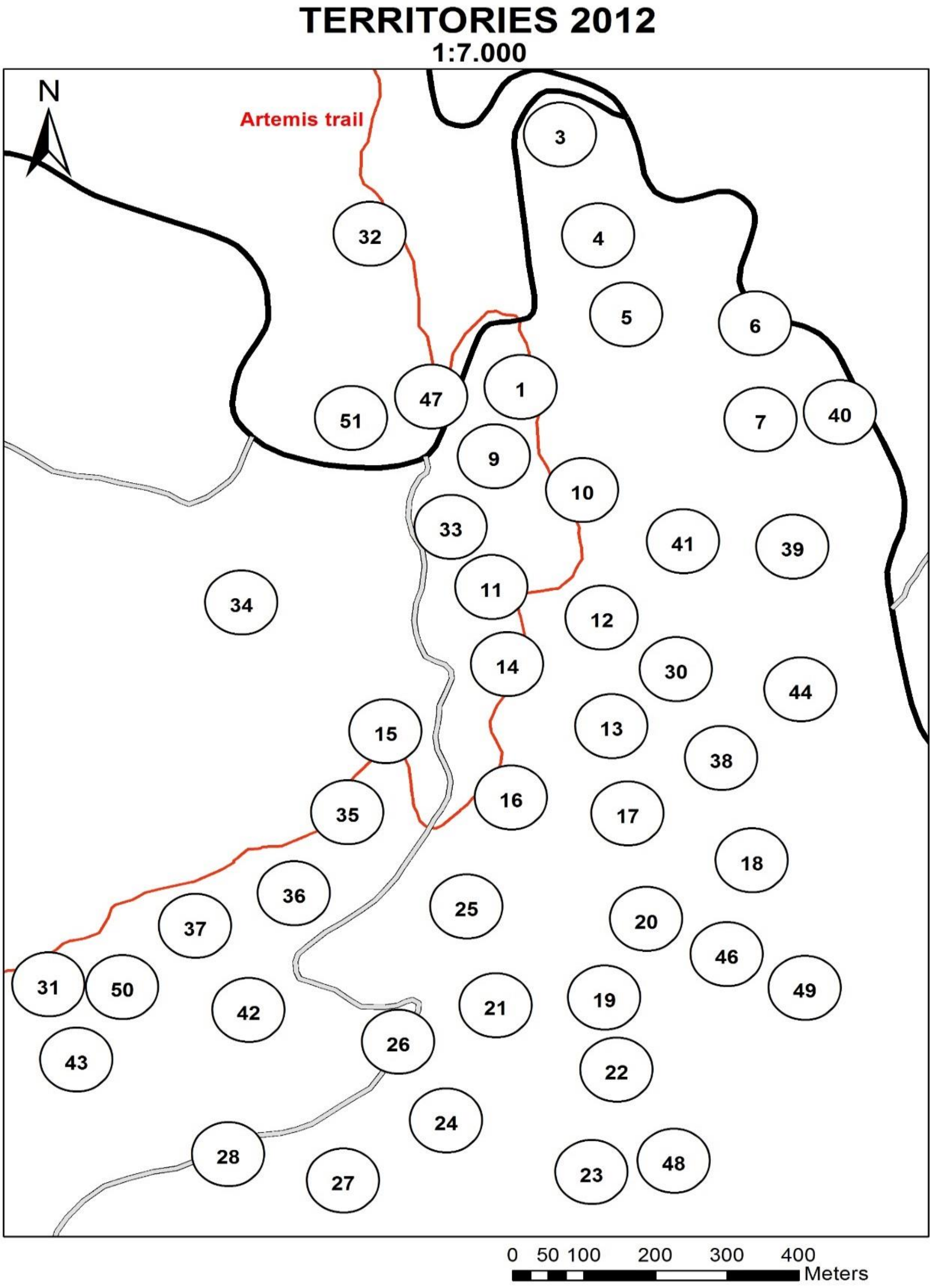

Figure D. Territory locations of Cyprus Wheatears during the breeding season 2012.

Observation and data recording started around mid-end of March each year when the first individuals arrived at the breeding grounds, and regular monitoring continued until the end of August, with sporadic visits until October. Birds were captured with spring traps that were baited with maggots throughout the season (but especially during arrival and territory establishment for the adults) and ringed with individual combinations of colour rings: playback using conspecific song was used to during trapping. Individuals were sexed, and all males were aged as young (1 year old) or adults (>1 years old) based on their plumage characteristics (contrast in the coverts so that first year males had brownish greater coverts – visible in the field – whereas adult males had dark, uniform sooty black wing feathers) (Sluys and Vandenberg 1982). The age of the female could not be reliably distinguished and so females were not aged. Territories were mapped on a paper using landmarks – the Artemis trail and tracks – and via a GPS. Territories were delimited by the outermost positions of the majority of all recorded positions of the resident pair or/and unpaired male. A GPS point was taken on the approximate centre of the territory sites (location), determined by multiple observations of colour-ringed birds (pairs) over several months, and nest location. Territory sites were largely stable across the years irrespective of territory holders. At each territory during 2010-2012, we recorded arrival dates of individuals, resighted colour-ringed birds, mapped territories, and monitored nesting stage, egg, nestling and fledgling survival, and depredated nest and females. Nests and fledglings were found opportunistically, the latter being extremely obvious – the number of fledglings was counted immediately after fledging and one month afterwards, although frequent visits meant that fledglings and their survival were recorded every few days. The study contained 324 individuals that were colour ringed over 2010-2013 (110 males, 91 females and 123 chicks). With respect to territories monitored: there were

45 during 2010, 69 during 2011 and 50 during 2012. Sample sizes of birds ringed and resighted in the different periods are given in Table 3.1.

I used resighting rates of individually marked Cyprus Wheatears to determine the annual survival rate of adult migratory birds and their offspring. Cyprus Wheatears are highly detectable. Typically both male and female birds could be seen on every visit to a territory particularly before incubation commenced. Cyprus Wheatears typically will allow approach to within 30 meters and their flushing response is to fly up to conspicuous perches rather than slipping away. They utilise lightly wooded habitats with large *Pinus nigra* trees that have a dense crown but few lower branches. The bare rocky hillsides of the study were largely devoid of low vegetation apart from occasional *Berberis cretica* and in any case, wheatears perch conspicuously on any tall vegetation present in their territory. Males sing for long periods from conspicuous song perches. Both male and female birds respond to playback of song particularly in April before incubation commences, moving to a few meters of a playback source within minutes. Males from adjacent territories and particularly males and females from new territories that have not become definite at the beginning of the season will also travel several hundred meters to check out playback. Females make a soft chacking call when people are near their nests adding to their detectability. Therefore, and also because of the intensive nature of the study, I considered a bird to have survived the previous winter if it was recorded at the study site the following April-May. No birds were ever not recorded in a season and then recorded in the next unless they had moved out of the study area (i.e. in 2013 when the search area was expanded to measure dispersal on a larger scale – see below). I considered a bird to have survived the breeding season if it was seen during August in its territory.

Dispersal was estimated by observing movements between breeding territories for adults between years and between natal and their first breeding territories for chicks. Each year all territories and territory holders were mapped and the number of territories moved for each bird was scored between consecutive years. In 2013 the study area was expanded to a distance of 2-3 territories beyond the study area used in 2009-2012 to increase sample sizes and to look for evidence that birds were surviving but being missed because of dispersal out of the study area. Six extra chicks from the previous year, one from two years previously, and one adult were found. These extra birds were not included in estimates of survival rates so that the three years' rates were directly comparable, but were included in the dispersal distance analysis. All adults were ringed wherever they could be caught but only a sample of chick broods were ringed each year, concentrating on chick broods within the centre of the study area to maximise chance of resighting the following year even with dispersal.

The proportion of birds that would have been detected assuming 100% return but with average territory movements as recorded above was estimated in the following way. The territory map for 2012 was used (the spatial arrangement and density of territories was broadly similar in all years) and each territory was scored for the number of territories adjacent to it, 1 territory away, 2 territories away, and so on until 7 territories (the largest dispersal distance observed) on the 4 ordinal compass bearings that were within the study area and therefore where I assumed a returning bird would be resighted. Thus a territory on the edge of the study area might have most of its adjacent territories – even at only one territory away – where a returning bird would not be resighted. In contrast a central territory would have a very high proportion of its adjacent territories within the study area. Then the proportion of adjacent territories in each distance band (1 – 7 territories away) within the study area was averaged across all territories (N = 44 territories): for example 89% of territories within 1 territory of the study area were monitored, 73% within 2, 58% within 3 and so on until 4% within 7 territories. The proportion of birds that were observed moving 1 territory was then multiplied by the proportion of territories that were monitored to calculate the proportion of birds that would have been resighted. This was repeated for all the distance bands and then the proportions were summed to give the overall proportion of dispersing birds that would have been detected in the study. The calculations were carried out separately for chicks and adults because of their different recorded dispersal distances (see below).

Resighting data were then corrected for the probability of dispersal by dividing the total number of either adults or chicks resighted in each year with the estimated resighting rate for adults or chicks due to dispersal respectively to give the total number of birds in each age class that were likely not to have been recorded due to dispersal. This was a trivial number for adults in each year (0-1) but a larger number of chicks (6-8): see results. Randomly chosen adults and chicks which were not resighted were then scored as having been resighted to match these annual estimated numbers of dispersing birds.

Analysis was carried out using R 2.13.1. Probability of survival was tested using resighting data for apparent survival and resighting data corrected for dispersal for true survival. Models to predict probability of resighting (0 or 1) were binomial logistic regressions with log-link functions. Overwinter survival considered all birds ringed that were seen alive at the end of the breeding season (August) that were then resighted the following April-May, and considered all chicks ringed. Chicks were all ringed in August apart from 4 in the last week of July and 11 in the first week of September (total N = 123). Annual survival considered all adult birds that were ringed between April-May and resighting during April-May the following year. Almost all adults were ringed in April and May apart from 3 in July and 14 in the first week of June (N = 221): these adults ringed outwith April-May were all known individuals associated with successful breeding territories monitored during April-May. Models included, where necessary, individual identity of the bird and brood identity as random effects in the model because some adults survived more than 1 year and more than one chick from the same brood survived respectively.

3.3.1 Models for overwinter survival considered were: Probability of resighting (0/1) ~ agesexclass + year + productivity + (1 | comb) + (1|terr) + agesexclass*year.

Note that there was no productivity associated with chicks so the initial model only included adults. Productivity was not a significant predictor and neither was the interaction so these variables were removed (see below).

3.3.2 Models for annual survival considered were: Probability of resighting (0/1) ~ sex + year + productivity + (1 | comb) + sex*year.

Note that the annual models only included adults (because all chicks were ringed more or less in August). Productivity was not a significant predictor and neither was the interaction so these variables were removed (see below).

3.3.3 Probability of dispersal was tested using territory movement data. Models to predict probability of dispersal (0 stayed in territory or 1 changed territories between years) were binomial logistic regressions with log-link functions. Models for dispersal considered were: Probability of moving (0/1) ~ sex + year + productivity + (1 | comb) + sex*year + sex*productivity.

3.4 RESULTS

Both annual and overwinter (Sept – April inclusive) apparent survival rate varied significantly by sex, age and year but were not affected by the productivity of a territory (Table 3.2, Figure 3.1). Males had the highest annual survival (0.50 – 0.70) compared to females (0.34 – 0.56) compared to chicks (0.19 – 0.35), and annual survival varied by a maximum of about 21%. Only 1.1% of ringed males were lost during the breeding season (May – August inclusive) compared to 8.2% of females; 71% of females that were lost (N = 7) were found depredated during incubation (Table 3.1). Apparent overwinter survival rates were therefore very similar to annual apparent survival rates (Table 3.1 and Figure 3.1).

Table 3.1: Numbers of birds ringed during the study used to estimate apparent survival. Overwinter refers to the number of birds alive in a year in August to start the overwinter period from September – April inclusive. Annual refers to all birds ringed during that year used to estimate annual survival rate. Resightings are for the following year (i.e. resightings in 2013 are reported for 2012).

	Number Ringed	Number Resighted	Proportion Resighted
2010			
Overwinter males	31	20	0.65
Annual males	31	20	0.65
Overwinter females	15	10	0.67
Annual females	16	10	0.63
Chicks	13	4	0.31
2011			
Overwinter males	58	32	0.55
Annual males	60	32	0.53
Overwinter females	47	13	0.28
Annual females	49	13	0.27
Chicks	66	15	0.23
2012			
Overwinter males	41	25	0.61
Annual males	41	25	0.61
Overwinter females	24	13	0.54

Annual females	28	13	0.46
Chicks study area	47	13	0.28
Chicks study area +	47	19	0.40

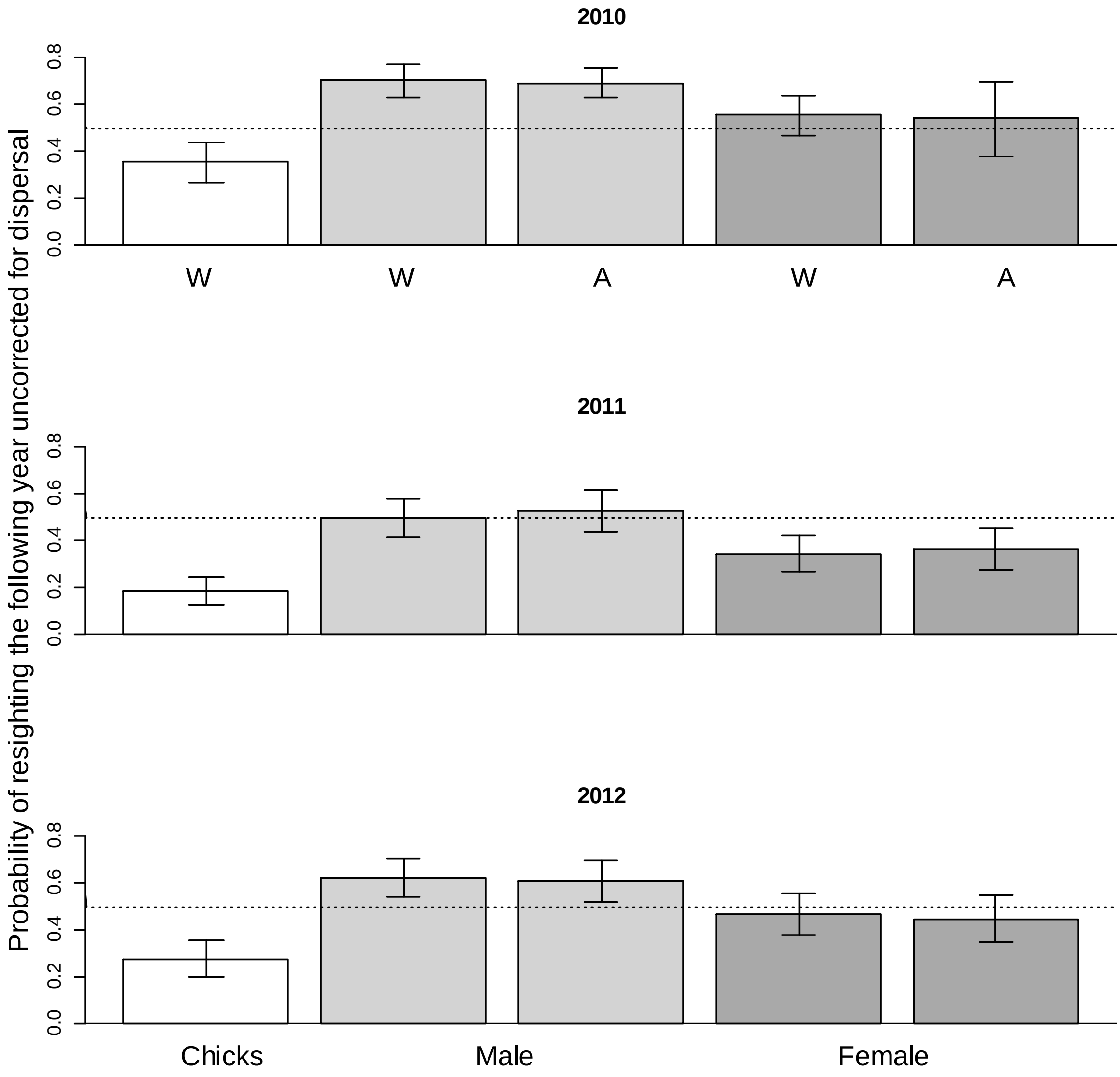

Figure 3.1: Predicted apparent overwinter survival (W: September – April inclusive) and annual survival (A) for Cyprus Wheatears by year, age and sex. Mean parameter estimates and 1 standard error plotted are from the model in Table 3.2. Note that only one chick value is plotted per year because only overwinter survival rates are relevant (some chicks were fledged in August). The dashed line is a survival rate of 0.5, plotted to allow the values to be read more easily.

Table 3.2: Results of the model to test whether apparent survival (a.) overwinter, between September and April inclusive was dependent on sex, age class or year and (b.) annually, was dependent on sex, year or annual productivity per territory. Individual identity of the bird (in models a. and b.) and brood identity (in model a. only) were included as random effects in the model because some adults survived more than 1 year and more than one chick from the same brood survived respectively.

a. Overwinter apparent survival

Variable	Estimate	SE	z	*p*
[1](Intercept)	-0.61	0.36	-1.7	0.09
Male	1.47	0.30	4.9	<0.001
Female	0.83	0.33	2.5	0.01
2011	-0.87	0.34	-2.6	0.01
2012	-0.36	0.36	-1.0	0.32

b. Annual apparent survival

	Estimate	SE	z	*p*
[2](Intercept)	0.82	0.33	2.5	0.012
Female	-0.67	0.28	-2.3	0.019
2011	-0.71	0.37	-1.9	0.05
2012	-0.37	0.40	-0.9	0.36

[1](Intercept) = Over winter apparent survival & chick & 2010

[2](Intercept) = Annual apparent survival & male & 2010

a. The interaction between year*age class was not significant (all *p* values > 0.19, delta AIC on removing interaction = -4.6)

a. Productivity was not significant when included in the model (*p* = 0.63, -0.049 ± 0.10, delta AIC on removing term = -1.8). Note only males and females were included in these model comparisons.

b. The interaction between year*age class was not significant (all p values > 0.25, delta AIC on removing interaction = - 2.7). Productivity was not significant when included in the model (*p* = 0.62, -0.048 ± 0.10, delta AIC on removing term = -1.8).

The probability that a Cyprus Wheatear changed territory between years was not dependent on sex, productivity or year (87% of adult birds did not change territory, 12% moved 1-4 territories away, and 1% 6 territories away, N = 109: Table 3.2, Figure 3.2). If an adult changed territories the distance it moved did not depend on sex ($t_{1,10}$ = -0.9, *p* = 0.41) or on productivity ($t_{1,10}$ = 1.7, *p* = 0.12) or on the interaction between sex*productivity ($t_{1,10}$ = -1.0, *p* = 0.33).

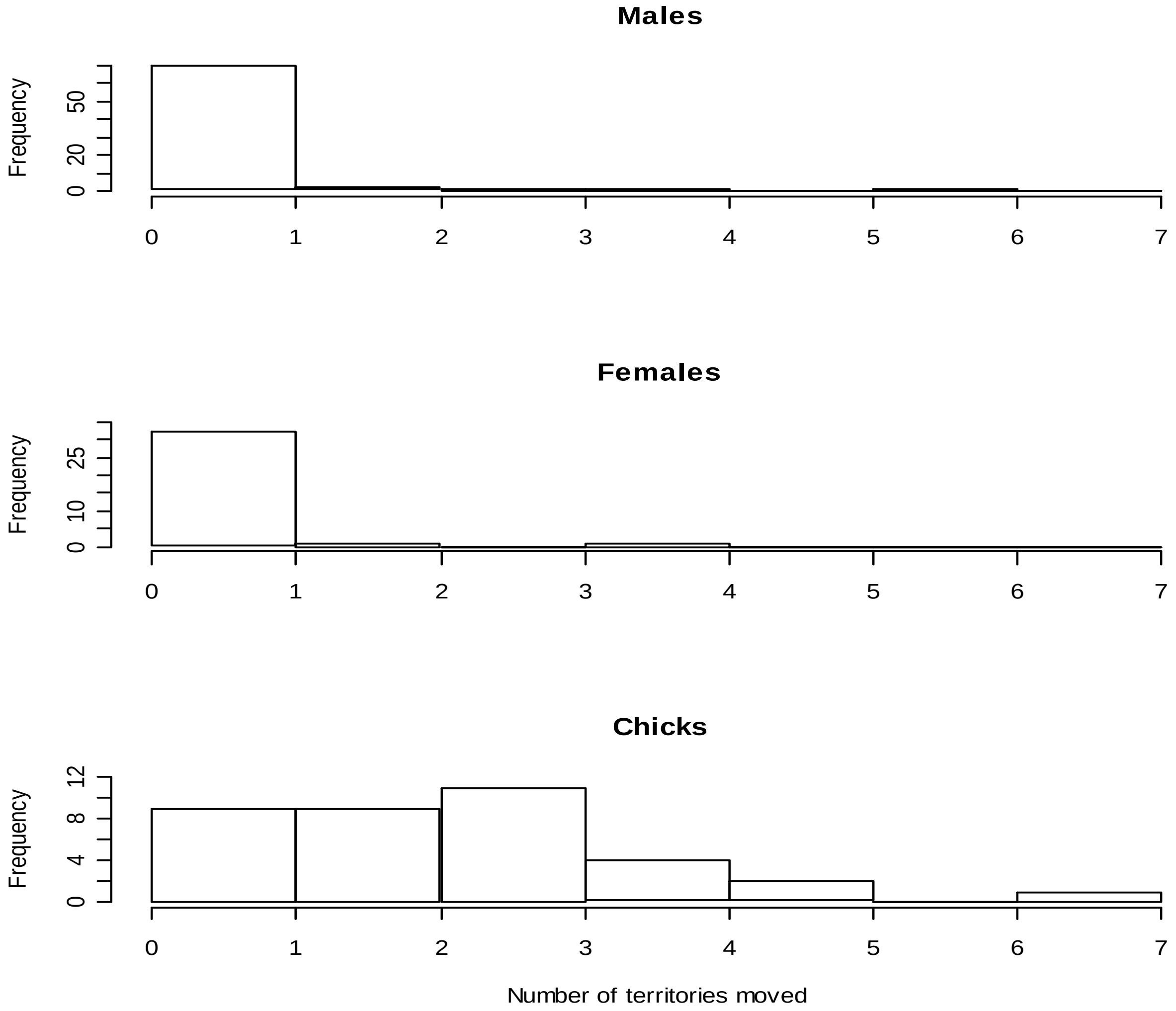

Figure 3.2: Frequency distributions of the number of territories moved by adult males and females, and chicks in the following year (0 if they reoccupied the territory used in/their natal territory in the following year). The distributions of male and females are very similar (Kruskall-Wallis 1- way ANOVA χ^2 = 0.1, *p* = 0.73).

More male chicks were resighted in a subsequent year compared to females (male 17, female 7: $\chi^2_1 = 4.4$, $p = 0.041$). The distance moved by a chick was not however dependent on the sex of the chick ($t_{1,22} = -0.8$, $p = 0.46$, including brood as a random effect). Chicks were significantly much more likely to change territories in their first year (mode 3 territories, range 0-7, N = 36) than adults (z = -6.1, $p < 0.001$, N = 139 including individual identity of adult birds and brood identity of chick as random effects: Table 3.3, Figure 3.3).

Table 3.3: Results of the model to test whether probability of an adult changing territory was dependent on sex, year or annual productivity per territory. Individual identity of the bird was included as a random effect in the model because some birds maintained territories in more than one year.

Probability of an adult changing territory

Variables	Estimate	SE	z	*p*
[1](Intercept)	-2.28	1.19	-1.91	0.06
Female	0.35	0.62	0.56	0.57
2011	0.94	0.73	1.29	0.20
2012	-0.60	0.96	-0.63	0.53
Productivity	0.0001	0.23	0.004	0.99

[1](Intercept) = male & 2010

The interaction between sex*year was not significant (all *p* values > 0.73)

The interaction between sex*productivity was not significant (*p* > 0.78)

Delta AIC on removing interactions = -1.8

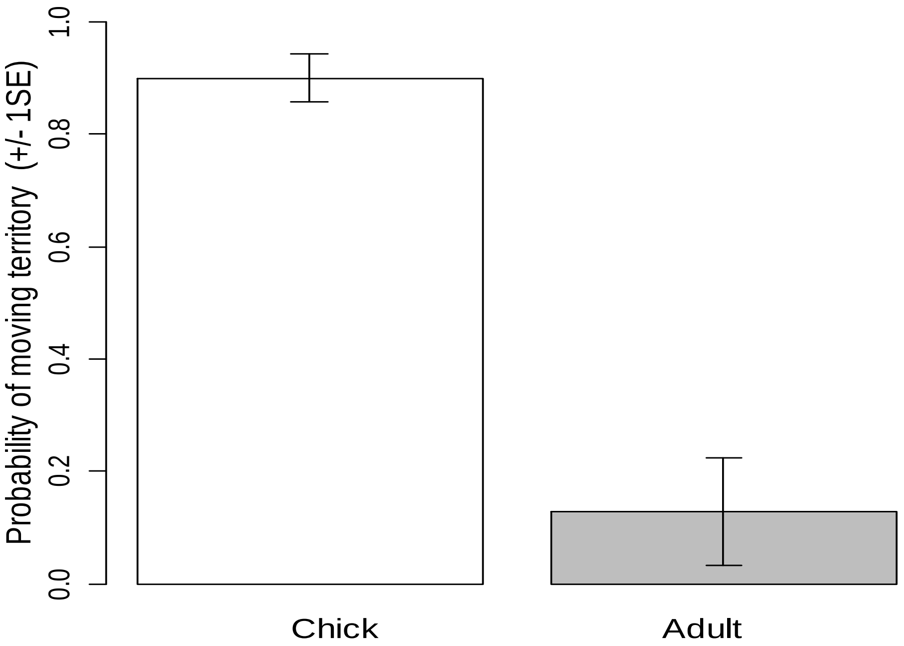

Figure 3.3: The probability of a chick or adult that survived over the winter moving from their natal or breeding territory, respectively, in the following breeding season. Mean parameter estimates and 1 standard error from a model of number of territories moved (range 0 – 7) by sex including individual identity and brood identity as random effects.

The probability that an adult that survived the winter would return to a territory in the study site (assuming a dispersal pattern according to the observed distribution illustrated in Figure 3.2) was calculated as 0.963 (i.e. very few dispersed and if they did, they moved only 1 or two territories so only some of those birds on the edge of the study area would be missed the next year). The probability that a chick that survived the winter would return to a territory in the study site (assuming a dispersal pattern according to the observed distribution illustrated in Figure 3.2) was calculated as 0.650 (e.g. 81% of chicks moved 3 territories or less and 87% of territories were within 3 territories of where chicks were ringed). This meant that I probably missed resighting

6 chicks and 1 male in 2010, 8 chicks, 1 male and 1 female in 2011 and 7 chicks, 1 male and 1 female in 2012. Consequently corrected predicted minimum true survival rates were very similar to apparent survival rates for males and females, but were much higher for chicks (Table 3.4 and Figure 3.4) where their high dispersal rates led to substantial underestimates.

Table 3.4: Results of the model to test whether true survival (a.) overwinter, between September to April inclusive was dependent on sex, age class or year and (b.) annually, was dependent on sex or year. Resighting rates were corrected for estimates of average dispersal (2010, 6 chicks and 1 male; 2011, 8 chicks, 1 male and 1 female; 2012, 7 chicks, 1 male and 1 female). Individual identity of the bird (in models a. and b.) and brood identity (in model a. only) were included as random effects in the model because some adults survived more than 1 year and more than one chick from the same brood survived respectively.

a. Overwinter

Variables	Estimate	SE	z	*p*
[1](Intercept)	0.58	0.35	1.6	0.10
Male	0.64	0.28	2.3	0.02
Female	0.049	0.31	0.31	0.87
2011	-1.2	0.34	0.34	<0.0001
2012	-0.62	0.37	0.37	0.09

b. Annual

	Estimate	SE	z	*p*
[2](Intercept)	0.92	0.33	2.8	0.01
Female	-0.69	0.28	-2.4	0.02
2011	-0.79	0.37	-2.1	0.03
2012	-0.31	0.40	-0.4	0.44

[1](Intercept) = Chick & 2010

[2](Intercept) = Male & 2010

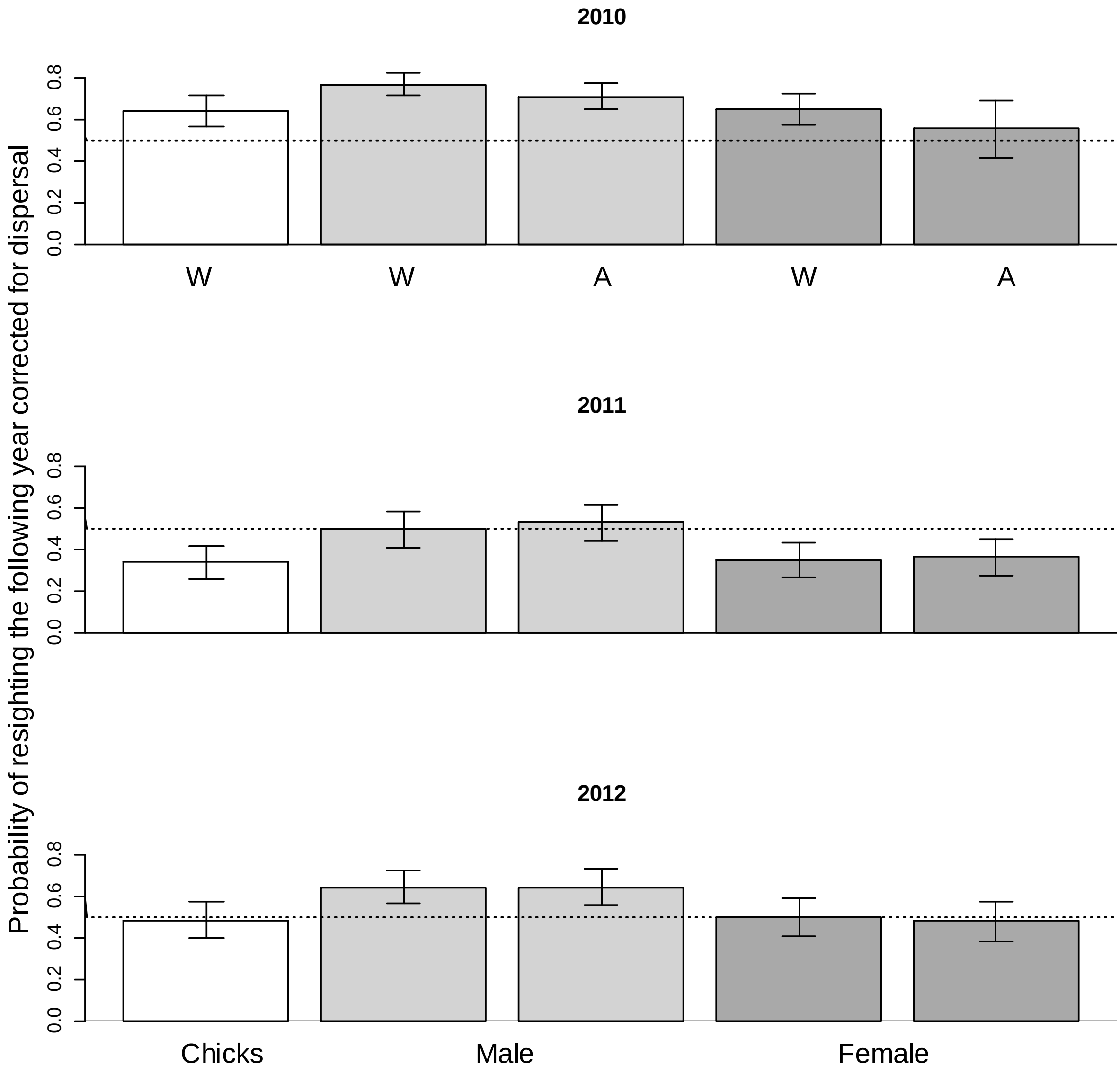

Figure 3.4: Predicted true overwinter survival (W: September – April inclusive) and annual survival (A) for Cyprus Wheatears by year, age and sex. Mean parameter estimates and 1 standard error plotted are from the model in Table 3.4. Note that only one chick value is plotted per year because only overwinter survival rates are relevant (some chicks were fledged in August). Mean number of resightings was corrected using an estimated probability of remaining in the study area of 0.963 for adults and 0.650 for chicks, if a bird survived. The dashed line is a survival rate of 0.5, plotted to allow the values to be read more easily.

Males had the highest true minimum annual survival (0.50 – 0.77) compared to females (0.35 – 0.65) which were very similar to chicks (0.34 – 0.64). Note that the minimum actual overwinter survival rate for chicks in 2012-2013 (including the chicks found from the wider dispersal search) was 19/47 = 40.4%: other raw unadjusted and therefore minimum real survival rates are high (Table 3.1) with a mean for males of 60.0%, females of 45.4% and chicks of 31.4%.

3.5 DISCUSSION

This study showed that Cyprus Wheatears are highly site faithful with little dispersal for adults and dispersal on the scale of only a few hundred meters for first year birds. This allowed me to estimate true survival. Minimum estimates of true survival were high but varied by sex and age: some females died from predation during incubation but overall survival rates were very high during the breeding season with most mortality occurring during migration or during the winter (Table 3.2). These results therefore require discussion in terms of the generality and population consequences of (i) low observed dispersal rate even for chicks, (ii) overall relatively high survival rates for a small passerine migrant (iii) higher survival rates for males versus females and (iv) lower survival rates for first year birds. These four results are then discussed in terms of informing our understanding of the population dynamics of Afro-Palearctic migrants in general.

Dispersal rates

Observed dispersal rates in my study were relatively low compared to other studies of migrant passerine but depended on age and sex with females and yearlings dispersing more than males (Table 3.3). This is consistent with other studies, for example, natal dispersal in the Collared Flycatcher *Ficedula albicollis* involved short-distances with most young returning to breed within one kilometre of their birth site, and females dispersed further than males (Part 1990). Kern *et al.* (2014), showed that in Pied Flycatchers, overall return rates for males was 53%, for females 42% and 3% for nestlings, thus suggesting that juveniles settled significantly further away from their natal sites than adults, and females further away than males.

The evolution of the Cyprus Wheatear, an island endemic, will have inevitably been associated with selection against long dispersal distance. Other island endemics also have relatively small dispersal distances, for example studies on the Reunion Grey White-eye *Zosterops borbonicus*, an endemic passerine to Reunion Island in the Mascarene archipelago indicated that the species shows extremely reduced propensity to disperse (Bertrand et al. 2014). Wheelwright and Mauck (1998) found that insular young Savannah Sparrows *Passerculus sandwichensis* were highly philopatric, returning to the same island, thus having a median dispersal distance between their natal nest and the first nest as an adult of about 228 m.

First year Cyprus Wheatears commonly dispersed from their natal site (90% moved) at the scale of a few hundred meters (most commonly 3 territories away), whereas adults, if they moved at all (only 13% moved), most commonly moved just one territory (Figure 3.3). First year birds typically disperse from their natal territory (Morton 1992) and this is primarily thought to be to avoid inbreeding (Doligez and Part 2008). For example, first year Northern Wheatears have been shown to disperse further than adults (Fulton 2010, Seward et al. 2013). Dispersal of offspring from their natal area has generally been interpreted as an inbreeding avoidance mechanism (Howard 1960, Lidicker 1962, Greenwood and Harvey 1976), with female birds being less philopatric and dispersing farther than males (Greenwood 1980). For example, Morton (1992), presented data on yearling and adult Mountain White-crowned Sparrows *Zonotrichia leucophrys oriantha*, showing overall return rates of 10% in females which were significantly lower than the 13.9% observed in male, suggested that females dispersed greater distances to avoid close male kin and the deleterious effects that could be caused by inbreeding. Lowered dispersal distances can lead to substantial inbreeding depression in insular populations of birds. For example, analyses of quantified inbreeding depression in survival and reproduction in the populations of Cactus Finches *Geospiza scandens* and Medium Ground Finches *Geospiza fortis* showed a strong reduction in recruitment and survival, although this was strongly modified by two environmental conditions: food availability and number of competitors (Keller et al. 2002).

Female birds have generally been found to be the dispersive sex (Clarke et al. 1997, Schjorring et al. 2000) but I found no evidence for this with chicks: although my sample size was not large (N = 24 chicks) there was no indication of females moving a greater distance than males, and the trend was for females to move slightly less (half a territory). There was no difference in dispersal rate observed for adult females compared to adult males (Figure 3.2). This seems unlikely in terms of results from other studies. For example, studies by Artl and Part (2008) showed that Northern Wheatear females disperse a greater distance than males, and detecting female (or indeed any) dispersal depends crucially on the scale of a study (Low et al. 2010). For example Winkler *et al.* (2002) showed that 11% of missing migratory Tree Swallows *Tachycineta bicolor* had in fact dispersed.

I noted a lower apparent overwinter survival rate for females (Table 3.4): one way this could arise could be that females had a bimodal distribution of dispersal distance – some females dispersed close to their last breeding territory in a similar way to all males (so accounting for our lack of a difference), whereas other females moved a larger distance away (and were not recorded as this distance exceeded the limits of our study area). Three pieces of evidence suggest that this may be the case.

First, I know of one case where a female moved 1.3 km within a season to breed again, after initial failure, outside the study area. Second, considering all territories monitored in all three years with both male and female of a pair colour-ringed, there were 33 territories where neither bird returned, 10 where both birds returned, 13 where the male only returned and 6 where the female only returned. If female survival and dispersal is the same as males then we would expect equal numbers of territories in each class. I do observe similar numbers for territories with both and for just males returning, but much lower numbers for females. More data are needed in future years to test this statistically, but this strongly suggests that females are more likely to move territories if they come back and find their mate from last year has not returned, whereas males stay put. That males can sing and attract a mate whereas females have to search to find a mate if they wish to find one may then account for the sex-specific difference in staying or going if only one of a pair returns to a territory. This effect may be enhanced by the fact that females of many migrants arrive back on the breeding grounds later than males (Dierschke et al. 2005), for example female Northern Wheatears arrived on average 8 days later than males (Horner and Hubbard 1982), so that a female's opportunity of occupying the territory they occupied last year, if their partner from the previous year has not returned, may be constrained by its current occupation by an unsuitable male (Arlt and Part 2008). Third, the sex ratio of returned chicks was male rather than female biased (71% male) when mortality (see below) and other studies (Breitwisch 1989, Donald 2007) suggest the reverse should be true.

Overall survival rates

The results indicate a very high survival rate for a small passerine migrant, with a minimum of 77% of males surviving in some years (Table 3.4; Figure 3.4). This is one of the highest survival rates recorded for any passerine migrant (Cuadrado et al. 1995, Gruebler et al. 2014). Similar high overwinter survival has been reported for both American Redstarts and Black-throated Blue Warblers that their rates were up to 80% and 66% respectively (Holmes et al. 1989) – but only within the winter period not including migration and breeding as in my estimates.

Other studies have found that apparent survival of short- and long-distance migrants was correlated with conditions experienced during the non-breeding season such as conditions in Africa (Salewski et al. 2013), and Nearctic tropical migrants had significantly higher survival rates at within-family level, which may be consequence of wintering in the tropics (Monkkonen 1992). Therefore if migration costs are minimised then a passerine migrant wintering in the tropics – and breeding in an area without few avian predators – as is the case with Cyprus Wheatears - then survival can be high. Cyprus Wheatears are relatively short distance Afro-Palearctic migrants with a flight distance of about 2,500 km to southern Sudan or Ethiopia (although exact wintering ground information is limited). Although survival rate information for most Palearctic migrants is limited, populations of long-distance migrants in Europe are declining most, suggesting migration distance influences survival rate (Sanderson et al. 2006, Jones and Cresswell 2010).

Another reason for such high survival rates may be because thecurrent study can measure true survival rather than apparent survival and because of low dispersal rates, particularly for males. Dispersal in many other populations of migrants is likely to be much higher and indeed in some populations dispersal may lead to very low apparent survival rates (e.g. (Shitikov et al. 2013). Even so, studies of passerine migrant survival that have considered dispersal have resulted in much lower survival rates than are reported here (Cuadrado et al. 1995, Gruebler et al. 2014).

Sex-dependent survival rates

I found that female Cyprus Wheatears had a higher mortality rate during the breeding season, with several females being killed during incubation on the nest. Because females are the sole incubators in Cyprus Wheatears (Randler et al. 2010b) and nested in cavities among rocks on the ground they exposed themselves to ground predators such as snakes, agamid lizards, foxes, dogs and possibly even rats, that were present on the study area, and the remains of 5 of the 7 females that disappeared during the breeding season were found on or very close to their nests, which also had been depredated or destroyed. Nest predation is an important cause of nest failure in birds and is the primary source of nesting mortality and can potentially affect life history traits in several ways, while also acting together with food limitation (Martin 1995). Accordingly, nest predation risk has been shown to be an important factor in shaping avian breeding habitat preferences and life history strategies that reduce predator impacts on nestling survival (Martin 1995, Roos and Part 2004). Predators can impose a similar high risk to incubating birds: an increased on-nest predation risk of females may explain the male biased adult sex ratios reported for many species (Donald 2007). For example, in Northern Wheatears nest predation of adult females occurred during 20 - 40% of all nest predation events and survival was markedly lower for females whose nests failed as compared to those successfully fledging young (Low et al. 2010).

I also observed differences in apparent survival rate between adult male and female Cyprus Wheatears, with females consistently showing a lower return rate than males. Some of this may be due to differences in dispersal as discussed above, where underestimates of survival rate arise for females, because of a female bias in between-year breeding site-fidelity (Clarke et al. 1997), especially among females with lower reproductive success (Hoover 2003). Nevertheless, lower annual survival rates for females that may not be entirely due to dispersal have been reported from other studies. These can arise through carry-over effects because females may invest more in breeding attempts and care of young, as shown in the example of the Northern Wheatear (Low et al. 2010) or because females can be disproportionately relegated to suboptimal habitats in winter by behavioural dominance of male conspecifics, as shown by the example of American Redstarts (Marra and Holmes 2001).

If females do have lower overwinter survival than males, as well as higher mortality during breeding, then this suggests that the sex ratio at birth may be female biased to compensate (Breitwisch 1989, Donald 2007). I have no data on this from this study. If this the case, however, then this means that the much greater numbers of male than female chicks (i.e. an observed *male* bias in the sex ratio) that were resighted in the study area could only have arisen if female chicks have a bimodal dispersal distance (i.e. there is a component of the population that does disperse on a greater than a kilometre scale rather than a 100m scale). Overall, therefore, it seems likely that sex-based differences in apparent survival for Cyprus Wheatears mostly arise through differences in dispersal rather than reflect differences in true survival, although small differences certainly occur during breeding and may occur on the wintering ground, although there is no information currently to inform this from any Palearctic passerine migrant.

Age-dependent survival rates

After accounting for dispersal (although only partly if female chicks also have long distance dispersal – see above), chicks had a lower overwinter survival than adults (chicks 13-16% less than adult males). Note that I estimated survival for chicks after the first month after fledging when chick mortality is much higher in many passerine species (Anders et al. 1997), and so any differences between adults and first years are associated with their first migration to and from Africa and their first wintering period in Africa. High mortality in the first month of fledging is well known and I examine this in detail in the productivity chapter. For example, Gruebler *et al.* (2014), used a population model to estimate survival rates of adult and juvenile Barn Swallows in both breeding and nonbreeding areas, and found that juvenile survival in the 3-week post-fledging period was low, whereas in the rest of the annual cycle survival estimates of adults and juveniles were high. Birds in their first year have been found generally to have lower survival than older birds (e.g. Sæther, 1989, Sæther and Bakke, 2000, Donovan et al. 1995) and this can arise, for example, because juveniles initially have no experience of migration routes (Strandberg et al. 2010) or their wintering ground (Cresswell 2014), and their inexperience in foraging ability (e.g. Desrochers 1992) or habitat choice (Cresswell 1994). It is not possible to further partition where the differences in survival lie between adults and first years without tracking juveniles and adults to the wintering grounds and studies based there.

Survival and the population dynamics of Afro-Palearctic migrants

Although the survival rates recorded were relatively high, they were probably sufficiently annually variable to profoundly affect the annual population dynamics of Cyprus Wheatears. When estimated, survival rates between fledging and the following breeding season have been shown to be important in the population dynamics of several migrant species (Baillie and Peach 1992, Newton 1998). Population dynamics of most migratory species are affected by ecological process that occur in their breeding, wintering and migration routes (Newton 2004, Calvert et al. 2009). For example, Amborsini *et al.* (2011), evaluated House Martins *Delichon urbicum* and Common Swifts *Apus apus* for both winter survival and population indices during the breeding period, and found that House Martins were affected by spring rainfall (43-47.7%) and NDVI (24-26.9%), and the Common Swift by NDVI (22.7-34.8%) on the wintering ground. Similarly, population dynamics of the migratory Red-backed Shrike *Lanius collurio* were analysed and findings suggested that negative density-dependent regulation of the species breeding population and conditions in the African staging and wintering areas influence population numbers breeding in Europe (Pasinelli et al. 2011). Inter-annual variation in adult and recruitment survival rates for a Sand Martin *Riparia riparia* population in Cheshire, UK, was positively related to rainfall in the sub-Saharan wintering grounds, but unrelated to weather conditions on the breeding ground (Norman and Peach 2013). Baillie and Peach (1992) presented analyses of the population dynamics of migrants generally and showed that variation in losses between fledging and the following breeding season (k_4) accounted for most of the variation in total losses (K_T) for all populations. They reported that fluctuation in k_4 were correlated with conditions (Sahel rainfall) on the wintering grounds for Sedge Warblers, Whitethroats and Swallows, whereas, populations of Sedge Warblers and Whitethroats were likely limited by density-dependent competition for resources on the wintering ground. Variable overwinter survival rates therefore are likely to have major implications for population dynamics of Palearctic migrants wintering in Africa.

Generally, annual survival rates appear to have a strong effect on population growth rates of many bird species, and thus, estimating and understanding survival rates are important for determining the causes of population declines. Wright *et al.* (2009), stated that the increased population growth of Woodlark *Lullula arborea* a multi-brooded ground nesting passerine was associated with higher first year survival rates, thus winter survival rates were likely to be responsible. Studies of the dynamics of a

Red-backed Shrike population, used estimates of temporal variability of population sizes, productivity, apparent survival, and immigration to assess how strongly the demographic rates were correlated with population growth Schaub *et al.* (2013). They found that the Red-backed Shrike population fluctuated and population was regulated by density dependence, but as population size increased, the proportion of immigrants decreased and the proportion of local recruits and surviving adults increased, suggested that other factors were responsible for the variability were environmental effects at staging or wintering areas.

In the case of the Cyprus Wheatear at NFP of Troodos survival rates are unarguably very high and must mean that this population has very few conservation issues both on migration and on the wintering ground. In Cyprus Wheatears survival could vary by c. 30% between years. Assuming an average 57% survival for adults (mean of all yearly minimum true values for males and females) and productivity of 4 young alive to migrate (see the productivity Chapter) with a 49% survival rate (mean of all yearly minimum true values for first years), this means that the population will have an average annual growth rate of 155%, with a minimum growth rate (-15% survival rate from average rates) of 110% and a maximum growth rate (+15% survival rate from average rates) of 200%. The rate of population growth therefore varies by 1.8 dependent on survival rate. Although in the Cyprus Wheatear population studied this is the difference between a rapidly growing or important source population and a very rapidly growing and very important source population, such differences if survival rates were lower would make the difference between a declining or increasing population. Reducing average survival rates in both age classes by 4% brings the poorest years to approximate breakeven point, and reducing survival rate by 18% in all cases brings the population to average stability.

Although survival probability for a Cyprus Wheatear is high, this is also annually variable and probably affected by environmental factors mainly along the migration route and/or at non-breeding ground, with consequently strongly annual effects on population dynamics. Future conservation research for Cyprus Wheatear should be focused on non-breeding mortality (extreme weather events during migration and wintering stage, predation and habitat destruction), which strongly impacts the annual survival of the species. High productivity (see productivity Chapter) however means that annual variation in survival probably makes little difference to its population size.

CHAPTER 4. REPRODUCTIVE SUCCESS AND PRODUCTIVITY

4.1 ABSTRACT

Population dynamics of annually breeding bird species depend crucially on productivity in any year. Initial clutch size and the survival of eggs, nestlings and fledged young all determine productivity, as does the probability of renesting after success or initial failure. These factors can all vary within and between years, determining whether overall productivity balances first year and adult survival and so whether the population size changes. I investigated variation in annual productivity in the Cyprus Wheatear, a small endemic migrant passerine. Clutch size was only recorded for first nests and was usually 5 eggs (4.91 + 0.06, N = 22), although -0.40 eggs lower in 2011. Nest survival did not vary between years, or nesting attempts, or with clutch initiation date but it was significantly higher in the chick stage (0.96; 0.88 – 0.98, 95%CI) versus the egg stage (0.74; 0.62-0.83, 95%CI). The number of chicks fledged from a successful nest varied with nest type – with first nests and second nests after failure being similar producing ~ 3 – 4.5 chicks dependent on year, and with second nests after success producing ~ 2 chicks, regardless of year. There were only weak positive or negative effects of clutch initiation date dependent on year, controlling for nest type; there was no effect of male age on productivity. If a nest fledged chicks then these had very high survival in the first month after fledging: 71% of broods lost no chicks, 26% 1 chick and 3% 2 chicks (N = 183). The probability that a brood lost a fledged chick in the first month increased from ~0.05 at the start of the season to 0.85 at the end on average, and this was independent of year and nest type. Renesting probability differed significantly between years (26%, 48% and 78%

renesting rate): 2010 had a much lower renesting rate after success with very few second broods (29% versus 76% and 73% in 2011 and 2012 respectively). Overall productivity per territory did not vary with year with 3.96 + 0.09 chicks alive 1 month after fledging. Cyprus Wheatears at Troodos showed several unusual breeding parameters including a highly variable renest probability, high nestling and very high fledgling survival, resulting in exceptionally high productivity. This high productivity combined with the already established high survival rates means that the population of Cyprus Wheatears at Troodos is a source population.

4.2 INTRODUCTION

Population dynamics of annually breeding bird species depend crucially on productivity in any year. Initial clutch size and the survival of eggs, nestlings and fledged young all determine productivity, as does the probability of renesting after success or initial failure. These factors can all vary within and between years, determining whether overall productivity balances first year and adult survival and so whether the population size changes. I investigated variation in these factors in the Cyprus Wheatear, a small endemic migrant passerine, in order to assess how its productivity varies, and to determine whether productivity is sufficient to offset annual variation in mortality.

Clutch size and its variation is fundamental to productivity. Clutch size varies interspecifically as a reflection of life history evolution in response to limits to food supply (Lack’s hypothesis). Clutch size is a fundamental life-history trait because it reflects both fecundity and reproductive effort (Lack 1947, Bennett and Owens 2002).

Lack's food-limitation hypothesis suggests that parents raise the maximum number of young allowed by food resources (Lack 1948). Clutch size also varies intraspecifically in response to climate and competition for food on a large spatial scale (Ashmole's hypothesis). Increasing seasonality causes greater overwinter mortality from resource scarcity at higher latitudes, so reducing breeding density and so providing more per capita resources for breeding that allow larger clutch size (Ashmole 1961). Clutch size also varies on a temporal scale through a season. Perrins (1965) hypothesised that the reduction in clutch-size with date is an adaptation to a steadily worsening food supply for the young. Although there will be selection to breed at the best time in the relation to food availability, the time that birds actually start to breed is related to the availability of spring food for females, and so clutch size in turn may show a quadratic function: initially low, peaking as the food supply peaks and then declining as this food availability declines through the season (Perrins 1965).

Nest survival or failure and its variation is fundamental to productivity. Nest predation is an important cause of nest failure in birds and is the primary source of nesting mortality and can potentially affect life history traits in several ways, while also acting together with food limitation (Martin 1995). Accordingly, nest predation risk has been shown to be an important factor in shaping avian breeding habitat preferences and life history strategies that reduce predator impacts on nestling survival (Martin 1995, Roos and Part 2004). Rates of nest predation can vary widely between species within a habitat (Martin 1993a), between nest stages (Peak et al. 2004, Cottam et al. 2009), and intraseasonally within a species (Shustack and Rodewald 2010). Much of the variation is probably due to differences in the abundance and/ or activity of nest predators (Cox et al. 2012), with breeding birds and their nests facing different predation risk, depending on their nest site (e.g. on the ground vs. in a tree cavity), habitat (forest vs. grassland), and geographic location (Thompson 2007). Nest predation risk varies with nest stage because eggs are much less conspicuous than nestlings which may be noisy and which require regular visits from the parents so revealing the nest location. Several studies have found a decline in nest success during the nestling stage (Young 1963, Robertso 1972, Schaub et al. 1992, Burhans et al. 2002), due to increased cues provided by the parents' feeding trips to the nest, and nestling noise. Adult birds themselves, of course, are at risk from accidents, disease and predators and this may increase due to nesting, thus for hole or ground nesters during incubation when predator exposure may be increased and escape options may be reduced (Moorhouse et al. 2003): nest failure may then result because of lack of or reduction in parental care. Life-history theory then predicts that short-lived species, such as the wheatears, should be more likely to trade their own survival for that of their current reproduction because the future prospects of reproduction are small (Charlesworth 1994).

The number of chicks fledged from successful nests and its variation is also crucial to productivity. Although this will often be a reflection of clutch size, many things can affect the proportion of a clutch that survives to fledging, and these can vary both within a breeding season and annually. Factors such as variable food supply affecting incubation scheduling and feeding rate, hatching asynchrony leading to competition between nestlings, partial predation, and brood parasitism can all affect brood survival. Food limitation frequently increases nestling mortality even under normal conditions (Quinney et al. 1986, Martin 1987). When food supply fails, hatching asynchrony of chicks provides a mechanism by which some young can be fledged because more developed chicks out-compete their less developed siblings (Amundsen and Slagsvold 1998, Lord et al. 2011). The overall costs and benefits of an asynchronous brood depend on complex interactions of factors such as food supply (Lack 1947, Ricklefs 1965, Hussell 1972), parental effort (Slagsvold 1986), and predation risk (Hussell 1985), but as these vary, brood asynchrony provides another way in which parents can match offspring production to the optima. Partial predation of chicks – where only one or two chicks from a brood are taken by a nest predator – can be a common cause of reduction in brood size, particularly when nest predators are relatively small (e.g. Part and Wretenberg (2002)), or parental nest defence is vigorous (Cresswell 1997, Grim and Honza 2001, Weidinger 2002). Brood-parasites can also reduce the breeding success of birds, either by lowering the body condition of the adults, or by lowering the body condition and survival of the chicks (Newton 1998) by removing host eggs when they deposit their own eggs in the host nest, by the resulting nestlings evicting host young from the nest or their more rapid growth, diminishing the growth and survival of any remaining host young (Rothstein 1990, Payne 1997).

The survival rate of chicks just after fledging is a very important component to productivity because post-fledging survival, particularly in the first month, is invariably low (Newton 1998). Newly fledged chicks have no experience of foraging or of predation and are often not fully developed in their physical ability to thermoregulate (Ricklefs and Hainsworth 1969), forage (Weathers and Sullivan 1989) or escape from predators. Although important, assessment of post-fledging survival is difficult because fledglings are hard to detect and follow as they disperse, therefore there are few estimates (Cox et al. 2014b).

A final crucial component to productivity is renesting probability (Lack 1954). Interspecific differences are related to life history in the same way as with variation in clutch size (Lack 1947, Bennett and Owens 2002) and will be mainly related to variation in food availability. Food resource availability is usually seasonally dependent, and so the timing of reproduction relative to the peak in food abundance, and the duration of this peak has been demonstrated to affect double brooding rates (Verboven et al. 2001, Lambrechts et al. 2008). Such seasonal variation in food supply will also lead to differences between the first and second breeding attempts in clutch size, egg size and fledging success (Ojanen et al. 1979, Orell and Ojanen 1983, Mägi and Mänd 2004). Passerines may be single brooded or multi-brooded but many species show a cline in this over time or their range in response to climate, suggesting this is a flexible trait (Pimentel and Nilsson 2007, Husby et al. 2009).

In this study I measured reproductive success in a colour-ringed population of Cyprus Wheatears over three years (2010-2012) from April – August, to determine how productivity arose from variation in clutch size, nest survival, number of fledged chicks and fledgling survival. As Cyprus Wheatears are also likely to be multi-brooded renesting probability was also measured. Therefore I measured:

4.2.1 Clutch size and how it varied with year. I predicted that clutch size would be reasonably constant with year but would decline as the season progressed as found for most other passerine species.

4.2.2 Nest survival rates during the egg and chick stage. I predicted that nest survival would be higher for the eggs than for the chicks because the chick feeding stage is much more conspicuous to nest predators.

4.2.3 The number of chicks fledged from successful nests and how it varied between and within years. I predicted that the number of chicks fledged would vary with year as annually variable factors affect nest survival, and within year with respect to clutch initiation date (a decrease later in the season because number of chicks is a proxy for clutch size) and whether the nest was a first or second nest (a decrease for second nests) as found for most other passerine species.

4.2.4 Survival of chicks in the first month of fledging. I predicted that survival would be low during this period and fairly uniform regardless of year as found for most other passerine species.

4.2.5 Renesting probability. I predicted that this would vary between years because of variable annual predation rates and weather conditions, but that the probability of renesting after a failed first nest would not change because renesting rate is important to maintain productivity.

4.2.6 Productivity per territory (pair) and its variation with year. This is important to model population trajectories in conjunction with annual survival rates.

4.3 METHODS

The study was conducted from 2009 to 2013 in a 130 ha area at National Forest Park of Troodos, Cyprus (34°56′11″N 32°51′48″E), at about 1800 m a.s.l. during the breeding season. The study area was the "Artemis Trail" with old low density coniferous forest, supporting the one of the densest breeding Cyprus Wheatear populations on the island (Flint and Stewart 1992). The National Forest Park of Troodos (NFP of Troodos) is located at the centre of Troodos massif that ranges from the northwest to the southeast part of Cyprus. The NFP of Troodos covers an area of 9,029 ha. with highest the peak of Chionistra at 1952 m, situated almost at the centre of an Ophiolite Complex. The main habitats that characterized the study area are those of the endemic *Pinus nigra* ssp. *pallasiana* forest, the Black Pine zone which starts from 1400 m and reaches up to the top of the mountains to 1952 m, and Juniper woodland *Juniperus foetidissima* and Serpentinophilous grasslands that are distributed at the highest parts and that occur in openings of the black pine forest in the form of small, scattered patches. The understorey of Black Pine consists of *Quercus alnifolia*, *Juniperus oxycedrus*, *Juniperus foetidissima*, *Sorbus aria* ssp. *cretica*, *Berberis cretica*, *Arbutus andrachne*, *Rosa chionistrae*, *Rosa canina*, *Cotoneaster racemiflorus* var. nummularius etc. Annual precipitation in the area is very high with more than 1100 mm being recorded and temperature varies through the year from freezing during winter to a maximum of about 35°C during very hot dry summers. The study area was characterized by high quality habitat types comprising homogenous coniferous forest with a low vegetation understorey consisting of open areas with sparse shrubs.

Figure 4.0. Examples of typical open areas within the forest

During 2009 a pilot study identified a study area and monitored and mapped territories but without colour-ringing of birds. In subsequent years 2010-2012, individuals were colour-ringed (Appendices: Table A, B and C) when they were actively defending a territory and locations of territories were plotted on maps; territories were intensively monitored to record details of breeding. The study area consisted of 4 parallel transects containing about 80 mapped territory locations over the 4 years, containing 30, 45, 69, and 50 focal territories over the four years of the conducted study. Observation and data recording started around mid-end of March each year when the first individuals arrived at breeding ground, and regular monitoring continued until the end of August, with sporadic visits until October.

Pairs were marked within their territory and at least one individual of the pair was coloured-ringed. The study contained 324 individuals that were colour ringed over 2010-2013 (110 males, 91 females and 123 chicks). Birds were captured with spring traps that were baited with maggots throughout the season (but especially during arrival and territory establishment for the adults) and ringed with individual combinations of colour rings: playback using conspecific song was used to during trapping. Individuals were sexed, and all males were aged as young (1 year old) or adults (>1 years old) based on their plumage characteristics (contrast in the coverts so that first year males had brownish greater coverts – visible in the field – whereas adult males had dark, uniform sooty black wing feathers). The age of the female could not be reliably distinguished and so females were not aged.

At each territory during 2010-2012, I recorded arrival dates of individuals, resighted colour-ringed birds, mapped territories, and monitored nesting stage, egg, nestling and fledgling survival, and depredated nest and females. Nests and fledglings were found opportunistically, the latter being extremely obvious – the number of fledglings was counted immediately after fledging and one month afterwards, although frequent visits meant that fledglings and their survival were recorded every few days. Records were systematically taken from all territories every second to third day from the arrival of the first birds to the study area each year.

Records of breeding activities were collected by systematic observation of the behaviour of birds in their territories every second to third day from the beginning of April to the end of August, thus, data consist of occupancy and activities of pair, nest stages (laying, incubation, hatching, fledglings), nest type (1 first, 2 renest after success, 3 renest after failure), breeding success (successful vs. failure) and male age. Not all territories could be monitored completely and so complete information is not available for all territories: some nests were not found, and many were found only in the chick stage when they become more conspicuous. Sample sizes vary throughout as a consequence.

Nests were on the ground in crevices among large rocks. Laying date was determined by direct observation of the first egg laid in a just completed nest, or by back calculation from the hatch date, or occasionally fledging date based on the mean duration of nestling and egg stage from known nests. Eggs and chicks were counted by direct observation or using an inspection camera on a flexible meter long stalk. A nest failure was defined as when a known nest (nest and eggs or chicks being monitored) lost its eggs or chicks and the parents resumed activities consistent with them renesting or stopping breeding. The day of failure was allocated to the mid-point between the last visit when the nest was active and the first visit when the nest was inactive. Breeding was defined to be successful when fledglings were observed, or intense warning calls of parents after fledging were heard (at ≥ 15 days after hatching). Fledglings were monitored for at least a month after fledging to record number of surviving chicks and the period of feeding by the parents. Chicks were reasonably conspicuous and stayed together in the small territories allowing a reasonable assessment of the number: nevertheless any estimates presented may be underestimates of survival because of imperfect detectability. Data collection on the number of fledglings surviving was restricted to the central territories of the study area.

Analysis

Clutch size was modelled with respect to year and clutch initiation date using a General Linear Model assuming a normal distribution. Clutch size was only recorded from first nests and so nest type was not included in the model: chicks fledged likely provided a proxy for clutch size and was available for most nests so the effects of nest type on clutch size were tested in the number of chicks fledged models (see below).

Nest survival rate was modelled with respect to nest stage (egg or chick), year and nest type using a linear logistic exposure-model (Shaffer 2004) with success or failure of a nest offset by the number of days exposure.

The number of chicks fledged was modelled from successful nests with respect to year, clutch initiation date and nest type using a General Linear Model assuming a normal distribution. The effects of male age were tested only by adding the variable to the final model because of missing values.

The survival of chicks in the first month of fledging was modelled with respect to the brood size (number of chicks initially fledged), clutch initiation date, year and nest type using a Generalised Linear Model assuming a binomial distribution. I predicted whether 1 or more chicks was lost during the month after fledging – 47 broods lost only 1 chick and 6 lost 2 chicks during the first month – versus all chicks surviving.

I assessed the overall relative frequency of renesting with year by simple comparison of the number of first and second nests across the three years using a chi-square test. I then assessed the relative frequency of renests after a successful first nest by a simple comparison of the number of successful first and second nests across the three years using a chi-square test. Renesting frequency was also analysed in more detail in Chapter 2.

I modelled overall productivity – the total number of chicks produced in a year within the same territory (almost always the same pair with occasional switches in one adult of the pair) – with respect to year using a General Linear Model assuming a normal distribution.

The potential confounding effect of territory and/or male quality was assessed by including male identity as a random effect in final models. Note that many males and females were not colour-ringed, and some individuals will appear in the study as unringed individuals in one year before being colour-ringed in the next. Therefore inclusion of male identity provides only a partial control for repeated samples from the same individual and territory across year. In all cases, even if male identity explained some of the variation, it did not change the biological or statistical significance of the result. The simpler, non-random effects models are therefore presented.

Analysis was carried out using R 2.13.1. Interactions were only tested where there was an a priori biological hypothesis to be tested; some interactions could not be tested because of sample sizes and missing information (e.g. clutch size). Quadratic effects of clutch initiation date were considered because breeding activities may have peaked mid-season rather than at the start: there was no strong evidence for quadratic effects. Full models were simplified by AIC comparison using the information theoretic approach (Akaike 1974, Burnham and Anderson 2002). Non-significant interactions were removed by default. The top models were then evaluated for both biological and statistical significance. Residuals of the top models met model assumptions reasonably well, as demonstrated by the plot command in *R* and according to criteria in Crawley (2007). Figures illustrate the results of models and plot the predicted values (parameter estimates) for the variable of interest, with other variable values set to their median (and so typical) values. Means are given +/- 1 standard error unless otherwise stated.

4.4 RESULTS

Clutch size was only recorded for first nests and was usually 5 eggs (4.91 ± 0.06, N = 22). There was significant variation in clutch size of first nests with year, although this was fairly small being slightly lower in 2011 (2010, 5.03 ± 0.25; 2011, 4.64 ± 0.23; 2012, 4.99 ± 0.21; with median clutch initiation date of 11th May) controlling for clutch initiation date (-0.0099 ± 0.0105): year, $F_{2,18} = 3.8$, $p = 0.041$; clutch initiation date, $F_{1,18} = 0.9$, $p = 0.36$.

Daily nest survival was higher during the nestling stage (0.997; 0.992-0.999, 95%CI) than the egg stage (0.982; 0.971 – 0.989, 95%CI): daily nest survival ~ nest stage; nestling stage, 1.70 ± 0.48, z = 3.6, $p < 0.001$. Overall probability of nest survival was higher during the chick stage (0.96; 0.88 – 0.98, 95%CI) than the egg stage (0.74; 0.62-0.83, 95%CI): Figure 4.1. Daily nest survival did not vary significantly between years (Figure 4.2), or nesting attempts, or with clutch initiation date, controlling for nest stage (Table 4.1). Most nest failure in our study site resulted from nest predation with a likelihood of the adult female wheatear being killed at the time (see Chapter 3).

It was impossible to determine the identity of the nest predators but they were likely to be Common Jays *Garrulus glandarius* that were often observed on the ground near nest sites, Starred Agama (Agamid lizards) *Stellagama stellio cypriaca*, mammals (foxes, dogs and rodents (rats)). One nest in a territory adjacent to the study area in 2011 was parasitized by a Common Cuckoo *Cuculus canorus* (an adult wheatear was seen feeding a newly fledged cuckoo chick) demonstrating that brood parasitism may also affect nest survival but at a very low frequency (i.e. it was not recorded in 173 fledged broods in three years in the study area).

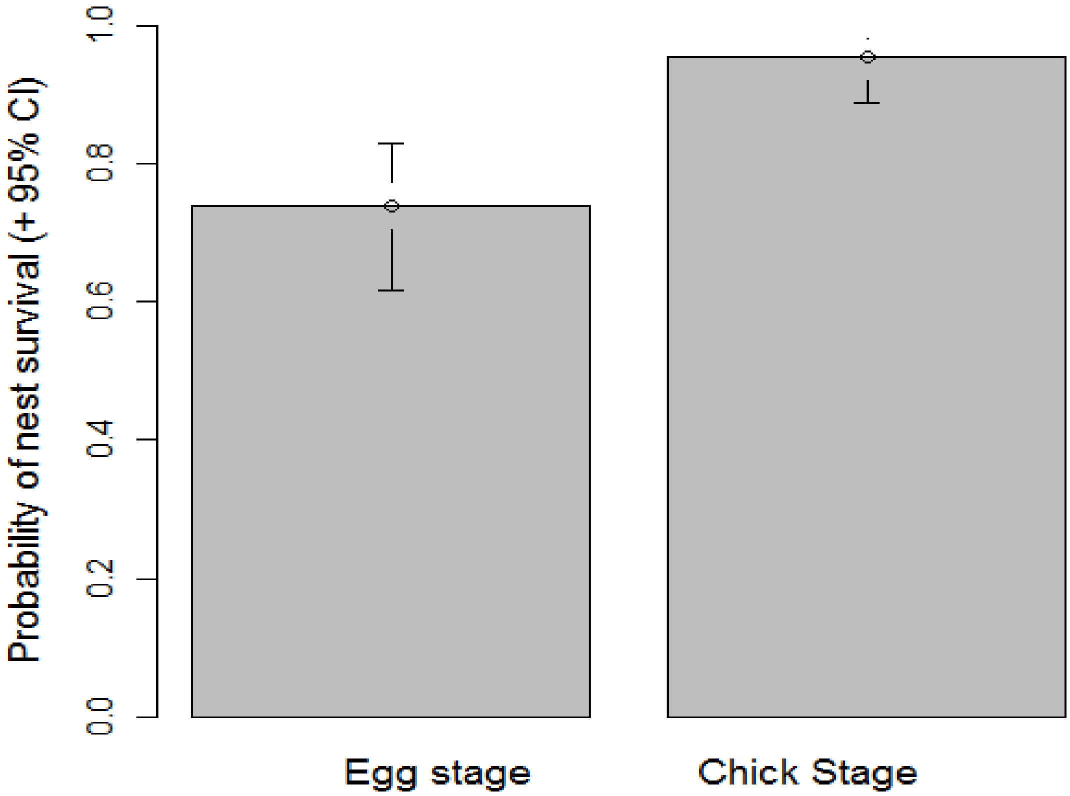

Figure 4.1 Predicted overall nest survival by stage (egg stage versus the chick stage).

Table 4.1: Daily nest survival variation with clutch initiation date, nest stage (egg or chick stage), year (intercept 2010) and nest type (first or second nest). N = 224 nests.

Variable	Estimate	SE	z	*p*
[1] (Intercept)	3.10	1.00	3.1	0.002
Clutch initiation date	0.03	0.02	1.4	0.15
Chick stage	1.66	0.50	3.4	<0.0001
2011	-0.94	0.66	-1.4	0.15
2012	-0.71	0.51	-1.4	0.16
2nd nest	-0.69	0.95	-0.7	0.47

[1] (Intercept) = Daily survival with clutch initiation date & nest stage & 2010

Interactions were not significant and were removed

Delta AIC with interactions in model = +6.3

The simplest model only included nest stage, delta AIC = -8.8

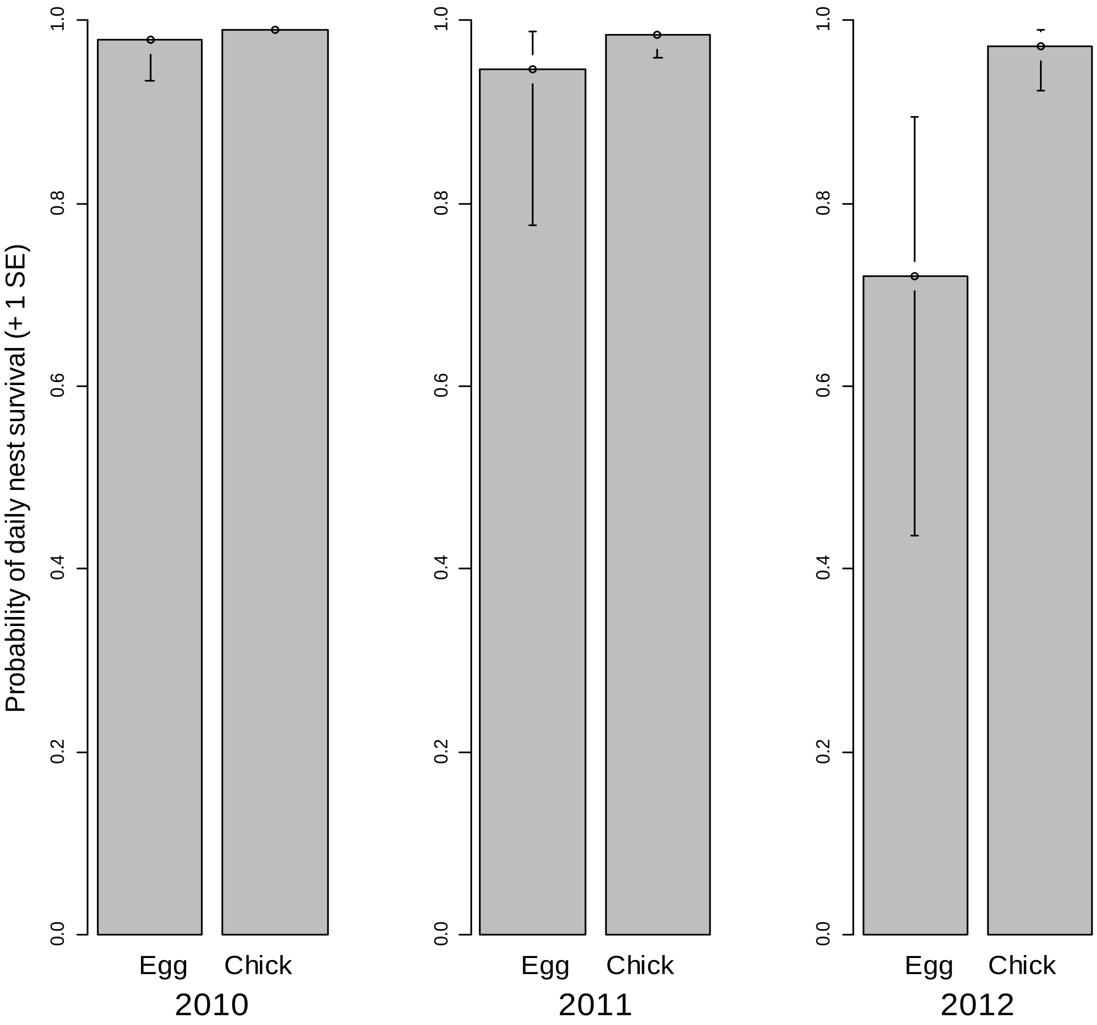

Figure 4.2: The probability of a daily nest survival during the egg and chick stage for three breeding seasons (2010-2012) modelled separately (parameter estimates +/- 1 standard error for nest stage plotted from the three annual models, daily nest survival ~ nest stage,). 2010 N = 60 nests, 2011 N = 57 nests, 2012 N = 66 nests.

The number of chicks produced by successful nests varied with clutch initiation date and nest type, but these relationships differed with year (i.e. the interactions between year*clutch initiation date and year*nest type were significant: Table 4.2). I therefore considered the effects of clutch initiation date and nest type separately by year (Table 4.3). Although effect sizes differed with year, there were no significant differences between first nests and second nests after failure (~ 3 – 4.5 chicks dependent on year), but significantly fewer chicks were produced from second nests after a first successful nest (~ 2 chicks, regardless of year): Table 4.3, Figure 4.3. There was a small change in number of fledged chicks from successful nests with clutch initiation date, with a negative trend in 2010 and 2011 and a positive trend in 2012 (Table 4.3, Figure 4.4). There was no effect of male age on productivity (Table 4.2) but sample sizes were small and the confounding effect of female age could not be considered.

Table 4.2: The number of fledged chicks by year, nest type and clutch initiation date. All interactions were tested but only significant interactions were retained in the model. The parameter estimates for the effects in separate years are given in Table 4.3.

Variable	Df	Sum of sq	*F*	*p*
[1] (Intercept)	41.3	-223.90		
Year	2	33.00	64.3	<0.0001
Nest type	2	6.70	13.2	<0.0001
Clutch initiation date	1	0.69	2.7	0.10
Year*Nest type	4	2.50	2.4	0.05
Year*Clutch initiation date	2	1.80	3.6	0.03

[1] (Intercept) = Number of fledged chicks

Main effects only model delta AIC = +22

Three way interactions model delta AIC = +6

All two way interactions model delta AIC = +3.1

Including male identity as a proxy for territory quality as a random effect did not change the model (i.e. it contributed no additional variance)

Addition of clutch initiation date as a quadratic term, or its interaction, in any model delta AIC > +3.6

Male age was not significant when added to the model, -0.086 +/- 0.090, $t_{1,136} = -0.01$, $p = 0.34$.

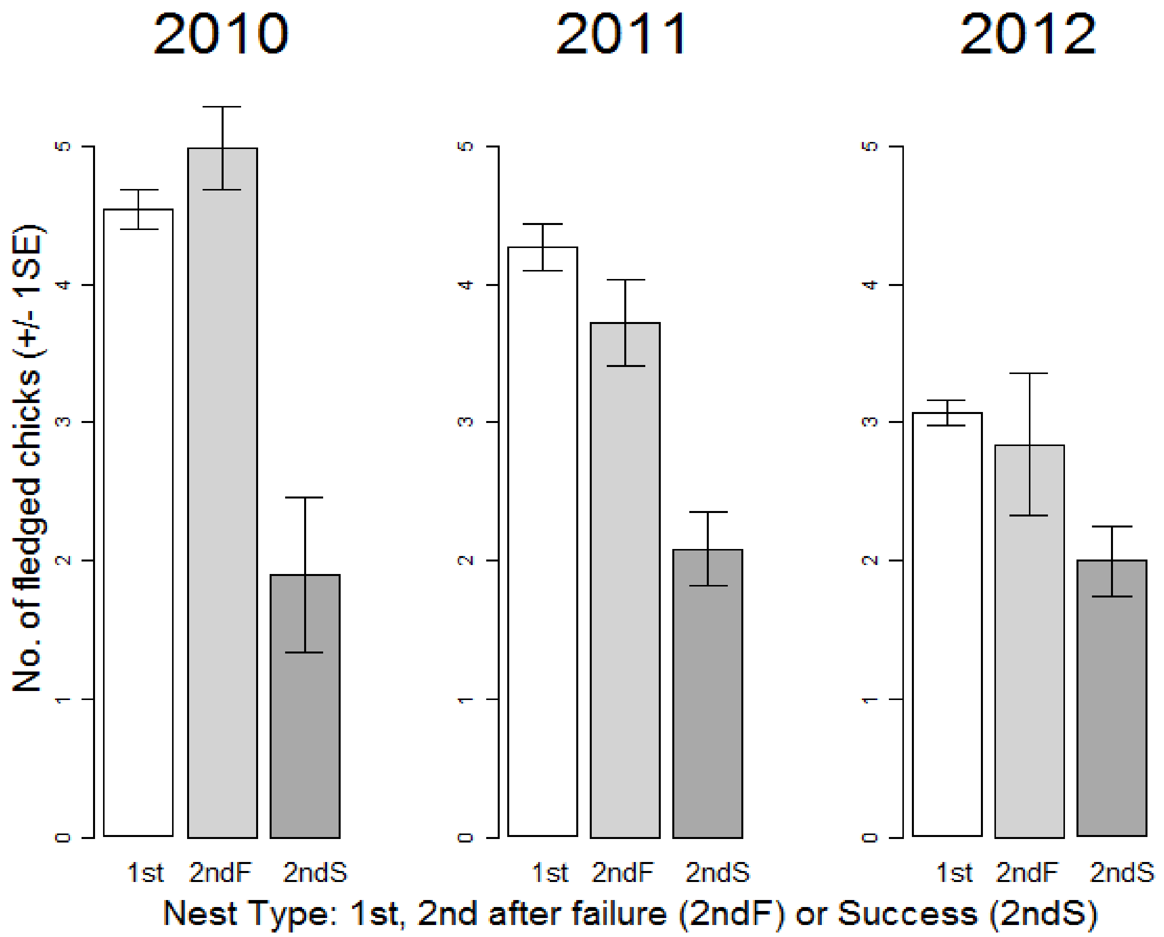

Figure 4.3: The number of fledged chicks produced each year with nest type. Predicted values (+/- 1 standard error) are plotted from the models in Table 4.3 using the median clutch initiation date for the particular year. 2010 N = 41, 2011 N = 66, 2012 N = 66.

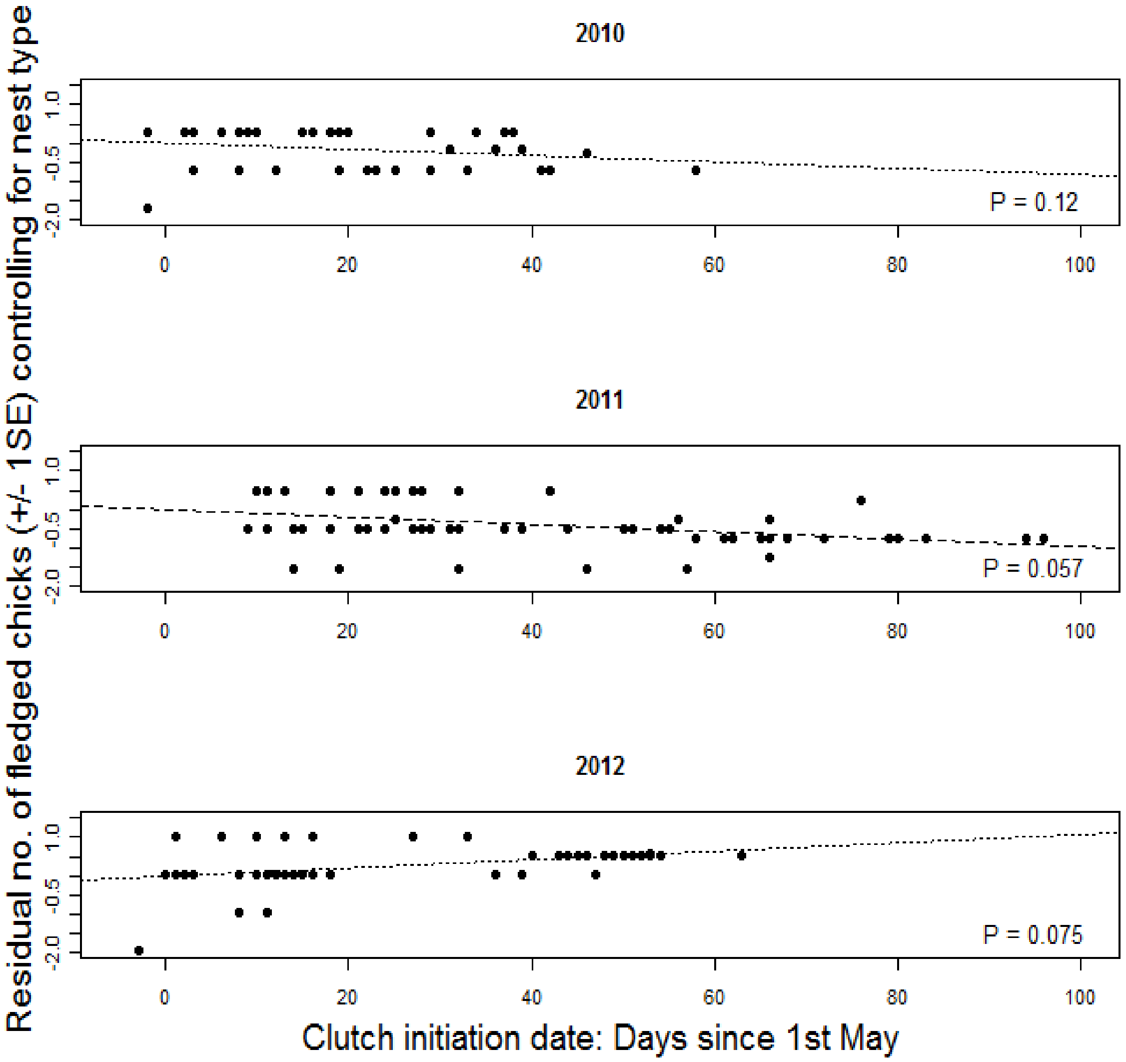

Figure 4.4: The decline in the number of fledged chicks from succesful nests with clutch initation date for each year of the study. The residual number of chicks controlling for nest type (from the models in Table 4.3) are plotted and the best fit regression line fitted to illustrate the effects predicted in Table 4.3.

Table 4.3: Results of individual year models to test whether the number of fledged chicks was dependent on clutch initiation date and nest type.

Variable a) 2010	Estimate	SE	t	*p*
[1] (Intercept – 1st nest)	4.70	0.14	33.2	<0.0001
2nd nest after success	-2.26	0.56	-4.0	<0.0001
2nd nest after failure	0.64	0.30	2.2	0.04
Clutch initiation date	-0.01	0.01	-1.6	0.13
With interaction delta AIC =+2				
b) 2011				
[1] (Intercept – 1st nest)	4.53	0.17	26.7	<0.0001
2nd nest after success	-1.78	0.26	-6.7	<0.0001
2nd nest after failure	-0.26	0.31	-0.8	0.41
Clutch initiation date	-0.01	0.01	-1.9	0.06
With interaction delta AIC =+2.5				
c) 2012				
[1] (Intercept – 1st nest)	2.96	0.09	31.8	<0.0001
2nd nest after success	-1.48	0.25	-5.9	<0.0001
2nd nest after failure	-0.52	0.51	-1.0	0.32
Clutch initiation date	0.01	0.01	1.8	0.08
With interaction delta AIC =+1.7				

[1] (Intercept) = Number of fledged chicks & first nest

There was a relatively high survival rate in the first month after fledging: 71% of broods lost no chicks, 26% 1 chick and 3% 2 chicks (N = 183 broods). However, the estimated probability that a brood lost a fledged chick in the first month increased from ~0.05 at the start of the season to 0.85 at the end, and this was independent of year and nest type (Table 4.4, Fig. 4.5).

Table 4.4: Results of the model to test whether chick survival in the first month after fledging was dependent on brood size (number of fledged chicks), clutch initiation date, year and nest type.

Variable	Estimate	SE	z	*p*
[1] (Intercept)	-9.84	1.53	-6.4	<0.0001
Brood size	1.89	0.30	6.3	<0.0001
Clutch initiation date	0.05	0.01	4.0	<0.0001

[1] (Intercept) = chick survival in the first month

Year and nest type were removed as non-significant terms, delta AIC if added to the model = +0.7

Including male identity as a proxy for territory quality as a random effect increased the power of the model (i.e. it contributed 11.4% additional variance and increased the parameter estimate for clutch initiation date slightly to 0.06 +/- 0.02).

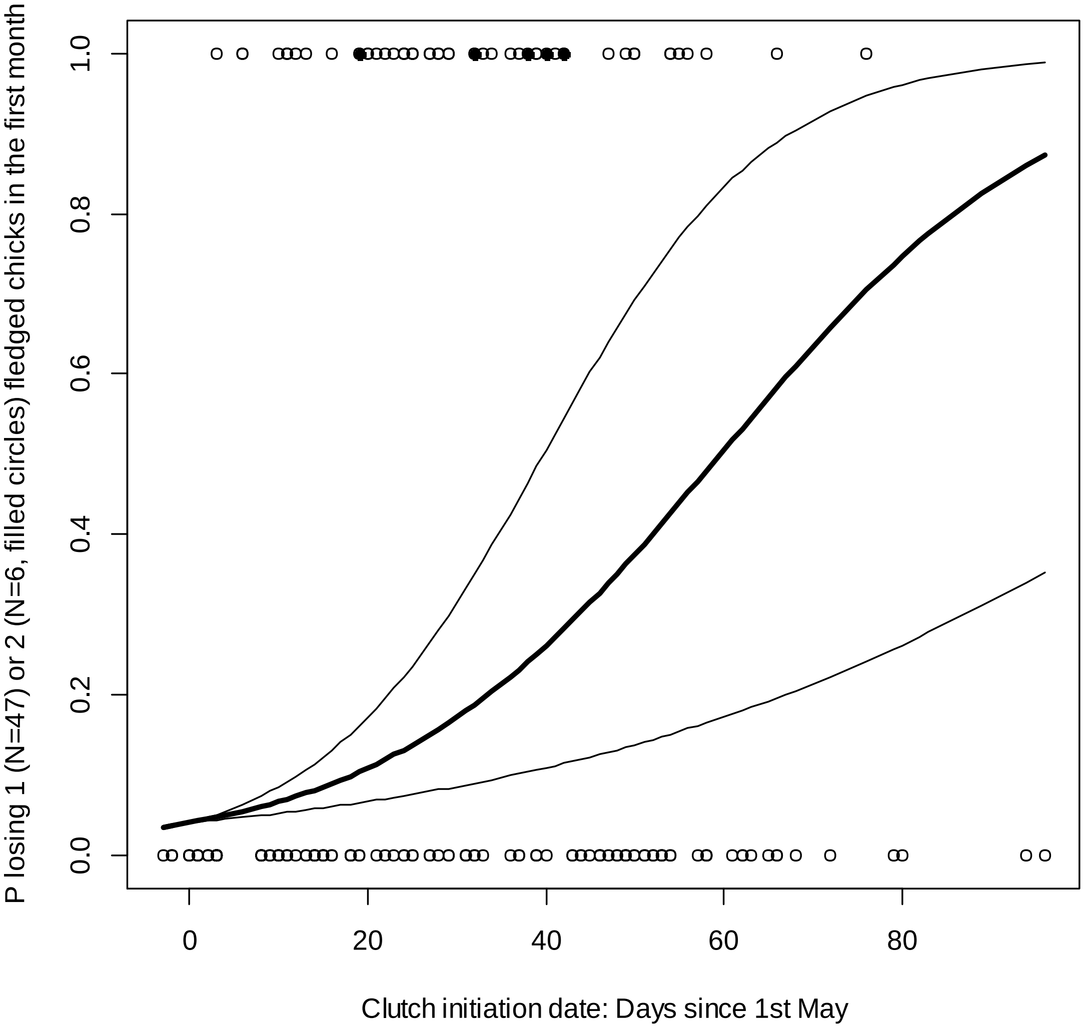

Figure 4.5: The change in probability of losing a chick in the first month after fledging with clutch initiation date. Mean predicted values (+/- 1 standard error) are plotted from the model in Table 4.4 with a mean value for brood size (number of fledged chicks) of 3.5 chicks (N = 227).

Overall renesting probability differed significantly across the three years (26%, 48% and 78% renesting rate; $\chi^2 = 20.8$, $p < 0.0001$: Figure 4.6a – see also Chapter 2). The probability that renesting occurred after a successful first nest also varied significantly by year: 2010 had a much lower renesting rate after success with very few second broods (29% versus 76% and 73% in 2011 and 2012 respectively: $\chi^2 = 6.2$, $p < 0.046$: Figure 4.6b – see also Chapter 2).

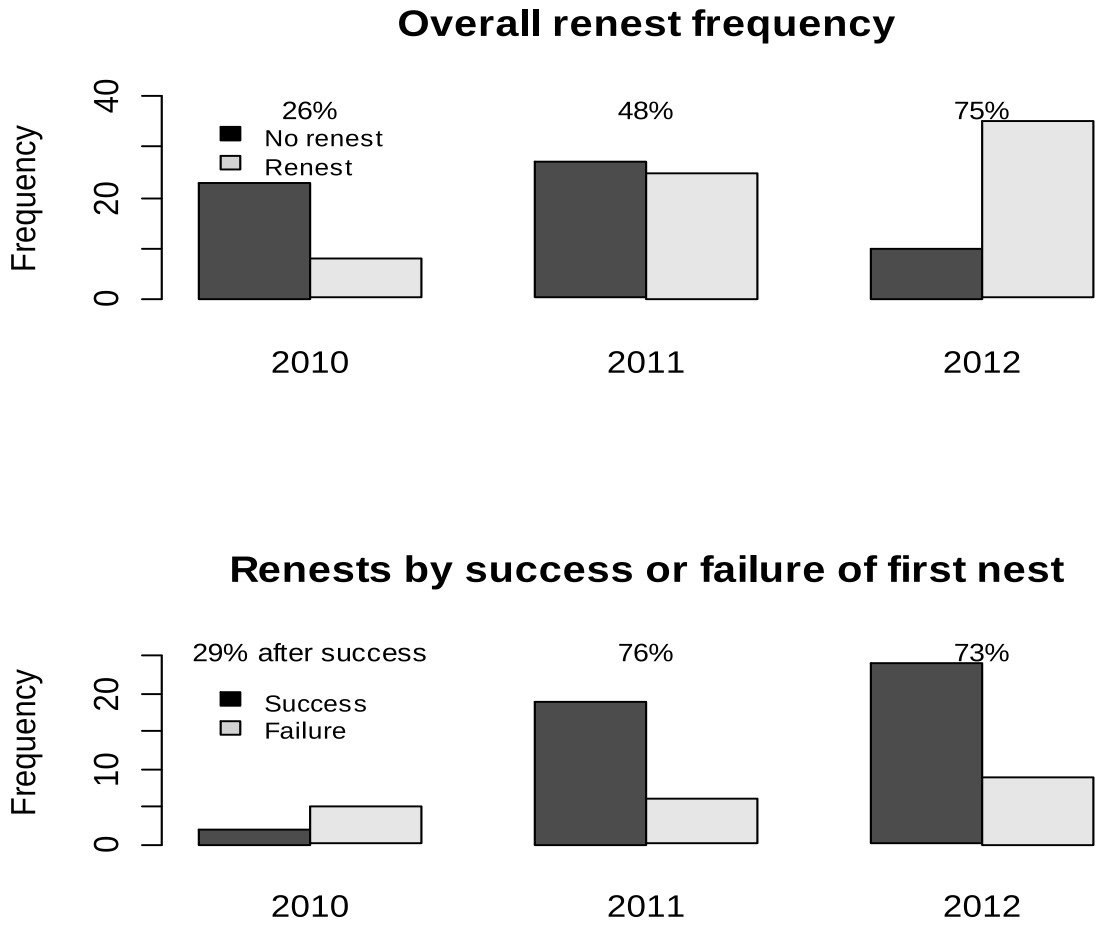

Figure 4.6: Variation in annual a) overall renesting rate regardless of nest type and b) renest frequency after success.

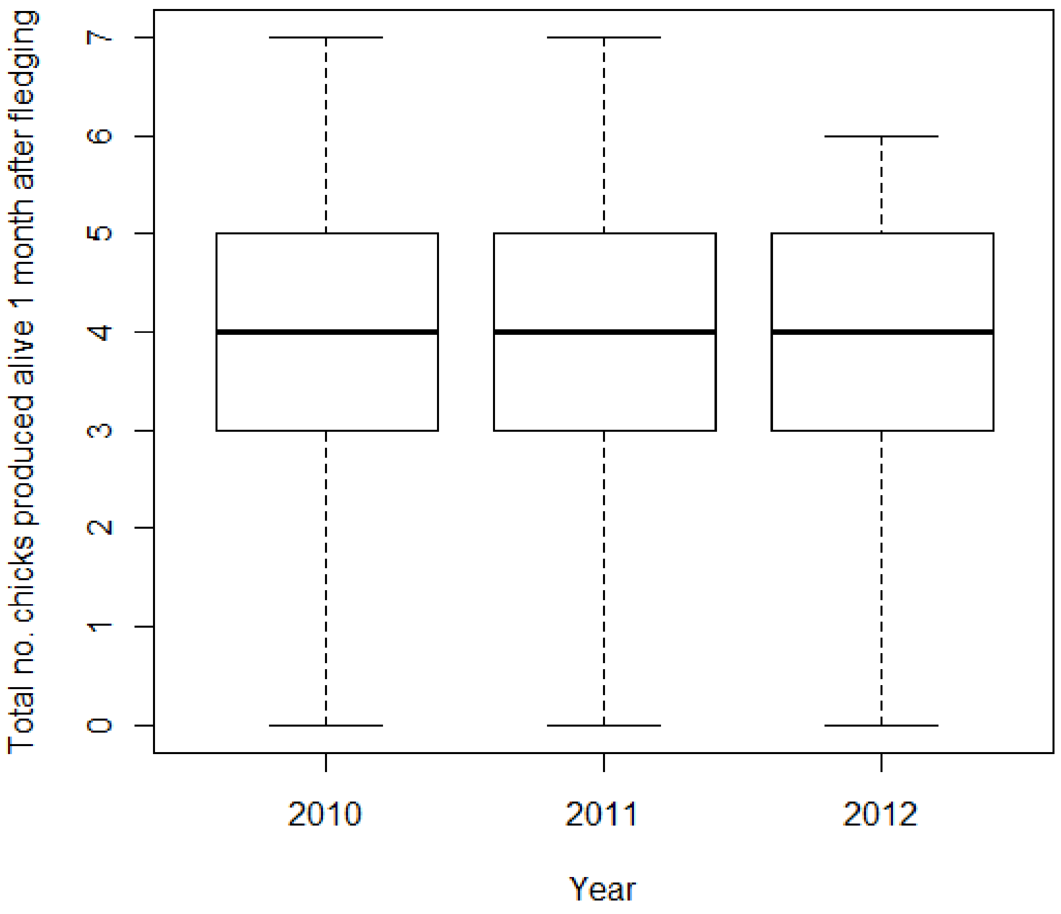

Figure 4.7: Boxplot of the annual variation in the number of chicks produced per pair (and that were alive 1 month after fledging).

Overall productivity of chicks per territory (pair), alive one month after fledging, did not vary significantly with year (2010, 4.00 ± 0.22; 2011, 4.00 ± 0.27; 2012, 3.87 ± 0.30, $F_{2,154} = 0.1$, $p = 0.87$: Figure 4.7). Average productivity was 3.96 ± 0.09 chicks, N = 227 broods. Including male identity as a proxy for territory quality as a random effect did not change the model (i.e. it contributed 0.5% additional variance).

4.5 DISCUSSION

Cyprus Wheatears had a clutch size of 5 for first nest, this declined slightly with clutch initiation date, but was probably substantially lower for second nests (c. 2 eggs) independently of clutch initiation date, as estimated from the number of chicks fledged. A clutch size of 5 is typical for similar passerines that attempt second broods, for example the Northern Wheatear (Hussell et al. 2014).

A decline in clutch size with season is typical for similar passerine species due to declining food availability, condition of the female and the timing of moult (Lack 1968). For example, Siikamaki (1998), showed that in birds the costs and benefits associated with later breeding dates caused variation in clutch size, which was the main cause of seasonal decline in reproductive success, resulting from seasonal variation in the environment or differences in parental/territory quality of early and late parents.

The present study indicates that the relationship between clutch size and season varies according to clutch initiation date, nest type and year. The observed seasonal decline in clutch size is likely an adaptive response to food availability (Rowe et al. 1994, Brommer et al. 2002), with conditions for producing offspring deteriorating after a peak of food availability in the spring (although we have no data in this study to test this). Furthermore the observed decline in clutch size with date may be related to increasing temperatures increasing the activity and so predation risk from snakes and lizards so reducing the value of larger clutches later in the season, but again we have no data in the study to test this. A lower clutch size for second broods is typical for passerines, for example several studies of great tit populations showed a decline through the breeding season (Verboven and Verhulst 1996).

Daily nest survival for Cyprus Wheatears was relatively high compared to most other passerine species (Willson and Gende 2000, Knutson et al. 2006, Schill and Yahner 2009). Nest predation is an important cause of nest failure in birds (Lack 1954), so much so that nest predation risk has been shown to be an important factor in shaping avian breeding habitat preferences and life-history strategies to reduce predator impacts on nestling survival (Martin 1995). As for many other bird species, nest predation was one of the major determinants of reproductive success of Cyprus Wheatear. However, daily nest survival was relatively high for the species compared to many other passerines (Willson and Gende 2000). The high survival rates found are equivalent to hole nesters, nesting in optimal often anti-predation designed cavities (Martin and Li 1992). Cyprus wheatears nest in narrow crevices or in tunnels under or between rocks which must provide a large degree of protection from nest predators.

Daily nest survival in Cyprus Wheatears was higher during nestling stage compared to egg stage (Figure 4.1). Many other studies have shown variation with nest stage, for example Suarez and Manrique (1992) showed high nesting mortality rates varying with nest stages and date for Mediterranean shrub steppe passerines including the Black-eared Wheatear *Oenanthe hispanica*. Most studies have however found that the stage associated with the highest mortality was the noisy and “busier” nestling stage (Skutch 1949). For example, Grant *et al.* (2005), studied variation in nest survival as a function of nest age and date in Clay-coloured *Spizella pallida* and Vesper Sparrows *Pooecetes gramineus*: survival rates were lowest during incubation and highest during brood rearing. Nests may experience higher predation after chicks have hatched than when eggs are present, because parental activity may be a cue to predators for the location of the nest (Young 1963). One possible explanation for my results is that they are due to lizard predation – that can effectively eat small eggs but that then do not preferentially target chicks because they do not hunt by sight or noise, or find chicks too large to eat. The endemic lizard subspecies, the Starred Agama (Cyprus Agamid) is very common on Cyprus and lives in a variety of habitats distributed along all altitudinal levels, and has frequently been observed at the study site. However, agamids are large lizards that eat most things and Hodar *et al.* (1996), studied the diet of the similar Ocellated Lizard *Lacerta lepida* and found that they preyed on Thekla Lark *Galerida theklae* nestlings.

Nest survival did not vary between years, or nesting attempts, or with clutch initiation date suggesting that seasonal changes in predator suites or behaviour or prey switching were not important. Predation could have arisen from lizards, mammals (canids'- mainly foxes and dogs, or rodents-rats) and avian predators (corvids - jay): all were seen at the study site and some nests were clearly dug up by large mammals. Cyprus Jays *Garrulus glandarius glaszneri* were seen often in the study. Both agamid lizard and jay species are well known predators of eggs and chicks (Kopan and Yom 1982, Sieving and Willson 1999). Both species' breeding period coincides with the Cyprus Wheatear's breeding cycle, and they both had a high population abundance in the study area. But specific identification of nest predators is lacking and although, for example Jays and Lizards were seen in the close vicinity of many nests, we have no direct evidence that any nest was taken by a Jay or a Lizard.

Survival of chicks in the first month after fledging was very high. Other studies have shown low rates of survival in relation to post-fledging stage of passerines. For example, Cox *et al.* (2014b) showed that fledgling age was a strong predictor of survival, with the highest mortality occurring during the first 3 weeks after birds fledged. In Barn Swallows (*Hirundo rustica*) juvenile survival in the first 3 weeks post-fledging was only 0.32 whereas after this period adults and juveniles had the same high survival of 0.96 (Gruebler et al. 2014). Studies of juvenile Eastern Meadowlarks (*Sturnella magna*) showed that mortality was very high during the first week of the postfledging period due to high rates of predation (Kershner et al. 2004). The same has been found in the Wood Thrush (Anders et al. 1997).

A very likely explanation for my contrasting result is the absence of aerial predators such as Sparrowhawks which are extremely rare breeders on Cyprus (never seen at Troodos during the study or concomitant prey alarm calling heard, W. Cresswell pers. obs.) Sparrowhawks are responsible for much of the mortality of passerines post fledging (Newton 1986). Other studies of species on islands that lack mainland predators (although there are many other predators on Cyprus) are lacking but the few available also show high post fledging survival rates in other passerines (Brouwer et al. 2006). Duration of parental care was unlikely to be a significant factor because this varied greatly between years (see Chapter 2) with nearly twice the length of post-fledging feeding in 2010 not resulting in any clear difference in the proportion of a brood surviving.

Renesting probability after failure of first nests was high and not particularly variable. This makes sense because failures are mostly “accidents” involving encounters with nest predators or loss of a partner: pairs should continue breeding afterwards because the strategic reason for breeding has not been modified. For example, Morton (2002) studied the reproductive biology of the migratory passerine the Mountain White-crowned Sparrow and found that more than half of the nesting attempts failed but there were rapid renesting efforts otherwise the reproductive opportunity for that year would be lost. Food abundance and nest predation were also associated with more renesting attempts in Song Sparrows *Melospiza melodia* (Zanette et al. 2006).

Renesting probability after the first succesful nest was highly variable within and between years, suggesting great flexibility in response to climatic cues (see Chapter 2). Here I discuss the implications for survival and productivity. Multiple breeding events in a year can greatly enhance productivity. For example, Nagy and Holmes (2005b) showed that 53% of female Black-throated Blue Warblers with successful first nests laid a second clutch and were thus double-brooded, effectively increasing productivity by half. Clutch initiation date and consequently food availability are likely to be the determinants of the occurrence of double brooding. If a second brood is possible then Cyprus Wheatears should have them unless there are trade-offs in the survival of the first brood (i.e. reduced duration of parental care – which occurs, see Chapter 2) or in the survival of adults (i.e. see Chapter 3). We have a limited number of years with which to examine this but there is no obvious coincidence between lower juvenile or adult survival and the occurrence of a second brood (see Chapters 2 & 3). Adults may however always invest a particular amount in their offspring whether entirely in their first brood or divided amongst a first and second brood and so there may be no survival trade-off for adults. And the number of juveniles produced in each year was the same regardless of their distribution between first and second broods (Figure 4.6), so there may be no particular survival benefit for an individual juvenile either.

Overall productivity was very high for a passerine (Chamberlain et al. 2009). This is particularly so because our productivity is one month after fledging – after the period of highest juvenile mortality - rather than estimated at fledging before this period as with most other studies. The high productivity suggests high adaptability to climatic conditions. Visser (2008), in his review argued that there are various mechanisms by which birds adapt to climate change which are primarily set by the rate of microevolution and different forms of phenotypic plasticity. In the last few decades, many bird species have responded to increasing spring temperature by advancing life cycle events (Ottersen et al. 2001) demonstrating that phenotypic plasticity is already widespread in many species. For example, in Pied Flycatcher populations early nesting has become increasingly important, associated with high fitness benefits, indicating adaptive phenotypic plasticity (Coppack and Both 2002). Pulido and Berthold (2004), however, hypothesise that long-distance migrants may take longer to adapt to changing conditions on the breeding grounds than short-distance migrant passerines because they are less phenotypically flexible. This perhaps does not appear to be the case with Cyprus Wheatears (as discussed in Chapter 2 and further in the final chapter): productivity is high regardless even in the face of variable conditions.

The population of Cyprus Wheatears at the NFP of Troodos Mountain was likely to be a source population with this level of productivity. With the lowest minimum annual survival rate recorded of 0.50 for males, 0.35 for females and 0.34 for chicks, the minimum annual productivity of 3.87 chicks would result in an 8.3% increase in the population over a year. With an average minimum survival rate for adults of 57% and for chicks of 49% (see Chapter 3), the average annual productivity would result in a

54.0% increase in the population over a year. The full implications of this high level of productivity, incorporating information from other areas of the study, are discussed in the final chapter.

CHAPTER 5. VARIATION IN ABUNDANCE, PRODUCTIVITY AND PHENOLOGY WITH ALTITUDE

5.1 ABSTRACT

The phenology of breeding of Afro-Palearctic migrants may be affected by climate change, leading to breeding success variation both within and between years. Determining such effects requires temperature variation data over many years, or a system where different populations breeding in a similar area are subject to different temperatures that lead to differing phenology. The Cyprus Wheatear is a migrant insectivorous passerine breeding throughout the island of Cyprus, from sea level to 1952 m, over a range of 20 - 30 km, so that its breeding phenology might be expected to vary considerably with the temperature variation that such a large altitudinal range over a small distance must represent. Here I used altitude as a proxy for variation in temperature and investigated how abundance, productivity and phenology in Cyprus Wheatears varied between and within years in relation to altitude.

One hundred and twenty two (122) transects of, on average, 12 km in length were carried out, with point counts made every 1 km recording the number and age of Cyprus Wheatears heard singing or calling, or seen, as an index of stage of breeding and productivity, along with altitude, date and habitat type.

First I confirmed that Cyprus Wheatears occurred and bred commonly over the full altitudinal range throughout the island. Second I found that adults were more abundant with increasing altitude, but this varied through the season so that they

became more common at lower altitudes from July. Using presence of singing males, which peaks at the start of breeding, to indicate the timing of breeding unconfounded by detectability, I found that probability of encountering a singing bird increased with altitude regardless of season and varied slightly but significantly between years and habitats. Third if adults were present on a transect, the timing of the appearance of any chicks did not vary significantly with altitude.

Overall therefore there was no indication that birds bred earlier at lower altitudes. However, where adults and chicks were both present, the ratio of chicks to adults (as an index of productivity of successful nests) depended significantly on both altitude and season with more chicks being apparent in May and June at lower altitudes, with higher altitudes catching up in July and August. This suggests that larger single broods were being produced at lower altitude and smaller double broods being produced at higher altitude. Overall, the transect results probably showed that altitudinal temperature variation affects the occurrence of double brooding and so the timing of chick production, but not variation in overall seasonal productivity. The results suggest that Cyprus Wheatears are already very well adapted to high variation in temperature within and between seasons, changing investment from a larger single brood to two smaller broods as temperature increases, as was also shown by the intensive nest-based study at NFP of Troodos.

5.2 INTRODUCTION

Changes in abundance, distribution and phenology of a broad range of plant and animal species have been correlated with patterns of atmospheric temperature, precipitation and other weather variables that have changed consistently over the last few decades (Walther et al. 2002a, Parmesan and Yohe 2003, Root et al. 2003). For example, Leech and Crick (2007) reviewed the effects of weather conditions on woodland bird species in temperate regions, and the climate mediated impacts on their abundance, distribution and phenology, to outline potential changes that may occur in light of future climatic scenarios. They found that changes in ambient temperatures and precipitation may have direct and indirect effects on the survival rates and productivity of bird species, thus, influencing population size. In addition they found that the dispersal rates of many woodland birds are low, so affecting their ability to move to new habitat if the current one became unsuitable. Thus climate change may profoundly affect the population dynamics of bird species.

The phenology of breeding of Afro-Palearctic migrants may be particularly affected by climate change, leading to breeding success variation both within and between years. Moussus *et al.* (2011), studied the ability of 20 common passerine species to adjust their breeding phenology to spring temperature variations, and suggested that the sensitivity of a species' breeding phenology to climate change related to its mean migration distance, thermal and habitat niche breadth and its brain mass. They stated that species with the broadest ecological and thermal niches, the shortest mean migration distances and the largest brains were most able to adjust their breeding phenology to temperature variation. Empirical examples from other Palearctic migrants confirm that some long-distance migrants have suffered population declines that may be associated with climate change. For example, Sanderson *et al.* (2006) showed that long-distance migrants may be particularly vulnerable to the impact of climate change, thus migratory passerines suffered greatest rates of decline. Both *et* *al.* (2010), analysed the consequence of climate change as an increasing mismatch between timing of food requirements and food availability in long-distance insectivorous migrant species and their results suggest that trophic mismatches could be among the major causes of population declines. A significant decline of long-distance migrants has been correlated with climate change, with increasingly warmer winters potentially also posing a severe threat to long distance migrants (Lemoine and Bohning-Gaese 2003).

Climate change may affect phenology in a number of ways. First, breeding may be initiated earlier, as shown by long-term trends in the seasonal distribution of laying dates of birds in the United kingdom reported by Crick *et al.* (1997), with migrant insectivores showing a tendency to lay earlier due to the rise in ambient temperature. For example, Forchhammer *et al.* (1998), showed that skylarks showed significant year to year responses to fluctuations in the North Atlantic Oscillation (NAO), with changes to an earlier breeding phenology with increasing average spring temperatures. Similarly, populations of Blue Tits *Cyanistes caeruleus* in Corsica advanced breeding responses to rising spring temperature (Thomas et al. 2010).

Second, productivity may be affected because of phenological mismatch of food supply which allows adults to reach breeding condition, lay large clutches and then to feed chicks. Przybylo *et al.* (2000), analysed cross-sectional correlations between the winter NAO-index and breeding performance of Collared Flycatchers, and found that within individuals the NAO-index significantly affected laying date and clutch size so that females laid earlier and produced larger clutches after warmer and moister winters. The potential consequences of mismatch have been shown for many species, for example, the Tree Swallow, where there is selection for laying earlier, the start of egg-laying is strongly related to food abundance and birds that lay earlier have larger clutches and fledge more young (Dunn et al. 2011).

Third, the duration of the breeding season may change, leading to greater or reduced opportunities for renesting after failure or initiation of second broods. Matthysen *et al.* (2011), studied the breeding cycle of the Blue Tit and the Great Tit, and found that both advanced their mean first-egg dates, fledging was shortened, through a decrease in laying interruptions, incubation time, and nestling development time, whereas this decrease was correlated with a gradual increase in temperature and consequently the occurrence of second clutches strongly decreased over time. The proportion of female Great Tits producing two clutches per year has declined over time and was strongly related to the timing of first clutch relative to the peak in caterpillar abundance. Adjustment to changing climatic conditions may involve shifts in life-history traits other than simply the timing of breeding, thus declines may only correlate indirectly with increasing spring temperature and changes in lay date (Husby et al. 2009).

Determining the effects of climate change on phenology requires temperature variation over many years (Cresswell and McCleery 2003, Both et al. 2004), or a system in which different populations breeding in a similar area are subject to different temperatures that lead to differing phenology such as was observed in Dutch Great Tits (Ahola et al. 2004, Nussey et al. 2005). The Cyprus Wheatear is migrant insectivorous passerine breeding throughout the island of Cyprus, from sea level to 2000 m, over a range of 20 - 30 km, so that its breeding phenology might be expected to vary considerably with the temperature variation that such a large altitudinal range over a small distance must represent. The species is common and distributed from sea level up to the highest mountainous area of the island, with the highest densities in forest, agriculture and abandoned agriculture areas and urban areas that still maintain small agricultural fields or gardens. Habitat quality has important effects on reproductive success, survival and fitness during breeding (Holmes et al. 1996, Part 2001) and on the wintering grounds (Strong and Sherry 2000) and so may confound any relationship between altitude as a proxy for temperature and phenology. However, van Oosten *et al.* (2014) showed that Northern Wheatears on the Dutch coast consider mainly variation in prey abundance and accessibility when considering where to forage. They studied the relationships between vegetation structure, habitat preference and densities of preferred prey and hypothesised that forager mobility (i.e. perches in open landscapes) and food accessibility were of greater importance during patch selection than food abundance per se in ground foraging birds. Therefore we might predict a relatively small confounding effect of habitat on Cyprus Wheatear breeding phenology, productivity and occurrence: as long as there are open areas with scattered perches a habitat is likely to be suitable for Cyprus Wheatears (Moreno 1984b, Randler et al. 2010b).

In this study I used altitude as a proxy for variation in temperature and investigated whether and how abundance, productivity and phenology in Cyprus Wheatears varied between and within years dependant on altitude. I investigated variation with respect to:

5.2.1 Distribution. I predicted that the species would be abundant on all transects regardless of altitude and habitat, as long as habitats were open and had perches (i.e. almost all Cypriot habitats).

5.2.2 Altitude. I predicted that the species occurrence and occurrence of breeding would vary with altitude because altitude will affect breeding phenology. I predicted that adults would occupy higher altitudes later in the season and breeding would commence later at higher altitudes.

5.2.3 Year and habitat. Variation in the occurrence of breeding by year and habitat can be investigated by using the presence of singing males that can be recorded without any confounding effects of detectability variation between habitats. I predicted that there would be annual variation in the probability of detecting a singing bird at a point (as an index of breeding density) between years because of inter-annual variation in survival (see Chapter 3). I predicted that there would be little variation in the probability of detecting a singing bird at a point across habitats (i.e. variation in breeding density with habitat) because Cyprus wheatears are very generalist in their breeding requirements.

5.2.4 Timing of breeding. I predicted that chicks would appear first at lower altitudes, because warmer temperatures at lower altitudes would allow earlier onset of breeding.

5.2.5 Productivity. I predicted variation in the timing of productivity with altitude because the duration of the breeding season will vary with altitude, allowing for variation in the number of broods produced. Because Cyprus has very high mid-summer temperatures, longer breeding seasons might be expected at higher altitudes allowing a higher frequency of double broods.

5.3 METHODS

Transect surveys to record the presence, abundance and behaviour of adult and fledged Cyprus Wheatears were carried out in three years 2010 – 2012 inclusive from March to October over much of the island of Cyprus (Geographic coordinates: 35 00 N, 33 00 E): no transects were repeated: Figure 5.1 a and b. Cyprus wheatears are Afro-Palearctic migrants and are present on Cyprus from March until early November, and then winter in Sudan and Ethiopia. A point transect method was used with point counts at 1km intervals along tarred or untarred minor roads.

Point transects were randomly selected across different habitats, altitudes and road types. I carried out 122 (43 in 2010, 57 in 2011 and 22 in 2012) transects ranging from near sea level to high elevation (>1500m) across 8 different habitat and 2 road types. Transects were carried out by randomly identifying minor roads on a large scale map and driving to the start. Point transects were almost all carried out in the evening between 16:00 and 19:30 during clear, warm and wind free conditions. At the start of each transect the car was parked and I walked 100m away from the car along the road. A point count was then conducted for 5 minutes recording several variables as below. After 5 minutes I returned to the car and moved exactly 1km along the road as measured by the car’s odometer. The car was parked and I walked 100m away from the car in the opposite direction to that of the last point, thus points were no closer than 800m. A second point count of 5 minutes was carried out. The procedure was repeated until 10 – 14 points had been carried out along the road. Overall 1,531 points were carried out across the 122 transects (Figure 5.1 a & b).

The following variables were recorded at each point:

5.3.1 Date, time, altitude and location using a Garmin GPS60x or a Garmin 12 GPS handheld unit, crosschecked with large scale topography and road maps of the island with an accuracy of +/- 10m or better.

5.3.2 The number of Cyprus Wheatears seen and their ages (adult or fledged chicks) and sex (male and female for adults only). The number of singing males and calling birds (the “chacking” call associated with the presence of a nest and presence of fledged chicks (Randler 2013) was also recorded).

5.3.3 Habitat type. Habitats were classified into 8 classes on the basis of the dominant habitat visible from the point: forest; agricultural; abandoned agricultural; mixture of forest, agricultural and abandoned agricultural; phrygana or grazed grassland; maquis; agricultural land within villages; and barren areas. The habitats in detail are:

5.3.3.1 Forest: Mostly Mediterranean conifer forests of Calabrian pine and Phoenician juniper maquis; occasionally sclerophyllous evergreen forest of golden oak and Kermes oak; occasionally deciduous, riparian forests and semi-deciduous oak woodlands; frequent mountain forests of Cyprus cedar and black pine and frequent Oro-Mediterranean-stage stands of arborescent junipers and thorny xerophytes.

5.3.3.2 Agriculture Land: Tilled land, cereal (including harvested crops), olive and carob groves, citrus groves, vineyards, etc. Agricultural land is widespread on the island covering sites from sea level up to the mountains. The Mesaoria plain which extends between the two mountainous ranges Troodos and Pentadaktylos is predominantly is under cereal cultivation, and represents a landscape type not found elsewhere on the island. Olives, carobs and vineyards are found across the whole island and a traditional mixed farming system is predominant in the mountainous sites mainly spread out along Troodos range. Citrus groves are predominant in the lowlands alongside the rivers and valleys especially the south-west but there are small patches of citrus all over the island.

5.3.3.3 Abandoned agricultural land: Common particularly in the mountains. All types of farming have been abandoned recently and many areas are in the process of succession back to more natural vegetation.

5.3.3.4 Mixed: A mixture of forest, agriculture and abandoned agriculture which is common particularly in upland areas. This category includes abandoned agriculture sites where succession has already taken place and a forest has become re-established. Small fields may still be being cultivated in this matrix.

5.3.3.5 Phrygana grassland: Phrygana and low shrubs in pasture land used for grazing especially by goats and sheep. Phrygana vegetation, corresponding to *Sarcopoterium spinosum* (Commission 2003), occurs as a forest degradation stage, most often in large openings of the maquis, or as a climax stage in sites with adverse conditions (aridity, poor soils, exposed, over grazing etc.).

5.3.3.6 Maquis: Olea and Ceratonia maquis including scrub and phrygana vegetation including thermophilic wild olive and pistacchio scrubs. The habitat is widely distributed from the Akamas peninsula, in the west, to the foothills of Troodos range where it is particularly common on the southern flanks.

5.3.3.7 Agricultural land within villages: Most rural housing in Cyprus including larger villages have fields and orchards interspersed among the houses. Essentially this habitat comprises of agricultural land with the presence of occupied houses.

5.3.3.8 Barren: Bare areas without vegetation such as steep slopes, quarries, areas cleared for development, rock falls and anthropogenically degraded and cleared bare areas.

5.3.4 Road type. Either tarred or dirt. All roads chosen were minor roads with very minimal traffic (1 car per 30 minutes at the time of survey) and there was little difference between the habitats around either type of road.

Analysis

Distribution was examined by plotting the coordinates of points over a map of Cyprus to evaluate whether the points had Cyprus Wheatears or not. The Arc GIS 10.2 package for Desktop was used for creating the maps of the species distribution along different habitat types and their distribution with altitude.

I tested for variation in occurrence with altitude and how this relationship varied through the breeding season by predicting the presence and absence of adults at points using a generalized linear mixed model (GLMM) with a binomial error structure and with transects as a random factor. Predictors were altitude (log transformed to better fit the assumptions of a GLMM) and month and their interaction, with year, habitat, road type and time of day included as confounding variables to control for variation in detectability.

I tested for variation in breeding occurrence with altitude and how this relationship varied through the breeding season by predicting the presence and absence of a singing male at points using a generalized linear mixed model (GLMM) with a binomial error structure and with transects as a random factor. Predictors were altitude (log transformed to better fit the assumptions of a GLMM) and month and their interaction, with year and habitat included as main effects to test for variation across these variables, and road type and time of day included as confounding variables. Note that there are no detectability confounds in this model because I recorded singing birds and therefore differences across habitats and years will represent true differences in breeding occurrence.

Models would not converge for analyses of timing of chick production and productivity so an aggregated data set was used reducing each transect to a single case, and so simplifying models by them not requiring a random effect to control for non-independence of points within transects. I aggregated the data for each individual transect (i.e. across 10 – 14 points) to calculate the total number of adult birds seen or heard and the total number of fledged chicks seen, and mean altitude and time of day. Habitat had to be ignored because transects could cross several habitat types, but transects were evenly spread across habitat types with respect to month and year reducing any bias from this. Sample size was reduced to the number of transects and so model complexity was reduced by using Julian date and its quadratic as covariates, as seasonal measure rather than individual month as a factor.

I tested for the timing of appearance of chicks with altitude and how this relationship varied through the breeding season by predicting the presence and absence of chicks on transects using a general linear model (GLM) with a binomial error structure. Predictors were altitude (log transformed to better fit the assumptions of the GLM) and Julian date and its square (because we expect a peak in breeding activity in temperate passerines), and the interaction between Julian date and its square term with altitude, with year and time of day included as confounding variables. Note that this model is not confounded by any effects of habitat on timing of breeding and covariation of habitat type with altitude (as above). Sample sizes were reduced to 111 transects because 11 transects where there were no adult Cyprus Wheatears present at any of the points were removed from the analysis.

I tested for the relationship between productivity and altitude by calculating an index of productivity for all transects where chicks were recorded. The total number of chicks recorded per transect was divided by the total number of adults, thus a high ratio indicates high productivity and a low ratio lower productivity. I then tested the relationship between this index of productivity and altitude using a general linear model (GLM) assuming a normal distribution. Predictors were altitude and Julian date and its square (because I expect a peak in productivity with season in temperate passerines), and the interaction between Julian date and its square term with altitude, with year and time of day included as confounding variables. Sample sizes were reduced to 64 transects because all transects where no chicks were recorded were removed from the analysis.

Analysis was carried out using R 3.0.2. Interactions were only tested where there was an a priori biological hypothesis to be tested; some interactions could not be tested because of sample sizes and missing information. Full models were simplified by AIC comparison using the information theoretic approach (Akaike 1974, Burnham and Anderson 2002). Non-significant interactions were removed by default. The top models were then evaluated for both biological and statistical significance. Residuals of the final models met model assumptions reasonably well, as demonstrated by the plot command in R and according to criteria in Crawley (2007). Figures illustrate the results of models and plot the predicted values (parameter estimates) for the variable of interest, with other variable values set to their median (and so typical) values unless otherwise stated. Means are given +/- 1 standard error unless otherwise stated.

5.4 RESULTS

Distribution

There was strong evidence that Cyprus Wheatears occurred commonly in all 122 surveyed localities visited in Cyprus with occurrence on all transects. The species was observed throughout the island from sea level up to the highest mountains. The species was commonly encountered in all three years 2010-2013, throughout the island, across all habitat classes and altitudinal gradients both during the species breeding season and migration (Figure 5.1 a & b).

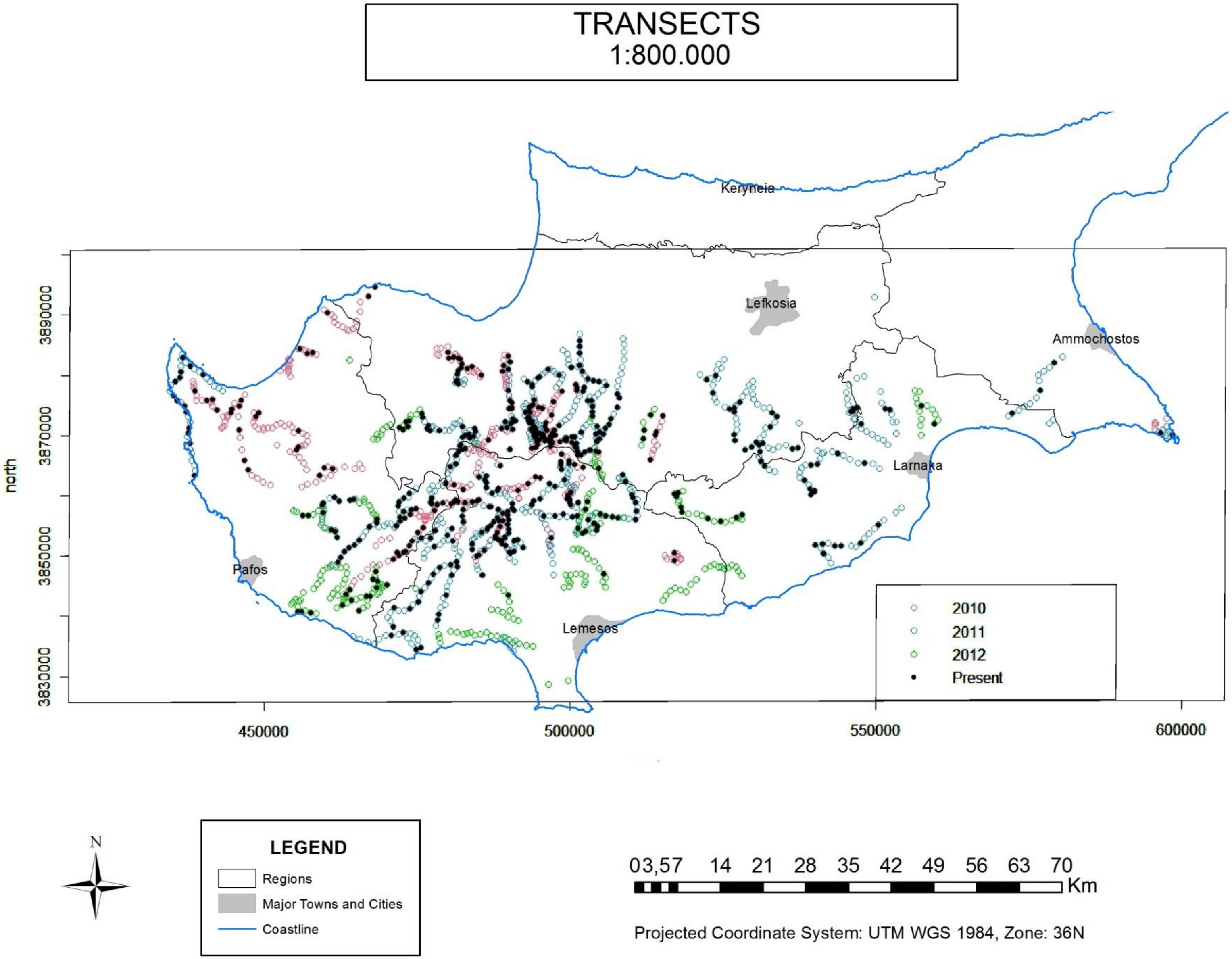

Figure 5.1 a: Transects of point counts (lines of circles with each circle representing a point count at 1km intervals) of Cyprus Wheatears over three consecutive years (2010 red circles, 2011 blue circles and 2012 green circles). Presence of at least one Cyprus wheatear at a point is indicated by that circle being filled in black. Transects were spread across the island in five of the six districts under the direct control of the government of the Republic of Cyprus.

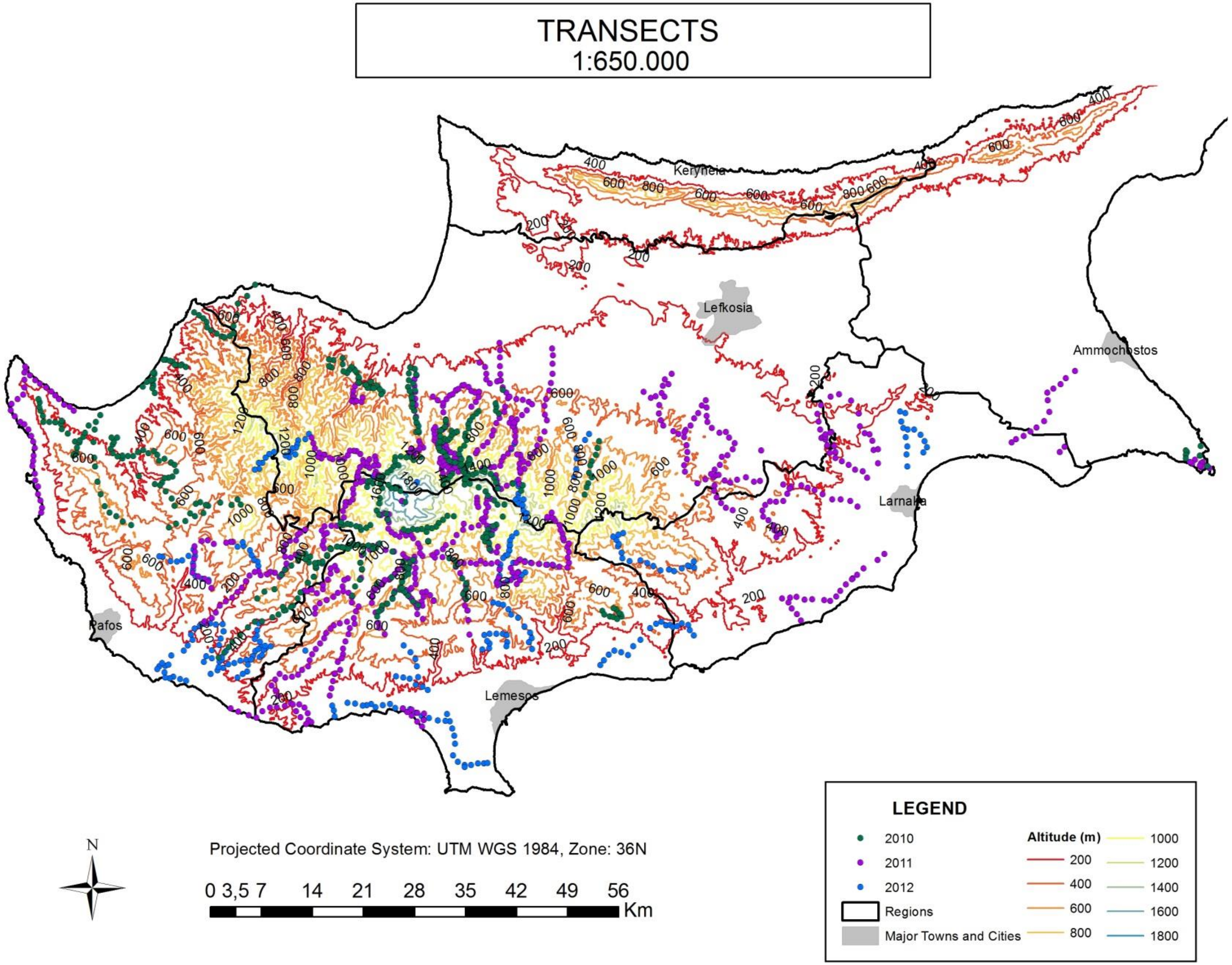

Figure 5.1 b: Transects of point counts with contours (lines of circles with each circle representing a point count at 1km intervals) of Cyprus Wheatears over three consecutive years (2010 red circles, 2011 blue circles and 2012 green circles). Presence of at least one Cyprus Wheatear at a point is indicated by that circle being filled in black. Transects were spread across the island in five of the six districts under the control of the government of the Republic of Cyprus.

Altitude

Although Cyprus Wheatears are ubiquitous in all areas in Cyprus they occurred at highest densities with increasing altitude, but this relationship depended on month of the breeding season (Table 5.1, Figure 5.2). Cyprus Wheatears were initially relatively more common at lower altitudes in March (although relatively uncommon at any altitude); during April to June the probability of occurrence increased strongly with altitude; in July and August Cyprus Wheatears then became more common at lower altitudes (Figure 5.2). For breeding occurrence (i.e. the presence of singing males during April to July), there was no significant interaction between altitude and month, but a strong positive main effect of altitude (Table 5.2, Figure 5.3). Breeding birds were more common at altitude regardless of month, but the overall level of singing declined significantly from April through to July (Figure 5.3).

Year and habitat

Using the presence or absence of a singing male at a point as an index to measure breeding density, there was significant variation in breeding density across years, with 2012 showing a significantly lower breeding density (Table 5.2, Figure 5.4). Similarly there was significant variation in the index of breeding density across habitats (Table 5.2, Figure 5.4). Cyprus Wheatears bred at similar densities in all habitats but were largely absent from Maquis and completely barren areas (Figure 5.5).

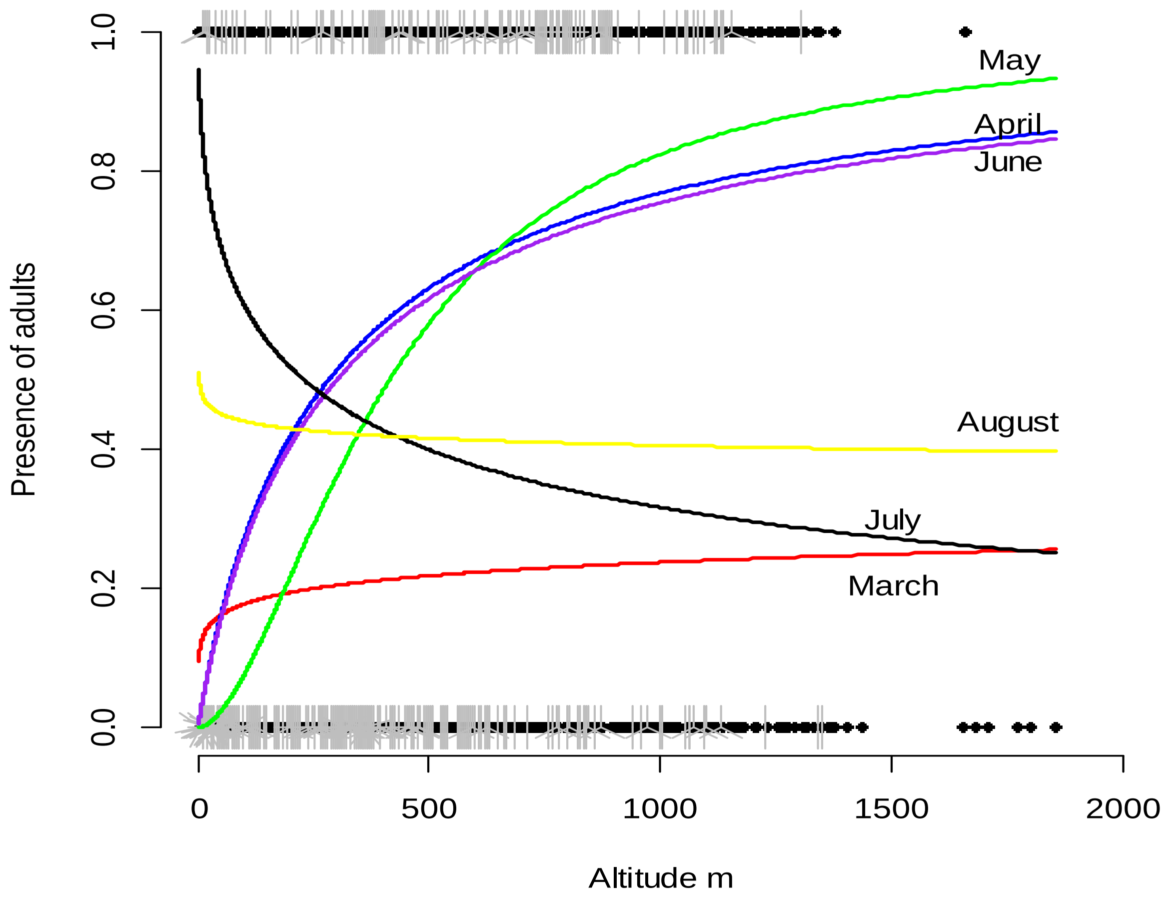

Figure 5.2: Variation in the presence of adult Cyprus Wheatears at a point with altitude, with separate lines plotted for each month to illustrate how this relationship varied through the breeding season. Predicted lines are plotted from the model in Table 5.1. Predicted values were set to Forest habitat, untarred roads, 2010 and median time of count.

Table 5.1. Results of a binomial GLMM to predict the probability that the presence of an adult Cyprus Wheatear was recorded at a point in a transect was dependent on altitude and whether this relationship varied by month, controlling for habitat type, road type, year and time of day. Transect was included as a random effect. N = 1531 points, 122 transects.

Variable	Estimate	SE	z	*p*
[1] (Intercept)	-3.61	1.11	-3.3	0.001
[3]Agricultural	0.01	0.22	0.0	0.98
Abandoned agricultural	0.54	0.27	2.0	0.04
Mixed	0.38	0.19	2.0	0.05
Grassland	0.50	0.38	1.3	0.19
Maquis	0.15	0.38	0.4	0.70
Village agriculture	0.52	0.24	2.1	0.04
Barren	1.95	1.17	1.7	0.09
Untarred road	0.30	0.17	1.7	0.08
[4]2011	0.14	0.19	0.7	0.47
2012	-1.03	0.28	-3.7	<0.001
April	-3.07	2.56	-1.2	0.23
May	-8.30	2.24	-3.7	<0.001
June	3.06	1.70	-1.8	0.07
July	5.11	3.88	1.3	0.19
August	2.31	1.27	1.8	0.07
September	1.27	1.43	0.9	0.37
October	-0.51	1.85	-0.3	0.78
Log(Altitude)	0.16	0.19	0.9	0.39
Time of day	0.06	0.02	3.1	0.002
[2]April * Log(Altitude)	0.79	0.42	1.9	0.060
May * Log(Altitude)	1.59	0.38	4.2	<0.0001
June * Log(Altitude)	0.77	0.29	2.7	0.007
July * Log(Altitude)	-0.68	0.58	-1.2	0.24
Aug * Log(Altitude)	-0.22	0.23	-1.0	0.32
Sep * Log(Altitude)	0.06	0.25	0.2	0.82
Oct * Log(Altitude)	0.23	0.30	0.8	0.44

[1] (Intercept) = Forest, Tarred road, March, 2010

[2] Removing the interaction of month * log (altitude) worsened the model (delta AIC = 28.8)

[3] Habitat had a significant effect (χ^2 = 16.0, *p* = 0.025, ANOVA removing habitat)

[4] Removing year from the model had a significant effect indicating that overall there was significant variation across years ($\chi^2 = 21.2$, $p < 0.0001$, ANOVA comparing model above with the same model without year).

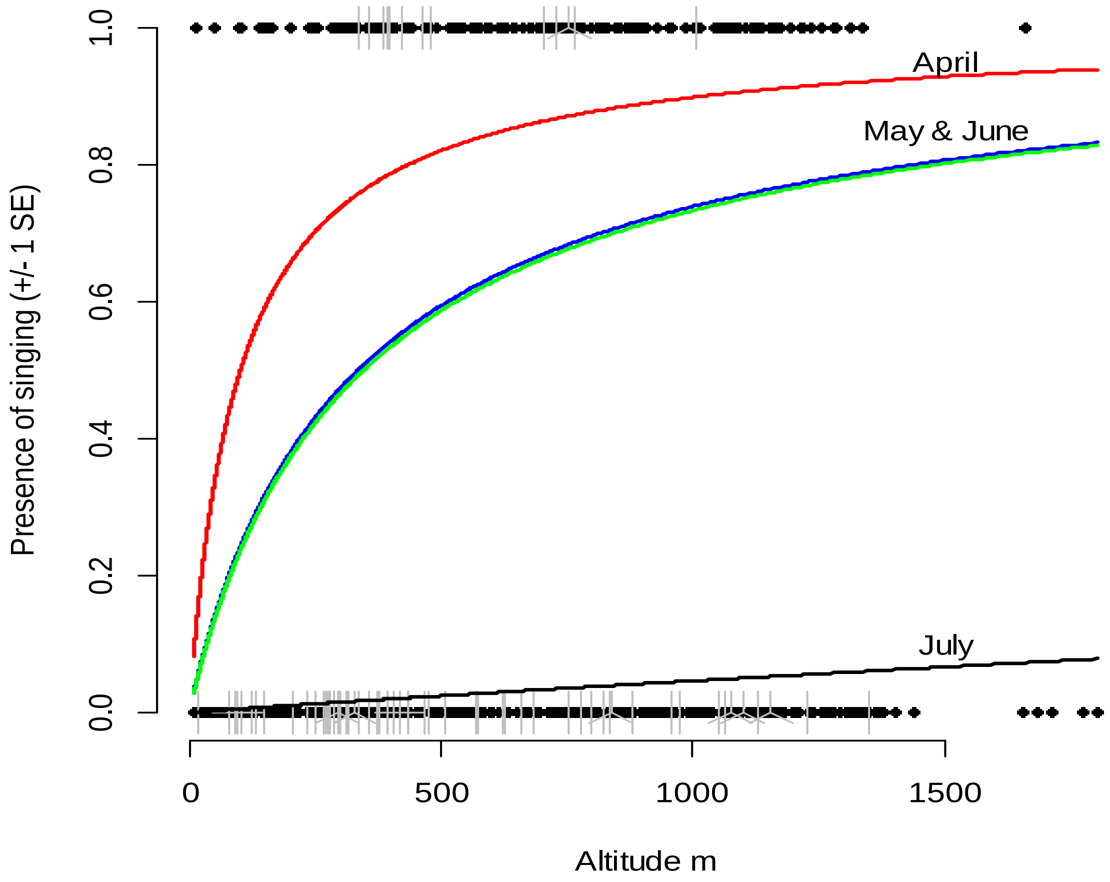

Figure 5.3: Variation in probability of hearing a male Cyprus Wheatear singing at a point (i.e. an index of breeding abundance) with altitude, and how this relationship varied by month during the breeding season. Predicted lines are plotted from the model in Table 5.2. Note that there was no significant interaction between month*altitude so although singing rate depends on month, it always is higher with altitude regardless of month. Predicted values were set to Forest habitat, untarred roads, 2010 and median time of count.

Table 5.2: Results of a binomial GLMM to predict the probability that singing was heard from a Cyprus Wheatear at a point in a transect was dependent on altitude and whether this relationship varied by month, controlling for habitat type, road type, year and time of day. Transect was included as a random effect. Only months April to July were considered in this analysis because singing is very rare outside these periods. N = 643 points, 54 transects.

Variable	Estimate	SE	z	*p*
[1] (Intercept)	-5.25	1.63	-3.2	0.001
Agricultural	-0.54	0.36	-1.5	0.13
Abandoned agricultural	-0.31	0.45	-0.7	0.49
Mixed	-0.49	0.31	-1.6	0.11
Grassland	-1.69	1.12	-1.5	0.13
Maquis	-15.18	850.20	-0.0	0.98
Village Agriculture	0.21	0.40	0.5	0.59
Barren	-15.53	9996.37	0.0	0.99
Untarred road	-0.02	0.31	-0.07	0.94
2011	-0.52	0.28	-1.88	0.06
2012	-1.67	0.43	-3.88	<0.0001
[2]Log (altitude)	0.95	0.19	5.02	<0.0001
Time of day	0.05	0.04	1.29	0.19
May	-1.14	0.35	-3.28	0.001
June	-1.17	0.41	-2.83	0.005
July	-5.20	0.61	-8.57	<0.0001

[1] (Intercept) = Forest, Tarred road, April, 2010

[2] Including the interaction between Month * log(altitude) did not improve the model (ANOVA comparing the model above with the model including Month * log(altitude), χ^2 = 1.8, *p* = 0.61, delta AIC = 4.2)

[3] Removing habitat from the model had a significant effect indicating that overall there was significant variation across habitats (χ^2 = 15.0, *p* = 0.035, ANOVA comparing model above with the same model without habitat).

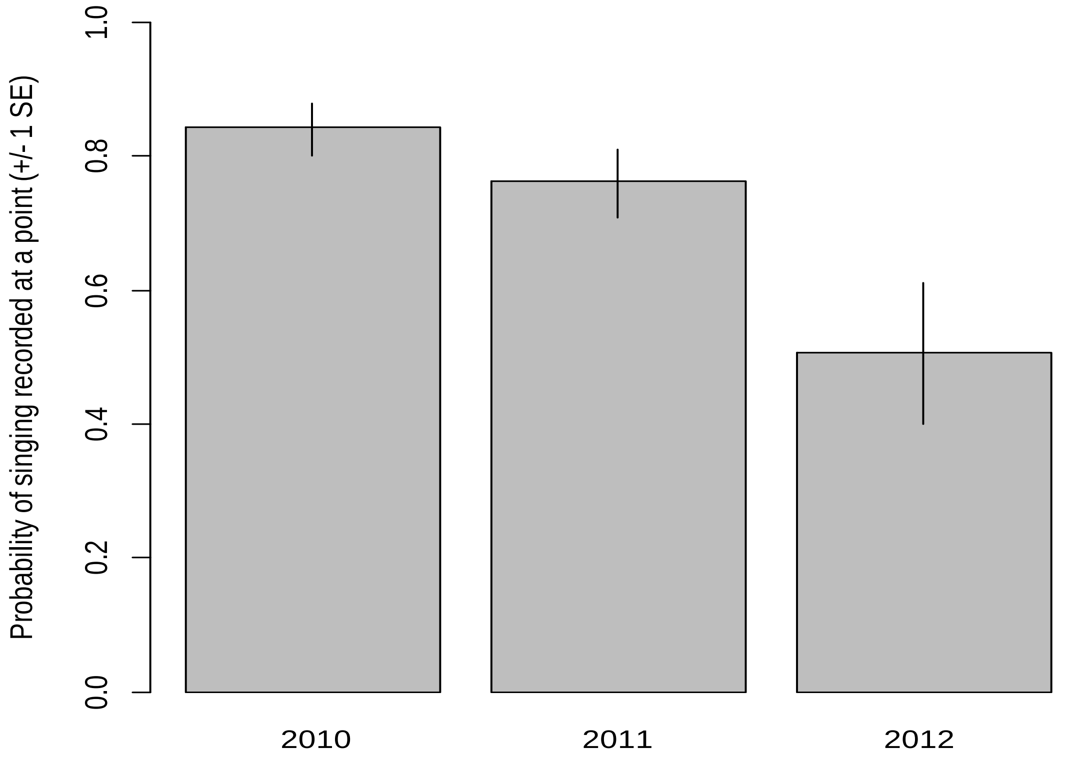

Figure 5.4: Variation in the probability of recording a singing male Cyprus wheatear at a point during a transect with year (i.e. variation in an index of breeding density across years). Predicted values are plotted from the model in Table 5.2. Predicted values were set to Forest habitat, untarred roads, median altitude and median time of count.

Initiation of breeding

The probability of recording chicks on a transect (if adults were present), as an index of the timing of breeding was dependent on altitude and date, but not their interaction (Table 5.3, Figure 5.6). Although there was a greater probability of encountering chicks at higher altitude, their peak of appearance did not vary with altitude showing that the timing of breeding was independent of altitude (Figure 5.6).

Table 5.3: Results of a binomial GLM model to predict whether variation in the presence of chicks with altitude was dependent on date (Julian day), i.e. whether chicks appear earlier at lower altitudes because breeding commences there earlier. Year and time of day were included as potentially confounding variables, but because analysis is at the level of the transect over a distance of up to 14km the analysis is confounded by habitat variation. Julian date included with its square term because breeding peaks in most temperate passerines so a quadratic function is more biologically likely. N = 111 transects (not 122 because 11 transects where no adult Cyprus Wheatears were recorded were removed from the analysis).

Variable	Estimate	SE	z	*p*
[1](Intercept)	-20.77	5.04	-4.1	<0.0001
[2]Log(Altitude)	0.78	0.36	2.2	0.03
2011	1.13	0.88	1.3	0.20
2012	-1.18	1.31	-0.9	0.37
Julian date	0.23	0.05	4.5	<0.0001
Julian date squared	-0.00	0.00	-4.2	<0.0001
Time of day	-0.01	0.09	-0.2	0.88

[1] (Intercept) = Presence of chicks & 2010

[2] The interaction altitude * Julian date was not significant $F_{1,102}$ = 0.0001, p = 0.99, nor was the interaction altitude * Julian date^2 was not significant $F_{1,102}$ = 0.0001, p = 0.78, Delta AIC = -0.7 with them both included and so the interactions were removed from the model.

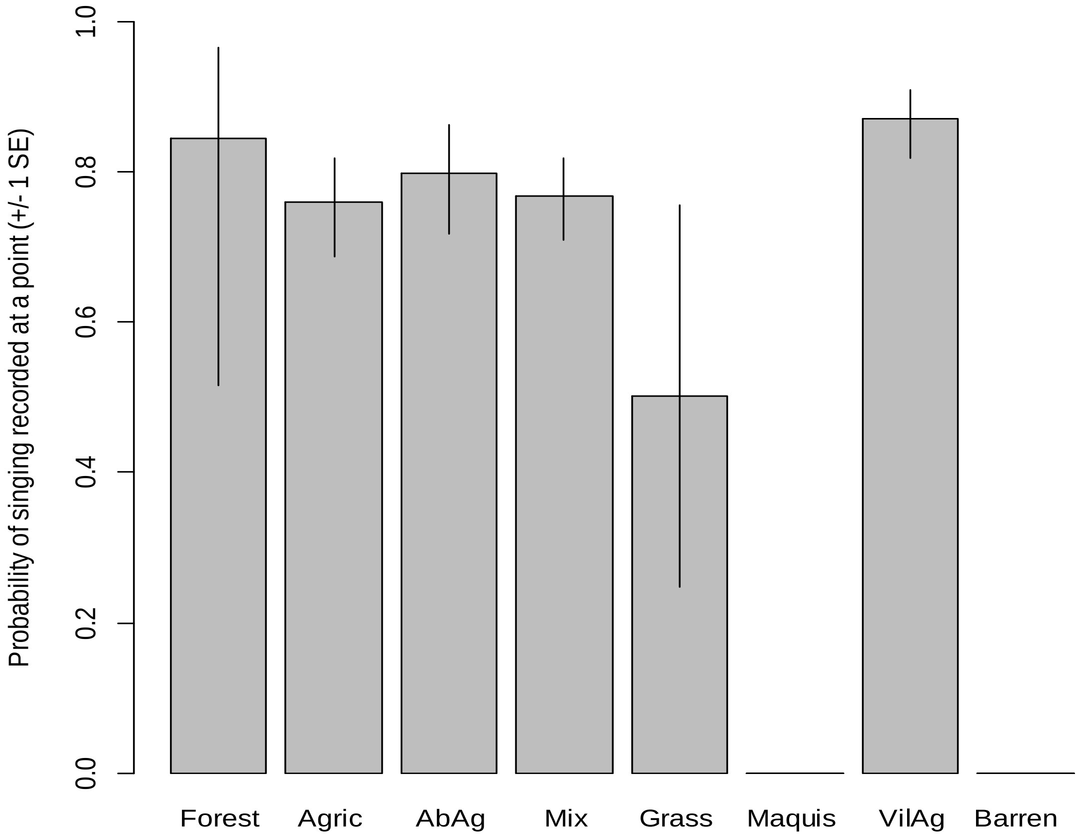

Figure 5.5: Variation in the probability of recording a singing male Cyprus Wheatear at a point during a transect with habitat (i.e. variation in an index of breeding density across habitats). Predicted values are plotted from the model in Table 5.2. Predicted values were set to 2010, untarred roads, median altitude and median time of count. Differences in abundance of Cyprus Wheatear between most habitats were minor except for Maquis and totally bare areas which were completely unsuitable. Habitat types are: Forest, Agric = Agricultural land under perennial cultivation, AbAg = Agricultural land no longer under active cultivation, Mix = Long term abandoned agricultural land where there is a mixture of successional forest, but some fields may be cultivated, Grass = pasture land used for grazing, Maquis = typical Mediterranean heathland scrub, VilAg = Villages with low density housing interspersed with land under cultivation, Barren = bare hillsides or anthropogenically degraded clear areas (quarries etc.).

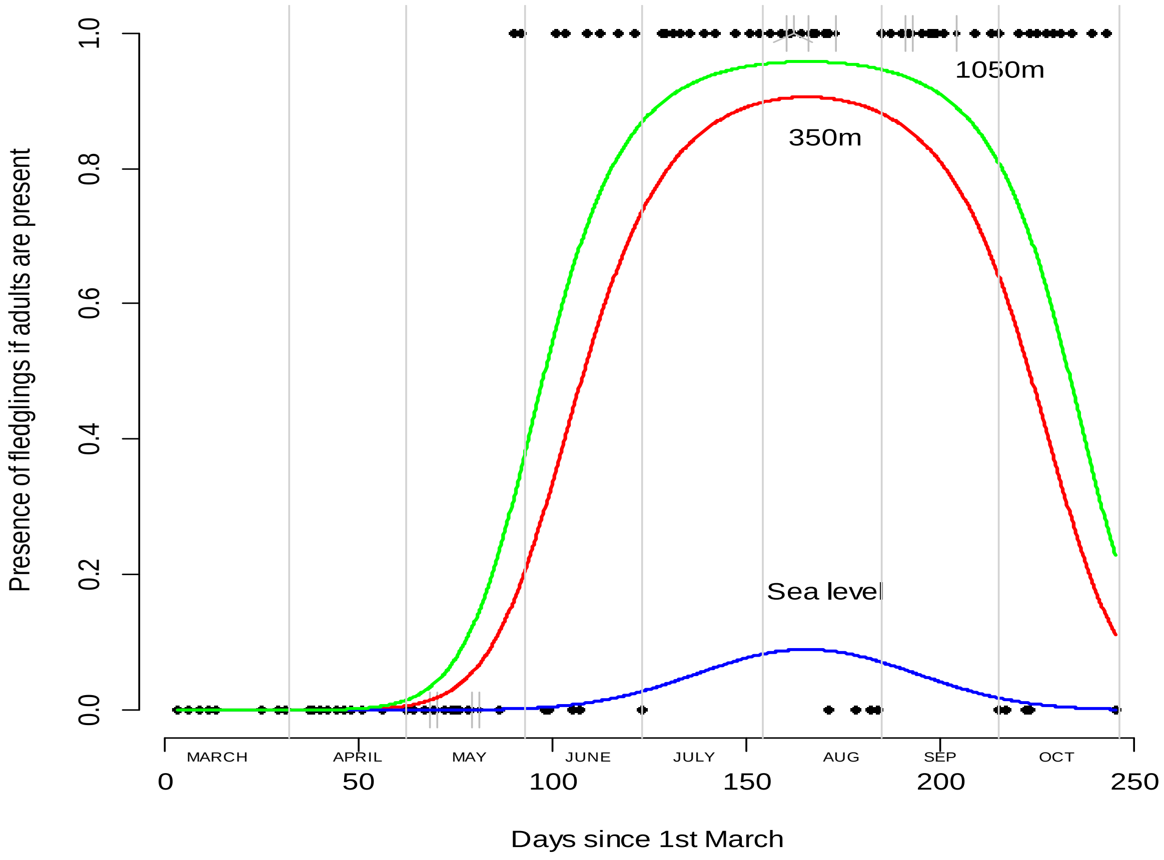

Figure 5.6: Illustration of the probability of fledglings being recorded (i.e. an index of the timing of local chick production and so onset of breeding) with time during the breeding season (date as days since the first of March) and how this relationship varies with altitude. Predicted values from the model in Table 5.3 are plotted. Parameters were set to 2010 and median time of day. Note that the interaction between altitude and date was not significant showing that chicks first appear at the same time regardless of altitude.

Productivity

The number of chicks produced per adult on transects that produced chicks (productivity index) was significantly dependent on the interaction between altitude and date (Table 5.4, Figures 5.7 & 5.8). If expressed in terms of seasonal variation

(Figure 5.7) then productivity was uniform across the season at lower altitudes and with a marked peak at higher altitude, with productivity at higher altitudes initially being lower than lower altitudes early in the season, but then exceeding that of lower altitudes in the middle of the season, before declining below the productivity at lower altitudes at the end of the season. If expressed in terms of altitude (Figure 5.8) then productivity declined with altitude early in the breeding season, but increased with altitude later in the breeding season. There was also significant variation in the index of productivity with year, with 2011 having a significantly higher productivity (Table 5.4, Figure 5.9).

Table 5.4: Results of a GLM model to test whether productivity (maximum number of fledged chicks recorded per transect) was dependent on altitude, and whether this relationship changed with time of year (Julian day or date, and also the quadratic of date because a seasonal peak in number of chicks would be expected). Year and time of day were included as confounding variables. Only transects where chicks were recorded were included so N = 64 transects.

Variable	Estimate	SE	t	*p*
[1](Intercept)	3.82	2.21	1.7	0.08
Altitude	-0.01	0.00	-2.5	0.02
2011	0.47	0.13	3.6	0.001
2012	-0.06	0.28	-0.2	0.83
Julian date	-0.04	0.03	-1.5	0.15
Julian date squared	0.00	0.00	1.3	0.19
Time of day	0.00	0.02	0.1	0.96
[2]Altitude * Julian date	0.00	0.00	2.5	0.02
[2]Altitude * Julian date^2	0.00	0.00	-2.5	0.02

[1] (Intercept) = Productivity & 2010

[2] Removing the interaction of date * altitude and date^2 * altitude substantially worsened the model (delta AIC = 3.1).

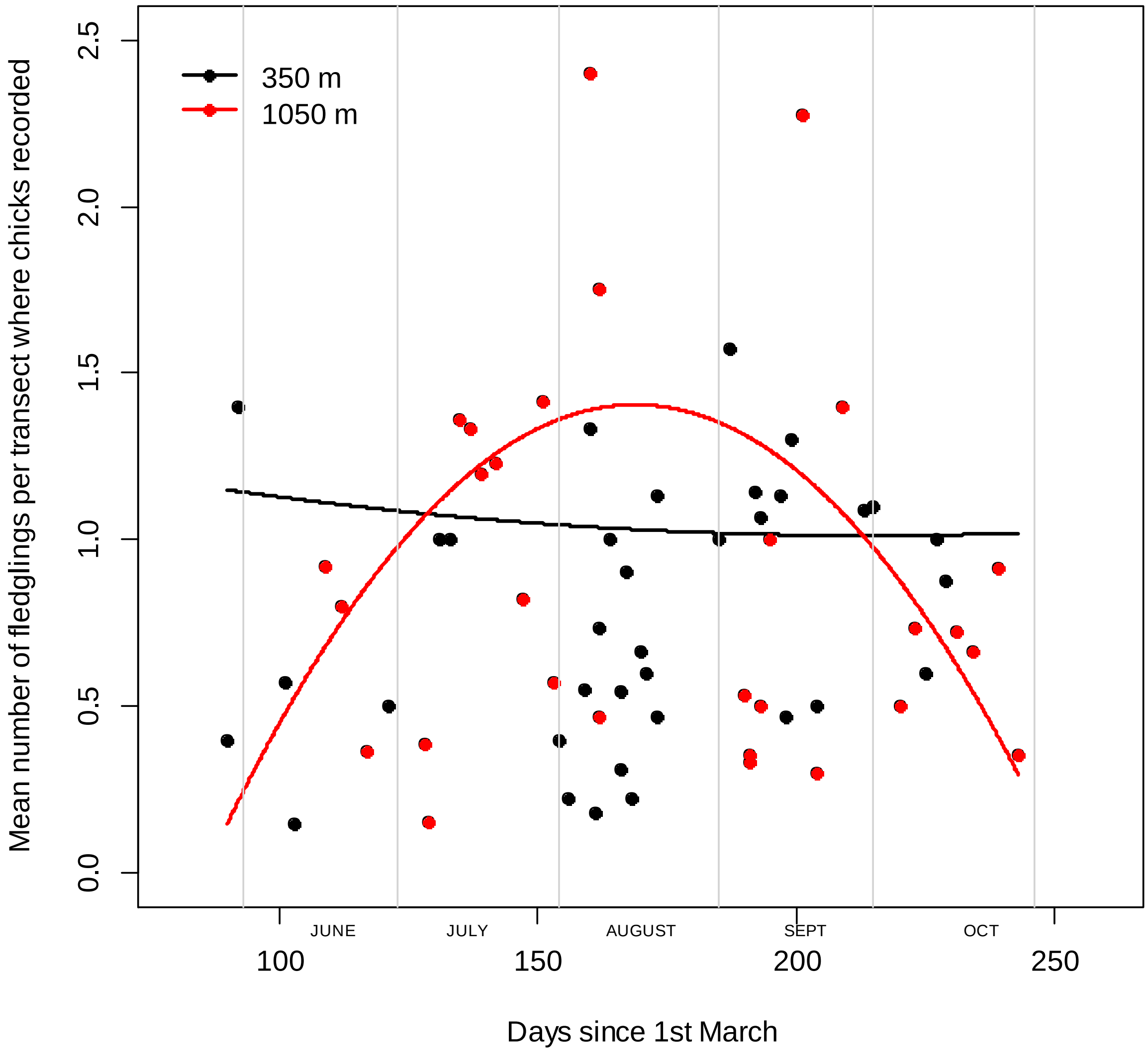

Figure 5.7: The relationship between the number of chicks produced per adult on transects that produced chicks (productivity index) and time during the breeding season and how this varied with altitude. The black line shows productivity with date at low altitudes and the red line productivity with date at higher altitudes. Predicted values from the model in Table 5.4 are plotted. Parameters were set to 2010 and median time of day.

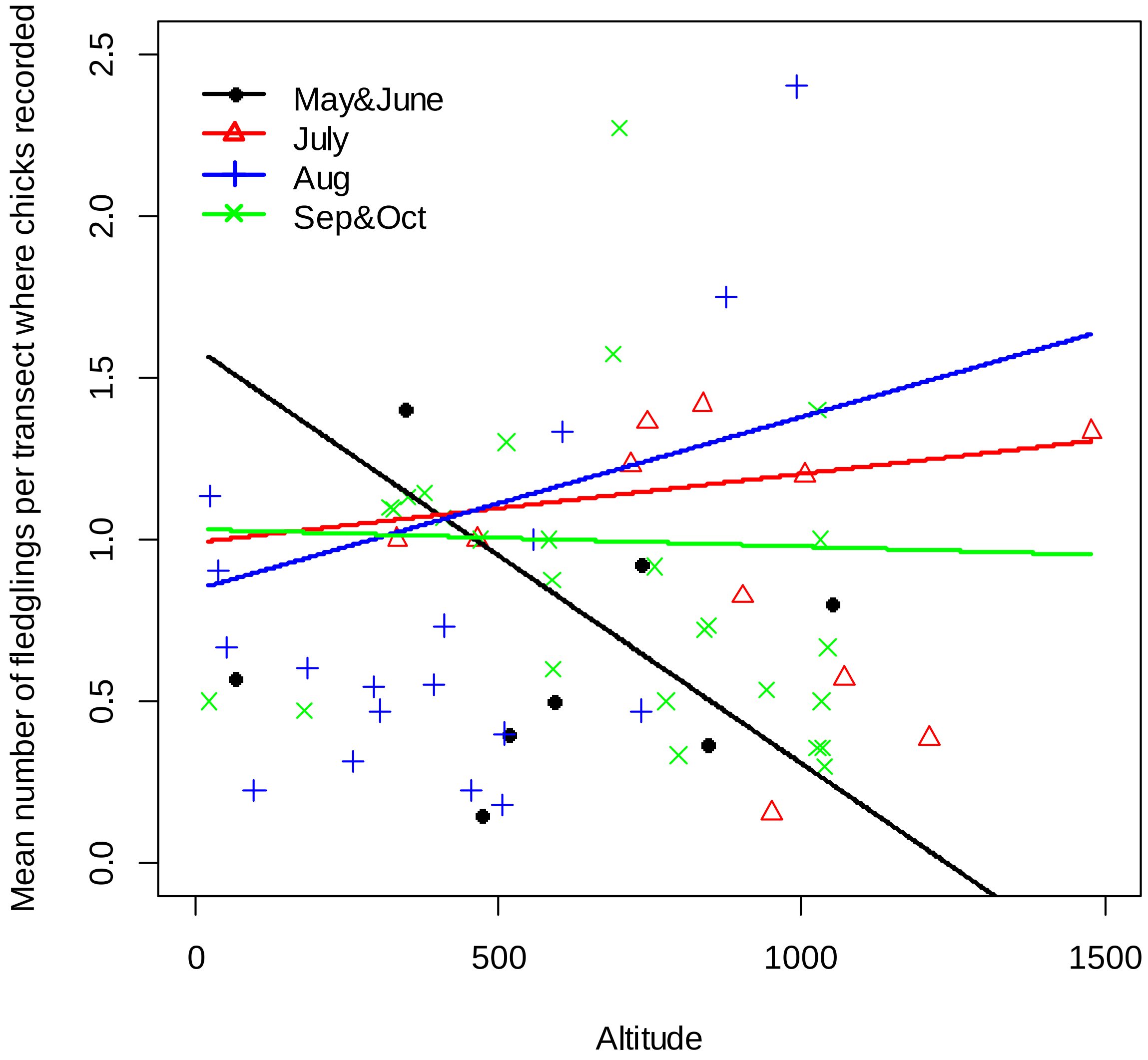

Figure 5.8: The relationship between the number of chicks produced per adult on transects that produced chicks (productivity index) and altitude and how this varied with time during the breeding season. The black line shows productivity with altitude early in the breeding season, the red and blue lines productivity late in the breeding season and the green line “productivity” after the breeding season. Predicted values from the model in Table 5.4 are plotted. Parameters were set to 2010 and median time of day.

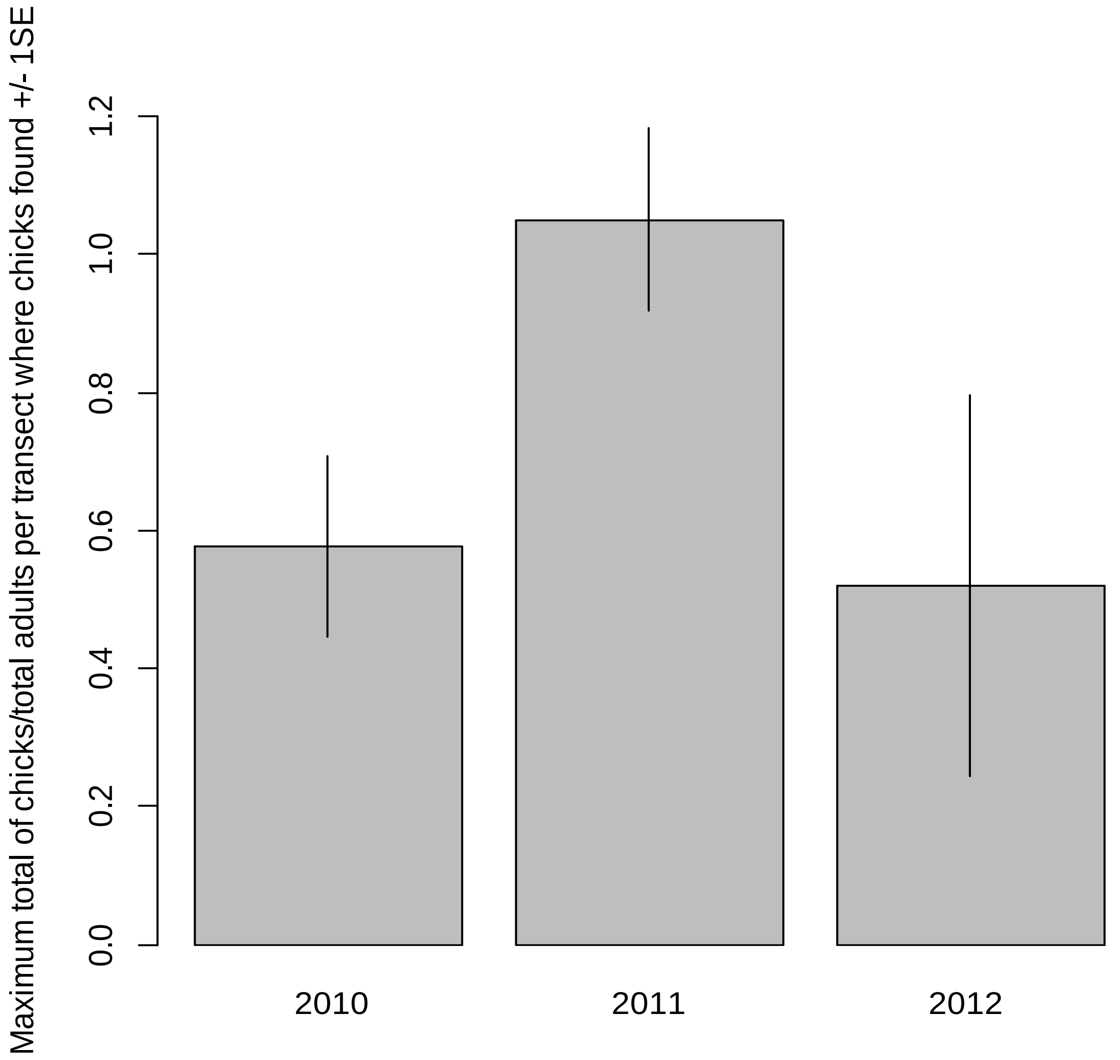

Figure 5.9: The number of chicks produced per adult on transects that produced chicks (productivity index) and how this varied across years. Predicted values from the model in Table 5.4 are plotted. Parameters were set to July 1st, median altitude and median time of day.

5.5 DISCUSSION

Occurrence

The Cyprus Wheatear is an apparently generalist species widely distributed across the island from sea level to the mountains inhabiting a variety of habitats, and most strongly associated with forest habitat and rural areas with traditional mixed agricultural land. Significant differences in the abundance of Cyprus Wheatear between low and high altitudes, along with differences in availability of habitat classes with altitude (not dealt with here in detail although forest occurs most at higher altitudes), suggest that the species is more widely distributed and at higher density at higher altitudes. Although Cyprus Wheatears are more common at higher altitudes, results showed that they were more likely to be present at any point above 200m than not, with a probability of >0.8 above 500m: they are therefore likely to occur everywhere on Cyprus except for maquis and barren areas.

Cyprus Wheatears are already established as a species occurring at high density on Cyprus and in a variety of habitats, found in every stage of vegetation from grassland to woodlands. Flint (2011) found them breeding over an extremely wide habitat range from urban to rural areas. They are encountered less frequently, but still commonly on arable land, in vineyards, on orchards of olive and carob trees, and only rarely in maquis, and completely barren land. They are most common in open forest in the mountains and hills. The island's population consists of *c* 90,000-180,000 pairs (BirdLife International 2004), and the species is the most widely distributed bird across the island (Randler et al. 2010b).

Cyprus Wheatears are likely to be generalists for a number of reasons including the fact that the limited fauna present on islands allows for greater niche space to be occupied without competition, the family traits of wheatears generally allow them great flexibility in feeding, and migrants are likely to be under strong selection to be generalists.

First, depauperate isolated (such as islands and montane areas) faunas generally allow those species that do colonise greater opportunities to expand their niche space, for example Cox *et al.* (2014a), studied White-eyes, genus *Zosterops*, represented by montane and lowland members, in order to assess the roles of niche conservatism versus niche divergence in the diversification and colonization of East Africa’s isolated montane “islands” as well as oceanic islands. They found that niche diversity was particularly large on oceanic islands, and continental diversity was relatively depauperate. Island populations of White-eyes *Zosteropidae* do consistently display a wide feeding niche, and in general, niche expansion and the adoption of generalist foraging behaviour play an important role in insular evolution in passerines (Scott et al. 2003). Similarly, nectar-feeding Hummingbirds and Bananaquit *Coereba flaveola* on the islands of Trinidad and Tobago were used for comparison of diverse and depauperate guilds: where there was reduced competition for nectar there was an increase in niche breadth (Feinsinger et al. 1981, Feinsinger et al. 1982, Feinsinger et al. 1985).

Second, wheatears are insectivores with a wide diet and foraging ability, thus Cyprus Wheatear use aerial sallying to hunt arthropods which can be found on both the ground and in the air; in Cyprus Wheatears males may use high perches more frequently and females may be more likely found on ground or at lower perches. Thus a wide range of arthropod prey must be being taken. Robinson and Holmes (1982), found that such diverse foraging tactics for arthropods in passerines results in the capture of many different kinds of prey. In short Cyprus Wheatears eat all small to medium size insects and these occur in all habitats in Cyprus.

Third, because initial selection of wintering location by juveniles is likely only to occur on a very large scale (see the serial residency hypothesis, Cresswell 2014), habitat generalisation is likely to be under strong selection. Migrant species are very likely always to be generalists because this allows them to be more flexible on migration and when locating a suitable wintering area. Island populations of White-eyes do consistently display a wide feeding niche, whereas niche expansion and the adoption of generalist foraging behaviour play an important role in insular evolution in passerine (Scott et al. 2003).

Significant variation in abundance was found with year in terms of density of singing birds. Although I identified annual variation in the pattern of singing in the intensive study (see Chapter 2), with a steeper decline in the rate of singing through the season in 2011, this was relatively subtle. Furthermore the year with the lowest density of singing birds was 2012. Therefore it seems likely that the lower probability of recording a Cyprus wheatear was not an artefact of variation in singing rate (and indeed the biological basis for any large inter-annual variation in singing rate not being related to density is not clear). It is interesting to note that the year that Cyprus Wheatears were least common (2012), coincided with the lowest survival rate for the preceding winter (see Chapter 3). It is also interesting to note that 2012 followed the year in which the highest productivity was recorded from the point transect data (this chapter), and at least equal productivity to other years in the intensive study (Chapter 4) suggesting that over-winter survival may be more important than productivity in determining the population of Cyprus wheatears (see final discussion chapter).

Phenology

There appeared to be no difference in the timing of breeding with altitude with respect to the onset of breeding or the appearance of chicks: there was no clear evidence for breeding to occur earlier at lower altitudes in contrast to predictions. Generally we might expect the breeding season to be later with increasing altitude because temperatures lapse about 0.5 – 1 degree with every 100m of altitude (Nagle and Cooke 2000) and the onset of breeding in many passerine species has been shown to depend on early season temperature. For example, studies of the European Starling *Sturnus vulgaris* indicated that increase in spring ambient temperature affected the onset of the breeding season, thus during laying in March timing of clutches was highly correlated with elevated temperature (Meijer et al. 1999). Similarly, Porlier *et al.* (2012) studied four Mediterranean populations of Blue Tits, and found earlier onset of breeding in warmer years in all populations with reduced plasticity in the less predictable environment. The reason that no such effects of temperature were found (i.e. altitude as a proxy for this) on the timing of the start of breeding could be for a number of reasons including poor resolution in data so leading to miss subtle effects, little temperature variation over the altitudinal range that was explored, or initial temperatures being favourable for starting breeding independent of altitude.

First, it is possible that the crude nature of the survey methods used here may be obscuring subtle patterns of variation in the timing of breeding. I used singing and appearance of chicks as an indication of timing of breeding. The former does not actually indicate when breeding starts, particularly if it is delayed after territory establishment or during the laying period (see Cresswell and McCleery 2003), although I have already shown a tight relationship between breeding and singing in the intensive study (see Chapter 2). Similarly the appearance of chicks depends on their detectability and there may have been many points where early fledged chicks were overlooked because they are less detectable. Nevertheless the same might be expected across all points regardless of timing, so on average this problem should not affect the estimate of *relative* timing with altitude, even if the actual timing recorded was later than the initial appearance of the chicks.

Second, there may have been little altitudinal variation in spring temperatures with altitude over the study area. This is unlikely to be the case because temperature differences recorded on Cyprus over the range of the study are equivalent to those considered to be significant for phenological change in temperate bird populations elsewhere. Temperature differences were calculated using three Meteorological stations (Meteorological Services, Cyprus) for the diurnal maximum temperature during 1st, 15th and 30th of April at sea level 10 m a.s.l., at 160 m a.s.l. and at 1100 m a.s.l. Maximum temperatures were found to be higher inland by c.1-3°C at Astromeritis village at 160 m a.s.l. than at Larnaka on the coast at 10 m a.s.l.. However, temperatures were lower by about c. 4°C at Agros village which is a mountainous area at 1100 m a.s.l. Temperatures varied significantly between locations in all years during April (data not presented): in April and May there may be a difference in 10 - 15 degrees between the top of Troodos and 200 m.

Third, even though temperature may have varied with altitude, if the temperature even at high altitude exceeds the threshold for the initiation of breeding then the altitudinal gradient will not be important. Many studies have shown that breeding in passerines commences when a certain temperature threshold is reached rather than a specific temperature. Delius (1965), for example, found that female Skylarks *Alauda arvensis*, depend on an individual temperature threshold, reached 4 to 7 days before laying. Great Tits and Pied Flycatchers breed earlier in the spring when the ‘warmth sum’ – where daily temperature exceeds some threshold temperature - is high (Lack 1950, Slagsvold 1976, O'Connor 1977). Temperatures at altitude on Cyprus do however appear to be limiting because evidence was found from the intensive study that onset of breeding varied by 13 days between years at 1800m (near the maximum altitude possible on Cyprus) suggesting that temperatures on Cyprus can limit the onset of breeding at least at higher altitudes. Monthly averages of the daily maximum temperature during April at 1100 m a.s.l. are 20^{o}C and daily minimum temperatures are 9^{o}C (data from Agros station): these are equivalent to many temperate populations which have been shown to be affected by spring temperatures.

Although there was no strong evidence for the timing of the breeding season to vary with altitude, there was some evidence that productivity differed with respect to altitude at different times during the season. Where adults and chicks were both present, the ratio of chicks to adults (as an index of productivity of successful nests) depended significantly on both altitude and season, with more chicks being apparent in May and June at lower altitudes, with higher altitudes catching up in July and August. This suggests that larger single broods were being produced at lower altitude with smaller double broods being produced at higher altitude. This is consistent with the results of the intensive study at NFP of Troodos where cooler conditions allowed second broods (see Chapter 2), and thus suggests that breeding attempts of Cyprus Wheatear are determined by temperatures. Other studies have also shown that the occurrence of double brooding is dependent in the duration of the breeding season (Moller et al. 2010, Townsend et al. 2013, Hussell et al. 2014). The duration of the breeding season is then usually dependent on the availability of food to feed chicks (Dawson 2008, Gruebler and Naef-Daenzer 2008a). This then suggests that the breeding season may be longer at altitude and that any food peaks which coincide with production of chicks are less pronounced and of longer duration at altitude. Further work on what the Cyprus Wheatears are eating and how this varies with altitude, and how the phenology of the prey itself varies with altitude is needed. Nonetheless, temperatures seem likely to affect food availability and consequently the decision whether to raise one or two broods.

Conclusion

Overall, the transect results probably show that altitudinal temperature variation affects the occurrence of double brooding and so the timing of chick production, but not variation in overall seasonal productivity. This suggests that Cyprus Wheatears are already very well adapted to high variation in temperature within and between seasons, changing investment from a larger single brood to two smaller broods as temperature increases, as also shown by the intensive nest-based study at Troodos

(Chapter 2). In Mediterranean climates, even those affected by moderate altitude, temperatures may not limit the onset of breeding as in more northerly temperate areas: the climate is already warm enough for breeding. The climate may then become too warm for breeding as the summer progresses.

Other abiotic factors such as precipitation may be important – whatever factor determines the phenology of the food that the chicks are fed on. However, if a species is already a generalist and able to feed its chicks on a wide variety of invertebrate prey any single abiotic factor may be relatively unimportant. Consequently, global temperature change may have a relatively small effect on a species like the Cyprus Wheatear breeding on a Mediterranean island, unless other abiotic factors such as precipitation change as a consequence. Cyprus already shows a great deal of variation in annual rainfall and, by and large, benign temperatures, making it perhaps more similar to arid tropical environments rather than more northerly European environments. Waters *et al.* (2010), for example argued that at present Cyprus has a semi-arid climate with strong seasonal rainfall patterns, mainly restricted to the winter months and rarely during summer cyclones, and the hot temperatures that characterize the island are typical of arid and tropical zones (Calabrisotto et al. 2013). The island's topography also creates great variation in rainfall and temperature with mean daily values reaching 29°C in summer along the central plain of Mesaoria and the coasts and 22°C in the mountains, whereas precipitation is as high as 1000 mm at the top of the Troodos Mountain and as low as 300 mm on the Mesaoria plain (Fall 2012).

Within this context, flexibility to large variation in annual conditions, including great flexibility in the occurrence of single or multiple broods might be expected in species where rainfall dominates more than temperature. For example, Hau *et al.* (2000), suggested that the insectivorous Spotted Antbirds *Hylophylax n. naevioides*, adjust reproduction to short-term cues such as food availability due to the onset of the rainy season and consequently insect abundance, and experiments showed that food stimuli enhance reproductive readiness in males by significantly increasing gonad size. Similarly, studies of the environmental and endocrine mechanisms that underlie the timing of reproduction in small ground finches from the equatorial arid Galapagos islands, reveal that short-term cues related to rainfall determine flexibility in the regulation of their breeding due to significant seasonal changes in growth of their gonads (Hau 2001), suggesting that the species are opportunistic breeders. The length of the breeding season for arid-zone birds in Australia is a function of annual rainfall and altitude (Wyndham 1986) further showing how rainfall may dominate breeding phenology outside temperate areas.

The missing part in this story is the food supply of the Cyprus wheatears and how this varies with altitude, and how breeding productivity is related to variation in food supply. The present results suggest that Cyprus Wheatears are flexible generalists able to breed successfully under different climates by varying the number and size of broods. This would predict therefore that breeding does not depend on any one particular food peak although if resources are present, are likely to be utilised.

CHAPTER 6. GENERAL DISCUSSION

Migratory bird populations in Europe are declining, due of anthropogenic changes associated with habitat destruction and losses and climate change, threats which affect individuals and populations on both the breeding and wintering grounds. Climate change and habitat loss can have a profound impact on a species' life cycle, which subsequently alters seasonal events such as migration and phenology of breeding (Visser et al. 2004, Carey 2009). Climate change influences bird breeding phenology (Laaksonen et al. 2006), their overall distribution and adaptation which then affect population dynamics, and consequently more or less all biological processes (Wright et al. 2009). Despites many studies that have examined climate change and breeding phenology changes in migratory birds (Crick and Sparks 1999, Stenseth et al. 2002, Cotton 2003, Both et al. 2005), our understanding of migratory bird ecology and the impact of changes on their breeding phenology and population dynamic still has to be improved.

This thesis studied the ecology of Cyprus Wheatears, a medium-distance endemic Palaearctic migrant, exploring their breeding phenology, productivity and reproductive success, their seasonal and annual survival rates and their variation in abundance, phenology and productivity with altitude, in the breeding season, in Cyprus. The findings allow us to draw conclusions about how climate variability may impact their behaviour and overall population size. The main results of the thesis were to discover that Cyprus Wheatears are already very flexible in their response to climatic variation. The results showed that breeding phenology of Cyprus Wheatears at Troodos displayed clear seasonality patterns and varied between years mostly because of inter-annual variation in clutch initiation date at the start of breeding. Furthermore I showed that renesting probability and duration of the fed fledged chick stage varied by year. I documented a highly variable renesting probability, high nestling and very high fledgling survival, resulting in exceptionally high productivity. This has been shown in several other species, for example, the migratory songbird the Black-throated Blue Warbler, showed initiation of breeding earlier in warming springs and thus was more likely to attempt a second brood, hence double-brooding and lay-date were linked to higher fecundity and productivity (Townsend et al. 2013).

My results also indicated a very high survival rate for a small passerine migrant, with a minimum of 77% of males surviving in some years, although females probably suffered greater mortality because only they incubate and they may also have lower overwinter survival than males do. As expected chicks also showed lower survival probability (although chick survival itself was relatively high). I extracted minimum estimates of true survival that were high but varied by sex, age and year. I showed that Cyprus Wheatears are highly site faithful with little dispersal for adults and that dispersal was usually on the scale of only a few hundred meters even for first year birds.

My results also showed strong evidence that Cyprus Wheatears occur commonly in a wide range of habitats in Cyprus with occurrence on all transects. I recorded Cyprus Wheatears occurring at highest densities at greater altitude, but this relationship depended on month of the breeding season. I documented that altitudinal temperature variation probably affects the occurrence of double-brooding and so the timing of chick production, but not the actual timing of onset of breeding.

These results lead to a number of potential general conclusions, although before I can consider these, we must ask the question of how typical Cyprus Wheatears might be. Are they a special island endemic or are they a model species? Having considered the differences, I then consider what general conclusions can be made.

How typical are Cyprus Wheatears?

The Cyprus Wheatear has a restricted distribution – an endemic to Cyprus – but it breeds throughout Cyprus in a wide range of habitat types and altitude, and winters probably over a wide area in East Africa (Sudan and Ethiopia). The species is particularly associated with forest habitats and agriculture especially vineyards and other land that maintains traditional landscape features (e.g. stone walls). The patterns in the breeding behaviour of the Cyprus Wheatear, and the phenology of its breeding, although distinct, have many similarities to other medium and long-distance migrant species. The Cyprus Wheatear is a multi-brooder and breeding onset and number of breeding attempts was documented to respond to temperature gradients. Clutch initiation date depended on nest type and year, with egg stage duration varying with year. Duration of the fed fledged chick stage varied with year and nest type in a way consistent with the many other studies that have shown such effects and that have linked this to variation in food supply, which depends on temperature. The examination of maximum daily temperature revealed fluctuations within and between seasons on the study site and this was reflected in variation in clutch initiation date and subsequently renesting attempts. As with other multi-brooding species (Naef-Daenzer et al. 2001, Gruebler and Naef-Daenzer 2008a, b), the probability that the

Cyprus Wheatear will renest varied with year and declined through the breeding season.

Cyprus Wheatear had a high frequency of second nesting attempts and this resulted in high chick output, which was very likely influenced by food availability being affected by high summer temperatures. Renesting attempts were lowest during 2010, the warmest year of the three years studied, which may indicate that the species responds strongly to climatic fluctuation and subsequently food availability. Nevertheless, despite this variation, there was no negative impact on the overall number of chicks produced and their survival. The overall renesting probability differed between years of the study indicating that both the clutch initiation date and temperature influence the phenology of the breeding of the species, but the overall productivity of chicks per territory (pair), alive one month after fledging, did not vary with year. So although very responsive to climatic variation in phenology, this did not result in variation in productivity: the former is typical, the latter may not be.

Productivity was similar, however, to many aspects of other migrants. Cyprus Wheatears varied in annual productivity output, with a typical clutch size of 5 for first nest, and this declined typically, slightly, with clutch initiation date, but was probably substantially lower for second nests (c. 2 eggs) – again this is fairly typical although the degree of change 5 to 2 is unusual. Predation rates in most migrants – the main influence on productivity - are typically higher during nestling and post-fledging stages. This has been documented by many studies since chicks are more conspicuous and noisy and thus are easily detected by predators, which consequently have lower survival rates compared to the egg stage (Part and Wretenberg 2002). In this study I showed the reverse, daily nest survival was higher during the nestling stage than the egg stage. But nest predation rates were not high even in the egg stage and consistent with other cavity nesters, and nest failure resulted from nest predation in a similar way to other studies, with the main predators likely being birds, reptiles and mammals (Martin and Li 1992, Martin 1993b, Martin et al. 2000b).

The survival rate for Cyprus Wheatears was relatively high in the first month after fledging, compared with other studies that show very low survival rates during the first three weeks after fledging. This may simply be because Troodos lacks Sparrowhawks which specialise in taking small bird fledglings in almost all other areas of Europe (Newton 1986). The annual survival rate in Cyprus Wheatears varied by sex, age and year males had the highest annual survival compared to females and chicks. The lower true survival rate for females may be related to a higher risk of predation during the breeding season because they are the sole incubator: this is similar to almost all other studies that have examined this (Martin 2002, Sillett and Holmes 2002, Low et al. 2010).

Cyprus Wheatears have a very high rate of site fidelity, with dispersal rates being greater for females than for males, but with chicks overall showing the highest dispersal rates. Thus my results resemble other studies that show higher dispersal rates for both females and particularly chicks which must avoid inbreeding (Verhulst et al. 1997, Wheelwright and Mauck 1998). Nevertheless the scale of chick dispersal is probably lower than in other migratory species reflecting the insular nature of the study system (large dispersal distances cannot by definition evolve in an island endemic).

Migratory birds have to time their breeding season so that chicks are reared during the peak of food availability. A species' geographical range and the seasonality it experiences is therefore very important for its productivity: this was true for the Cyprus Wheatear just at a condensed spatial scale. Cyprus Wheatears bred at higher densities at higher altitudes reflecting the correlation of temperature with altitude, suggesting that climatic fluctuation can influence the onset of breeding at least at higher altitudes, which is equivalent to other temperate populations at more northerly latitudes which have been shown to be affected by spring temperatures (Muller et al. 2005, Both and te Marvelde 2007). The abundance of the species throughout the island was strongly associated with altitude and showed evidence that temporal productivity variation reflects seasonality. There was a suggestion that the species may have larger single broods at lower altitude with smaller double broods being produced at higher altitude, for example Sanz (1998) studied variation in laying date, clutch size and number of fledglings in the Great Tit in relation to elevation, and found that laying date increased with elevation. In addition Bears *et al.* (2009) found that with an increase in breeding elevation, Dark-eyed Juncos *Junco hyemalis* delayed reproduction and reduced the duration of their reproductive period. Such variation is typical across species, or across larger spatial scales within species in Europe (Fargallo 2004, Pimentel and Nilsson 2007), but may be unusual in the Cyprus Wheatear in that such large variation exists here within a single species within a small spatial area. Paradoxically this may make the Cyprus Wheatear a particularly good model, resembling other migrant species. The frequency of double brooding and clutch size may vary over the scale of just a few kilometres.

Higher nest predation rates in egg stage – unusual

Cyprus Wheatears make their nests in narrow crevices or in tunnels under or between rocks which must provide a large degree of protection from nest predators. Nest predation in hole-nesting species is usually higher during the nestling stage (Martin 1993b). However my results indicated higher nest predation in the egg stage, which may reflect the type of predator and nest concealment (Cresswell 1997). One possible explanation for my results is that egg predation may arise from a lizard predator – that can effectively eat small eggs but then does not preferentially target chicks because they do not hunt by sight or sound, or find chicks too large to eat. Further work with nest cameras is needed to confirm this hypothesis: for example, miniature video cameras deployed at 69 nests of 10 passerine species in North America revealed that eggs or nestlings were destroyed by mice, ground squirrels, weasel, badgers, canids, deer, cowbirds and hawks - both nocturnal and diurnal predators - with predation risk increasing with nestling age from 0 to 8 days (Pietz and Granfors 2000). If this hypothesis is correct then seasonality and warmer springs may affect the pattern of nest predation via its effects on lizard activity and so climate change may have an impact in this way. Synchronisation of breeding outwith the main activity times of predators is logical to maximise fitness and is perhaps much more of a problem for birds in tropical areas where climatic synchronisation may be relatively less important.

Very high post fledging survival – unusual

The highly productive, obviously high quality habitat of the Troodos Mountains also engendered very high post-fledging survival for the Cyprus Wheatear. A very likely explanation for this unexpected result (at least in the context of almost all other studies where survival post-fledging is very low) is the already mentioned absence of aerial predators such as Sparrowhawks which are extremely rare breeders on Cyprus. There was also little evidence of other avian, mammalian or reptile predation on chicks from hatching onwards: but predators are present and Cyprus Wheatears are abundant so this lack of predation generally is odd. After about the third week after fledging juveniles behave much as adults, but in the intervening period they are slow, uncoordinated and obvious – again the lack of predators on this vulnerable stage seems odd. One other relevant observation is that chicks were able to feed on *Berberis cretica* fruits which may well lead to higher survival rates even during the hot late summer period.

High survival of adults and chicks – might be unusual

Cyprus Wheatears showed very high survival rates during the breeding season which probably reflect the high quality habitat at Troodos where the species was found in particularly high densities. The high survival rates must reflect seasonally very abundant food (this must be so because of the very high densities still resulting in very high productivity) and low predation. Only females suffered any kind of mortality during the breeding season which paralleled the risk of nest failure due to predation during the incubation stage (Slagsvold and Dale 1996). Results from the intensive study indicated that most losses occurred overwinter, with apparent overwinter survival rates being very similar to annual rates. Males had the highest true minimum annual survival compared to females which were very similar to chicks. The results indicate a very high survival rate for a small passerine migrant, although they probably vary sufficiently between years to affect annual population dynamics profoundly. If females suffer greater mortality (Kessel 1957) because only they incubate, and may also have lower overwinter survival compared to males, then the sex ratio at birth may be female biased to compensate. Females may, however, have longer range dispersal than measured in our study, particularly if they respond to their mates not returning by moving territories, leading to an underestimate of their true survival (Greenwood and Harvey 1982, Clarke et al. 1997). Whether the high survival rates in this study are unusual is hard to say.

Most studies have very low site fidelity (Shitikov et al. 2015) so cannot approach true survival as was estimated in this system, so comparisons have little value. We do know however that survival for migrants can be both high on the breeding and wintering grounds, that migration itself leads to lower survival and that population dynamics of migrant populations are affected by the length of their migration. Therefore high survival in Cyprus Wheatears may reflect their relatively short distance migration: from Cyprus to Southern Sudan represents a flight distance of about 2,400 km, which it may be a straightforward single continuous flight for a migrant of the size of a Cyprus Wheatear (based on unpublished geolocator data from Emma Blackburn’s PhD running concurrently with mine on Whinchats *Saxicola rubetra*).

High survival rates for chicks (after the post-fledging period) may then also reflect the relatively short migration distance for Cyprus Wheatears (Perez-Tris and Telleria 2002, Heldbjerg and Fox 2008). The “multiple-jeopardy” hypothesis put forward by Newton (2008) states that migrants are likely to be more vulnerable to habitat change because they rely on a series of interconnected sites, and if any one fails, then the chain is broken, leading to reduced survival. Juvenile birds will be particularly susceptible to this because they are likely to migrate in shorter stages on their first migration (juveniles universally seem to take longer to reach the wintering grounds suggesting at least their exposure to multiple-jeopardy is increased relative to adults). Juvenile Cyprus Wheatears may be able to make the migration to Sudan in a single flight as adults do, or with only a single stop over for many individuals, so reducing the survival differential between adults and juveniles and leading to a much higher juvenile survival relative to other longer distance “long-distance” migrants. We know that survival for juveniles when they reach the wintering ground is similar to adults and that survival rates between first years and adults are the same after the first migration from unpublished data from Whinchats (again Emma Blackburn’s PhD thesis on Whinchats, and several neotropical studies already cited). Therefore this hypothesis seems very likely: juvenile Cyprus Wheatears reach their wintering ground, as do adults, by a single flight, leading to high survival. This hypothesis will hopefully be tested with geolocators in future years.

Condition-dependent variation in probability of second broods – unusual in a temperate context

The renesting probability after failure of first nests was high for Cyprus Wheatear: this is typical and a fairly trivial result (Morton 2002, Kershner et al. 2004). If a species is to have any fitness it must breed, nest predation rates are high in passerines and they deal with this by renesting as long as the breeding season is long enough. Of much greater interest is the variability in renesting probability after success because then trade-offs develop between survival and care of the first brood, the adults own survival and maintenance and the timing of migration and moult (Hemborg and Lundberg 1998). Renesting probability after the first successful nest was highly variable within and between years, suggesting a great flexibility in response to climatic cues. Clutch initiation date and consequently food availability are likely to be the determinants of the occurrence of double brooding (Verboven and Verhulst 1996, Nagy and Holmes 2005b). Such flexibility may be unusual for northern temperate migrants but is probably not unusual from a tropical bird perspective – in many respects the life history of Cyprus Wheatears could be considered to resemble much more, a tropical species, just one that lives in Southern Europe and migrates. Although, the variation in probability of second broods may depend on trade-offs of first brood survival, fitness condition of adults, and habitat quality, a major determinant for the Cyprus Wheatear seems to be temperature fluctuations. This has been shown in other species also. For example, spring temperatures in temperate regions have increased over the past two decades and 24 populations of tits *Parus* spp. from six European countries have shown a phenological response to large-scale changes in spring temperature across their range and also a link between rising temperature and the probability of second broods (Visser et al. 2003). The results showed that larger single broods were being produced at lower altitude with smaller double broods being produced at higher altitude are particularly suggestive that this is determined by climatic conditions and consequently food availability. The evidence from the transects is however less good compared to that from the intensive study and further work is needed, at the individual nest level across the altitudinal gradient to confirm this.

Can Cyprus Wheatears be used as any type of model species?

Although Cyprus Wheatears show some extreme values of traits (like high productivity and survival) their values arise because of similar processes operating on all passerine migrants. And indeed, the high productivity combined with high survival rates may mean that the population of Cyprus Wheatears at Troodos can be used particularly as a model species for studying migrant passerines. The logic of this is that studies of productivity and survival are possible – if 100 juvenile whinchats from Russia are fitted with geolocators, only 1 or 2 birds might return to the same breeding area to be recovered, whereas we might expect up to 50 juvenile Cyprus Wheatears. Similarly if we study nesting behaviour and productivity, stochastic events of less interest, such as nest predation are at sufficiently low rates that they do not dominate productivity or phenology. The Cyprus Wheatear is also an apparently generalist species widely distributed across the island from sea level to the mountains inhabiting a variety of habitats so many aspects of its ecology can probably be compared realistically with a wide variety of other migrant species. The species also shows that migration itself does not rule out high survival and high productivity, and indeed high survival itself does not preclude high productivity: it has a potentially variable suite of life-history trade-offs again making comparison to a wide variety of other migrant species reasonable. And perhaps best of all Cyprus Wheatears, as shown by this study, are relatively easy to study being very common and accessible. Cyprus Wheatears may therefore provide a tractable and excellent model study system in which to study the population dynamics of a migrant.

Final Conclusions

Having considered whether Cyprus Wheatears are particularly unusual, I now consider the general conclusions – first specific to Cyprus Wheatears and their population dynamics in the face of environmental variation and then for migrants generally.

What are the population dynamics of Cyprus wheatears?

The population of Cyprus Wheatears at Troodos was likely to be a source population due to its high level of productivity, survival and densities, suggesting that populations at higher altitude may be source populations generally. This then implies that lower altitude areas must be sink areas otherwise the island would soon be overrun with Cyprus wheatears (although to some extent it is!). Consider a hypothetical population of 50 pairs of Cyprus Wheatears in the National Forest Park (NFP) of Troodos. With an average minimum true survival of an adult (all years and both sexes = 0.56), the average minimum true survival of a chick (all years = 0.49) and average productivity (all years = 4.0 chicks) then the population in the following year will be 77 pairs, or an increase in the population of 54%. In other words the population will double every two years on average! Troodos may be (must be) particularly productive. Set against this fairly astounding rate of population increase is the fact that population levels across Cyprus apparently vary with year – 2012 in particular was noted by other observers on Cyprus as having lower densities of Cyprus Wheatears as was observed in the transect data. This suggests that there may well be periodic much lower survival years, or productivity years particularly at lower altitudes on the island. The results showed that there are indications that most losses of Cyprus Wheatears occurred overwinter, with apparent overwinter survival rates being very similar to annual rates. Variable overwinter survival rates therefore are likely to have major implications for Cyprus Wheatears and indeed for the population dynamics of Palearctic migrants wintering in Africa. Although survival rate for a Cyprus Wheatear was high it also varied annually and probably affected by environmental factors mainly along the migration route and/or at non-breeding ground, with consequently strongly annual effects on population dynamics through mortality or carry over effects. Further work is needed at lower altitude sites at the level of detail employed in the NFP of Troodos and further years of survival data would be particularly useful.

Key to a better understanding of the population dynamics of Cyprus Wheatears will be productivity variation and perhaps survival of chicks post fledging at lower altitudes. Although overwinter survival varies between years and was much lower in one year, the population at Troodos still broke even. Survival data for 2014 (collected too late for the thesis but also very high and most similar to 2010 values) adds to the suggestion that high survival is typical for this population. We know that connectivity is likely to operate at a very large scale (>1000 km) in almost all passerine migrants (see Cresswell 2014) so therefore winter survival is unlikely to be different for Troodos birds than for those that bred 40 km away at lower altitude. Therefore breeding productivity or post-fledging survival must largely determine the population dynamics of the Cyprus Wheatear.

Cyprus Wheatears are insectivores with a wide diet and foraging ability and are established in a wide variety of habitats. Therefore it seems likely that variation in factors such as extreme summer heat shortening the breeding season and/or nest predation rate, rather than habitat quality per se might account for differences in productivity with altitude.

Overall, the transect results probably show that altitudinal temperature variation affects the occurrence of double brooding and so the timing of chick production, but not variation in overall seasonal productivity per pair. This suggest that Cyprus Wheatears are already very well adapted to high variation in temperature within and between seasons, changing investment from a larger single brood to two smaller broods as temperature increases. Productivity variation with altitude suggests that the species' populations in the lowlands may be sink populations and at higher altitudes, sources. Population growth and limitations may apply for high quality habitats and in poorer habitats. However I found a relatively small confounding effect of habitat on Cyprus Wheatear productivity and occurrence. Hence populations are probably not declining but are annually variable. Populations at higher altitudes can be characterized as source populations and therefore crucial. Thus factors that may change its status globally are habitat destruction/degradation/losses and climate change at higher altitude. These factors have been identified as the biggest threat for species such as migrants that are particularly vulnerable to the impact of such changes. It is perhaps noteworthy that Cyprus has undergone massive development in the last few decades (Italos et al. 2014), but most of this is in the lowlands: if such development had been preferentially targeted on upland areas then perhaps the conservation status of the Cyprus Wheatear would be more questionable.

How are Cyprus wheatears affected by climate variation and so change?

Overall, the transect results probably show that altitudinal temperature variation affects the occurrence of double brooding and so the timing of chick production, but not variation in overall seasonal productivity. This suggests that Cyprus Wheatears are already very well adapted to high variation in temperature within and between seasons, changing investment from a larger single brood to two smaller broods as temperature increases, as also shown by the intensive nest-based study at Troodos. In Mediterranean climates, even those affected by moderate altitude, temperatures may not limit the onset of breeding as in more northerly temperate areas: the climate is already warm enough for breeding. Temperatures at sea level in March, however, may exceed those at Troodos in early May. Therefore, that Cyprus Wheatears do not start breeding earlier at lower altitudes seems strange: intensive nesting studies at low altitude are again needed. The climate may then become too warm for breeding as the summer progresses. This then suggests that the breeding season may be longer at altitude and that any food peaks which coincide with production of chicks are less pronounced and of longer duration at altitude. Rainfall in the island also tends to be associated with altitude and this in turn could influence wheatears availability of food.

A key issue is probably the degree to which extreme summer temperatures and rainfall limit breeding in the Cyprus wheatear rather than earlier warm temperatures. For example, Ockendon *et al.* (2013), investigated the impact of wintering ground precipitation and breeding ground temperature of 19 migratory birds and found that arid zone precipitation was significantly correlated with laying date. Again this comes back to requiring information on what food is required for breeding. It seems most likely, considering the very large productivity and source populations at altitude, that there must be some limitation, probably by summer drought and heat, to the duration of the breeding season at lower altitude. Nestling and post-fledging mortality might be expected to be high for later broods at lower altitudes. If this is the case then future climate change that increases summer temperatures (and probably reduces rainfall) may then reduce the altitudinal range of the source populations (i.e. still in favourable long breeding season conditions). Consequently the population dynamics of the Cyprus Wheatear will be affected. A transect of nesting populations from sea level to Troodos to monitor productivity would tell us the point at which sink switches to source and so would inform us of whether future climate change would reduce Cyprus Wheatear populations. If the switch was at 400m for example then there would be more resilience than if it was at 1000m. The transect data only give indirect evidence for this, but Figure 5.6 in Chapter 5 might suggest that differences in productivity related to altitude conservatively become more pronounced below about 400m. Nevertheless, with an average lapse rate with altitude of about 0.5 degrees per 100m, then a local average temperature change of two degrees for example would raise the shift point to 800m, greatly reducing the area of Cyprus with source populations. There is a need for longer term studies to test these hypotheses with more than three (N=3) years of data. In particular I would predict that in early hot years there will be early initiation of breeding, extended post-fledging care and a low proportion of second broods, with productivity shifting from a net decrease to a net increase at higher altitudes.

Consequently, global temperature change may have an effect on a species like the Cyprus Wheatear breeding on a Mediterranean island, even when altitude acts as a refuge. Other abiotic factors such as precipitation may also change as a consequence with unknown effects on food supply to either strengthen or weaken effects. The species, however, already shows great flexibility to the large variation in annual and altitudinal conditions, including great flexibility in the occurrence of single or multiple broods as perhaps might be expected in species where rainfall dominates more than temperature and so a species is pre-adapted to environmental change. Cyprus already shows a great deal of variation in annual rainfall and, by and large, benign temperatures, making it perhaps more similar to arid tropical environments rather than more northerly European environments. The carrying capacity of the island for Cyprus Wheatears may decrease with increasing global temperatures, although the exact effect on density is harder to predict because of the sink-source dynamics. If higher altitude sites export 54% of their populations to the lowlands, then Cyprus wheatears may remain common there.

What are the general implications for other migrant species in the face of climate change?

Climate change has a significant influence on many organisms at all trophic levels, and for birds there is much evidence to suggest a shift in their breeding phenology and mismatch with their food resources (Both and te Marvelde 2007, Jones and Cresswell 2010, Dunn and Møller 2014). Cyprus Wheatears arrive in March but do not start breeding until mid-April even at lower altitudes so the potential for phenological mismatch may be low. Other more northerly breeding species may be in a similar situation, arriving before breeding can actually commence. Phenology mismatch has been widely trumpeted as a potential cause of Palearctic migrant declines, but outside a few populations (particularly Pied Flycatcher in Western Europe, e.g. (Both et al. 2010) more evidence is needed to determine whether this is a fundamental problem. Climate change that reduces food peaks or that shortens the breeding season, or that affects post-fledging survival, or survival during first migration is perhaps more worrying. Climate change effects may be more subtle, for example warmer springs may make reptiles active earlier and increase nest predation rates. Thus climate change may profoundly affect the population dynamics of a migrant bird species in any number of ways. There are many ways that breeding can be varied in timing and effort within a season, and coupled with high overwinter survival of migrants, over several years. Migrants are by nature flexible generalists that evolved to exploit climate change at the end of the last ice age (Moussus et al. 2011) and many potential solutions involving life history traits at all stages might be expected.

The Cyprus Wheatear case study presented here highlights the likelihood that each species will respond differently. The Cyprus wheatear is a flexible multi-brooded migrant and my findings indicate that the species can maintain a high productivity, maximising the number of offspring produced within a season, by changing number of broods they produce and the duration of their post-fledging care period. For Cyprus Wheatears on Troodos – everything is apparently working very well for the species even with a variable climate. The exact nature of the sink/source dynamics across the island and with altitude remain to be determined, but at the moment the species seems resilient and well adapted to climate variability and perhaps future change.

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APPENDICES

Figure E. National Forest Park of Troodos Mountain (Intensive study site) - Cyprus Wheatears (*Oenanthe cypriaca*) – top left adult female, top right adult male and middle right juvenile – bottom study site.

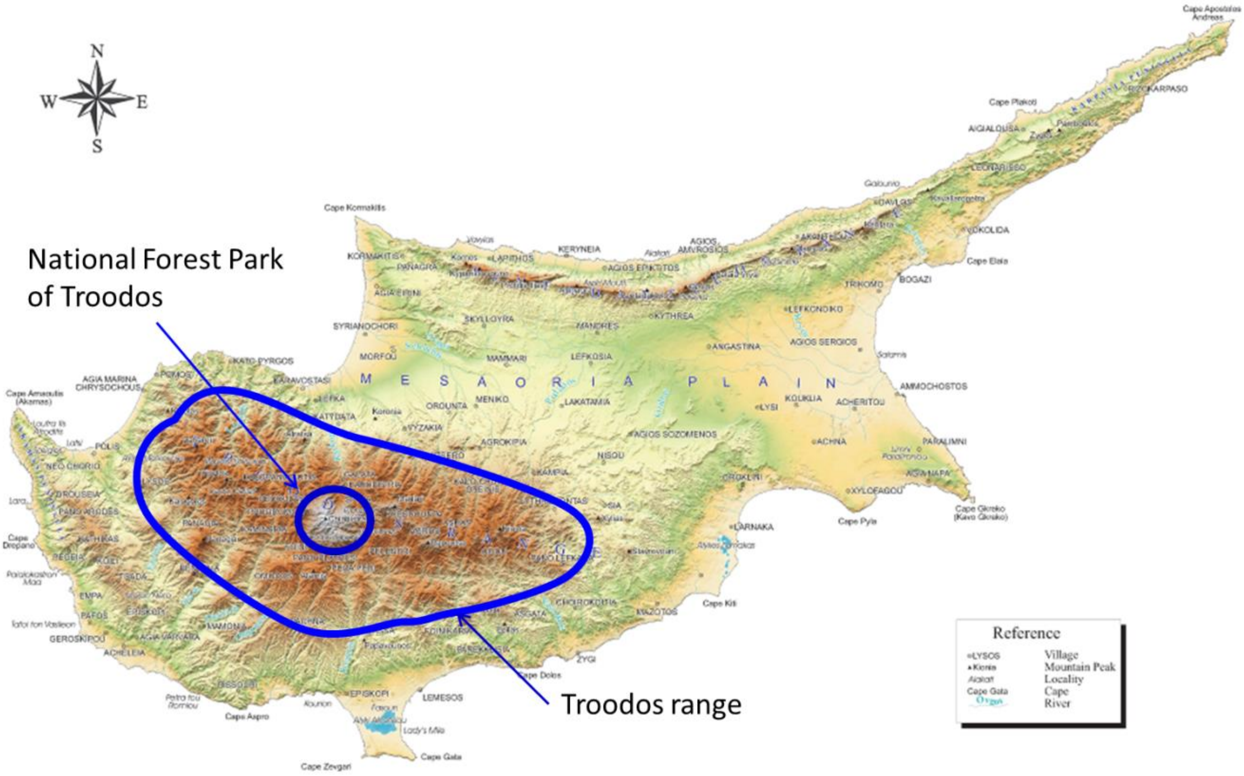

Figure F: The NFP of Troodos covers an area of 9,029 ha. The main habitats that characterize the study area are those of the endemic *Pinus nigra* subsp. pallasiana forest (Black Pine zone which starts from 1400 m and reaches up to 1952 m), the Juniper woodland *Juniperus foetidissima* (Stinking Juniper) and Serpentinophilous grasslands that are distributed at the highest parts and that occur in openings of the black pine forest in the form of small, scattered patches. The understorey of Black Pine consists of Golden Oak *Quercus alnifolia*, Prickly Juniper *Juniperus oxycedrus*, Stinking Juniper *Juniperus foetidissima*, Whitebeam *Sorbus aria* subsp. *cretica*, Cretan Berberry *Berberis cretica*, Greek Strawberry Tree *Arbutus andrachne*, Chionistra Rose *Rosa chionistrae*, Dog Rose *Rosa canina*, *Cotoneaster racemiflorus* var. *nummularius* etc.

Table A: Territories with ringed individuals during 2010 (UF stands for unringed female and UM for unringed male).

Sex	Terr. No.	Ring Comb.	Terr. No.	Ring Comb.
Male	1	UM	24	WOWR
Female	1	WRWY	24	WNWR
Male	2	YY	25	WYWN
Female	2	UF	25	UF
Male	3	UM	26	BWRW
Female	3	YR	26	RWYW
Male	4	WNWY	27	YWRW
Female	4	UF	27	WBWO
Male	5	YB	28	UM
Female	5	UF	28	OWOW
Male	6	WNWO	29	BWYW
Female	6	UF	29	UF
Male	8	WYWB	30	NWYW
Female	8	UF	30	UF
Male	9	WYWO	31	RWOW
Female	9	UF	31	RWBW
Male	10	UM	32	RWNW
Female	10	UF	32	NWRW
Male	11	WOWY	33	WBWN
Female	11	UF	33	WNWN
Male	12	UM	34	UM
Female	12	BWOW	34	UF
Male	13	UM	35	OWNW
Female	13	WBWY	35	OWBW
Male	14	WOWN	36	YOWR
Female	14	UF	36	UF
Male	15	UM	37	YOWB
Female	15	YWNW	37	UF
Male	16	OWYW	38	OWRW
Female	16	UF	38	UF
Male	17	WRWR	39	UM
Female	17	YYWY	39	YRWB
Male	18	WRWB	40	UM
Female	18	UF	40	UF
Male	19	WBWR	41	YWBW
Female	19	WRWO	41	UF
Male	20	WOWB	42	YWOW
Female	20	UF	42	UF
Male	21	WOWO	43	UM
Female	21	UF	43	YWYW
Male	22	WRWN	44	RWRW
Female	22	UF	44	UF
Male	23	WBWB	45	UM
Female	23	UF	45	UF

Table B: Territories with ringed individuals during 2011(UF stands for unringed female and UM for unringed male).

Sex	Terr. No.	Ring Comb.	Terr. No.	Ring Comb.	Terr. No.	Ring Comb.	Terr. No.	Ring Comb.
Male	1	WBYB	24	WOWR	56	NYOY	72	BYNW
Female	1	BWBY	24	WNWR	56	BYRY	72	UF
Male	2	UM	29	WBWB	57	RYBY	73	WRYR
Female	2	BWNW	29	OYBY	57	NYRY	73	UF
Male	3	OWRY	30	BYOY	58	BWOY	74	OYOY
Female	3	OWOY	30	UF	58	BWNY	74	UF
Male	5	YB	31	RWOW	59	YBYB	75	RYYY
Female	5	BYYY	31	RWBW	59	YBWY	75	UF
Male	8	WYWB	35	OWNW	60	RWOY	76	WNYN
Female	8	NWOY	35	OWBW	60	RWNY	76	WOYN
Male	9	NYRW	36	YOWR	61	RYNW	77	RYRY
Female	9	WRYO	36	RYOY	61	RYBW	77	WNYY
Male	10	BYBW	39	BYYW	62	WBYN	79	WRYN
Female	10	UF	39	YRWB	62	RWYY	79	UF
Male	12	WOWY	40	UM	63	OYNW	80	WYYB
Female	12	BWOW	40	OYRY	63	RWBY	80	UF
Male	13	UM	41	YWBW	64	OWYW	81	PWOW
Female	13	WBWY	41	UF	64	BWYY	81	UF
Male	14	NYOW	43	WRYB	65	OWYY	82	WYYR
Female	14	YBWY	43	RYOW	65	OWBY	82	OYYW
Male	15	NYYY	44	UM	66	OYBW	83	UM
Female	15	YWNW	44	BYRW	66	UF	83	BYBY
Male	17	WRWR	51	RYNY	67	WBYY	84	NWRW
Female	17	YYWY	51	UF	67	UF	84	UF
Male	19	WOWO	52	WBYO	68	NYNY	86	NWOW
Female	19	NWNW	52	UF	68	WOYB	86	OWNY
Male	20	WOWB	53	WBYR	69	WOYR		
Female	20	NYYW	53	RYOW	69	UF		
Male	22	BWRY	54	NYNW	70	BYOW		
Female	22	BWRY	54	BWBW	70	OYRW		
Male	23	WBWR	55	OYNY	71	UF		
Female	23	UF	55	OYOW	71	YOYN		

Table C: Territories with ringed individuals during 2012 (UF stands for unringed female and UM for unringed male). X frond of the combination stands for missing ring.

Sex	Terr. No.	Ring Comb.	Terr. No.	Ring Comb.	Terr. No.	Ring Comb.
Male	1	BWBY	24	WYNY	45	OYNY
Female	1	BROW	24	UF	45	UF
Male	3	WBYO	25	WBWB	46	WOYY
Female	3	RONW	25	UF	46	WNYY
Male	4	RYNY	26	BNRR	47	NYOY
Female	4	WBYR	26	UF	47	BWNW
Male	5	OYNW	27	UM	48	OYOY
Female	5	BROO	27	BNRW	48	UF
Male	6	BYYY	28	OYNY	49	OYYY
Female	6	UF	28	UF	49	UF
Male	7	BNNO	29	WBYY	50	ROOW
Female	7	BNBN	29	UF	50	OYWY
Male	9	OWRY	30	RWYY	51	UM
Female	9	OWOY	30	ORBW	51	YRWY
Male	10	YB	31	OWNW		
Female	10	BYYY	31	RORW		
Male	11	WYWB	32	YWBW		
Female	11	BNNW	32	UF		
Male	12	BNOW	33	OOOW		
Female	12	UF	33	OWOY		
Male	13	BOOW	34	YBWR		
Female	13	BORR	34	OYRY		
Male	14	BOBW	35	OWYY		
Female	14	UF	35	UF		
Male	15	UM	36	XWWB		
Female	15	RYOY	36	UF		
Male	16	WOWY	37	WRYR		
Female	16	YYWY	37	BORW		
Male	17	OWYW	38	WYYR		
Female	17	BWYY	38	UF		
Male	18	RYRY	39	YBYB		
Female	18	NORY	39	UF		
Male	19	UM	40	RWOY		
Female	19	BBNB	40	BYRY		
Male	20	PWOW	41	NORW		
Female	20	BONW	41	UF		
Male	21	ONWB	42	UM		
Female	21	BONO	42	BOBN		
Male	22	UM	43	UM		
Female	22	UF	43	ROWW		
Male	23	BNWO	44	BOWR		
Female	23	BNWR	44	UF		