DETERMINANTS OF VARIATION IN PRODUCTIVITY, ADULT SURVIVAL AND RECRUITMENT IN A DECLINING MIGRANT BIRD: THE WHINCHAT (*SAXICOLA RUBETRA*)

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Declaration

I declare that the work presented in this thesis is my own, except where acknowledged, and has not been submitted elsewhere for the award of a degree of Doctor of Philosophy.

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Abstract

Populations of many species of Afro-Palearctic migrant birds, including the Whinchat (*Saxicola rubetra*), have shown severe declines over the last few decades. Habitat change on the breeding grounds, especially agricultural intensification, is thought to be the main driver of the decline in Whinchats. However, recent evidence also suggests that the decline may have a common source, such as low over-winter survival, which affects the whole UK population. To better understand the declines, this study investigated the key demographic parameters driving the breeding Whinchat population change on Salisbury Plain, UK, which is an area of agriculturally unimproved grassland where Whinchats are still relatively common.

Territory settlement and nesting attempts of colour-ringed individual Whinchats were monitored intensively during 2012-2014. Pairs were significantly more likely to breed in sheltered valleys with long, grassy, structurally diverse vegetation and a high density of tussocks. Territories with an abundance of perches, for use in foraging, were also preferred. The first occupied territories, by returning birds in spring, tended to have higher invertebrate availability, and the order of territory occupancy was positively correlated between years, which suggests that territory quality was consistently perceived. Nestling starvation was rare because food availability did not limit reproductive output. Neither did the availability of suitable breeding habitat apparently limit the population, but nest productivity was lower than expected, mainly because of a high rate of nest failure due to nocturnal predators. Adult apparent survival was high relative to other open-nesting passerine migrants; however, the survival and recruitment of Whinchats in their first breeding year was low. This low apparent survival could partly be explained by natal dispersal, which was greater than breeding dispersal. From the reproductive output, survival and recruitment quantified in this study, it is apparent that the Salisbury Plain population is not currently self-sustaining.

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An adult male Whinchat in flight

1.1 Understanding population change

The number of individuals within a population is determined by the balance between reproduction, mortality, immigration and emigration (the intrinsic features), all of which may be influenced by a wide range of external factors such as climate, habitat, predation, food availability, disease and competition (Newton 1998). By quantifying these environmental variables along with the intrinsic features, it is possible to quantify the relative impact of such factors on population change (Caswell 2001; Robinson *et al.* 2004; Fletcher *et al*. 2006; Wright *et al*. 2009; Sim *et al.* 2011; Hastings & Gross 2012; Grüebler *et al.* 2014).

The limitation effect of external factors may differ in impact depending on the density of a population (density dependent) due to interactions within or between species; or may have the same impact regardless of population density (density independent) (Newton 1998). For example, common density dependent limiting factors include availability of food and suitable nesting habitat, whereas density independent effects include severe weather events. Generally, density dependent factors have a stabilising effect on populations whereas density independent effects have a destabilising impact, causing populations to fluctuate in an unpredictable manner (Newton 1998). To separate the relative impact of external factors on a population it is necessary to know the extent of density dependent and density independent effects in all areas the population inhabits: the ultimate limiting factor on population size occurs in whichever area the '*per capita* effects' on survival and productivity are greatest (Newton 2004a, 2008). As the causes of a long-term population trend may differ from causes of stochastic yearly variation, it is also important to separate these factors where possible (Newton 1998, 2004a, 2008, Jenouvrier *et al.* 2005; Robinson *et al*. 2004; Coulson *et al.* 2005; Krüger 2007; Wright *et al.* 2009). Information on the key demographic parameters and potential limiting factors can be collected to determine the most vulnerable life-history phase and the limiting factors acting on a particular population (Robinson *et al.* 2004; Fletcher *et al*. 2006; Wright *et al.* 2009; Caswell 2001; Calvert *et al*. 2009; Sim *et al.* 2011; Hastings & Gross 2012; Grüebler *et al.* 2014). Population trends and limiting factors may vary across a species range (e.g. Morrison *et al*. 2010), but by comparing and contrasting environmental factors between populations, and identifying which demographic parameters are most influential to population change, it is possible to improve our overall understanding of a species' population dynamics. Furthermore, this approach enables us to gain insights into factors that may be affecting declining populations with similar life-histories, thereby applying the acquired knowledge more widely for more effective conservation management (Martin *et al.* 2007; Bolger *et al.* 2008; Robinson *et al.* 2008; Calvert *et al.* 2009).

1.2 Population change in migrants

Migration is a taxonomically widespread phenomenon where animal populations make geographical movements to track resources. In birds, migration is generally the annual seasonal movement of populations between breeding and non-breeding grounds (Berthold 2001). Migrants may be ‘obligate’, where they undertake approximately similar seasonal movements each year, between breeding and non-breeding areas, or ‘facultative’, where migration distance and timing is variable, and only occurs if conditions are unfavourable (Newton 2008, 2011). Migratory distances vary with some species travelling hundreds of thousands of kilometres between continents (e.g. Arctic Terns), whereas others may only travel a couple of thousand kilometres within a continent (e.g. Blackcap) (Berthold *et al.* 1992; Newton 2008). Around 126 bird species are Afro-Palearctic migrants (Birdlife International 2004; Vickery *et al.* 2014). By definition, Afro-Palearctic migrant species move between breeding grounds in the Palearctic region and non-breeding grounds in Sub-Saharan Africa (Moreau 1972; Newton 2004a, 2008).

Over the last 30 years, long-distance Afro-Palearctic migrants as a group have shown severe declines in Europe compared to mean trends of closely related, sedentary and short-distance migrants (Berthold *et al.* 1998; Sanderson *et al.* 2006; Newton 2004a, 2008; Heldbjerg & Fox 2008; van Turnhout *et al.* 2010). This suggests a population limiting effect that is acting on migrants and has led to them increasingly becoming a subject of scientific and political agendas (Vickery *et al.* 2014). Under the Convention on the Conservation of Migratory Species of Wild Animals (CMS), the UK and many other European countries have an obligation to conserve migratory species (UNEP/CMS 2014). To achieve this objective effectively and efficiently, it is necessary to understand the factors causing the decline of migrant birds in detail and how they interact with the migrants' population demographics to exert their effect (Sanderson *et al.* 2006; Calvert *et al.* 2009; Vickery *et al.* 2014; Grüebler *et al.* 2014).

Interactions between different limiting factors are often complex, interlinked and may change over time (Newton 1998, 2004a, 2008). With migrants, there is the added complication that individuals spend a significant portion of their lives in several different geographical areas: breeding, stopover and non-breeding sites. This greatly limits the opportunity for year-round monitoring and makes it difficult to determine where limiting factors operate (Newton 2004a, 2008). In addition, influences from one area may have carryover effects on an individual’s breeding success or survival in another area (Calvert *et al.* 2009, Table 2; Harrison *et al*. 2011). There have been several reviews in the last decade attempting to uncover the reasons behind the large scale declines in migrants, but these largely highlight the need for more studies to fill gaps in our knowledge (Newton 2004a, 2008, Sanderson *et al.* 2006; Vickery *et al.* 2014). In this introduction, I aim to review our current understanding of the main population limitations operating in long-distance migrant populations.

1.3 Limiting factors operating in the breeding season

Limiting factors in the breeding season have the potential to have a big effect on an individual's life-time fitness as they may directly impact on both survival and productivity. This life-cycle phase is the best studied and consequently breeding season limitations are better understood than limitations in the wintering grounds or during migration (Calvert *et al*. 2009; Vickery *et al.* 2014). A review by Vickery *et al.* (2014) found that degradation of breeding habitats was the most common breeding season influence on demography.

1.3.1 Loss of suitable breeding habitat

Currently, potential breeding habitats are changing at an alarming rate (Goldewijk 2001). Common causes of habitat degradation are agricultural intensification (Aebischer *et al.* 2000; Vickery *et al*. 2001; Donald *et al*. 2001, 2006; Newton 2004b), forestry and deforestation (Santos *et al.* 2002; Hausner *et al.* 2003), reed harvesting, (Graveland 1998; Barbraud *et al.* 2002) land drainage (Kozulin & Flade 1999), burning and over-grazing (Soderstrom *et al.* 2001) and deterioration of water quality (Beintema 1997). Climatic conditions can compound the effect of breeding habitat loss, for example by shifting breeding ranges and thereby leading to a reduction in suitable habitat (Thomas & Lennon 1999): climate models predict a reduction in breeding ranges of 11% for Afro-Palearctic migrants (Huntley *et al.* 2008).

For breeding, birds need suitable habitat for both nesting and foraging (Vickery & Arlettaz 2012), but may require very different habitat characteristics for these activities (Benton *et al.* 2003). For example, Common Whitethroats favour tall herbaceous vegetation and bramble for nesting and woody vegetation for foraging in, but do not generally nest in close proximity to woody vegetation (Halupka *et al*. 2002). A common effect of habitat degradation is homogenisation of the landscape which leads to a loss of combinations of habitat types required to meet both foraging and nesting requirements (e.g. Bradbury & Bradter 2004; Barbaro *et al.* 2008; Schaub *et al.* 2010; Weisshaupt *et al.* 2011; Vickery & Arlettaz 2012; Vickery *et al.*

2014). For example, agricultural intensification leads to the removal of hedges that many farmland birds rely on for nesting, as well as ditches and grassy margins used for foraging (e.g. Bradbury *et al.* 2000). Additionally, logging may remove natural cavities, used for nesting by some species (Newton 1998), and dead trees, which are a source of invertebrate food (Ehnstrom 2001; Hannon & Drapeau 2005). Loss of suitable breeding habitat may reduce the number of pairs attempting to breed (reviewed in Newton 1998), or act indirectly to reduce breeding success by forcing breeders into poor quality breeding habitat, which may have lower food availability (Martin 1987; Beintema 1997; Britschgi *et al.* 2006; Vickery & Arlettaz 2012), an increased probability of nest failure due to predation or increased predation risk and energetic costs to incubating adults (Baines 1990; Martin 1993; Ost & Steele 2010; Vickery & Arlettaz 2012; Seltmann *et al.* 2014).

Habitat change within the breeding season, which causes the habitat to become unsuitable, can be particularly damaging, because once its eggs are laid, a bird is tied to its breeding site until either the breeding attempt fails or the chicks fledge (Anteau *et al*. 2012). For example, the shift from hay to silage, and the associated earlier mowing date has been detrimental to populations of many ground nesting grassland birds, causing high nest loss (Baines 1990; Green *et al.* 1997; Müller *et al.* 2005; Perlut *et al*. 2006; Broyer 2007, 2009, 2011; Grüebler *et al.* 2012; Perkins *et al*. 2013; Fischer *et al.* 2013; Grüebler *et al*. 2015; Strebel *et al.* 2015) and increased female mortality (Grüebler *et al*. 2008). The loss of females prevents re-nesting, reducing reproductive output, and could potentially skew the population sex ratio, which may therefore limit further growth (Steifetten & Dale 2006; reviewed by Donald 2007). Mid-season mowing can also deter repeated nesting attempts and thereby effectively shorten the breeding season (Gilroy *et al*. 2009; Grüebler *et al*. 2015).

Habitat degradation can lead to fragmentation and a rise in associated edge effects, such as reduction in food availability and higher foraging costs (Newton 1998, 2004a, 2008; Hinsley *et al.* 2008). Fragmentation has also been linked to higher incidences of predation, especially for ground nesting birds (Herkert *et al*. 2003; Lampila *et al.* 2005). The severity of the edge effect from habitat fragmentation depends on the type of habitat that replaces the original habitat: agricultural land replacing forest appears to have a greater negative effect on population numbers and breeding success for the forest inhabitants than just felling part of the forest (Schmiegelow & Monkkonen 2002). The degree of isolation and the area of remaining habitat can also affect the impact of habitat degradation (Newton 1998), but not in all cases (Schmiegelow & Monkkonen 2002).

Habitat change does not necessarily always have a negative impact on birds and, for some species, it may actually introduce new nesting or foraging opportunities (Newton 1998). The range expansion of Barn Swallows in Europe and North America, for example, has been associated with the widespread availability of nest sites in man-made buildings (Zink *et al.* 2006) and foraging opportunities from livestock farming (Møller 2001; Ambrosini *et al.* 2002; Grüebler *et al.* 2010). However, examples of positive effects are few are far between, for the vast majority of species anthropogenic habitat change has been implicated in population declines (Newton 1998, 2004ab, 2008; van Turnhout *et al.* 2010; Sheehan & Sanderson 2012; Vickery *et al*. 2014).

1.3.2 Limited food supply

Habitat change (e.g. Beintema 1997; Britschgi *et al.* 2006) and inclement weather (e.g. Rotenberry & Wiens 1991; Rodriguez & Bustamante 2003) may both interactively limit food availability during the breeding season, which can negatively affect reproductive success (Wiklund 1984; Martin 1987; Siikamaki 1998, Britschgi *et al.* 2006, Lu *et al*. 2011). Lack of food may also be caused by an inability to respond to the earlier arrival of spring (IPCC 2014) on breeding grounds (Forchhammer *et al.* 2002; Crick 2004; Rubolini *et al.* 2007; Saino *et al.* 2011, but see Stervander *et al.* 2005; Jonzén *et al.* 2006), leading to a mismatch in the timing of breeding and peak food abundance (Both & Visser 2001; Visser *et al.* 2004; Both *et al.* 2006; Both *et al.* 2009; Knudsen *et al*. 2011).

Low food availability early in the breeding season can reduce female condition, leading to lower clutch sizes (Martin 1987; Slagsvold & Lifjeld 1988; Konarzewski 1993; Devries *et al*. 2008), reduced egg quality (Martin 1987; Graveland & Drent 1997), lower hatching success (Martin 1987; Serrano *et al.* 2005) and reduced levels of parental care (Martin 1987; Slagsvold & Lifjeld 1988). Reduced food supplies later in the season may lead to nestling starvation (e.g. Wiklund 1984; Beintema 1997; Lu *et al*. 2011). Lack of food can potentially make nestlings more vulnerable to predation by increasing the frequency and volume of vocal begging behaviours (Cotton *et al.* 1996; Diego *et al.* 2012). Reduced food supplies may also increase parental foraging time and distance (Tremblay *et al.* 2005; Britschgi *et al.* 2006), causing parents to spend less time guarding the nest from predators (Martin 1987; Komdeur & Kats 1999; Rastogi *et al.* 2006). Alternatively, a reduction in the quality of food (e.g. Britschgi *et al.* 2006) may lead to parents needing to make more provisioning visits to the nest and therefore increase the probability of disclosing its location (Martin *et al.* 2000). Food shortages have also been shown to influence adult survival, as parents have to expend more effort provisioning nestlings (Lima 2009; Low *et al.* 2010). As well as directly reducing the abundance and quality of food supplies, habitat change and weather may reduce food availability by changing the habitat structure, making efficient foraging more difficult (Oppermann 1992; Schaub 1996; Whittingham & Evans 2004; Wilson *et al.* 2005; Atkinson *et al.* 2005; Brambilla *et al.* 2007; Hoste-Danylow *et al*. 2010).

1.3.3 Predation and disturbance

Predation has often been invoked as a major cause of reproductive failure in nesting birds, especially ground nesters (Vickery *et. al* 1992; Martin 1993; Patterson & Best 1996; Donald *et. al* 2002; Zanette *et. al* 2006a; Bellebaum & Bock 2009). Weather may interact with predation risk, for example by increasing the activity and population size of certain predators (Rotenberry & Wiens 1989; Morrison & Bolger 2002; Chase *et al.* 2005), or reducing vegetation growth and thereby nest concealment (Chase *et al.* 2005). Predation risk is usually density dependent and therefore unlikely to cause prolonged population declines on its own (Newton 1998). However, it may have a greater impact when combined with negative anthropogenic changes, for example predation has commonly been found to increase with increasing habitat fragmentation, and these combined effects have been suggested as a factor in Neo-tropical migrant bird declines (reviewed in Newton 2004a, 2008).

The disturbance to breeding birds caused by predators may also have indirect negative effects on reproductive success (Cresswell 2008; Lima 2009; Martin & Briskie 2009). Birds generally perceive human disturbance as a potential predation risk and react accordingly, leading to similar indirect negative effects (Frid & Dill 2002; Beale & Monaghan 2004; Price 2008). With the growing human population and concurrent increasing use of outdoor space for recreation, the impact of human disturbance on breeding birds is predicted to increase (Hill *et al.*1997; Price 2008). Disturbance can reduce reproductive output by limiting distribution (Ebbinge & Spaans 2002; Cresswell 2008), restricting foraging opportunities (Klaassen *et al.* 2006; Cresswell 2008), interrupting incubation (e.g. Ghalambor & Martin 2002; Kovarik & Pavel 2011; Zanette *et al.* 2011; Ibanez-Alamo & Soler 2012), reducing clutch sizes (Lima 2009) and reducing provisioning efficiency (Eggers *et al.* 2005; Zhao 2005; Ghalambor *et al.* 2013). Disturbance can also increase predation risk by prompting temporary or permanent nest abandonment (Tremblay & Ellison 1979; Piatt *et al.* 1990), causing parents to inadvertently draw attention to the nest location, or damaging the concealing vegetation surrounding a nest (Major 1990; Weidinger 2008; Jacobson *et al.* 2011). Nest monitoring by researchers inevitably involves a degree of disturbance and there are worries that this disturbance may reduce breeding success, not only harming the population the researchers are trying to conserve but also biasing estimates of demographic parameters (Price 2008; Reynolds *&* Schoech 2012). It is therefore particularly important for researchers to monitor the effect of disturbance from their research activities and use this information when interpreting their findings and when planning future research projects (O'Grady *et al.* 1996; Price 2008; Reynolds *&* Schoech 2012).

1.4 Limiting factors during the non-breeding season

Factors that limit migrant population growth in the non-breeding season are far less clear (Clavert *et al.* 2009). Over-winter survival has occasionally been measured directly (Ketterson & Nolan 1982; Conroy *et al.* 1989; Conway *et al*. 1995; Sillett & Holmes 2002; Marra & Holmes 2001; Blackburn & Cresswell 2015a) but, due to logistical constraints, survival estimates are usually based on re-sightings of colour-ringed birds during the breeding season (e.g. Saether & Bakke 2000; Stahl & Oli 2006; Ezard *et al.* 2006; Fletcher *et al*. 2006; Clark & Martin 2007; Wright *et al.* 2009; Calvert *et al*. 2009; Sim *et al.* 2011). Comparative studies suggest that population change in migrant species is 'almost always' most sensitive to change in adult survival (Saether & Bakke 2000; Calvert *et al.* 2009), and most adult mortality is thought to occur in the non-breeding season, especially during migration itself (Sillet & Holmes 2002; Newton 2006; Calvert *et al.* 2009; Klaassen *et al.* 2014). Migration requires large amounts of energy (Klaassen *et al.* 2012), and has the associated risks of strong competition at stopover sites and increased exposure to bad weather and predation risk (Bulter 2000; Newton 2006, 2007). Intraspecific competition due to differences in dominance (e.g. Rappole & Warner 1976; Lindström *et al*. 1990), age (e.g. Rguibi-Idrissi *et al.* 2003) and sex (e.g. Yosef & Wineman 2010) can affect migration speed and survival probability on migration (Newton 2004a, 2006, 2008). In the non-breeding grounds, it is thought that climate variation and habitat degradation are the two main factors causing changes in population demographic rates (Vickery *et al.* 2014).

1.4.1 Limiting factors during migration

Birds migrate in stages, with large numbers of birds using the same stopover sites (reviewed in Newton 2006, 2008). This can lead to high levels of competition (Salewski *et al.* 2007; Moore & Yong 1991), food depletion (e.g. in Bewick's Swans, Nolet & Drent 1998 and Red Knots, Baker *et al.* 2004), increased risk of predation (Lank *et al.* 2003) and parasitism (Figuerola & Green 2000), especially as time pressures and extreme energy requirements cause birds to focus more on feeding, rather than vigilance behaviours (reviewed in Newton 2004a, 2006, 2008). For example, low weight Western Sandpipers in the Strait of Georgia favoured feeding in a high predation risk area with a high fattening rate, rather than at a site with lower predation risk and a low fattening rate (Ydenberg *et al.* 2002). They may also be heavier due to an increase in energy stores, and therefore less able to escape attacks (Metcalfe & Ure 1995; Lind *et al.* 1999; reviewed in Newton 2006). Human influenced habitat degradation has exacerbated the situation by further limiting resources (Norris *et al*. 2004; Drent *et al.* 2006; Verkuli *et al.* 2012). Additionally global warming is shifting breeding ranges northwards and therefore migration distances between wintering and breeding grounds are predicted to increase, leading to higher energetic costs (Doswald *et al.* 2009). Birds may also suffer high mortality during migration due to severe weather (reviewed in Newton 2007), which can increase energetic costs (e.g. Ligon 1968; Kennedy 1970; Jehl *et al.* 1999; Montalti *et al.* 1999) or kill directly (e.g. lightening, (Glasrud 1976), hunting (Magnin 1991; McCulloch *et al.* 1992; Stronach *et al.* 2002; Baha el Din & Salama 1991; Vickery *et al.* 2014; Newton 2008) and collisions with man-made structures (US FWS 2002; Newton 2007, 2008)). Due to global warming the frequency of severe weather events (IPCC 2014) is predicted to increase, as is the number of wind turbines (Newton 2007), therefore these mortality causes may be more prevalent in the future.

1.4.2 Limiting factors on the wintering grounds

The Sahel zone is a key wintering and staging ground for many Afro-Palearctic migrants (Vickery *et al.* 2014). Drought conditions have dominated here from 1968-1997 causing long term habitat change (Nicholson 2000; Zwarts *et al.* 2009). In these areas the amount of vegetation, and correspondingly the availability of suitable habitat and food (e.g. Dingle & Khamala 1972; Sinclair 1978) depends on the amount of rainfall in the wet season (July-September): low rainfall leads to reduced habitat and food availability (Newton 2004a, 2008; Vickery *et al.* 2014). Changes in Sahel rainfall patterns and primary productivity have been linked to population fluctuations in various Afro-Palearctic migratory species (e.g. Sedge Warbler and Common Whitethroat, Peach *et al.* 1991, Baillie & Peach 1992; hirundines, Robinson *et al.* 2008, Norman & Peach 2013; Purple Heron, Den Held 1981; White Stork, Schaub *et al.* 2005; Lesser Kestrel, Mihoub *et al.* 2010; Red-backed Shrike, Pasinelli *et al.* 2011). There is strong evidence for a direct link between non-breeding season rainfall, food availability and body condition in migratory birds (Strong & Sherry 2000; Brown & Sherry 2006; Vickery *et al.* 2014). Lack of food can cause direct mortality from increased starvation risk, or has indirect effects, such as increasing susceptibility to predators and parasites (Martin 1987; Newton 1998, 2004a, 2008) and causing poor quality feather replacement in moulting birds (van den Brink *et al.* 2000; Sanio *et al.* 2004a) which reduces foraging efficiency and increases energetic costs (Møller *et al.* 1995; Nilsson & Svensson 1996; Rubolini *et al.* 2002). The effects of weather on availability of suitable habitat and food are compounded by anthropogenic habitat change (Zwarts *et al.* 2009; Vickery *et al.* 2014). Almost five million heactres of natural vegetation are lost to agriculture each year in Sub-Saharan Africa (Brink & Eva 2009), and this trend is predicted to continue as the human population expands (Gaiser *et al.* 2011; Heubes *et al.* 2011). Agricultural intensification is associated with increased pesticide use, which also reduces available food resources (Newton 1998, 2004a, 2008) and causes mortality and reduced body condition through bioaccumulation (Mineau 2002). Widespread locust control measures can be particularly damaging (Dallinga & Shoenmakers 1987; Newton 2004a, Sanchez-Zapata *et al.* 2007; Vickery *et al.* 2014).

1.5 Carry-over effects

Poor conditions on wintering, breeding, or migration stopover sites can also have carry-over effects which influence breeding success and survival (Newton 2004a, 2006, 2008; Calvert *et al*. 2009 (see Table 2) & Harrison *et al.* 2011; Vickery *et al.* 2014). For example, birds in better condition tend to arrive earlier at breeding sites (Møller 1994; Marra *et al.* 1998; Drent *et al*. 2003; Saino *et al.* 2004a,b; Norris *et al.* 2004; Gunnarsson *et al*. 2005; Reudink *et al.* 2009), and therefore can access the best territories, have a greater choice of potential mates, and a longer breeding season, and thereby have higher reproductive success (Smith & Moore 2005; Saino *et al.* 2004a,b; Marra *et al.* 1998; Norris *et al.* 2004; Møller 1994; Møller *et al.* 2009; Reudink *et al.* 2009; Tryjanowski *et al.* 2004; Cooper *et al.* 2011; Aebischer *et al.* 1996; Currie *et al.* 2000; Bensch & Hasselquist 1991; Dalhaug *et al*. 1996, also reviewed in Newton 2006, 2008). Poor conditions on wintering, stopover or breeding grounds, leading to increased competition for resources, can reduce an individual's body condition and subsequent breeding success (Ebbinge & Spaans 1995; Marra & Studds 2006; Mainguy *et al.* 2002; Reed *et al.* 2004; for more examples of studies linking body condition and breeding success see Newton 2006: Table 2). This, in turn, can increase the probability of mortality during the next life-cycle phase

(Dit Durell *et al.* 1997; Schmutz & Ely 1999; Marra & Holmes 2001; Baker *et al*. 2004; Kéry *et al.* 2006; and see review in Newton 2006: Table 1).

1.6 Difficulties in determining population limitations

The impact of a potentially limiting factor depends strongly on the species' range, habitat requirements and behaviour (Wunderle & Waide 1994; Vickery *et al.* 2014; Newton 2004a, 2008). There is also individual variation in responses, for example a more efficient forager will be able to cope with the effects of reduced food supply better than a less efficient one and a bird with plentiful fat supplies is less likely to die in a sudden cold snap than a bird near to starvation (Newton 1998, 2008). Additionally, limiting factors can act indirectly and in combination with each other, confounding results. For example, habitat change may force an individual to move to a habitat with lower food availability, which reduces its breeding success, or it may remain where it is but be more susceptible to predators because the nesting habitat has been degraded (Newton 1998, 2008). It is also hard to measure annual survival in migrants due to the limited opportunities for year-round monitoring (Newton 2004a, 2008). In addition, problems are compounded by a lack of data. Few field studies have been carried out on the non-breeding grounds and knowledge on variation in migratory speed, routes and staging areas is lacking for many species; though the advent of technology enabling smaller satellite trackers and geolocators is working to fill this gap (reviewed in Bridge *et al.* 2011, Vickery *et al.* 2014 & Newton 2008). It is necessary, therefore, to rely on models to statistically account for the effects of immeasurable variables and temporal variability (Newton 1998, 2008). In Europe, more connectivity between different study populations is needed to uncover spatial and temporal variation in demographic parameters and deduce the differences in habitat or climate responsible for this (Vickery *et al.* 2014).

1.7 Conclusions

The populations of many species of Afro-Palearctic migrants have shown severe declines over the last 30 years (Berthold *et al*. 1998; Sanderson *et al.* 2006; Heldbjerg & Fox 2008; Newton 2004a, 2008; Van Turnhout *et al.* 2010; Vickery *et al*. 2014). These declines are widespread and affect species from a range of taxa and from different habitats (Sanderson *et al.* 2006; Newton 2004a, 2008, Vickery *et al.* 2014). Currently, the reasons behind the widespread declines are not fully understood and are thought to vary between population and species (Newton 2004a,2008; Sanderson *et al.* 2006; Vickery *et al.* 2014), though current evidence suggests degradation of habitat on breeding grounds and climate interacting with habitat loss on the over-wintering grounds may be particularly influential (Vickery *et al.* 2014). Migrants are likely to be more susceptible to environmental change than residents due to their dependence on multiple sites during their life-cycle (Newton 2004a). Sanderson *et al.* (2006) also suggested that migrants may be more vulnerable to environmental change than residents due to their smaller brain size (Sol *et al*. 2005), which suggests that they have less capacity to adapt their behaviour. To enable positive conservation management action to try to halt these declines, we need to understand why so many migrant species are declining. One way to achieve this aim is through detailed studies of a sample population, were we quantify all the key demographic parameters and the associated environmental factors that affect them (e.g. Fletcher *et al*. 2006; Hoekmann *et al*. 2006; Wright *et al*. 2009; Sim *et al.* 2011; Grüebler *et al.* 2014). Findings from such studies can then be applied to the species more widely, taking account of key differences between the quality of habitat and resources available to different populations and tailoring recommended conservation management action accordingly.

1.8 The Whinchat

The Whinchat, *Saxicola rubetra*, is an example of a grassland, ground nesting, insectivorous, Afro-Palearctic migrant that was once common across Europe but has suffered major and widespread declines over the last 50-60 years (Sharrock 1976; Holloway & Gibbons 1996; Baillie *et al.* 2014; EBCC 2012). Whinchat populations in the UK have declined by 57% between 1995-2010, making them an amber listed species (Baillie *et al.* 2014), and by 67% in Europe between 1980-2009 (EBCC 2012), causing them to feature on the IUCN red list (Birdlife International 2012). Whinchats are now restricted to marginal upland habitat in much of Europe (Müller *et al.* 2005; Henderson *et al.* 2014; Bergmüller & Frühauf 2015) and have recently become extinct as a breeding bird in Luxembourg (Bastian, M. 2015).

1.8.1 Current threats

Agricultural intensification on the breeding grounds is commonly cited as the main cause of Whinchat declines (Grotenhuis & Van 1986; Bastian 1989; Richter & Düttmann 2004; Grüebler *et. al* 2008; Broyer 2009; Fischer *et. al* 2013; Elts 2015; Kurlavicus 2015). Earlier mowing in particular has frequently been implicated (Müller *et al.* 2005; Britschgi *et al.* 2006; Broyer 2009; Broyer *et al.* 2012; Tome & Denac 2012; Strebel *et al*. 2015), and causes destruction of nests (Müller *et al.* 2005; Grüebler *et al.*2008), a reduction in food supplies (Britschgi *et al.*

2006), and increased female mortality when incubating (Grüebler *et al.*2008). Müller *et al.* (2005) found that switching to earlier mowing regimes led to the Swiss lowlands becoming population sinks (Pulliam 1988, 1996): the Whinchats could not change their behaviour and start breeding earlier to adapt to this change, consequently their breeding success was reduced. Intensification practises in general, such as using large quantities of fertiliser and changing the structure of the habitat through intensive grassland management and extensive drainage also have negative impacts. The associated change in the vegetation structure limits suitable nesting habitat and reduces food availability, both directly, by reducing invertebrate diversity and abundance, and indirectly, by reducing access to invertebrates and foraging efficiency (Oppermann 1990; Opperman 1992; Bastian *et al*. 1994; Bastian & Bastian 1996; Oppermann 1999; Orlowski 2004; Britschgi *et al.* 2006; Fischer *et al.* 2013). On the other hand, a recent study by Hulme & Cresswell (2012) found that Whinchats may actually benefit from the moderately intensive farming in their wintering grounds if it leads to the creation of more open habitat. So far, however, this has been the only research project on population limitations in Whinchats on the wintering grounds, and as it was limited to one area within Nigeria, the results may not be representative for Whinchats across the whole of their wintering range.

Predation has also been implicated as a factor in reduced Whinchat breeding success (Frankiewicz 2008; Tome & Denac 2012; Shitikov *et al*. 2015), though it has not yet been shown to have effects at the population level. Fledglings are particularly vulnerable in their first 10 – 15 days after leaving the nest, before they switch from their initial ‘sit and hide’ method of predator evasion to escape by flying (Tome & Denac 2012). However, other studies, from more intensively farmed land, have suggested that predation rates on Whinchats are generally lower than for other ground nesting birds (Grüebler *et al.* 2012). Nests may also be lost from occasional events such as trampling from livestock and flooding (Gray 1974; Frankiewicz 2008).

It is also thought that climate change may negatively affect Whinchats, by reducing habitat quality or causing a mismatch in peak food supply and demand (Bastian, H-V. 2015). However, currently this has not been specifically studied and consequently there is no evidence for any effect of climate change. Illegal hunting during migration may also reduce Whinchat populations: Whinchats are the most commonly trapped species in Southern Italy (Heyd 2015). More study is needed to determine the overall impact of hunting on the Whinchat population (Bastian & Feulner 2015b).

1.8.2 Conservation action

Conservation methods suggested to reduce the decline in Whinchats generally focus on delaying mowing (Broyer 2007, 2009, 2011, Broyer *et al.* 2014a, 2014b; Tome & Denac 2012; Fischer *et al*. 2013; Grüebler *et al.* 2015), reducing the speed of mowing machines, changing the angle of the cutting bar, leaving strips of the field uncut and marking nests for farmers to avoid (Grüebler *et al.* 2008; Grüebler *et al.* 2012; Siems-wedhorn 2015). Grüebler *et al.* (2015) used models to determine the best strategy of mowing dates and the proportions of early and late mown meadows necessary for a stable Whinchat population. Grüebler *et al.* (2012) found that marking nests for protection from mowing was effective and did not increase the predation risk, but was only a 'short time fix', time consuming and costly, and did not solve the associated problems of reduced food availability and loss of suitable nesting habitat. Uhl (2015) found leaving fallow strips and wooden poles in fields improved Whinchat breeding success. However, Horch & Spaar (2015) found that in the long-term only large scale late cutting of flower meadows was likely to be effective. Horch & Birrer (2011) tried to determine the minimum area necessary to conserve to benefit breeding Whinchats by erecting fences to exclude cattle from some parts of the field. Their results suggested that the fenced off areas need to be at least one hectare and represent '10% of the area of favourable grassland' to have any positive effect on territory establishment.

1.8.3 Why Whinchats?

Degradation of breeding habitats was found to be the most likely breeding season influence on the declines in Afro-Palearctic migrants (Vickery *et al.* 2014). In Europe one of the biggest causes of habitat change is agricultural intensification (Donald *et al.* 2006; Thaxter *et al.* 2010; Vickery *et al*. 2014). Due to their habitat preferences (section 2.1.2), Whinchats would be expected to be particularly sensitive to agricultural intensification on their breeding grounds (Müller *et al*. 2005), and indeed agricultural intensification on the breeding grounds is commonly thought to be responsible for the Whinchat decline (Grotenhuis & Van 1986; Bastian 1989; Richter & Düttmann 2004; Grüebler *et. al* 2008; Broyer 2009; Fischer *et. al* 2013; Elts 2015; Kurlavicus 2015). However, a recent study has found evidence to suggest that events in the non-breeding season may also play a role (Henderson *et al.* 2014). My study area, Salisbury Plain, is a habitat that has largely escaped agricultural intensification (Ash *et al.* 2011; section 2.2). Therefore, it offers the perfect opportunity to investigate whether agricultural intensification on the breeding grounds is the sole reason for the Whinchat decline. Whinchats make a good study species. They are relatively conspicuous, often sitting on highly visible perches and have a distinctive song. They keep clearly defined territories in the breeding season, allowing tracking of the same individuals, and show site fidelity (Bastian 1992; Müller *et al.* 2005), enabling the measurement of adult survival and population turnover. Whinchats also are single brooded which greatly simplifies calculations of reproductive success (Cramp 1988). They are becoming increasingly well studied across Europe, with study groups currently working on Whinchats in 18 European countries (1st European Whinchat symposium: Bastian & Feulner 2015a) and the recent formation of an International Whinchat working Group, thereby allowing broad-scale comparisons of trends in populations with different quality breeding habitat. The high availability of data, combined with the sensitivity of Whinchats to declines in grassland and farmland habitat quality make them a good indicator species for assessing the impacts of anthropogenic activity on migrant populations and grassland biodiversity.

1.8 Thesis outline

This thesis aims to quantify the vital demographic parameters of reproductive success, adult survival and juvenile survival and recruitment, and to determine how these vary according to habitat quality in a population of Whinchats on an unimproved grassland habitat. First, background information on the study site and methods is provided (Chapter 2). Then, in Chapter 3, I investigated the hypothesis that Whinchat settlement will vary in relation to the vegetation and topographical features and invertebrate fauna of an area. The habitat features that are associated with Whinchat occupancy were determined (Chapter 3) and this information was used to develop a habitat suitability model to determine how much suitable breeding habitat was present in the study area (Chapter 4). This model, in conjunction with ground truthing surveys, was used to test the hypothesis that suitable breeding habitat is not a limiting resource on Salisbury Plain. Additionally, the hypothesis that Whinchat occurrence would be affected by the suitability of the surrounding habitat was also tested, thereby investigating potential effects of habitat fragmentation. Next, I aimed to investigate which external factors were limiting breeding success (Chapter 5) by assessing the variation in environmental factors associated with the observed variation in breeding success. The breeding success estimates for the study population was compared to other Whinchat studies to see how it differed and these differences were interpreted in relation to differences in habitat between the populations. In Chapter 6 I aimed to determine whether researcher nest monitoring activity affected the observed Whinchat breeding success. Through two experiments, the effects of nest monitoring on egg phase daily survival rates and nestling provisioning rates were quantified (Chapter 6). In Chapter 7 apparent survival estimates for adult males, adult females and Whinchats in their first breeding year were determined. The results were interpreted relative to results from other Whinchats studies and other studies on Afro-Palearctic migrants. To improve our understanding of the accuracy of the apparent survival estimates, I tested the hypothesis that breeding and natal dispersal distances would vary according to age, sex and breeding success the previous year. I also aimed to investigate the pattern of arrival on the breeding grounds and territory settlement, and to determine how this varied according to age and sex, whether it was related to territory quality and whether arriving earlier was linked to higher breeding success. Finally, the demographic parameters determined from the previous chapters were brought together in a population model which aimed to predict the future population trend and aid in suggestion of the most appropriate conservation actions (Chapter 8).

Chapter 2: General Methods

Soldiers training on Salisbury Plain

2.1 Study Species

2.1.1 Life history

Whinchats are grassland, ground nesting, Passerines from the family Turdidae which also includes Wheatears, Stonechats and Redstarts. Whinchats are approximately 12 cm high (Robinson 2005) and the mean adult body mass is 15.9 g during the breeding season (n = 127, pers. obs.). A typical lifespan is two years and the maximum recorded age is four years 11 months (Robinson 2005).

On average, Whinchats start arriving in their UK breeding grounds from the 16th April (Robinson 2005). They are territorial during the breeding season, and form monogamous pair bonds (Cramp 1988) but will change partners between seasons and sometimes within a season (pers. obs.). Cases of polygyny and polyandry have been rarely observed (pers. obs.). First breeding occurs in their first spring. Clutch sizes are usually 5-6 blue eggs (Gray 1974; Cramp 1988; Müller *et al.* 2005; Robinson 2005; Britschgi *et al*. 2006; Frankiewicz 2008; Tome 2015; pers. obs), though larger mean clutch sizes of 6.75 have been found for one site in Russia (Shitikov *et al.* 2015). For the Salisbury Plain population the mean clutch size was 5.6 (range 3 3 – 7). Whinchats generally only lay a single clutch (Cramp 1988; Robinson 2005) but may have another attempt if the first fails: this occurred for 55.3% of pairs on Salisbury Plain and some males were observed having four attempts (pers. obs.). Nests are usually at ground level, well hidden in dense vegetation, with existing hollows sometimes used (Cramp 1988; Frankiewicz 2008). On Salisbury Plain, nests were commonly built close to a tall protruding piece of vegetation used as a perch (pers. obs.). The female builds the nest of grass stems, leaves and moss, incubates the eggs and broods the young, but both sexes will provision the nestlings (Cramp 1988; Frankiewicz 2008; pers. obs). Eggs are laid one a day, and incubation starts with the last egg and lasts around 13 days (Robinson 2005, pers obs.). Whinchat nestlings are altricial, and hatch blind and naked, apart from sparse down. Hatching success ranges between 76 and 92% (Frankiewicz 2008; Britschgi *et al.* 2006). After hatching, nestlings grow following a logistic growth curve, with peak growth rates between 3 – 7 days and adult weight achieved by nine days old (Bastian & Bastian 1993). Fledglings leave the nest at 12 - 15 days old, fly at 17 – 20 days old and are independent by 28 – 30 days (Cramp 1988; Tome & Denac 2012; pers. obs.). Estimates of nest success based on daily survival rates generally range between 35 – 55.7% for a 29 day breeding cycle (adapted from Grüebler *et al*. 2012; Shitikov *et al*. 2015; M.; Tome, D., pers comm.) but can vary widely between years (from 1 – 57%, Shitikov *et al.* 2015) and are considerably lower for early mown sites (12.2%, Grüebler *et al.*

2012). The mean number of fledglings produced per pair ranges from 3.3 – 4.17 (Frankiewicz 2008; Fischer *et al.* 2013; Shitikov *et al.* 2015), but again is lower for early mown areas (1.8, Fischer *et al.* 2013). On Salisbury Plain, the breeding season lasted a mean of 55.3 days (+/- 2.19 days), with the earliest first egg date ranging from 5th – 7th May and the latest first egg date from the 1st – 3rd July (from 2012 – 2014), which was similar to other European sites (Frankiewicz 2008; Fischer *et al.* 2013; Shitikov *et al.* 2015; Tome 2015).

Whinchats winter in open vegetated areas in Sub-Saharan Africa in two distinct zones: Senegal to Cameroon, and North East Zaire and Uganda to Zambia (Cramp 1988). Whinchats are solitary on the wintering grounds but will form feeding and roosting flocks while on migration (Koce & Denac 2010). They exhibit breeding site fidelity, with site fidelity higher in adults (older than their first breeding year) compared to birds in their first breeding year. A mean of 50% of adult males (range 37.5 – 73.6%), 30% of adult females (range 11.8 – 57.1%) and 11% of first-years (range 1 – 26.2%) return to the study site the following year (Schmidt & Hantge 1954; Bezzel & Stiel 1982; Rebstock & Maulbetsch 1988; Bastian 1992; Müller *et al.* 2005; Shitikov *et al*. 2015; Tome, D. pers. comm.).

2.1.2 Habitat and resources

Whinchats are generally insectivorous, though they will eat berries on migration (Cramp 1988). They feed on a wide range of invertebrates (Britschgi *et al.* 2006) and generally forage by searching from perches and diving to catch their prey, but they will also catch insects on the wing and forage on the ground (Ritcher & Düttmann 2004; Barshep *et al.* 2012; pers. obs). In the breeding season, Whinchats need an area of grassland that is not heavily managed for agriculture, that is within their altitudinal limits (500 - 1800 m; Cramp 1988; Calladine & Bray 2012), has plenty of perches (such as tall herbaceous plants and fence posts) and has a rich diversity of medium to large invertebrates (Opperman 1990; Opperman 1992; Bastian *et al.* 1994; Orlowski 2004; Müller *et al.* 2005; Britschgi *et al.* 2006; Broyer 2009; Grüebler *et al*. 2012; Fischer *et al.* 2013). Territory sizes range between 0.38 – 4.14 ha (Bastian 1987; Cramp 1988; Bastian & Bastian 1996; Calladine & Bray 2012), though this varies depending on habitat quality (Calladine & Bray 2012), as does territory density, which can range from 0.8 to 33.3 territories per 10 ha (Orlowski 2004; Frankiewicz 2008).

2.2 Study area

Salisbury Plain is in Wiltshire, southwest England. It is a large area covering 40,000ha (40 km east to west, 15 km north to south) which has been set aside as an army training area since 1897 (Ash *et al.* 2011). Due to this, the habitat on Salisbury Plain effectively escaped the agricultural advancement which has affected much of the rest of the UK. The main study site consists of an area of 92.76 km^2 in the western part of Salisbury Plain (Latitude 51°11'52"N-51°16'4"N; Longitude 1°57'32"W- 2° 9'32"W; Figure 2.1). This area was chosen because large scale Breeding Bird Surveys carried out by the Royal Society for the Protection of Birds (RSPB) and the Defence Estates in 2000 and 2005 revealed a strong, widespread population of Whinchats in this area (Stanbury *et al.* 2000, 2005). Also, it is not generally used for live firing military exercises, so regular access is possible. The center area, which appears to have a larger Whinchat population, is impossible to gain regular access to because it is a live firing zone. The East area is mostly low intensity farmland and has a much smaller Whinchat population. This area would have made an interesting comparison population of Whinchats compared to the unimproved grassland in the west. However, due to time constraints with the east area taking 1-2 hours to drive to, it was not possible to study the Whinchats in this area too.

Salisbury Plain is the largest area of unimproved chalk grassland in northwest Europe and as such has high biodiversity value, supporting 104 species included on the UK Biodiversity Action Plans (BAP) (see JNCC 2007 for more explanation on BAP) and 34 birds species listed as red or amber status indicating a need for conservation concern (Ash & Toynton 2000; Eaton *et al*. 2009). Due to this, 20,000 hectares of the plain are designated as a Site of Special Scientific Interest (SSI), a Special Area for Conservation (SAC) and a Special Protected Area (SPA) (Ash & Toynton 2000; Ash *et al.* 2011). Salisbury Plain held an estimated 429 pairs of Whinchats in 2005 (Stanbury *et al.* 2005), approximately 1% of the population in Great Britain (47,000 pairs) (Musgrove *et al.* 2013).

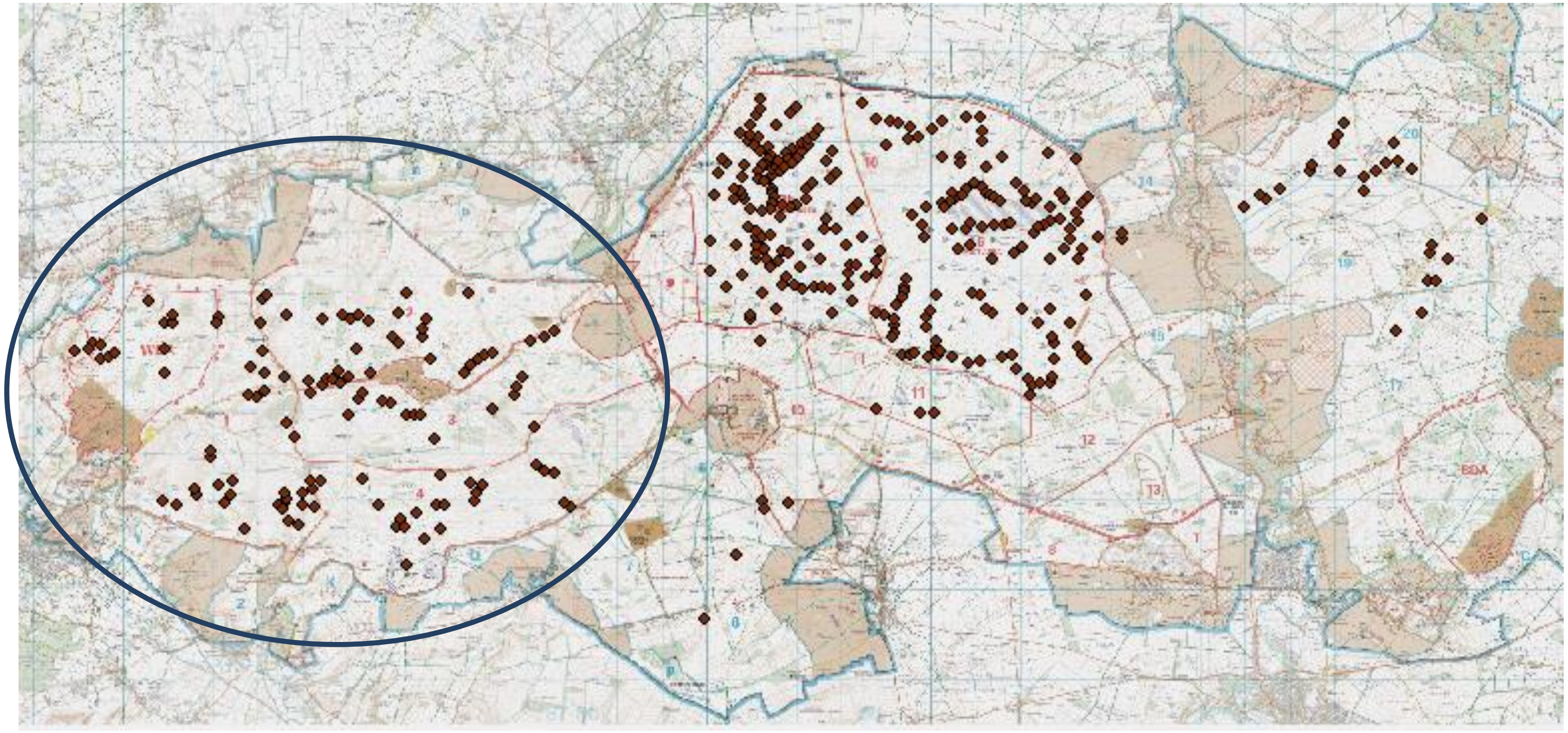


Figure 2.1. A map of Salisbury Plain. The red dots depict whinchat sightings from surveys carried out by Stanbury *et al.* 2000 and 2005. The circled area is the study site in the western part of Salisbury Plain. Based on [2011, Salisbury Plain – West, 1:25,000]. Map produced on behalf of The Controller of Her Majesty’s Stationary Office © Crown Copyright. Lancaster University, Bailrigg, Lancaster, OS Licence No. 100028811.

The majority of the study area is classified as agriculturally unimproved grassland (Walker & Pywell 2000; Figure 2.2), mainly *Bromus erectus* grassland with *Festuca rubra - Festuca arundinacea* sub-community and *Arrhenatherum elatius* grassland with *Festuca rubra* sub-community (Rodwell 1992). In some areas there is also scattered scrub and small blocks of plantations created for military training, but these covered less than 4% of the total study area. Low level grazing was reintroduced to parts of the plain around 1995 to prevent excessive scrub encroachment but, prior to this, the area was un-grazed for over 50 years (Stanbury *et. al* 2002; Ash & Toynton 2000). All land management on the site is strictly controlled by the Defence Estates to limit any potential impacts on the fauna and flora (Ash *et al.* 2011; Ash & Toynton 2000). Some grazing by cattle and sheep occurs year round. Grazing is limited to 10-14 days on areas of 8.2 ha or when the sward height reaches 5 cm (Ash & Toynton 2000). Fertilisers are not allowed on the majority of the study area. Mowing is restricted to a few small fields on the edge of the study area and none is allowed until after the 1st July to minimise the impact on breeding birds (Ash & Toynton 2000).

Some preliminary work was undertaken in three valleys in the study area in 2010 and 2011 (Figure 2.3: Berril, K-crossing, Imber; Henderson, I. pers. comm.), and focused on colour-ringing Whinchats, and finding and monitoring nests. These three valleys, along with two others (Figure 2.3: Southdown Track and West Hill), were selected for more intensive study including territory mapping, nest monitoring and habitat sampling. The two additional valleys were chosen because preliminary surveys in 2010 and 2011 suggested they supported large populations of Whinchats and they were relatively easy to access. In 2013 and 2014, due to a reduced number of breeding pairs in the five sites already established, an additional site, Ic Valley (Figure 2.3), was also studied.

Figure 2.2. View across Salisbury Plain

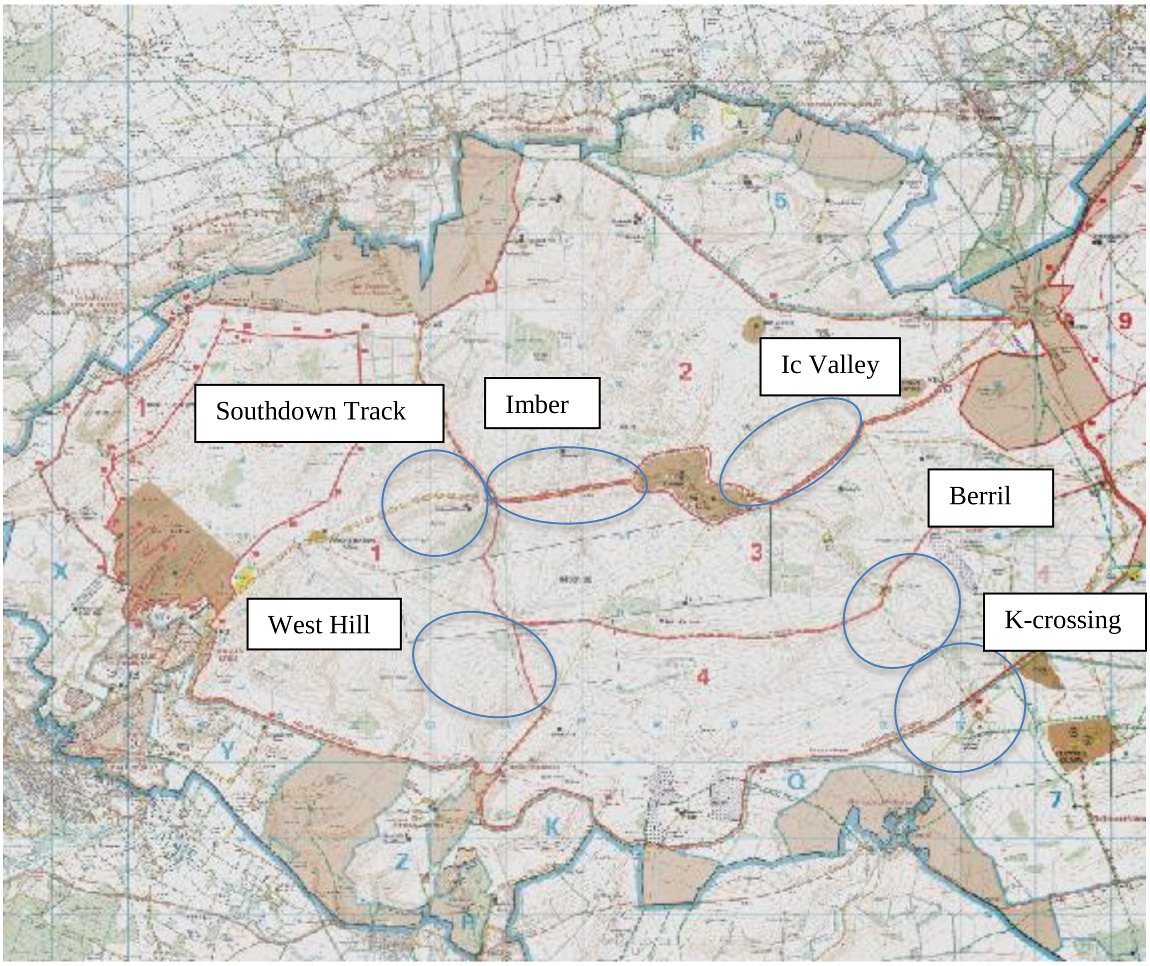


Figure 2.3. A map of the study sites. Total Map Area = 15km by 12 km. Based on [2011, Salisbury Plain – West, 1:25,000]. Map produced on behalf of The Controller of Her Majesty's Stationary Office © Crown Copyright. Lancaster University, Bailrigg, Lancaster, OS Licence No. 100028811.

2.2.1 The Salisbury Plain population is stable relative to the UK trend

A large, relatively stable population of Whinchats persists on Salisbury Plain. Figures 2.4 and 2.5 compare the population trend in UK Whinchats between 1994 and 2013 (Figure 2.4) and the population trend for the west of Salisbury Plain from three surveys carried out in 2000, 2005 and 2012-2013 (Figure 2.5). The UK Whinchat population has declined by 57% between 1994 and 2013 whereas the Salisbury Plain population has remained stable: population estimate in 2000 = 402 (95% CI: 234 - 613) (Stanbury *et al*. 2000), population estimate in 2012 – 2013 = 411 (95% CI: 263 - 644)). See section 2.2.2 for details on how the 2012 – 2013 distance estimate was calculated.

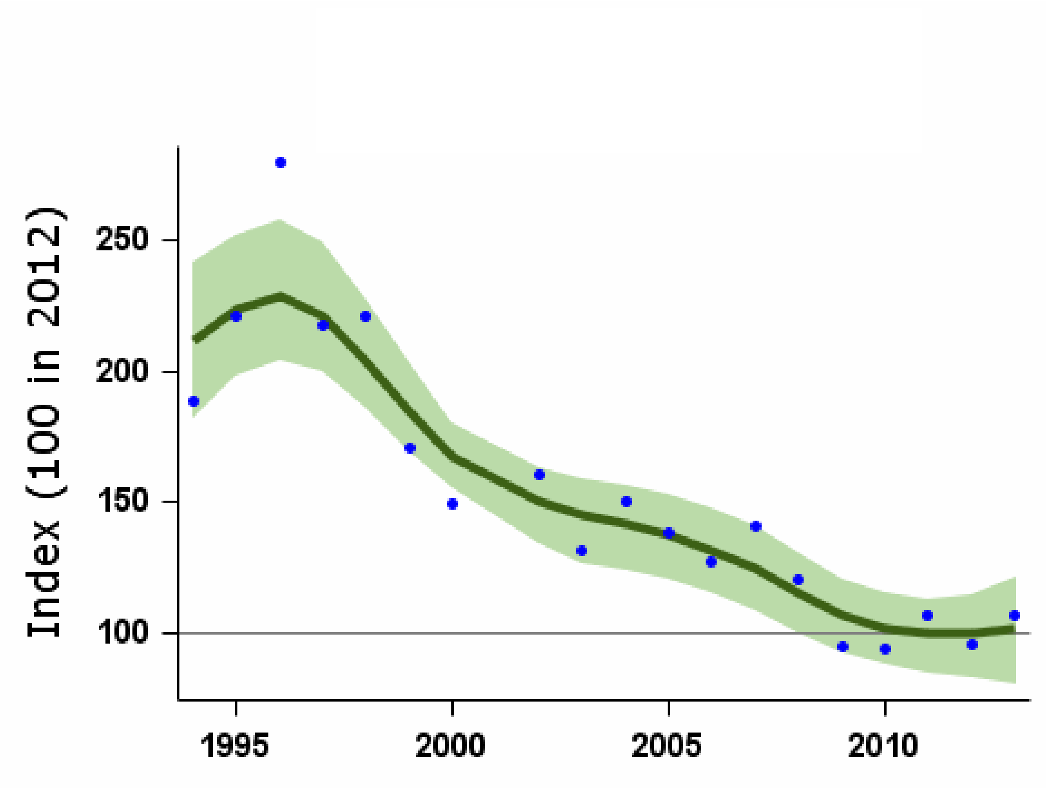


Figure 2.4. Figure of the yearly UK Breeding Bird Survey estimates of the Whinchat population size from 1994 – 2013 taken from Baillie *et al.* (2014), available at: http://blx1.bto.org/birdtrends/species.jsp?year=2014&s=whinc. The green band depicts the 85% confidence intervals, the dots are the population estimates for each year and the solid line depicts the smoothed population trend. The population size for each year is shown relative to 2012, which is set at 100.

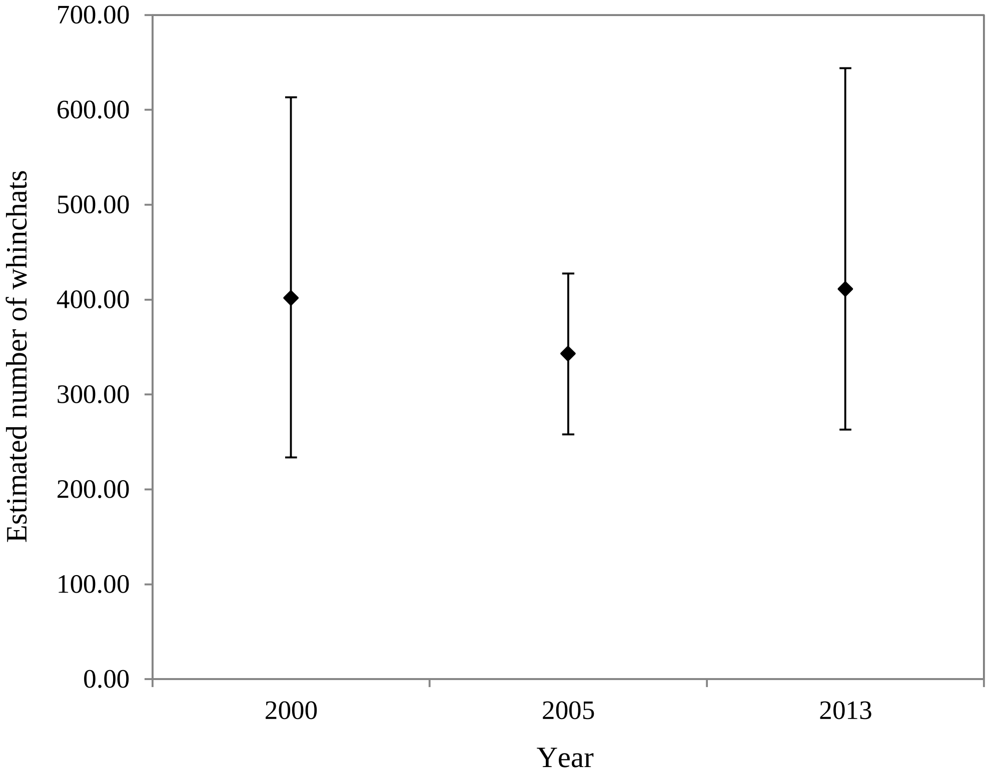


Figure 2.5. The predicted number of Whinchats in 92.76 km^2 of the west of Salisbury Plain during 2000, 2005 and 2012 – 2013. Predictions are based on distance adjusted estimates of density (km^{-2}) (Thomas *et al.* 2010). The 2000 and 2005 results come from Stanbury *et. al.* (2000, 2005); 45 one-kilometre British National Grid squares in the west of the Plain were surveyed using Breeding Bird Survey methods (Norman *et al*. 2012). The 2012 – 2013 results are from a survey using the same methods sampling 33 one-kilometer squares in the west of the Plain (see section 2.2.2). The dots mark the population estimates from the three surveys and the bars are the upper and lower 95% confidence intervals derived from 999 bootstrapped resamples.

2.2.2 Large scale surveys to assess the population size

During 2012 and 2013, 33 one kilometre by one kilometre squares were selected for surveying; one of these squares was covered by a local volunteer. Squares were selected to give a good coverage of the west of Salisbury Plain and include the six study sites. The original bird surveys undertaken by Stanbury *et al.* (2000, 2005) covered 45 one kilometre by one kilometre squares. The survey in 2012 – 2013 covered 70% of this area.

The surveys in 2012 – 2013 followed the same methodology as Stanbury *et al*. (2000, 2005), and were based on the British Trust for Ornithology's Breeding Bird Survey (Gregory & Bashford 1996). Two one kilometre line transects (500 m apart) in each one kilometre by one kilometre square were walked at a slow constant pace (30 – 40 minutes per transect), in good visibility, between 6:00 – 10:30 in the morning and 16:30 – 19:30 in the evening. The orientation of the lines (east to west or north to south) was randomly assigned. The first visit took place between 20th May – 3rd June in 2012 and the 20th May – 26th May in 2013. The second visit, between the 8 – 11th July in 2012 and 3 – 7th July in 2013, accounted for any movement of Whinchats due to the loss of first broods. All Whinchats seen or heard during the transect were recorded along with their perpendicular distance from the transect line. Distances were estimated by eye. To ensure accuracy, a sample of distance estimates were initially tested used a hand held GPS device (Garmin exTrex).

Distance version 6.0 (Thomas *et al.* 2009) was used to calculate the population size of Whinchats on the whole west of Salisbury Plain. For each 200 m section of the one kilometre transects, the maximum recorded number of Whinchats on a single visit was used in the analysis. This value was chosen, rather than the mean of the two visits, to follow the same methods that Stanbury *et al.* (2000, 2005) used for the other two surveys. Using only the second visit would have missed pairs that finished breeding early and using only the first visit may have missed late arrivals. The data were truncated, so that only Whinchats observed within 250 m were used to increase the precision of the detection function (Thomas *et al.* 2010). Three models were compared using AICc: a half-normal key with cosine adjustments (AICc = 142), a uniform key with cosine adjustments (AICc = 144) and a hazard-rate key with simple polynomial adjustments (AICc = 146). A half-normal key with cosine adjustments was the best fitting model. To ensure the distance adjusted estimates were accurate, distance estimated Whinchat numbers for 10 one kilometre survey squares that covered the four main study sites in 2012 (Imber, Berril, West Hill and K-crossing) were compared to the number of Whinchats determined from intensive surveys within these sites in the same year (see Chapter 7 for details on study site survey effort each year). The correlation from the graph does not appear strong (Figure 2.6). However, the Whinchat counts from the intensive surveys and the distance surveys were significantly correlated (PMCC = 0.638, p = 0.047, n = 10) and the relationship between the variables did not deviate significantly from 1:1 (T-test: t = 0.591, df = 9, p = 0.569; Figure 2.6). This suggests the distance estimates performed relatively well, though were not as accurate as the intensive surveys when applied at the smaller scale of a one kilometre by one kilometre square.

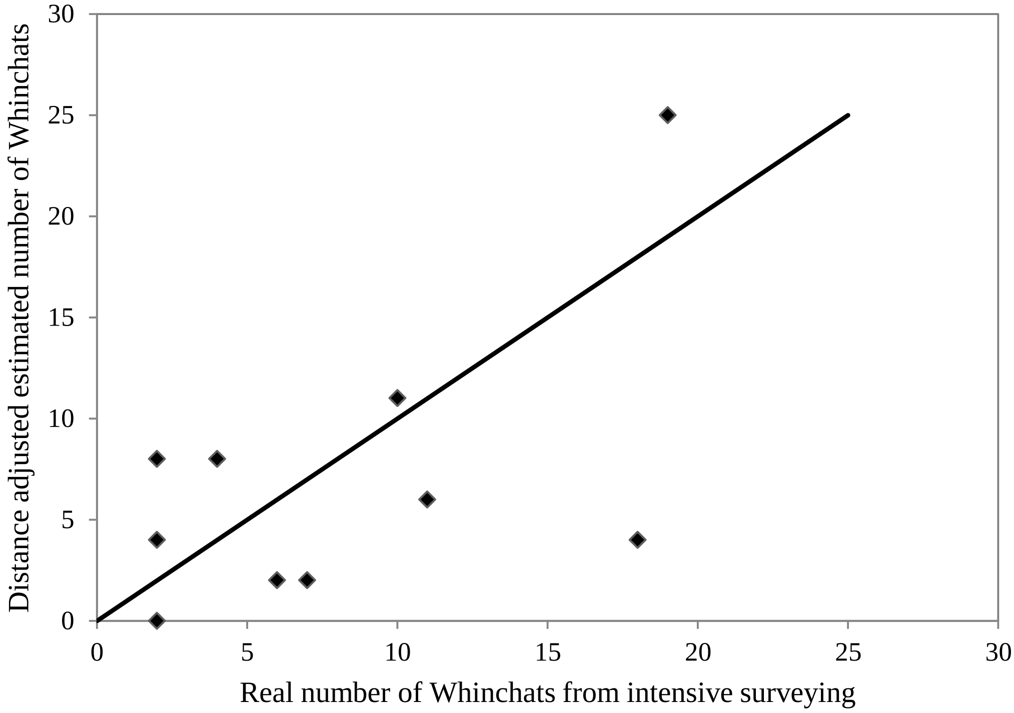


Figure 2.6. Verification of distance adjusted estimates of Whinchat abundance: comparing number of Whinchats estimated to occur in 10 one kilometre by one-kilometre squares from distance adjusted estimates of transect surveys in 2012 to the real number of Whinchats known to be within the squares from regular intensive surveying throughout 2012 (T-test: t = 0.591, df = 9, p = 0.569). The line is a 1:1 line.

2.3 Nest finding and monitoring

Nests were found for all known pairs within the study sites. Nests were found by observing breeding pairs from a distance, using RSPB optics binoculars (10 x 42 HD) and a Leica telescope (25 – 60 x 65). The location where females were nest building or incubating was then determined. This location was approached and marked with a cane. UK Ordnance Survey coordinates were recorded for each nest site to the nearest 1 m using a hand held GPS device (Garmin exTrex). Figure 2.7 shows two Whinchat nests. Generally nest were monitored at least every two days until failure or fledging. However, occasionally due to access restrictions this was not possible, therefore the visitation intervals varied between one to five days (mean 2.85 +/- 0.02 days). A nest was considered as failed due to predation if the contents had disappeared or the eggs were damaged, and was considered abandoned if the parents were not present in the territory on three consecutive visits and the eggs were cold but undamaged or the nestlings were dead. Nests designated as abandoned may also include cases where parents were predated as it was not possible to separate these two scenarios. A nest was considered successful if at least one nestling fledged.

a)

b)

Figure 2.7. Two Whinchat nests, the arrows mark the nest. In b) the woody cane used to mark the nest is also shown to the right of the arrow.

2.4 Biometrics

During the 2010-2014 breeding seasons (May – July), as many adults as possible that bred within the six study sites were caught and individually marked with colour rings. Whinchats were trapped before breeding and during the incubation and nestling rearing phases but not during nest building and egg laying. Whinchats were caught mainly using baited spring traps located within their breeding territory, and for each bird their sex, age (Jenni & Winkler 1994; Svennson 1992), wing length (mm), fat and muscle scores (Redfern & Clark 2001) were recorded (Table 2.1). Nestlings were weighed and the tarsus measured at three time intervals (unless predated), 3, 6 and 9 days after hatching, with day zero referring to the hatching date, although due to occasional access restrictions or inclement weather, this occurred a day either side in a minority of cases.

2.4.1 Ageing and sexing Whinchats

Male Female

Figure 2.8. Picture of a male and a female Whinchat (RSPB 2015: https://www.rspb.org.uk/discoverandenjoynature/discoverandlearn/birdguide/name/w/whinchat/).

Sexing adult Whinchats is relatively simple, the males are darker with a redder breast and a sharper contrast between the eye stripe and the rest of the face (Figure 2.8). There is little difference in male and female size and weight (males: mean wing = 76.4 +/- 0.193 mm, mean weight = 15.4 +/- 0.130 g, females: mean wing = 73.7 +/- 0.241 mm, mean weight = 15.5 +/- 0.171). It is not possible to sex fledgling Whinchats based on appearance.

Ageing Whinchats is notoriously difficult (Jenni & Winkler 1994; Svennson 1992). Adults exhibit a complete moult before migration, whereas juveniles only exhibit a partial moult. Both adults and birds in their first year also exhibit a partial moult on the wintering grounds before returning to breed (Svennson 1992). Ageing criteria for birds in their first breeding year are: the moult limit in the greater coverts between changed inner greater coverts and retained outer greater coverts (shown by 76% of first-years), a moult limit in the median coverts, and wear on the remiges or rectrices (Jenni & Winker 1994; Svennson 1992). The majority of Whinchats were aged retrospectively using a photo taken of the right wing to avoid a lengthy handling time.

a)

b)

Figure 2.9. a) A male Whinchat in his first breeding year, the moult limit is circled, b) a male either in his second breeding year or older.

Table 2.1. Biometrics taken from Whinchats

Measurement	**Method**
Wing (adults and first-years only)	Wing length: the distance from the carpal joint to the tip of the longest primary on a flattened wing measured using a stop rule
Weight (± 0.05g)	Measured using a battery powered, digital pan balance. The birds were placed in a small pot while weighing to prevent escape
Minimum Tarsus (± 0.05mm)	Distance between the depression in the intertarsal joint, “notch” to the tarso-metatarsal joint
Fat Score (adults and first-years only)	Scored between 0-8, (0=none, 8=overflowing), see Redfern & Clark 2001, p227-228
Pectoral Muscle Score (adults only)	Scored between 0-3, (0=little muscle, 3=thick muscle), see Redfern & Clark 2001, p229-300

2.4.2 Nestling growth curve

To estimate nestling age for nests which were found after the hatching date, a growth curve model was created for nestlings where the exact hatching date was known. The data were modelled in R version 2.3.1 (R development Core Team 2014) using a Non-linear least squares model (NLS) of a logistic growth curve:

$$\mathrm{a}/(1+\exp(-\mathrm{k}\ \times(\mathrm{age}-\mathrm{b})))$$

a= asymptote, b = inflection point on the age axis where growth changes from accelerating to decelerating, k = constant scale parameter for rate of growth (Ricklefs 1998; Bastian & Bastian 1993; Remes & Martin 2002; Mainwaring *et al*. 2011).

Models were created separately for nestling mass and tarsus length. Starting values for the model were estimated from plotting the initial curve of nestling mass (g) against age: a = 16, b = 6, k = 0.4 and nestling tarsus length (mm) against age: a = 18, b = 5, k = 0.4 (Table 2.2; Figure 2.10).

The two growth curve models, along with observations on feather development and eye status (closed, opening, open) (King & Hubard 1981; Murphy 1981; Jongsomjit *et al.* 2007), were used to age nestlings found after hatching, as using a combination of features is the most reliable method of ageing (King & Hubard 1981; Murphy 1981; Lepczyk *et al.* 2000; Podlesak & Blem 2002; Jongsomjit *et al.* 2007).

Table 2.2. NLS model of a) the change in nestling weight (g) and b) the change in nesting tarsus length (mm) with age, using 252 measurements from known age nestlings. The weight model has the formula: Nestling Weight (g) = 17.3 / (1 + exp (-0.53 × (Nestling Age – 4.12))), starting values: a = 16, b = 6, k = 0.4. The tarsus model has the formula: Nesting Tarsus (mm) = 24.8 / (1 + exp (-0.39 × (Nestling Age – 3.63))), starting values: a = 18, b = 5, k = 0.4.

a) Nestling Weight (g)	Parameter Estimates
Constant scale parameter for growth rate (k)	0.53 +/- 0.033
Inflection point (b)	4.12 +/- 0.131
Asymptote	17.3 +/- 0.381
b) Nesting Tarsus (mm)	
Constant scale parameter for growth rate (k)	0.39 +/- 0.027
Inflection point (b)	3.63 +/- 0.165
Asymptote	24.8 +/- 0.639

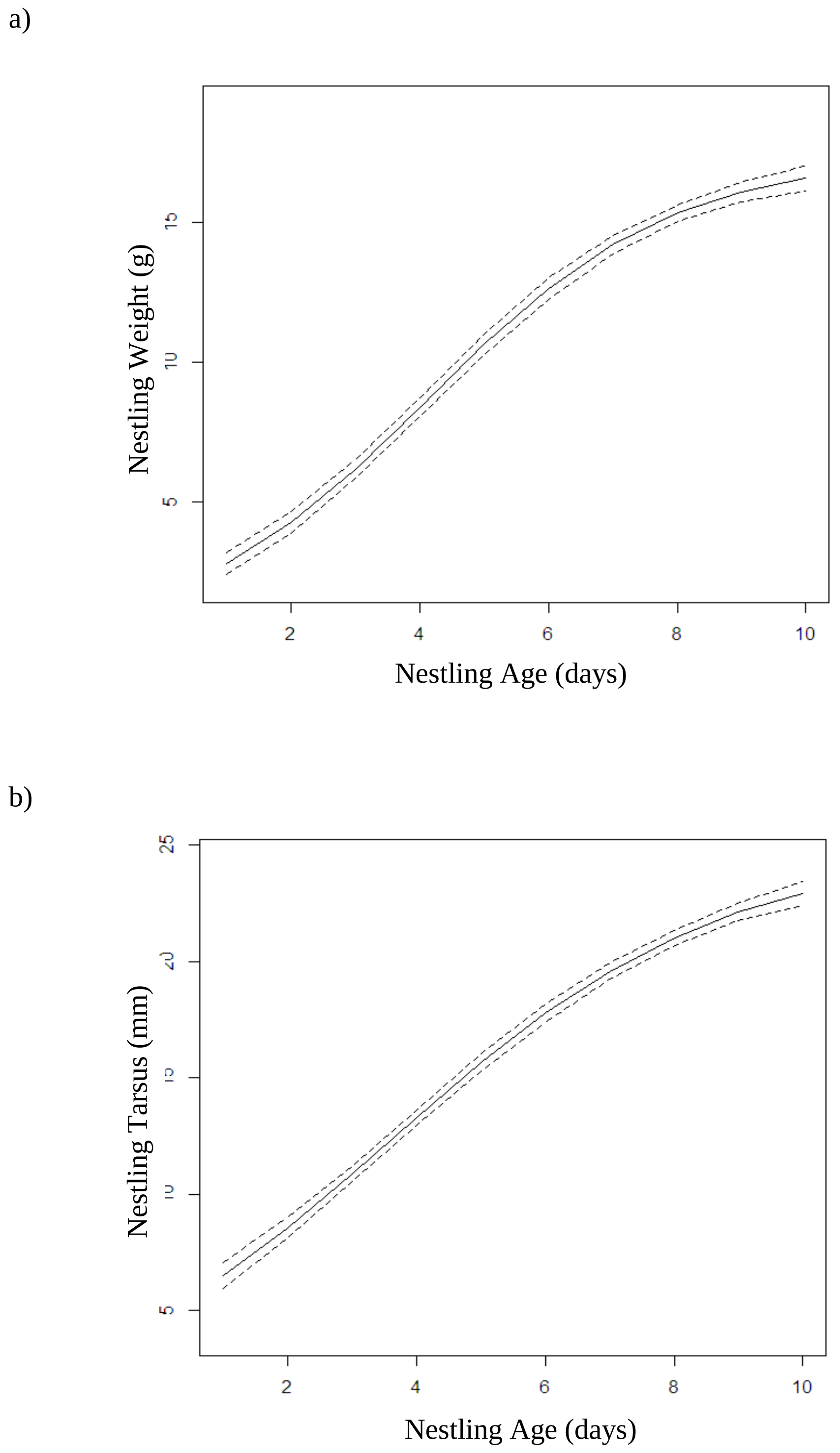


Figure 2.10. a) Growth curve of increasing nestling mass (g) with age (days), b) Growth curve of increased nestling tarsus length (mm) with age. Based on 252 measurements from known age nestlings. The weight model has the formula: Nestling Weight (g) = 17.3 / (1+ exp (-0.53 × (Nestling Age – 4.12))), starting values: a = 16, b = 6, k = 0.4. The tarsus model has the formula: Nesting Tarsus (mm) = 24.8 / (1 + exp (-0.39 × (Nestling Age – 3.63))), starting values: a = 18, b = 5, k = 0.4.

2.5 Effective sampling of Whinchat habitat requirements

2.5.1 Effective vegetation sampling

In Chapter 3, vegetation was measured for 317 200 m long transect sections. Initially in 2012 three quadrat samples of the vegetation and three sweep net samples of the invertebrate fauna were taken per 200 m section for 187 200 m sections. However, it was thought that this may not be enough to capture all the variation in a 200 m section. To test this, the sample size was doubled and six samples instead of three were taken for each of the first 10 transect sections sampled in 2013. In the program R, version 2.3.1, (R core Development team 2014), diminishing returns curves were created for each measured vegetation variable for each of the 10 sections by randomly sampling the collected data with replacement 1000 times for each of a range of sample sizes (2, 3, 4, 5, 10, 15, 20), for each of the 10 transect sections. The mean and standard error of these 1000 random samples for each sample size were calculated and the standard error plotted to create the diminishing returns curve (e.g. Figure 2.11) (Lowry 2013). The diminishing returns curves suggested that 10 – 15 samples would be needed to capture all the variation for every vegetation variable within a 200 m section. It was, however, not possible in the time available to complete this many samples per 200 m section and still ensure a good survey coverage of the sites for arriving Whinchats. Therefore as a compromise between effective sampling and time available, six samples were taken for every 200 m section in 2013, which took about six hours per ten 200 m sections.

The same analysis was conducted using the habitat data collected from Whinchat territories. The diminishing returns curves suggested that five samples would be sufficient to capture the majority of the variety in the measured vegetation characteristics; therefore, I am confident that the nine samples taken for each territory effectively sampled the vegetation.

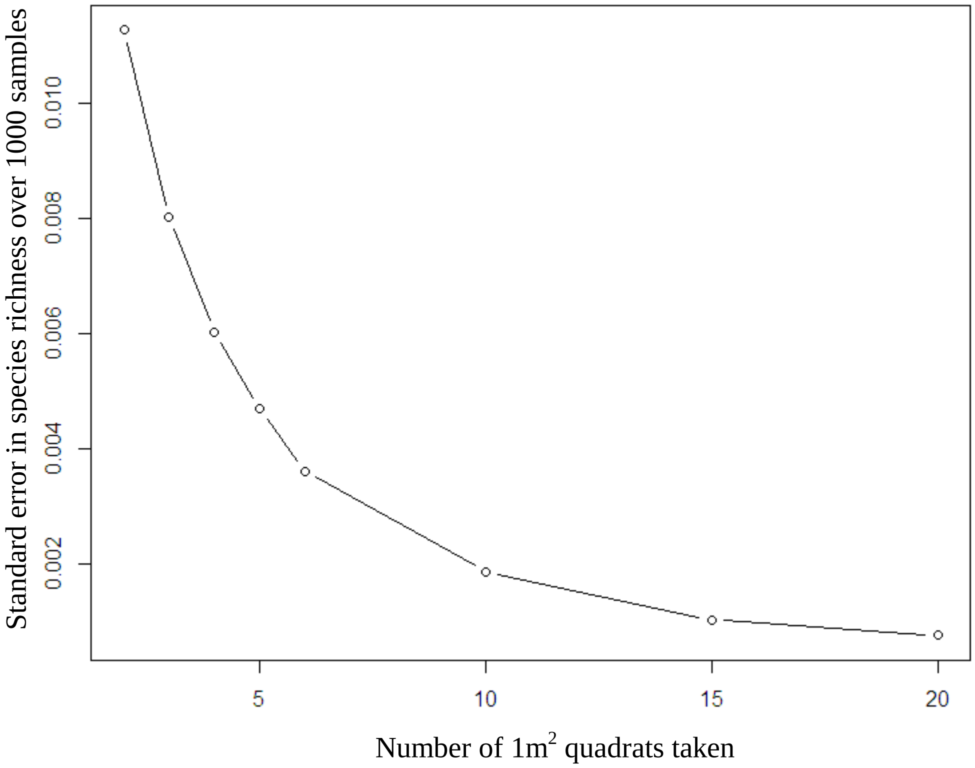


Figure 2.11. Example of a diminishing returns curve for the variation in the plant species richness count within a 200 m section with increasing numbers of quadrat samples taken. The standard error of 1000 randomly selected samples of 2, 3, 4, 5, 6, 10, 15 and 20 (from the original data with 6 samples per section), is plotted.

2.5.2 Effective food sampling

In 2012, faecal samples were collected as the opportunity arose from nestlings while weighing and measuring. Eighty-five samples were collected from 26 nests. These samples were stored in ethanol for later examination under a low-power binocular microscope (using guidance from Moreby 1988 and Davies 1977). Additionally, a video camera on a tripod was placed 1 m from the nests, pointing at a perch used by parents before entering the nest with a feed. A total of 246 feeds from 13 nests were captured on video. Prey items were identified by freezing the video and using an insect identification guide (Chinery 1986) and advice from an entomologist (pers. comm. Tomazella, V.). The information on nestling diet obtained via these methods is presented in Table 2.3.

In 2012, invertebrates were sampled with a Vortis suction sampler (Burkland Ltd, Rickmansworth, UK) using 12 second suction bursts, with three samples per transect section (Chapter 3) and nine samples per territory (Chapter 5). These samples consisted mostly of *Collembola* and *Acari*, which do not form a large proportion of the nestling diet (Table 2.3), and were heavily skewed towards insects less than 2 mm which, again, would not be expected to form a large component of the nestlings' diet (Britschgi *et al.* 2006; Pudil & Exnerovà 2015; Koce 2015). After 2012, therefore, the method of sampling invertebrate food availability was changed to sweep netting, which was more effective for sampling the invertebrates observed in the diet (pers. obs. and see Doxon *et al.* 2011). Only the 2013 and 2014 invertebrate sampling data are used in the analyses. The invertebrate sampling data were summarised in three measures: overall abundance, order richness and inferred biomass. Inferred biomass was estimated from body length in millimetres (L) using a formula from Rogers *et al.* (1976): Weight (mg) = $0.0305L^{2.62}$. The body length was taken to be the length of the main body of the insect, excluding antenna or other protrusions. Invertebrates were measured in the field, and assigned to size categories in 2 mm bands: 0 – 2 mm, 2 – 4 mm, etc. The median length for each of these size categories (i.e. 1, 3, 5 etc.) was multiplied by the number of insects in the size category and these values were summed to give an inferred biomass value for each sample.

Table 2.3. The percentage of nestling faecal samples (collected in 2012) containing different invertebrate orders, n = 85 from 26 nests, and the percentage of feeds from provisioning parents (recorded in 2012) containing different invertebrate orders from video footage taken at the nest for comparison, n = 246 from 13 nests.

	% of nestling faecal samples containing each invertebrate order	% of provisioning feeds containing each invertebrate order
Coleoptera	97.7%	33.1%
Araneae	62.4%	18.4%
Lepidoptera	38.8%	8.57%
Hymenoptera Larvae	32.9%	-
Diptera	28.3%	16.7%
Eggs	25.9%	2.04%
Lepidotera Larvae	16.5%	11.4%
Orthoptera	11.8%	10.2%
Pulmonata	8.24%	0.41%
Hymenoptera	5.88%	4.49%
Acari	5.88%	0.41%
Collembola	3.53%	
Coleoptera Larvae	3.53%	-
Neuroptera	2.35%	-
Cicadellid	2.35%	-
Hemiptera	-	1.22%
Dermaptera	-	0.41%

Chapter 3. Habitat selection by breeding Whinchats on lowland grassland

An adult male about to feed his nestlings

3.1 Abstract

Habitat degradation is thought to be the most important breeding ground influence on migrant population change. To determine the impacts of habitat change on a population, and suggest appropriate conservation action, we first have to identify which habitat features they require. Previous studies have identified habitat features which are linked to Whinchat habitat preferences. However, these have been limited to areas which have already undergone change, due to agricultural intensification, and so they may not represent the full range of habitat features that might influence breeding Whinchats. Salisbury Plain is the largest area of unimproved chalk grassland in northwest Europe. Due to its role as an army training ground it has escaped much of the agricultural intensification that has affected the rest of the UK. In this chapter, I aim to explore the habitat requirements of breeding Whinchats on a site where habitat choices have not been restricted by recent habitat change. The vegetation and invertebrate food availability of 317 200 m sections of habitat were assessed and an index of Whinchat abundance in these areas was determined. Additionally, the consistency of territory occupation from 2012 to 2013 was determined and linked to the variation in vegetation between territories. Breeding Whinchats selected sheltered valleys, with a high percentage cover of tall, dense, structurally diverse grassy vegetation and a high density of tussocks. They also preferred areas with an abundance of perches from which to forage. On Salisbury Plain, invertebrate abundance, diversity and biomass did not differ between areas with Whinchats and areas without, suggesting invertebrate availability was not limiting. Whinchats did, however, tend to select areas with less variation in insect abundance, diversity and biomass, suggesting a preference for a consistent food source. Habitat choices for nesting Whinchats were thought to minimise thermoregulatory costs and predation risk to both incubating females and the nest contents.

3.2 Introduction

Over the past three decades, the populations of many species of Afro-Palearctic migrant birds have shown severe declines, compared to populations of ecologically similar and closely related sedentary species (Berthold *et al*. 1998; Sanderson *et al.* 2006; Newton 2004a, 2008; Heldbjerg & Fox 2008; Van Turnhout *et al.* 2010). A recent review by Vickery *et al.* (2014) found that the most important breeding ground influence on Afro-Palearctic migrants' population size was habitat change. Habitat change can cause population declines either directly, via loss of nesting habitat (e.g. Newton 1998; Malpas 2013a) or indirectly, via reductions in food availability (e.g.

Schmidt *et al.* 2005; Britschgi *et. al.* 2006) and increases in the risk of predation (e.g. Ejsmond 2008) and parasitism (Newton 1998, 2004a, 2008). Agricultural intensification is frequently cited as the cause of breeding ground habitat change (Donald *et al.* 2006; Thaxter *et al.* 2010; many examples reviewed in Vickery *et al*. 2014). In Europe, the global area of cropland has increased 5.5 fold between 1700 and 1990, while pasture has increased 6.6 fold (Goldewijk 2001). Many Afro-Palearctic migrants choose open habitats, such as agricultural land, for breeding whereas residents and short distance migrants do not show this preference (Bohning-Gaese & Oberrath 2003). They may, therefore, be disproportionately affected by European agricultural intensification (Vickery *et al.* 2014). Successive governments have pledged to halt the decline of biodiversity throughout the European Union (2002 UNEP/CBD/COP 6 Decision VI/26) and to conserve migratory species (UNEP / CMS 2014). Accordingly, a range of agri-environment schemes aimed at reducing the declines of farmland biodiversity have been compulsory in European Union member states since Regulation 1257 in 1997. In order to focus conservation action and ensure the best use of limited funds, it is necessary to identify a breeding species' key habitat preferences and requirements.

Selection of a good breeding territory is particularly important as once a bird has built a nest and laid eggs it is tied to that area until its breeding attempts either fail or succeed (Anteau *et al.* 2012). A breeding territory encompasses the nesting site and foraging area: these two components may have different requirements. A nest site should provide a suitable microclimate and an environment to minimise predation risk (Gillis *et al.* 2012). Often both these features cannot be optimised simultaneously (Amat & Masero 2004) and parents must engage in a trade-off to maximise the chances of the current brood fledging without compromising the production of future offspring (Trivers 1974; Robertson 2009; Seltmann *et al.* 2014). In ground nesting birds especially, higher concealment by increased vegetation may reduce the risk of a nest being detected and improve thermoregulatory ability, but often makes it more difficult for the adult to see predators and to escape quickly (Ost & Steele 2010; Seltmann *et al.* 2014). A similar trade-off exists for foraging habitats, with short vegetation increasing foraging efficiency and reducing predation risk by improving visibility, whereas longer vegetation is associated with higher food abundance but a greater predation risk (Whittingham & Evans 2004). Individuals under selection to maximise their fitness have to balance these various costs and benefits to select the optimal breeding territory (Martin 1998).

Habitat change can create conditions different from those under which the species evolved, meaning that specific resource cues used in habitat selection may no longer maximise fitness and reproductive success, and so create an 'ecological trap' (Misenhelter & Rottenberg 2000;

Anteau *et. al* 2012; Hollander *et. al* 2013). This can even occur within a breeding season with no prior warning. For example, a switch from hay to silage production could result in the mid-season mowing of meadows, bringing with it the associated high mortality of nesting females and nestlings (Müller *et al.* 2005; Grüebler *et al.* 2008; Tome & Denac 2012; Broyer *et al.* 2012; Grüebler *et al*. 2015). Additionally, habitat change may mean that individuals cannot display their true preferences because the optimal habitats are rare or absent. It is important to understand evolved habitat cues to prevent the creation of ecological traps and to encourage species towards suitable breeding habitats in a changed environment (Anteau *et al.* 2012).

The ground nesting Whinchat is one example of a declining Afro-Palearctic migrant that was once common across Europe. It has declined by 67% between 1980 and 2009 (EBCC 2012) and this is mainly thought to be due to agricultural intensification on the breeding grounds (Grötenhuis & Van Os 1986; Bastian 1989; Richter & Düttmann 2004; Grüebler *et al.* 2008; Broyer 2009; Fischer *et al* 2013). Various studies have looked at Whinchat habitat preferences in the breeding grounds and identified important features (Opperman 1990; Oppermann 1992; Bastian *et. al.* 1994; Bastian & Bastian 1996; Orlowski 2004; Richter & Düttmann 2004; Müller *et al.* 2005; Britshgi *et al.* 2006; Frankiewicz 2008; Broyer 2009; Grüebler *et al*. 2012; Fischer *et al.* 2013). However, most of these studies have worked on declining Whinchat populations in agricultural areas (albeit of different management intensities). It is therefore possible that some habitat features that would be beneficial to Whinchats were unavailable due to the effects of agricultural intensification.

Different populations may live in habitats of varying qualities which can affect their vulnerability (Both *et al.* 2010). It is possible to use this variation within a species to find stable local populations which have not suffered from habitat change, from which to draw conclusions on beneficial habitat features that may be missing in declining populations. In order to uncover the naturally evolved resource cues Whinchats use when selecting breeding territories, here we study an apparently stable (section 2.2.1) stronghold Whinchat population on an agriculturally unimproved grassland site, Salisbury Plain. Salisbury Plain has been under military ownership since 1897 and consequentially has escaped much of the agricultural intensification that has affected the rest of the UK (section 2.2). Despite the habitat quality, past surveys (Stanbury *et al*. 2002 & 2005), revealed variations in breeding densities of Whinchats, which imply settlement decisions are not random but must be based on habitat quality or biological factors such as conspecific attraction. If habitat quality is the main settlement cue this implies variations in food availability or variation in habitat structure, composition and extent. Using this natural variation in habitat provides an opportunity to examine what resource cues Whinchats are selecting in a habitat similar to the pre-decline habitat.

In this Chapter, we intend to uncover the naturally evolved resource cues used by Whinchats when selecting breeding territories in agriculturally undeveloped grassland habitat. Invertebrate fauna and vegetation and topography features were measured for a sample of line transects and the same areas were surveyed for Whinchats. Additionally, vegetation and topography features from known Whinchat territories in 2012 were assessed at the beginning of 2013 and surveyed to determine which of the territories were occupied again by Whinchats. The differences in habitat features between areas with Whinchats and areas without were assessed. Whinchats need a good source of food close to the nest when breeding (Andersson 1981), and they are single brooded, with a short breeding season, suggesting they may be more vulnerable to fluctuations in food availability than closely related multi-brooded species (Henderson *et al.* 2014). To maximise reproductive success during their short breeding season, Whinchats would also be expected to select breeding habitat to reduce thermoregulatory stress and minimise predation risk (Gillis *et. al* 2012). Based on findings from previous studies, I predict that Whinchats will select breeding territories with thicker more structurally diverse vegetation, more perches and a higher food supply (Opperman 1990; Oppermann 1992; Bastian *et. al.* 1994; Orlowski 2004; Richter & Düttmann 2004; Fischer *et al.* 2013). The null hypotheses may expect no significant association with food or habitat, particularly if neither was currently limiting breeding densities at this site.

3.3 Methods

3.3.1 Study area

The study site was an area of 92.76 km^2 in the west part of Salisbury Plain (see section 2.2 for more details).

3.3.2 Survey design

Within the site, 32 one-kilometre British National Grid squares were selected for surveying over a two year period: 2012 and 2013. Squares were selected from the map before visiting the site to ensure a balance between a good coverage of the area and accessibility. The surveys consisted of two one-kilometre transect lines from each grid square, positioned 500m apart, based on the British Trust for Ornithology’s Breeding Bird Survey design (Gregory & Bashford 1996) (Figure 3.1). The orientation of the lines (east to west or north to south), was randomly assigned. Each transect line was then further split into 200 m sections. A handheld Global Positioning Systems (GPS) device (Garmin eTrex) was used to navigate each transect.

Vegetation, invertebrate fauna, topography and Whinchat abundance were sampled for each 200 m section. The features of habitat measured were selected based on results from previous studies of Whinchat habitat preferences to cover all possible important variables. All vegetation and invertebrate measures were carried out by the same observer for consistency. A small proportion of the bird surveys were conducted by other observers but all observers were experienced bird surveyors.

Vegetation was also sampled for known Whinchat territories from 2012, at the beginning of 2013. These territories were then surveyed throughout the 2013 season to record occupation of the same area by breeding Whinchats.

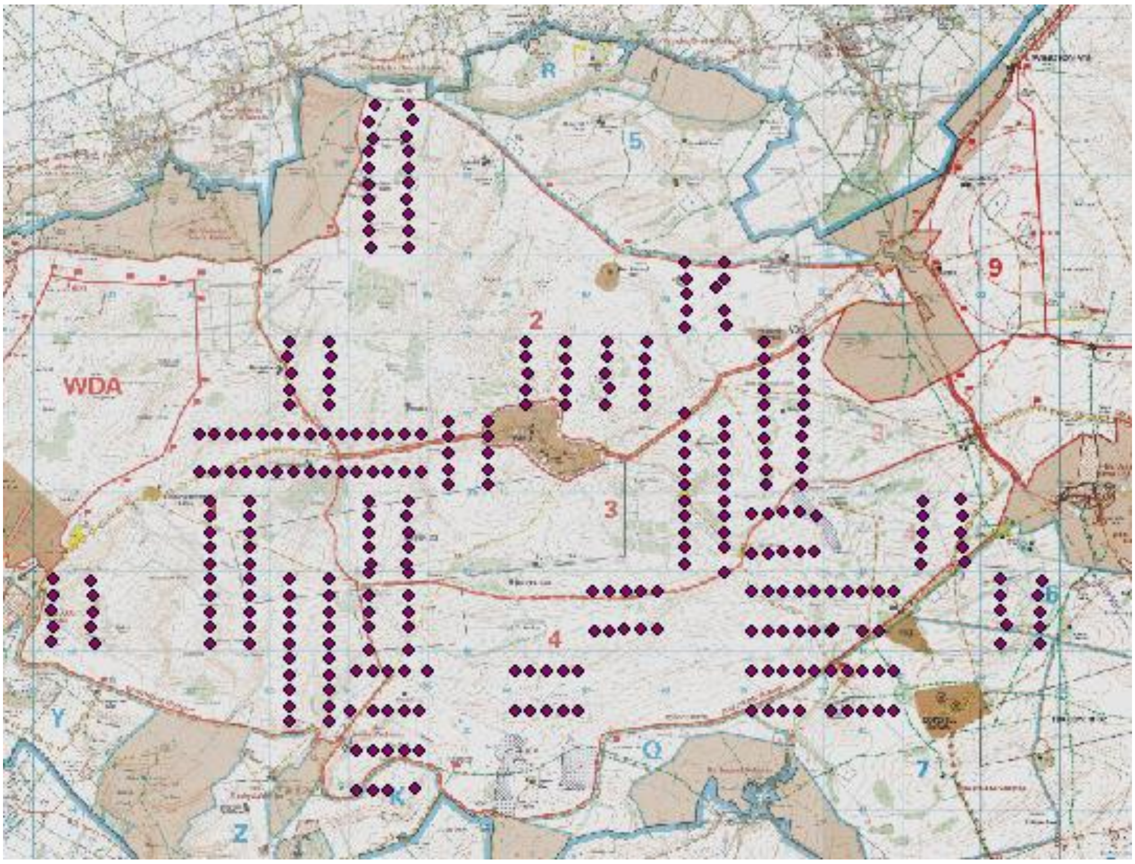


Figure 3.1. Lay out of the survey design. The dotted lines show the transect lines for each square. The map covers an area of approximately 11 km by 14 km. Based on [2011, Salisbury Plain – West, 1:25,000]. Map produced on behalf of The Controller of Her Majesty’s Stationary Office © Crown Copyright. Lancaster University, Bailrigg, Lancaster, OS Licence No. 100028811.

3.3.3 Vegetation sampling

Vegetation was sampled between 19thApril – 9th May in 2012 and 16th – 26th April in 2013 to coincide with Whinchat arrival and thereby reflect any habitat cues the Whinchats were selecting near to the time of settlement. Ten 200 m segments were sampled later on the 11th May due to access restrictions. In 2012, three 1m^2 quadrats were recorded at 0, 10 and 20 m from the start of each 200 m section. A diminishing return curve of the variance in the samples (Lowry 2013) suggested three samples were not enough to capture all the variation in a 200 m section (section 2.5.1). In 2013, therefore, the sampling effort was doubled to six samples, taken every 33 m. These replicates were averaged to give one mean value for each 200 m section. In total, ten vegetation characteristics were measured to capture the structure of the grassland (Table 3.1).

For known territories from 2012, vegetation was recorded in nine 1m^2 quadrats in 2013 between 27th April – 4th May. The centre quadrat was based on the nest location the previous year and then four quadrats at 20 m intervals were taken going north and west from the nest (20 – 80 m). The average size of a Whinchat breeding territory on agriculturally unimproved grassland is 0.015 – 0.018 km^2 (Bastian & Bastian 1996), which gives a radius of approximately 76 m, therefore this provides an appropriate scale at which to sample the vegetation to capture the habitat features important to breeding Whinchats.

Table 3.1. Vegetation variables measured for each 1 m^2 quadrat in 2012 and 2013, all measurements were observed by eye.

Variable	Definition
Plant species richness	Number of plant species when viewed from above
% Cover ground level	Percentage of ground covered with vegetation viewed from above
% Cover 20 cm above ground level	Percentage of vegetation cover 20 cm above ground viewed from above
% Grass to herb ratio	Percentage of grass relative to herb viewed from above
Mean vegetation height	The mean of 5 measurements taken (one in each corner of the quadrat and one in the centre). A plastic sward disk (weight 135 g, diameter = 20 cm) was dropped from a height of 1 m with a bamboo cane though the centre
Standard deviation (SD) in vegetation height	The standard deviation of 5 measurements taken (one in each corner of the quadrat and one in the centre). A plastic sward disk (weight 135 g, diameter = 20 cm) was dropped from a height of 1 m with a bamboo cane though the centre
Perch abundance	Number of perches in quadrat. A perch is any projection, above the height of the general vegetation that can support approximately 16 g (the mean weight of a Salisbury Plain Whinchat)
Minimum perch height	The height of the smallest perch in the quadrat measured from the ground vertically upwards
Maximum perch height	The height of the tallest perch in the quadrat measured from the ground vertically upwards
% Cover tussocks	Percentage of quadrat area covered by tussocks when viewed from above, a tussock is defined as a clump of grass

3.3.4 Invertebrate sampling

Invertebrates were sampled between 09:30 and 17:00 on days when the grass was dry and the wind speed was less than 12 mph (Beaufort scale 0 – 3). In 2012, invertebrates were sampled via a Vortis suction sampler (Burkland Ltd, Rickmansworth, UK) using three 12 second suction bursts at 0m, 10m and 20m from the start of each 200 m section. However, data on nestling diet in 2012, collected from video footage at nests and nestling faecal samples, demonstrated that this was not an effective method of sampling the Whinchats' diet. Sweep netting was tried and found to be a much more effective and efficient method (section 2.5.2). In 2013, invertebrate samples were taken using a sweep net (37 cm diameter by 82 cm) with 10 sweeps of an equal depth and intensity forming one sample. Invertebrates were sampled three times on three separate visits for each square, with samples taken at 0 m, 66 m, and 133 m from the start of each 200 m section. The order of sampling the survey squares was rotated to minimise bias. Time periods for the three survey visits were the 8th – 21st June, the 1st – 7th July, and the 15th – 20th July to capture the change in invertebrate fauna for each 200 m section through the season. Some 200 m sections were mown before the last visit in July, which drastically altered the habitat and led to a large reduction the number of invertebrates for these sections. Therefore these samples were not used in the analysis to avoid biasing the results. As this was only a small percentage of the total sample area (eight out of 390 200 m sections) any effect should be minimal. The invertebrate sampling data were summarised in three measures: overall abundance, order richness and inferred biomass (section 2.5.2).

3.3.5 Topography

UK Ordance Survey coordinates were taken from each 33 m sampling point in 2013 and at the beginning of each 200 m section in 2012 using a handheld Geographic Positioning System device (Garmin eTrex). These coordinates were used to calculate altitude, aspect and slope from the Digital Elevation Model (DEM; NERC Earth Observation Data Centre 2007; Redhead, J. Pers. Comm.).

3.3.6 Whinchat surveys

The Whinchat surveys aimed to establish a comparable index of abundance for each 200 m by 250 m section rather than provide an absolute value of population size. Each kilometre square was surveyed twice, the first visit being between 20th May – 3rd June in 2012 and 20th May – 26th May in 2013 and the second visit , between 8 – 11th July in 2012 and 3 – 7th July in 2013.

Surveys were conducted after the Whinchats had settled onto territories and therefore should reflect breeding habitat choices. The second visit allows sightings of any new Whinchats moving territories after a failed first nesting attempt. In 2012, surveys took place between 06:00-10:30 and 16:30-19:30; in 2013 surveys took place between 06:00 – 09:30. Surveys were only carried out in good visibility and the order of the surveys was rotated to ensure no bias. As the purpose of this analysis was to identify suitable areas of Whinchat habitat, the maximum count of Whinchats observed for each 200 m section out of the two visits was used in the analysis.

To account for any difference in detectability of Whinchats in the different 200 m sections, two more variables, visibility and percentage scrub cover, were included in the analysis. Visibility was calculated individually for each transect using the DEM of Salisbury Plain (NERC Earth Observation Data Centre 2007) and the arc Viewshed tool (from ARGIS 10.0; ESRI, 2010). Percentage scrub cover was calculated using data from a survey by the Centre for Hydrology and Ecology (CEH) (Redhead *et al.* 2012). Aerial photographs were used to count the number of 0.25 m by 0.25 m squares with scrub and this value was then transformed into percentage cover for each 100 m by 100 m square. Zonal histograms and zonal statistics were then used to determine the percentage area visible and the mean percentage scrub cover for a 250 m radius from the mid-point of each 200 m section along the transects. This value was chosen to cover as much of the survey area as possible while avoiding overlap between parallel lines as the transect lines were 500 m apart.

In the 2012 season, four areas within the study site with high Whinchat populations were regularly surveyed (at least every two days) between mid-April and mid-July and the Whinchat territories mapped (Bibby 2000). These territories were then regularly surveyed throughout the 2013 season; each area was visited at least every two days and scored either as occupied or unoccupied.

3.4 Data analysis

3.4.1 Whinchat habitat preferences

The data were analysed in the R statistical package version 3.1.2 (R Development Core Team 2014). All variables were tested for outliers, only one outlier was present, a particularly tall piece of vegetation in the mean vegetation height data; this was an accurate value. The analysis was re-run without this value to test for any effect: the results were the same, therefore the analysis is presented using the full dataset. All variables were tested for normality and transformed where necessary; the transformations are listed in Table 3.2.

Due to the large number of variables and because six of the vegetation variables were highly correlated, a Principal Components Analysis (PCA) was used to summarise the main variability of these vegetation characteristics. Principal Components were selected to explain at least 80% of the variation in the original variables (Zuur *et al.* 2007).

Initially a Generalised Additive Model (GAM) was fitted to the data to check for non-linear trends using the gam function in the mgcv library (Wood 2014). The graphical trends from this model were approximately linear and the effective degrees of freedom (edf) equalled one, which both indicated that a linear model was suitable.

The dependent variable, the counts for Whinchats per 200 m section, was found to be highly zero inflated with the excess zero counts causing over-dispersion, so a hurdle model was used (Mullahy 1986; Zeileis *et. al* 2008). This model consists of two parts: a zero truncated count component modelled with a poisson distribution (a negative binomial distribution did not improve the AIC: 315 as opposed to 313), and a hurdle component which models the zeros versus larger counts using a binomial distribution. A hurdle model was chosen instead of a zero-inflated model as the excess number of zeros were deemed to be real values rather than false zeros (Zeileis *et al.* 2008; Zuur *et al.* 2009). Each square was surveyed an additional four times to collect data on vegetation and invertebrates and from this it was found that the original survey detected 90% of Whinchats, adding in these missed Whinchats did not remove the zero-inflation. Additionally, a habitat suitability model in Chapter 4 found a large proportion of suitable Whinchat breeding habitat was unoccupied, suggesting the population is well below carrying capacity. Therefore, the occurrence of false zeros was considered to be marginal. Initially all variables were included in both components of the model along with an interaction term for altitude and aspect because a study by Calladine & Bray (2012) found the effect of aspect on Whinchat abundance was different at different altitudes. Stepwise deletion was used to simplify the model until only significant terms were left. Nested models were compared via likelihood ratio tests using the lrtest function from the lmtest package (Zeileis & Hothorn 2002) which corrects for testing on the boundary (Zuur *et al.* 2009). A spline correlogram from the ncf package (Bjørnstad & Falck 2001), was used to check the model Pearson residuals for spatial autocorrelation (Zuur *et al.* 2009). A correlogram graphically represents the spatial autocorrelation between locations at a range of lag distances up to a maximum. A spline correlogram with 95% bootstrap confidence intervals and a maximum lag distance of 10km showed no spatial autocorrelation in the Pearson model residuals, therefore a spatial correlation structure was deemed unnecessary.

The invertebrate data could not be analysed across years as a different, less effective, sampling method was trialled in 2012 (section 2.5.2). Therefore, invertebrate abundance, invertebrate order richness and invertebrate biomass were modelled against Whinchat number per 200 m section for the 2013 data only. Invertebrate biomass was logged transformed to make it conform to an approximately normal distribution; invertebrate abundance and invertebrate order richness were already approximately normally distributed.

Table 3.2. Transformations used to make variables for the Whinchat habitat preference model conform to a normal distribution. After transformation all variables were approximately normally distributed.

Variables	Transformations
% Ground cover	Log (ground cover)
% Ground Cover at 20 cm height	Log (ground cover at 20cm + 1)
%Grass to herb: once transformed = % Herb to grass	Log (101 - % grass to herb)
Maximum perch height (cm)	Log (max perch height + 1)
Perch abundance	Log (perches abundance + 1)
Mean vegetation height (cm)	Log (mean vegetation height)
Standard deviation in vegetation height (cm)	Log (sd vegetation height + 1)
% Tussock cover	Log (% tussock cover + 1)
Slope (degrees)	Sqrt (slope)
% Scrub Cover	Log (% scrub cover + 1)
% Visibility	No transformation necessary
Minimum perch height (cm)	No transformation necessary
Plant species richness	No transformation necessary
Aspect (NW or SE)	No transformation necessary
Altitude (m)	No transformation necessary

3.4.2 Occupancy of territories from 2012

For the territory vegetation data, only one vegetation variable did not follow an approximately normal distribution and was therefore log transformed: perch abundance. No outliers were present in the data. A binomial Generalized Linear Model (GLM) was used with a logit link, the response variable was whether a territory from 2012 was re-occupied in 2013 or not. Site, depicting the four survey sites was added as a random effect to account for any correlation between territories from the same site but it did not improve the AIC (AIC = 49 for GLM and 51 for GLMM) and gave exactly the same end model result, therefore it was deemed unnecessary. The model was simplified by stepwise deletion using the drop1 command in R (Chambers 1992). Each explanatory variable was dropped in turn and the difference in residual deviance calculated and compared to a Chi-square distribution, the least significant term causing the smallest change in residual deviance was dropped and the process was repeated until every term was significant.

3.5 Results

3.5.1 Whinchat habitat preferences

A total of 317 different 200 m sections were sampled; 130 in 2013 and 187 in 2012. Three 200 m sections were missed from sampling in 2012 due to inability to access these sites.

Six vegetation variables were highly correlated (Pearson Product Moment Correlation Coefficient (PPMCC) >0.5, Figure 3.2). A principal components analysis was performed on these variables using the prcomp package (Venables & Ripley 2002; Crawley 2007). The first two principal components summarised 80% of the variation. These two components were then used as variables in the model. PC1, which explained 60% of the variation in the vegetation variables, represented areas with longer grass and more vegetation cover higher up, more variation in grass structure, lower species richness, lower percentage of herb to grass, and higher tussock cover. PC2 explained a further 20% of the variation in the vegetation variables and represented areas with high species richness and high herb to grass ratio, low tussock cover and shorter grass with less structural variation (Table 3.3). Minimum and maximum perch height was also highly correlated, therefore only maximum perch height was used in the analysis. Invertebrate order richness was correlated with invertebrate abundance and invertebrate biomass and was, therefore, modelled separately to these two variables.

PC1 and PC2 were both found to be correlated with log(perch abundance + 1) (PPMCC = 0.446 and 0.417 respectively). Therefore, perch abundance was modelled separately to PC1 and PC2. No other variables were strongly correlated with each other.

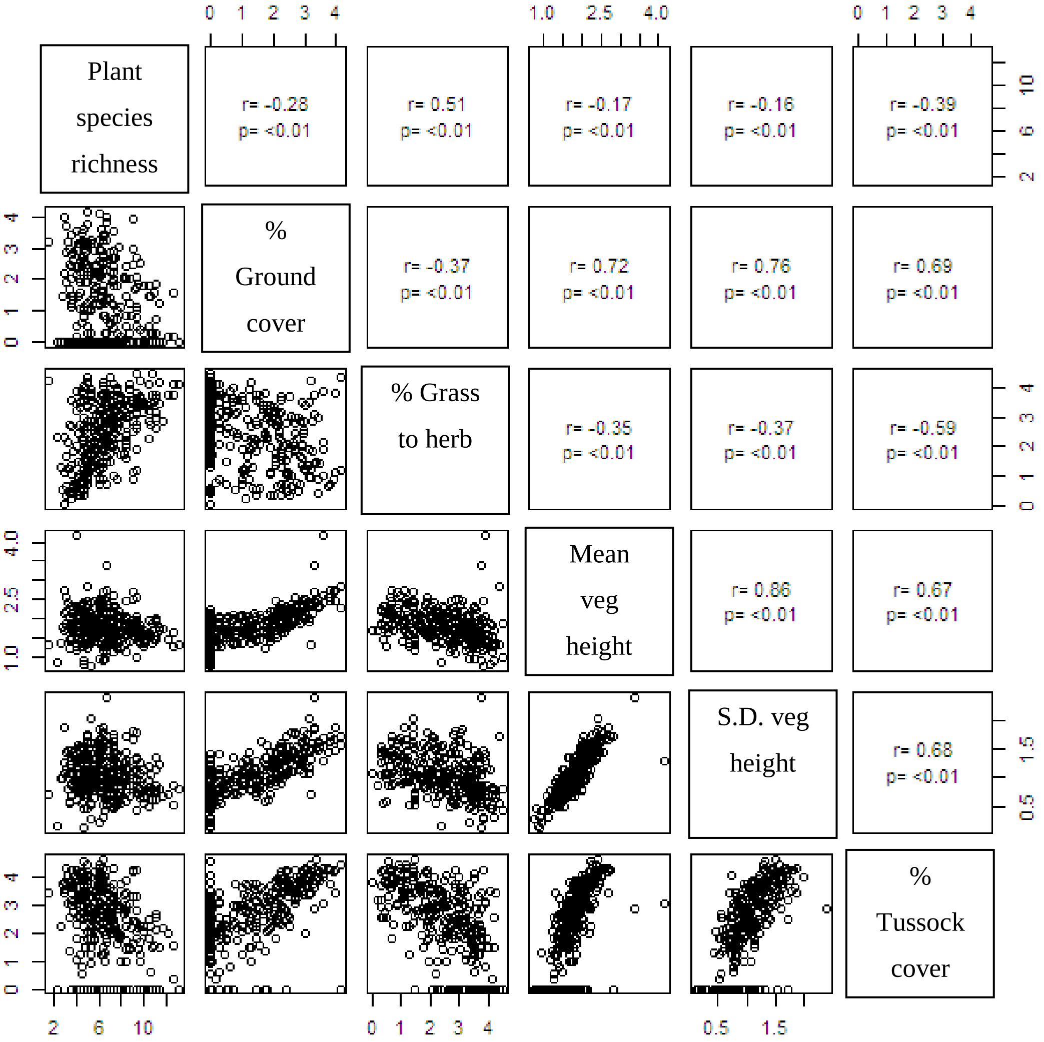


Figure 3.2. Correlations between the six correlated vegetation variables. The Pearson's Product Moment Correlation Coefficient(r) and p values for each correlation are shown in the upper right panels and a plot of each variable pair is shown in the lower left panels.

Table 3.3. Results of a Principal Component Analysis for vegetation data from the 200 m transect sections. Variables included in the PCA were: plant species richness, percentage of ground cover at 20cm height, herb to grass ratio, mean vegetation height, standard deviation in vegetation height and percentage tussock cover. Firstly the cumulative proportion of the variance explained by each component is presented and then the correlation coefficients for the relationship between each habitat variable and the two principal components. Lastly a verbal interpretation of each component is given. The first two principal components summarised 80% of the variation.

Variables	PC1	PC2
Cumulative proportion of variance	0.605	0.804
Plant species richness	-0.239	0.697
% Ground cover 20cm above ground	0.450	0.184
% Herb to grass	-0.338	0.518
Mean vegetation height (cm)	0.449	0.322
Standard deviation in vegetation height (cm)	0.459	0.320
% Tussock cover	0.462	-0.072
Interpretation	Areas with longer grass and more vegetation cover higher up, more variation in grass structure, lower plant species richness, lower percentage of herb to grass, and higher tussock cover	Areas with high plant species richness and high herb to grass ratio, low tussock cover, shorter grass with less structural variation

The best model contained PC1 in the count component, which models the counts for areas where Whinchats were present, and PC1 and altitude in the hurdle component, which models the presence and absence of Whinchats (Table 3.4). Table 3.5 gives the final model parameter estimates. Whinchat presence was positively associated with PC1 and in areas of habitat where Whinchats were present, the number of Whinchats increased as the amount of PC1-type vegetation increased (Table 3.5). Therefore, an increase in the amount of long dense grassy vegetation with more variation in height, low plant species richness and a high density of tussocks, encourages settlement of breeding Whinchats. Ordination methods such as PCA make it difficult to interpret the individual effects of the variables that make up the principal components (Zuur *et al.* 2007; Davies *et al.* 2014). However, it is possible to get an idea of the magnitude of the influence for the different variables that form PC1 from examining the means and standard errors from the raw data for 200 m sections where Whinchats were present and 200 m sections where Whinchats were absent (Table 3.6).

Whinchats were also more likely to be observed at lower altitudes regardless of vegetation type (Table 3.5). From the raw data the mean altitude for 200 m sections with Whinchats was 14.2 m lower than 200 m sections without Whinchats. Visibility and percentage scrub cover, which were included to account for any differences in detectability between 200 m sections, did not affect the observed number of Whinchats and were therefore dropped from the model (Likelihood ratio test: $p > 0.05$). Slope, aspect, the interaction of altitude and aspect, percentage ground cover and maximum perch height did not show significant relationships with Whinchat presence and were also dropped from the model (Likelihood ratio test: $p > 0.05$). However, from examining the raw data means (Table 3.6) it is apparent that there is a trend for Whinchats to occur in 200 m sections with taller perches (43.9 +/- 3.12 cm as opposed to 35.3 +/- 1.94 cm).

The model results are presented graphically in Figure 3.3. The fitted values for the hurdle part of the model, modelling Whinchat presence versus absence, are plotted against PC1 and altitude, and the fitted values from the count part are plotted against PC1. There is some curvature in the plot of Whinchat count against PC1 and Whinchat presence against altitude but the addition of a higher order polynomial terms did not increase the explanatory power of the model. Diagnostic plots of the final model residuals against every potential explanatory variable validated that this model is a suitable fit.

An alternative model using perch abundance instead of PC1 and PC2 was created to investigate the effect of perches, as explained earlier, the perch abundance was highly correlated to PC1 and PC2, though not to the individual variables that formed these components, therefore it was modelled separately to PC1 and PC2. The perch abundance was significantly positively correlated with Whinchat occurrence (Hurdle: Est =0.935 +/- 0.316, z =2.96, p = 0.003). On average 0.5 more perches were presence in 200 m section with Whinchats than those without (Table 3.6). Altitude was also significant in this model, showing the same trend as observed in the final model, discussed above. The model using perch abundance had a higher AIC compared to the model built with PC1 and PC2 (318 as opposed to 313) and therefore was not chosen as the best model.

Table 3.4. The chi-squared values from the likelihood ratio tests for the best model selected by stepwise deletion examining the relationship between the abundance and presence of Whinchats per 200 m section in relation to habitat variables. The model is a hurdle model combining a truncated poisson with a log link to model Whinchat abundance for sections with Whinchats and a zero hurdle component to model Whinchat presence versus absence using a binomial distribution with a logit link (n =317).

Count Model	χ^2	Df	P value
PC1	7.85	1	0.005
Zero Hurdle Model	χ^2	Df	P value
PC1	8.13	1	0.004
Altitude	10.4	1	0.001

Table 3.5. The parameter estimates for the best model selected by stepwise deletion examining the relationship between the abundance and presence of Whinchats per 200 m section in relation to habitat variables. The model is a hurdle model combining a truncated poisson with a log link to model Whinchat abundance for sections with Whinchats and a zero hurdle component to model Whinchat presence versus absence using a binomial distribution with a logit link (n =317).

Count Model	Estimate	Std.error	Z value	P value
Intercept	-0.24	0.28	-0.85	0.396
PC1	0.31	0.12	2.61	0.009
Zero hurdle model				
Intercept	1.60	1.14	1.40	0.162
PC1	0.26	0.09	2.78	0.005
Altitude	-0.02	0.008	-3.11	0.002

Table 3.6. The mean +/- 1 standard error for each predictor variable for 200 m sections where Whinchats were present and 200 m sections where Whinchats were absent. The raw data values for each variable are used (n = 317).

	200 m sections with Whinchats	200 m sections without Whinchats
Plant Species Richness (number)	6.00 +/- 0.32	6.65 +/- 0.13
% Ground cover at 20 cm height	9.43 +/- 1.88	6.24 +/- 0.62
% Herb to grass ratio	12.5 +/- 2.17	19.8 +/- 1.12
Mean vegetation height (cm)	7.54 +/- 0.44	6.60 +/- 0.27
Standard deviation in vegetation height (cm)	2.47 +/- 0.18	1.94 +/- 0.07
% Tussocks cover	25.3 +/- 3.10	18.1 +/- 1.23
% Ground cover	92.2 +/- 1.61	90.5 +/- 0.73
Perch abundance	1.43 +/- 0.18	0.93 +/- 0.08
Minimum perch height (cm)	33.6 +/- 3.12	27.0 +/- 1.42
Maximum perch height (cm)	43.9 +/- 4.13	35.3 +/- 1.94
Altitude (m)	144 +/- 4.04	158.2 +/- 1.50
Aspect	SE	SE
Slope (°)	5.15 +/- 0.51	5.24 +/- 0.22
% Scrub cover	15.1 +/- 1.67	18.9 +/- 0.88

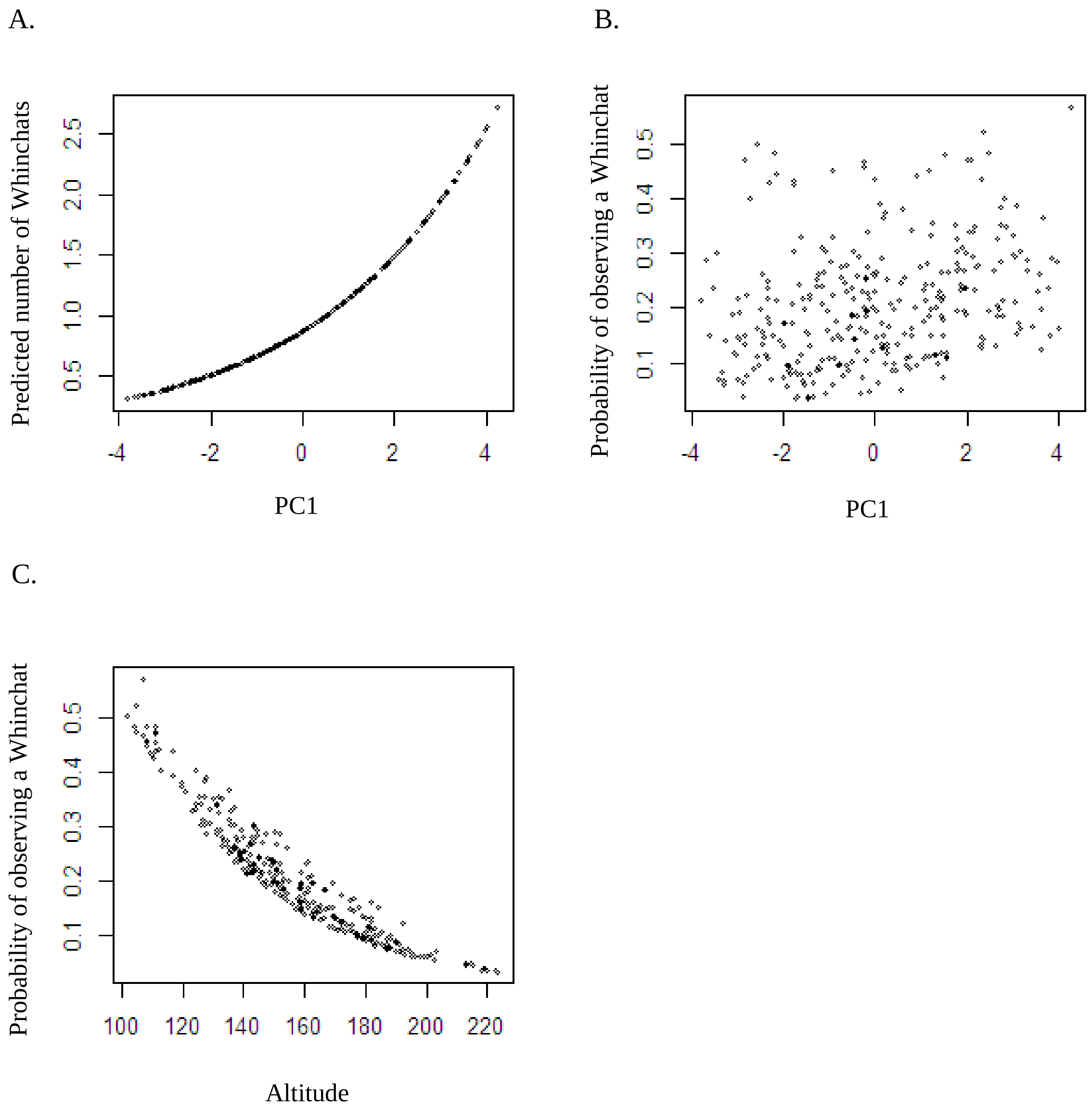


Figure 3.3. Plots of fitted values for the best model for the relationship between Whinchat abundance and habitat characteristics. A: fitted values for the count component of the model (Whinchat abundance in areas with Whinchats) against PC1, B: fitted values for the hurdle component (Whinchat presence versus absence) of the model against PC1, C: fitted values for the hurdle component (Whinchat presence versus absence) of the model against altitude.

3.5.2 Invertebrate resources and Whinchat distribution

The abundance, order richness and inferred biomass of invertebrates showed no relationship to the abundance or the presence of Whinchats per 200 m section when tested individually or in a full model with the vegetation and topography variables (Table 3.7 and Figure 3.4). It does appear that the variability in mean invertebrate abundance, order richness and biomass is lower in areas with Whinchats as opposed to areas without but the sample size of areas with Whinchats is much smaller (23 as opposed to 107).

Table 3.7. The best model selected by stepwise deletion examining; A: The relationship between the number of Whinchats per 200 m section and invertebrate abundance and inferred biomass, B: The relationship between the number of Whinchats per 200 m section and invertebrate order richness. The variables are presented with the associated chi squared values from the likelihood ratio test upon their removal from the model. Invertebrate order richness was modelled separately from the other two invertebrate variables as it was highly correlated with them (PPMCC > 0.6). The model is a hurdle model combining a truncated poisson with a log link to model Whinchat abundance for sections with Whinchats and a zero hurdle component to model Whinchat presence versus absence using a binomial distribution with a logit link (n =130).

A. Count Model	χ^2	Df	P
Invertebrate Abundance	0.145	1	0.703
Invertebrate Biomass	0.063	1	0.803
A. Zero hurdle Model	χ^2	Df	P
Invertebrate Abundance	0.040	1	0.842
Invertebrate Biomass	0.105	1	0.746
B. Count Model			
Invertebrate Order Richness	0.368	1	0.544
B. Zero hurdle Model			
Invertebrate Order Richness	0.114	1	0.736

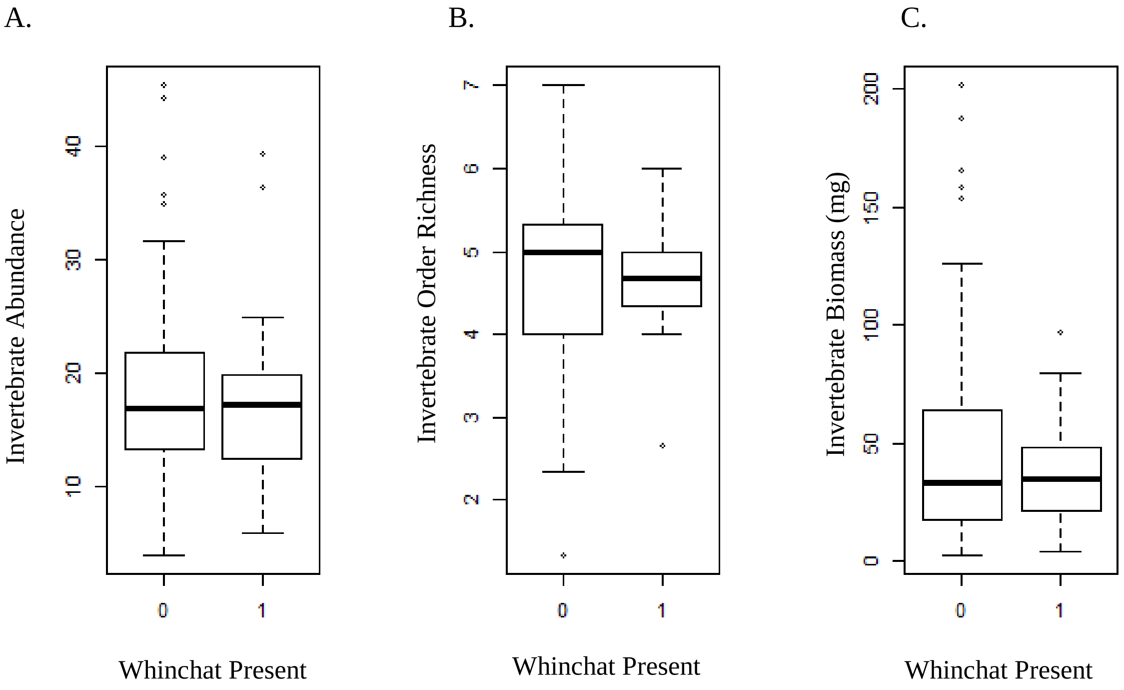


Figure 3.4. Boxplots displaying A. invertebrate abundance, B. invertebrate order richness and C. invertebrate biomass for 200 m sections where no Whinchats were observed (n = 107) and at least one Whinchat was observed (n = 23 whinchat presences). The boxes display the Median, Upper Quartile, Lower Quartile and Inter-Quartile Range (IQR), the lines display the Range: top = 1.5*IQR + upper quartile, bottom = 1.5*IQR – lower quartile.

3.5.3 Occupancy of territories from 2012

A PCA was used again due to collinearity between six of the vegetation variables (Figure 3.5). The first two principal components explained 88.7% of the variance in the vegetation variables (Table 3.8) and were used in the full model. Maximum perch height and minimum perch height were correlated, therefore only maximum perch height was included in the model.

The best model was a binomial GLM with PC1 as the only explanatory variable (Table 3.9). Whinchat territories were more likely to be occupied if PC1 was high (Table 3.10, Figure 3.6). Table 3.11 presents the mean values from the raw data of all the variables for occupied territories as opposed to unoccupied territories, with the accompanying standard errors for a quantitative comparison.

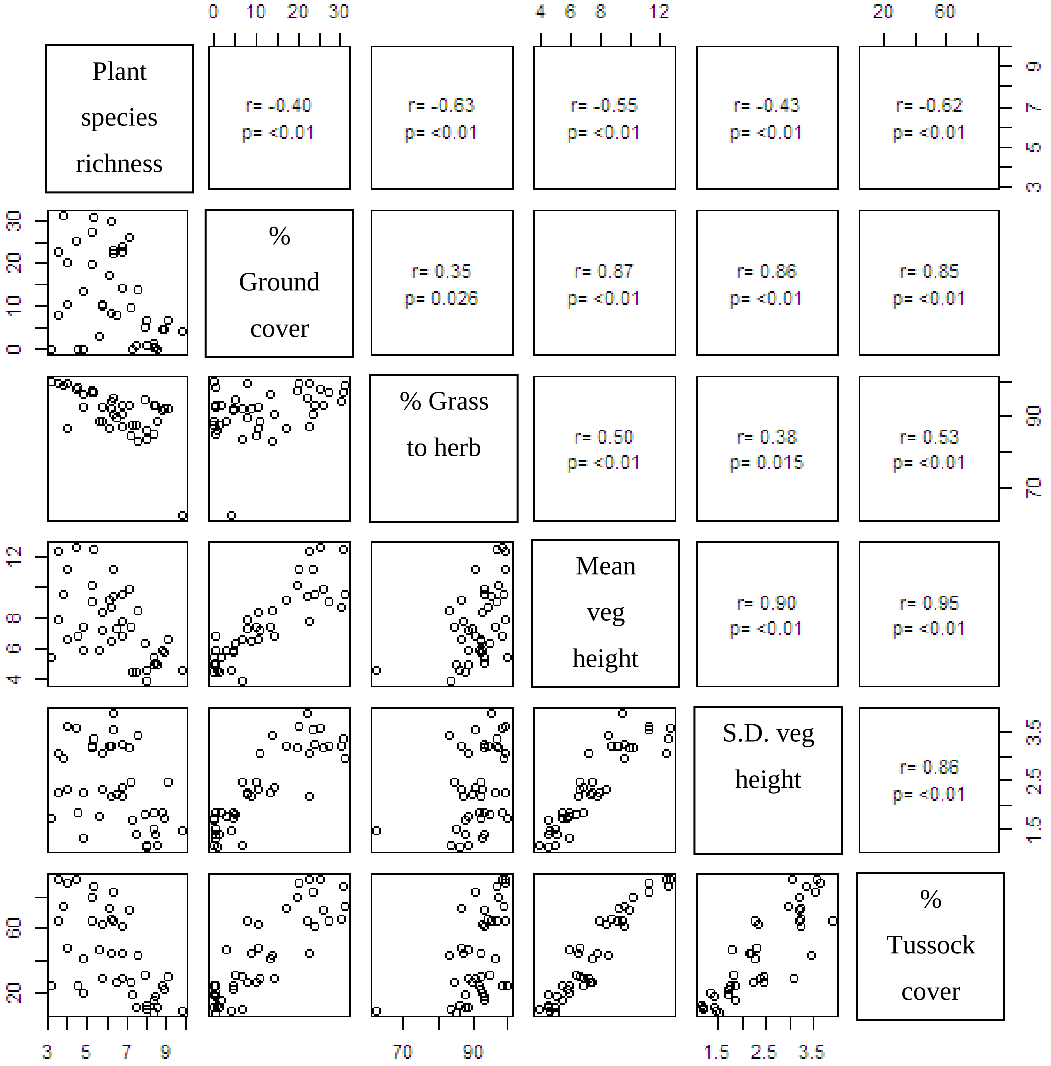


Figure 3.5. Correlations between the six highly correlated vegetation variables. The Pearson's Product Moment Correlation Coefficient (r) and p values for each correlation are shown in the upper right panels and a plot of each variable pair is shown in the lower left panels.

Table 3.8. Results of a Principal Component Analysis with vegetation data from Whinchat territories. Variables included in the PCA were: plant species richness, percentage of ground cover at 20cm height, grass to herb ratio, mean vegetation height, standard deviation in vegetation height and percentage tussock cover. Firstly the cumulative proportion of the variance explained by each component is presented and then the correlation coefficients for the relationship between each habitat variable and the two principal components. Lastly a verbal interpretation of each component is given. The first two principal components summarised 89% of the variation and were used in the full model.

Variables	PC1	PC2
Cumulative proportion	0.718	0.887
Plant species richness	-0.329	0.578
% Ground cover 20 cm above ground	0.426	0.340
% Grass to herb	0.301	-0.652
Mean vegetation height	0.463	0.154
Standard Variation in vegetation height	0.434	0.308
% Tussock cover	0.465	0.0780
Interpretation	Areas with longer grass and more cover higher up, more variation in grass structure, lower plant species richness, higher percentage of grass to herb, and higher tussock cover	Areas with high plant species richness and more herbs as opposed to grass, low tussock cover, shorter grass with less structural variation

Table 3.9. Model selection for the relationship between the occupancy of a territory and the territory vegetation. The model deviance, change in residual deviance (LRT) and p value for each term as it was dropped from the model are included. The change in residual deviance follows an approximately Chi-squared distribution. The model is a binomial GLM with a logit link (n= 41).

Variables	DF	Deviance	LRT	P value
PC1	1	56.81	12.06	<0.001
PC2	1	43.5	0.041	0.839
% Ground cover	1	44.0	0.468	0.494
Perch abundance	1	44.8	0.772	0.380
Maximum perch height (cm)	1	41.7	0.006	0.938

Table 3.10. The best model selected by stepwise deletion examining the relationship between territory occupancy and habitat variables. The model is a Generalised Linear Model of the binomial family with a logit link (n = 41).

Model	Estimate	Std.error	Z value	P value
Intercept	0.09	0.37	0.25	0.804
PC1	0.62	0.21	2.95	0.003

Table 3.11. The mean +/- 1 standard error for each predictor variable for territories identified in 2012 that were occupied again by Whinchats in 2013 and territories identified in 2012 that were not occupied again in 2013 (n=41).

	Territories from 2012 occupied in 2013	Territories from 2012 not occupied in 2013
Plant Species Richness	5.95 +/- 0.20	6.87 +/- 0.32
% Ground cover at 20 cm height	17.2 +/- 1.53	6.31 +/- 1.16
% Grass to herb ratio	93.2 +/- 0.67	89.6 +/- 1.29
Mean vegetation height (cm)	8.64 +/- 0.33	6.30 +/- 0.34
Standard deviation in vegetation height (cm)	2.78 +/- 0.12	1.97 +/- 0.10
% tussocks cover	55.8 +/- 3.72	30.9 +/- 3.84
% Ground cover	94.6 +/- 0.72	93.6 +/- 0.69
Perch abundance	1.25 +/- 0.11	1.01+/- 0.16
Minimum perch height (cm)	25.1 +/- 1.97	19.0 +/- 1.55
Maximum perch height (cm)	33.5 +/- 2.51	25.4 +/- 2.36

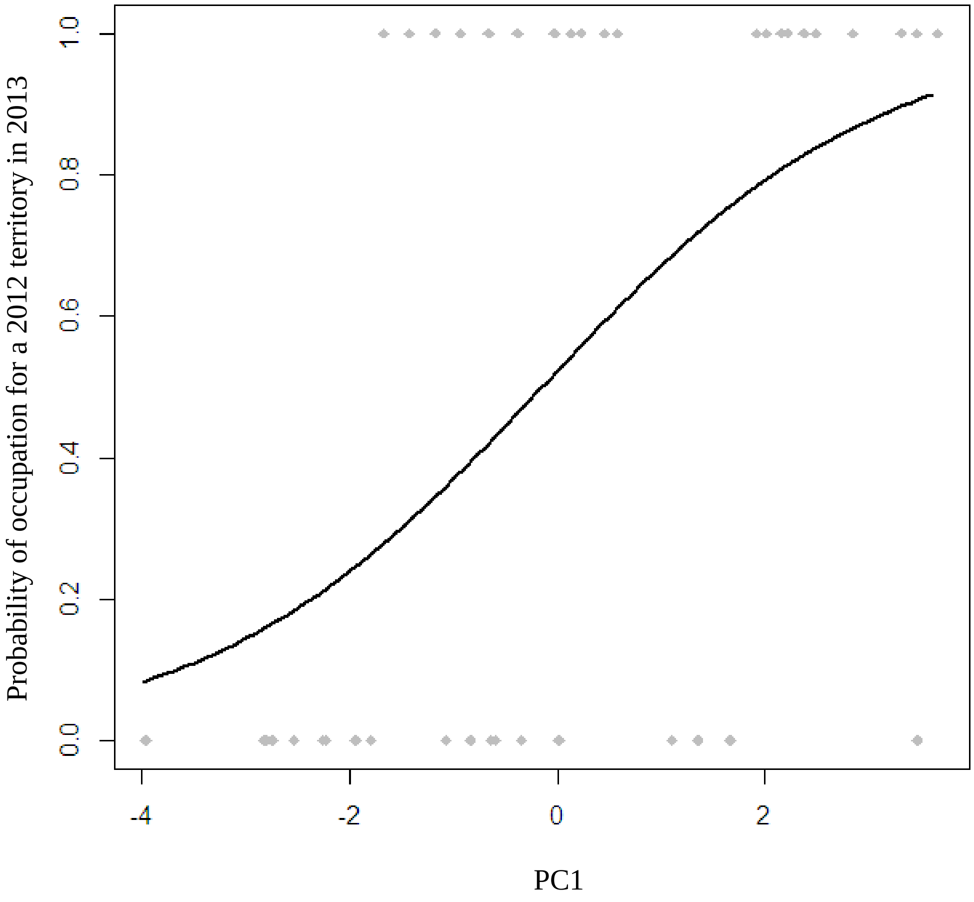


Figure 3.6. The fitted values (solid line) from the best model for the relationship between PC1 and Whinchat occupancy of a 2012 territory in 2013 (n = 41), the dots are the observed values. The model is a binomial GLM with a logit link.

3.6 Discussion

Whinchats were more likely to be present at lower altitudes and in areas with more PC1 type vegetation (Table 3.5; Figure 3.3); long dense grassy vegetation with more variation in vegetation height, low species richness and a high percentage cover of tussocks. In sections where Whinchats were present, their abundance increased with increasing PC1 vegetation (Table 3.5; Figure 3.3). Additionally, Whinchat territories from 2012 were more likely to be occupied in 2013 if they had more PC1 type vegetation (Table 3.10). Whinchats were also more likely to be present in areas with a higher abundance of perches. Aspect, slope, percentage ground cover and perch height were not significantly associated with Whinchat occurrence or abundance. Visibility and scrub cover were not significant in the final model suggesting the results were not an artefact of variations in detectability. As stated in the introduction, Whinchats were expected to select breeding habitat to maximise the chances of breeding successfully without compromising their ability to reproduce successfully in the future (Trivers 1974). Habitat would be expected to be selected to maintain a suitable microclimate but still minimising predation risk (Gillis *et al.* 2012) and to ensure a good local food supply close to the nest (Andersson 1981).

3.6.1 A preference for valleys

Whinchats were more likely to be observed at lower altitudes. The altitude of the 200 m sections surveyed on Salisbury Plain ranged from 102 m to 223 m above sea level, which is well within a Whinchats physiological limits (Whinchats have been found up to 500 m above sea level in the UK; Calladine & Bray 2012). Salisbury Plain topography consists of a series of low hills and valleys. The lower altitude sections of the transects refer to the valleys, therefore in this case a preference for lower altitude reflects a preference for valleys. Similar results have been found in other studies on the Plain (Stanbury *et al.* 2002; Redhead 2011) and differences in vegetation between the valleys and hilltops has been suggested as the reason. In this study, however, vegetation type was also accounted for in the model and the correlation between altitude and PC1 type vegetation was low (PPMCC = -0.114). The top 20 % of sections with the highest altitudes (above 180 m) contain some sections which also had very high values of PC1 (2.0 – 4.0) and despite the highly suitable vegetation these areas were not occupied by Whinchats. Therefore, the observed preference for valleys must be to do with the structure of the valleys themselves rather than any correlation with the vegetation type. Salisbury Plain is subject to strong winds due to the open nature of the plain, with few features to act as wind barriers. In this situation, valleys may present a more sheltered microclimate than hilltops.

Extreme temperatures when incubating have been found to increase the energetic costs to incubating birds (Rauter & Reyer 2000) and can also result in slow offspring growth (Robertson 2009), reduced immunity (Ardia *et al*. 2010) and reduced fledging success (Ardia 2013). For altricial passerines, like Whinchats, an insulated microclimate is especially important, as the nestlings are unable to thermoregulate until about 6 – 9 days old (Visser 1998).

3.6.2 Vegetation preferences

PC1, which decribed areas with a high percentage of long grass, a higher percentage cover at 20 cm height (indicating a higher vegetation density), higher tussock density and more variation in vegetation heights, was significantly positively correlated with both Whinchat occurrence and the number of Whinchats in an area. The importance of PC1 is again exemplified in the second analysis looking at territory occupation. Whinchat territories from 2012 with a higher level of PC1 were significantly more likely to be occupied again in 2013. This suggests PC1 type vegetation is strongly selected when Whinchats are choosing breeding territories.

Whinchats build concealed nests, deep inside tussocks (pers. obs.), therefore the increased tussock density and vegetation height associated with increased PC1 type vegetation would be beneficial. Other studies, including several on Whinchats (Richter & Düttman 2004; Pearce-Higgins & Grant 2006; Broyer *et al.* 2012) have found that ground nesting birds will preferentially select areas with taller, denser vegetation to nest in, which is thought to be due to increased protection from predators and improved thermoregulatory benefits (Martin 1993; Davis 2005; Kim & Monahan 2005; Gillis *et al.* 2012). For many bird species, more exposed nests have been found to have a higher risk of predation; Martin (1992) found that in 29 of 36 studies, predation rates were lower for nests with greater concealment. As well as concealment, dense, long, vegetation can make it more difficult for a predator to find the nest by increasing the amount of vegetation to search through and the number of potential nest sites to check (Martin 1993). However, long vegetation can also increase predation risk for parents by obstructing their view while foraging or on the nest (Whittingham & Evans 2004; Wilson *et al.* 2005; Seltmann *et al.* 2014), and tall vegetation may also limit foraging efficiency by impeding the birds movement and access to prey (Whittingham & Evans 2004; Wilson *et al.* 2005; Devereux *et al.* 2006; Hoste-Danylow *et al.* 2010). This is where the increased structural variation in vegetation, reflected in PC1 by standard deviation in vegetation height, is also important. It provides both tall dense vegetation for shelter and concealment and shorter more open vegetation suitable for foraging in close proximity (Wilson *et al*. 2005; Fischer *et al*. 2013;

Murray *et al.* in prep). PC1 also includes a higher percentage of grass cover but as the areas with long, dense vegetation also tended to be the areas with a higher percentage of grass, this does necessarily indicate a preference for grass specifically. In fact, Whinchats have been shown to preferentially select areas of bracken cover at sites in North England and Scotland (Pearce-Higgins & Grant 2006) but there is no bracken on Salisbury Plain.

Perch abundance had a significant positive effect on Whinchat occurrence but not on Whinchat abundance in areas where Whinchats occurred. Other studies have also found an association of Whinchats with increased perch abundance (Oppermann 1990; Opperman 1992; Bastian & Bastian 1994; Richter & Düttmann 2004). Oppermann (1992) even found that adding artificial perches to a habitat encouraged uptake by Whinchats. Whinchats rely on perches for hunting, detecting prey from a perch and pouncing (pers. obs.; Richter & Düttmann 2004; Barshep *et al.* 2012), therefore an increase in perch abundance improves their foraging efficiency. Perches could also act as look-out posts, aiding early detection of predators by improving the range of vision (e.g. Yasukawa *et al.* 1992) and in the case of males, as song posts for territorial defence (Orlowski 2004).

3.6.3 Features not significantly associated with settlement

Slope and aspect were not significantly related to Whinchat occurence. The preference shown for valleys, as already discussed, would suggest a preference for slopes. However, the fact that this relationship was not apparent in the analysis suggest the preference for lower altitudes and PC1 type vegetation was more important for breeding Whinchats than slope. Slope and aspect affect the soil moisture content and surface temperature (Bennie *et al.* 2008) and this has been shown to affect the energetic costs of incubation (Rauter & Reyer 2000). Calladine & Bray (2012) found Whinchats favoured south and east facing aspects, especially at higher altitudes. However, it is important to note that all sample altitudes from this study were low (less than 223 m) compared to Calladine & Bray’s paper where altitudes ranged between 225 – 610 m above sea level, therefore selecting aspect to maximise surface temperature may not be necessary.

The maximum perch height was not significantly associated with Whinchat occurrence. Taller perches might be preferred as they would allow a wider field of view to detect approaching predators (as found for Red-winged blackbirds in Yasukawa *et al*. 1992) and potential prey items (e.g. Poole 2005; Andersson *et al.* 2009). Hulme & Cresswell (2012) found that

Whinchats in their study preferred perches of 108 cm which was significantly higher than randomly selected potential perches (mean height 52 cm). Other studies have also suggested perch height might be important in male song post selection (Castrale 1983) and could act as an indication of male quality (Sprau *et al.* 2012), with the best quality males risking higher exposure to predations and increased thermoregulatory costs (Ward *et al*. 2005) by singing from more prominent posts (Møller *et al.* 2006). Harrison (1977) actually tested the hypothesis that taller perches are preferred as song perches for six territorial grassland bird species and concluded that in general individuals will use virtually any elevated perch regardless of height but Castrale (1983) found that if there is a choice between two perches in close proximity the highest one was used almost exclusively. However, my study only looked at maximum perch height with Whinchat occurrence and abundance, not the maximum height of perches the Whinchats actually used, Whinchats may have been using the taller perches within an area more. On average perches were 8 cm taller in areas with Whinchats as opposed to areas without (Table 3.6) suggesting a trend towards selecting areas with taller perches.

Percentage of ground cover, which refers to the cover of vegetation as opposed to bare earth, was also not statistically significantly related to Whinchat occurrence or abundance. Bare ground was expected to be a significant component of Whinchat occupancy since they are visual predators and bare ground may improve prey accessibility and foraging efficiency. At the scale of sampling, however, there was no detectable variation in the percentage of bare ground in sections with and without Whinchats (Table 3.6).

Invertebrate abundance, diversity and inferred biomass were not related to Whinchat presence or abundance which suggests food abundance, diversity and biomass are not influencing variation in Whinchat settlement on Salisbury Plain. Comparisons of invertebrate abundance, diversity and biomass for 200 m sections with and without Whinchats (Figure 3.4) suggest little difference in average values at this scale of sampling. Field observations suggest that food was not limiting on Salisbury Plain. Out of the 199 nests monitored over the 2012, 2013 and 2014 seasons, only four nestlings starved to death in the nest (Chapter 5) and the condition of nestlings in fledged nests (based on residual weight) was not significantly different to failed nests. Therefore, it appears justified to assume that invertebrate abundance, diversity and biomass in the sampling area is uniformly sufficient for Whinchat breeding needs. Other studies of Whinchat habitat preferences have found high invertebrate diversity and biomass to be important in settlement decisions; for example, Bastian *et al.* (1994) found species richness and biomass of invertebrates was greater on Whinchat occupied plots, but the abundance was lower, and Opperman (1999) also suggests a clear relationship between Whinchat habitat use and food availability. However, both of these studies compared Whinchat settlement between habitats with very different invertebrate populations due to different levels of agricultural management, whereas Salisbury Plain is virtually all agriculturally unimproved grassland (Ash & Toynton 2000; Ash *et al*. 2011). It is also important to recognise that availability of invertebrates to foraging Whinchats is not the same as invertebrate abundance, diversity and biomass. Availability of invertebrates may rely more on the vegetation structure: Hoste-Danylow *et al*. (2010) found that vegetation structure influenced birds in their choice of a foraging spot far more than prey abundance. Variation in vegetation height may increase access to invertebrates while still providing concealment from predators (Whittingham & Evans 2004) and high perch abundance and tall perches may improve the visual field for searching (Poole 2005).

3.6.4 Conclusions

In conclusion this research suggests that in unimproved grassland where food appears not to be limiting, breeding season occupancy of habitat is biased towards valleys and areas where the dominant vegetation is tall, structurally diverse, grass with high tussock density and abundant perch availability. Occupancy of this habitat is likely to minimise nest predation risk and thermoregulatory stress and increase foraging efficiency. Salisbury Plain allows us to look at Whinchat habitat choices in a stable population in optimal habitat, where food abundance and diversity is not limiting enough to determine habitat occupancy. This information can then be used to guide effective conservation management for Whinchats. For example if we want to encourage Whinchats into an area and we have already taken action to ensure a healthy insect population then the other priorities to focus on are to ensure a sufficient area of dense, structural diverse vegetation with a high density of tussocks and perches to maximise foraging efficiency while minimising predation risk and thermoregulatory stress, and to consider the shelter topography can offer when selecting sites to conserve. Increasing structural heterogeneity would also benefit other grassland nesting birds and grassland biodiversity in general (Benton *et al.* 2003; Wilson *et al.* 2005; Vickery & Arlettaz 2012). Studying stable populations of a declining species in optimal habitat can thus help to uncover important habitat selection cues and thereby guide effective conservation management action for the species as a whole.

Chapter 4: Using Habitat Suitability Modelling to determine whether breeding habitat is limiting for a declining migrant bird

One of the core survey valleys with a large Whinchat population

4.1 Abstract

As the trend in anthropogenic habitat loss continues it is becoming increasing important to identify strongholds of suitable habitat that still exist to enable implementation of effective conservation management strategies. In the previous chapter the breeding habitat requirements of Whinchats were established. Here, I use this information to create a Habitat Suitability Model for Salisbury Plain from Whinchat occurrence data and large scale environmental data. The predictive power of the model is tested via a ground truthing survey, with 267 random points in the west Salisbury Plain area surveyed for Whinchats and the results compared to the habitat model predictions. The habitat suitability model, in conjunction with the ground truthing surveys, is used to investigate the vulnerability of Whinchats to fragmentation and to determine if suitable breeding habitat is a limiting resource. The habitat suitability model successfully predicted areas where breeding Whinchats were more likely to be observed. In general, Whinchats were not sensitive to fragmentation at the level present on Salisbury Plain. The number of Whinchats sighted was far below the value expected in highly suitable and moderately suitable habitats, with whinchats observed at only 24.3% of predicted highly suitable points. This suggests a large proportion of apparently suitable habitat was unoccupied on Salisbury Plain.

4.2 Introduction

Anthropogenic habitat change has been the most important cause of declines in bird populations in the past century (Sala *et al.* 2000, Green *et al.* 2005). Habitat change can cause declines via loss of suitable breeding and foraging habitat (e.g. Newton 1998, Table 8.2; Schmidt *et al.* 2005, Britschgi *et al.* 2006; Barbaro *et al.* 2008) and via reduced patch size, increased isolation and increased edge habitat due to fragmentation (Andren 1994; Herkert *et al*. 2003; Hinsley *et al.* 2008). As this trend continues it is becoming increasingly important to identify strongholds of suitable habitat that still exist so we can implement effective conservation management strategies (e.g. Sage Grouse, Yost *et al.* 2008; Stony Corals, Tittensor *et al.* 2009; European Bison, Kuemmerle *et al.* 2010; Eleonora's Falcon, Kassara *et al.* 2014). It is possible to do this on a small scale, with detailed habitat sampling and corresponding surveys on the relative abundance of a particular species (e.g. Chapter 3) but this method is very labour intensive and therefore often not possible to conduct over a large area, or in more remote locations (e.g. Buchanan *et al.* 2005). However, it is also possible to use habitat preference data to model expected species distributions. Due to advances in remote sensing technology and large scale environmental monitoring, there is currently a large range of climatic, vegetative, aquatic and topographic data available at different resolutions and covering different geographical areas (Buchanan *et al.* 2005; Tittensor *et al.* 2009; Elith *et al.* 2011). Species occurrence data have also become increasingly available over the last decade, with a much broader coverage, due to the rise of the internet providing easier data sharing and the corresponding increase in citizen science (Lepczyk *et al.* 2009). Advances in Geographical Information Systems (GIS) software and statistical modelling now mean we can predict areas of suitable habitat for key species on a scale of our choosing, provided there is readily available species occurrence data and habitat data for the area of interest (Buchanan *et al.* 2005; Yost *et al.* 2008; Elith *et al.* 2011). We have the capacity, therefore, to create large scale habitat suitability maps for a particular species, making it much easier to determine how much suitable habitat is left and which areas are most important to conserve (Tinoco *et al.* 2009).

Habitat suitability models can also be useful for assessing the effect of fragmentation on a target species. Species differ in their vulnerability to the effects of habitat fragmentation depending on their requirements, mobility and ability to exploit matrix habitats between their preferred habitat patches (Schmiegelow & Monkkonen 2002; Antongiovanni & Metzger 2005). There is currently a lack of data on the response of grassland birds, such as Whinchats, to variations in patch size and landscape composition (Winter *et al.* 2006). Assessing a species' vulnerability to fragmentation enables us to determine the minimum patch size necessary for persistence and thereby provides evidence for conservation initiatives (Pereira *et al.* 2004). In most studies of habitat fragmentation, patch size assignment is based on contiguity of a broad habitat type (Girvetz & Greco 2007). However, what is commonly not taken into account is the perceptual responses and behaviour of the study organism (Girvetz & Greco 2007; Lu *et al.* 2012). What is a patch for the organism, due to its mobility and behaviour, may be different to the patch assigned by contiguity. Habitat suitability models use a variety of environmental variables important to the study organism to predict suitable habitat and therefore it would be expected that these predicted patches of suitable habitat will be a closer approximation to the patches as the study organism perceives them than patches determined by contiguity. Patches defined in this way can then be assessed for the study organism's occurrence and this will help to determine if isolation and size affect patch occupancy.

Habitat suitability models may also be used to determine how much of the suitable habitat is currently in use (e.g. Lauver & Busby 2002) and thereby help to understand the population limitations better. Many studies on Whinchats have invoked habitat loss on the breeding grounds as the main cause of the population decline (e.g. Grotenhius & Van 1986; Bastian 1989; Richter & Düttmann 2004; Grüebler *et al.* 2008; Broyer 2009; Fischer *et al.* 2013).

However, it has been suggested that the recent sharp decline of Whinchats may actually be driven by reduced survival during winter, or on migration (Henderson *et al.* 2014). Large areas of suitable, but unoccupied, breeding habitat on Salisbury Plain would suggest that, in this population at least, breeding habitat is not limiting. This information combined with data on productivity, over-winter survival and recruitment (Chapters 5 & 7) can give us clues as to the cause of the population decline.

In this chapter, Whinchat occurrence data collected from 2010 – 2013 and available large scale environmental data were used to create a map of Whinchat habitat suitability for the west of Salisbury Plain. The west of the plain was chosen as that is the region where the most Whinchat occurrence data were available. The program Maxent was used to create the habitat suitability model as it has been found to perform particularly well when compared to other habitat suitability modelling methods, giving robust and precise estimates even when the sample size is small (Elith *et al.* 2006; Hernandez *et al.* 2006; Phillips *et al.* 2006). To test the predictive power of the model, ground truthing surveys were conducted, with random points in the west Salisbury Plain area surveyed for Whinchats and the results were compared to the habitat suitability model predictions. The habitat suitability model in conjunction with the ground truthing surveys was used to investigate the vulnerability of Whinchats to fragmentation and determine if suitable breeding habitat was limiting. The predictions were that Whinchats would be less likely to be present in small isolated patches of suitable habitat compared to large well connected areas, and that not all suitable breeding habitat would be occupied. This chapter aims to improve our understanding of the role of breeding habitat availability in Whinchat population dynamics.

4.3 Methods

4.3.1 Study area

The study site was a section of Salisbury Plain, Wiltshire, in southwest England (Latitude 51°11'52"N-51°16'4"N; Longitude 1°57'32"W- 2° 9'32"W; Woodcock *et. al* (2005)). The study area covered 178 km^2 in the west part of the plain, which is predominantly used by the military for combat training including large scale troop manoeuvres and tank exercises but also includes Warminster live firing range. The majority of the study site is classified as agriculturally unimproved grassland (Walker & Pywell 2000), mainly *Bromus erectus* grassland with *Festuca rubra - Festuca arundinacea* sub-community and *Arrhenatherum elatius* grassland with *Festuca rubra* sub-community (Rodwell 1992) (see section 2.2 for more details).

4.3.2 Habitat Suitability Model

Maxent software version 3.3.3k (Phillips *et al*. 2007) was used to create a map of habitat suitability for the study area based on sightings of Whinchats from 2010 – 2013 and environmental variables. The program works by using maximum likelihood to estimate the likely distribution of a species over a finite area, such as the study area, based on a set of environmental predictor variables and the values these variables take at a sample of species occurrence points. Initially it is assumed that the probability of a species occurring is uniform in geographic space and therefore a species will occur in proportion to the availability of an environmental predictor variable. The data on species presence, in relation to an environmental predictor variable, places constraints on the model, forcing it away from a uniform distribution towards the mean value for the variable at presence locations. New parameter variables for the predictor functions are proposed and accepted if they improve the fit of the distribution compared to a uniform distribution (for details see Phillips *et al.* 2006; Phillips & Dudik 2008; Baldwin *et al.* 2009; Elith *et al.* 2011). The pixels of the study area define the probability distribution, which can be viewed in ArcGIS (ESRI 2010). The output is logistic, scaled to be between 0 and 1. Areas with high values are predicted to be very suitable habitat and areas with low values are predicted to be unsuitable habitat. For a more detailed statictical explanation of how Maxent works please see Elith *et al.* (2011).

4.3.3 Occurrence data

All Whinchat sightings recorded on Salisbury Plain from 2010 – 2013 were used as occurrence data. These data consist of sightings from line transect surveys (section 3.3.6), unstructured valley surveys and regular surveys of the six study sites (section 7.3.3). Occurrence data need to be a series of coordinates rather than areas, therefore to encompass a Whinchat territory, 100 m radius circular buffers were created around all Whinchat sightings in ArcGIS 10.0 (ESRI 2010). A grid of 100 m by 100 m squares was then overlaid onto the circular buffer and the average X and Y coordinates of the intersections of each grid cell within the buffer were calculated (Figure 4.1). In this way a cluster of points surrounding each sighting which represented the area of habitat use was created. The mean size of a Whinchat breeding territory in natural grassland is 0.015 – 0.018 km^2 (Bastian & Bastian 1996), which gives a radius of approximately 76 m, and from nest watches (Chapter 6) it was found that 99.4% of recorded Whinchat foraging took place 100 m or less from the nest location. A 100 m radius should, therefore, encompass the majority of the habitat the Whinchats use. The model uses clusters for occurrence data also avoids making stringent assumptions on where Whinchats will and will not occur. This was preferable because there was a lack of high quality vegetation data available for use as a predictor variable in the model, which was likely to affect the model's accuracy. A model was also run with just the original Whinchat sighting locations, to check for any substantial differences in the model output.

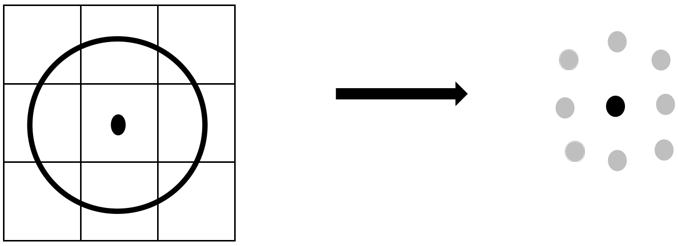


Figure 4.1. Diagram of how the cluster of points depicting territory use from each Whinchat sighting was created. The dot is a Whinchat sighting, the circle is a 100 m radius buffer and the grid is the 100 m by 100 m grid that was overlaid. The average X and Y coordinates of the intersections of each grid cell within the buffer were then calculated to give a cluster of points.

Maxent relies on an unbiased sample of presence data points for species occurrence. These points provide data on the values of environmental variables where the species occurs and Maxent will also randomly draw environmental data from background points where there are no occurrences as ‘pseudo species absence points’ (Phillips *et al.* 2006). The structured and unstructured survey coverage that provided the Whinchat occurrence data did not extend over the whole of the west of Salisbury Plain, meaning that for some areas it was not known if Whinchats were present or not. Therefore a mask layer was used to depict survey effort and avoid potential bias. A mask is a raster with a value of one for all surveyed 100 m by 100 m pixels and a value of zero for un-surveyed pixels. It works by restricting the Maxent model to only draw background environmental data (pseudo species absence points) from the area surveyed (Elith *et al.* 2011). Additionally, six regions in the surveyed area were study sites for Whinchat nest monitoring (see sections 2.2 & 2.3) and therefore had much better coverage than the other areas. To account for any possible biasing effect from this variation in survey effort, a bias file was also created (Phillips & Dudik 2008). A bias file works in a similar way to the survey area mask, proportionally weighting background samples towards more heavily surveyed areas. Models with and without a bias file were run and compared to see if including a bias layer improved the model fit.

4.3.4 Predictor variables

Any available large scale data can be used as predictor variables in Maxent modelling, including climatic, edaphic and biogeographic variables (Phillips & Dudik 2008). Maxent is not strongly influenced by the number of parameters used in model building and will automatically ignore non-informative predictors (Phillips *et al.* 2006; Tinco *et al.* 2009). This allows for the selection of many environmental parameters that might be important and the assessment of their influence, without a reduction in model precision.

All chosen predictor variables were on a 100 m by 100 m cell raster resolution to correspond with a Whinchat's approximate territory size. Variables were selected based on the findings from chapter 3, findings from other studies of Whinchat habitat preferences, and the availability of environmental data at an appropriate spatial scale (Table 4.1). The only vegetation data available at the appropriate spatial scale was a National Vegetation Classification (NVC) (Rodwell 1992) map from 1996 (Walker & Pywell 2000). Preliminary analysis identified CG3d and MG1 as the most common habitat types for Whinchat territories, therefore the area of these two habitat types in each 100 m by 100 m cell was chosen as an environmental predictor for the model. The perimeter of CG3d and MG1 vegetation in each 100 m by 100 m cell was also included to explore a possible edge effect. CG3d is mainly *Bromus erectus* grassland with *Festuca rubra - Festuca arundinacea* sub-community, which in common terms describes rank tussocky chalk grassland associated with low level grazing. MG1 is mainly *Arrhenatherum elatius* grassland with *Festuca rubra* sub-community and could also be described as reverting arable grassland (Rodwell 1992). As the vegetation variables came from a NVC survey from 1996 and therefore may not be accurate for the habitat in 2014, models were run with and without the vegetation variables to see which fitted the data better. All environmental predictor variables were converted to American Standard Code for Information Interchange (ASCII) files for input to Maxent.

Table 4.1. Description and source for the predictor variables used in the Maxent model.

Variable	Description	Source
Percentage scrub cover	Percentage of a 100 m by 100 m cell covered in scrub. This is converted from the original data of the number of 0.25 by 0.25 m cells designated as scrub in a 100 m by 100 m cell.	Image analysis of aerial photography (Redhead *et al.* 2012)
Percentage bare ground	Percentage of a 100 m by 100 m cell that is bare ground. This is converted from the original data of the number of 0.25 by 0.25 m cells designated as bare ground in a 100 m by 100 m cell.	Image analysis of aerial photography (Redhead *et al.* 2012)
Altitude (m)	Height in meters above sea level	NextMap Digital Elevation Model (DEM; NERC Earth Observation Data Centre 2007).
Slope (°)	Steepness of the slope in degrees above flat	Calculated from DEM (Redhead, J. pers. comm.)
Northness (°)	Northness = cos ((aspect in degrees * π) / 180)	Calculated from DEM (Redhead, J. pers. Comm.)
Eastness (°)	Eastness = sin ((aspect in degrees * π) / 180)	Calculated from DEM (Redhead, J. pers. Comm.)
Area of CG3d (m^2)	Square meters of CG3d type vegetation in a 100 m by 100 m cell	Vegetation survey (Walker & Pywell 2000)
Area of MG1 (m^2)	Square meters of MG1 type vegetation in a 100m by 100m cell	Vegetation survey (Walker & Pywell 2000)
Perimeter of CG3d (m)	Edge of CG3d vegetation in meters in a 100 m by 100 m cell	Vegetation survey (Walker & Pywell 2000)
Perimeter of MG1 (m)	Edge of MG1 vegetation in meters in a 100 m by 100 m cell	Vegetation survey (Walker & Pywell 2000)

Transformations of the predictor variables are used in the program rather than the raw data, these are called features (see Phillips *et al.* 2006 for a list of feature types and definitions). When specifying a model it is possible to restrict the set of transformations Maxent can apply to the data and for smaller sample sizes this is recommended. However, the default settings have been validated using a large dataset covering 226 species and six regions of the world, with sample sizes ranging from 2 – 5822 and with 11 – 13 environmental predictors for each and have been found to have ‘a performance almost as good as if they had been tuned on the evaluation data itself’ (Phillips & Dudik 2008). For this analysis, therefore, the default settings were used but models were also tried using a simpler set of features, to see if a simpler and smoother model improved the fit (as suggested in Elith *et al.* 2010 and Kuemmerle *et al.* 2010).

ENMTools version 1.4.3 was used to check for correlations between the predictor variables (Warren *et al.* 2010). The only correlation evident was between the area and length variables for MG1 and CG3d (Pearson Correlation Coeffcient = 0.57), and no effect of correlation was evident from the model response curves (Phillips *et al*. 2007). Additionally Maxent models have been found to be relatively robust to correlations between predictor variables (Phillips *et al.* 2006; Tittensor *et al.* 2009).

4.3.5 Model selection and validation

The candidate models were compared using AICc (Burham & Andersson 2002) (with ENMTools) which Warren & Seifert (2011) found to perform better than alternative methods.

The Area Under the Receiver Operator Characteristic Curve (AUC) was used to evaluate the final model fit. AUC measures the probability that a randomly chosen presence site will be ranked with a higher suitability than a randomly chosen background site (Phillips *et al.* 2006). Values of AUC between 0.7 – 0.9 indicate a moderately useful model, with values above 0.9 indicating excellent performance (Pearce & Ferrier 2000). Maxent also performs binomial tests on the AUC to determine whether a model will predict the test localities significantly better than random. AUC has been used in many other studies to evaluate model fit (e.g. Wollan *et al.* 2008; Yost *et al.* 2008; Tinoco *et al.* 2009; Tittensor *et al*. 2009; Boubli & Lima 2009; Kuemmerle *et al*. 2010) and is one of the most widely used accuracy measures in ecology (Liu *et al.* 2009), though there is some controversy over its use (Lobo *et al.* 2008). However, other suggested methods such as Kappa and the True Skills Statistic (TSS) do not allow model cross validation and are only suitable when a binary threshold for habitat suitability is wanted (Allouche *et al.* 2006). As the model will also be tested in the field by surveying random points, AUC was deemed a sufficient measure of fit.

Cross validation was used on the final model to improve accuracy and create confidence intervals (Phillips *et al.* 2006; Boubli & Lima 2009; Tinoco *et al.* 2009; Titterson *et al.* 2009; Elith *et al.* 2010; Elith *et al.* 2011). The data were split into 10 subsets, and for each subset the model was run with 90% of the data with the remaining 10% withheld and used for testing.

4.3.6 Ground truthing

To test the final Maxent model prediction, 400 random points were generated in ArcGIS 10.0 (ESRI 2010). The points were restricted to be at least 100 m apart to avoid overlapping samples. The spread of these random points was assessed to ensure a good coverage of a range of predicted habitat suitabilities, and different levels of fragmentation.

The predicted suitability value for each point was extracted from the raster. A 150 m radius buffer was used to isolate the pixels surrounding each point and the average suitability of the habitat within 150 m of each point was calculated to determine the average predicted suitability of the 100 m by 100 m squares immediately surrounding the survey point. To assess the effect of patch isolation as determined by predicted habitat suitability, the habitat suitability raster was split into three classes of polygons (0 < = unsuitable < 0.3, 0.3< = moderately suitable < 0.6, 0.6 < = highly suitable < 1.0), depicting areas of highly suitable habitat, areas of moderately suitable habitat and areas of unsuitable habitat. For each random point, the area of the fragment it was in was then calculated, along with the shortest distance from the point to each of the habitat types (highly suitable, moderately suitable and unsuitable), using the ‘nearest neighbour’ tool in ArcGIS.

For all of these different variables (predicted habitat suitability, surrounding predicted habitat suitability, area of fragment, distance to highly suitable habitat, distance to moderately suitable habitat and distance to unsuitable habitat) histograms were created and the data distribution examined to determine if coverage was even. It was found that too few points were in habitat predicted to be highly suitable so another 200 points were randomly generated just in the highly suitable habitat polygons and a random sample of 120 of these points were added to the main group of survey points. Such a large number of points were generated to allow for uncertainty in how many it would be possible to survey during the field season, and allow for any that might prove inaccessible. A total of 267 randomly selected points were surveyed in 2014, between the 19th May – 28th June. The points were surveyed in tetrads to make sampling quicker and more efficient, and ensure a good coverage of the whole study area.

To allow more points to be surveyed, the Imber Conservation Group, a local volunteer group, carried out some of the surveys. All the points were surveyed before 11 am or after 4 pm, when Whinchats were observed to be most active (pers. obs.). Handheld Global Positioning (GPS) Units were used to navigate to each point. Upon arrival the observer watched for five minutes, listening for Whinchat song and scanning all around with binoculars. Five minutes was chosen as a compromise between allowing detection of any Whinchats present and reducing sampling time to allow more points to be sampled. Prior knowledge from surveys in 2012 and 2013 suggested five minutes should be long enough to detect a breeding Whinchat if the observer is within the Whinchat’s territory. Each point was only sampled once, again to maximise the number of points sampled. The start time, weather, number and sex of Whinchats seen were all recorded. An approximate measure of distance was also recorded, whether the Whinchats seen were within 100 m of the observer, or between 100 m and 250 m.

Some of the 267 sampling points had to be moved from their original location due to inaccessibility (crop fields, buildings etc.), therefore the predicted suitability value, suitability of the surrounding 150 m radius of habitat, the area of the fragment it was in, and the shortest distance from the point to each of the habitat types (highly suitable, moderately suitable and unsuitable), was re-calculated to look at Whinchat sensitivity to fragmentation. Additionally the average suitability of the surrounding habitat for a 250 m radius and a 500 m radius around the sampling point was calculated to allow assessment of Whinchat response to fragmentation at different scales.

4.3.7 Assessing model fit

The Maxent model predictions were tested against Whinchat presence within a 100 m survey radius and a 250 m survey radius using the statistical program R version 2.3.1 (R Development Core Team 2014). Exact counts were not used as few Whinchats were encountered and therefore the model would have been zero inflated. A binomial Generalised Linear Model (GLM), with a logit link, was used. The ‘lm.moran’ test function (Cliff & Ord 1981; Bivan 2014) was used to test for spatial autocorrelation in the model residuals, using an inverse weighted distance matrix, and found no significant autocorrelation (Moran's I = 0.121, p = 0.106). However, the moran test function was created for testing residuals of a linear regression, and has not been validated for use on GLMs, therefore a spline correlogram with 999 bootstrapped 95% confidence intervals (Zuur *et al.* 2009) was also used; the correlogram also did not indicate significant autocorrelation.

4.3.8 Vulnerability to fragmentation

Salisbury Plain is the largest area of continuous grassland in northwest Europe (Ash *et al.* 2011). Compared to habitats such as abandoned farmland interspersed with forest (e.g. Shitikov *et al*. 2015), Salisbury Plain would appear relatively un-fragmented. However, here I am considering finer scale fragmentation which is less obvious from visual observation. Fragmentation here is defined by the lack of necessary habitat features for breeding Whinchats. The habitat predicted as suitable by the model should contain all the habitat features necessary for breeding Whinchats, whereas habitat predicted as unsuitable should not. Therefore the habitat is fragmented in the sense that Whinchats cannot breed everywhere in the habitat but can only breeding in areas of habitat above a certain suitability value. To assess Whinchat vulnerability to this level of fragmentation, the presence of Whinchats within 100 m of a survey point was modelled against the various measures of fragmentation determined by the predicted suitability values of the surrounding habitat. The variables used to measure fragmentation were all correlated with each other and with the survey point’s predicted suitability (Pearson’s Product Moment Correlation Coefficient > 0.5), therefore they were modelled separately in a series of GLMs using R version 2.3.1 (R Development Core Team 2014). To separate the effects of surrounding habitat suitability on the probability of Whinchat presence, from the effect of survey point suitability on Whinchat presence, the data were split into three categories based on the predicted suitability value, which from here on will be called the suitability category (unsuitable < 0.3, 0.3 < = moderately suitable < 0.6, highly suitable > = 0.6). Fragment area had a skewed distribution for all suitability categories with areas either small or very large. Therefore area was split into two categorical variables (based on the fragment size) for moderately suitable and unsuitable survey points and into three categorical variables for highly suitable survey points. All model residuals were examined for spatial autocorrelation with Moran’s I using lm.moran, but none showed significant spatial autocorrelation.

4.3.9 Proportion of suitable habitat occupied

To determine whether most of the suitable habitat was occupied by Whinchats, the number of sampling points where an individual was observed within a 100 m radius of each sampling point was compared to the maximum, mean and minimum number that would be expected from the model if all suitable breeding habitat was occupied. It is important to note here that the model predicts the probability of an area of habitat being suitable for breeding, not the probability of a Whinchat being in a particular area (Kuemmerle *et al.* 2010). If availability of breeding habitat was limiting we would expect all suitable habitat to be occupied. Using the suitability categories, the predicted number of sample points with Whinchats was calculated by multiplying the number of sample points in each category (sample size) by the minimum, maximum and mean predicted suitability for that category. However, it is also necessary to account for the reliability of the Maxent predictor model. The AUC of the model effectively provides a measure of model accuracy, an AUC of 0.715 means that in 71.5% of cases a randomly selected point with Whinchats will have a greater habitat suitability score than a randomly selected point where there were no Whinchats. Therefore the AUC value of the final model was used to adjust minimum and maximum estimates to account for the prediction model accuracy. The following formulas were used for these calculations:

Predicted maximum number of Whinchats in the habitat suitability category = maximum suitability value for the category × number of squares in the category+ (maximum suitability value for the category × number of squares in the category) × (1-AUC).

Predicted minimum number of Whinchats in the habitat suitability category = minimum suitability value for the category × number of squares in the category − (minimum suitability value for the category × number of squares in the category) × (1-AUC).

Predicted mean number of Whinchats in a habitat suitability category = mean suitability value for the category × number of squares in the category

4.4 Results

4.4.1 Habitat Suitability Model

The Maxent model with the lowest AICc was selected (Table 4.2), this model used all the variables, all feature types and no bias layer. The final, cross-validated model had an average AUC of 0.715 (+/- SD 0.028). This means that in 71.5% of cases, a randomly selected point where there were Whinchats will have a greater habitat suitability score than a randomly selected point where there were no Whinchats (Yost *et al.* 2008). All tested models performed significantly better than a random model (Binomial test of omission: $p < 0.0001$).

Table 4.2. AICc scores for candidate models, with sample size, number of model parameters and log likehood. The model description is in the left column, with the difference in variable specification compared to the other models in bold. Three factors were changed in models: variables of low contribution to the model output were removed and simpler feature types and a bias layer were trialled. The models are listed in order of increasing AICc. All models used a maximum of 5000 iterations.

Model	Log Likelihood	Parameters	Sample Size	AICc Score
All variables, restricted survey area, all feature types	-6217	85	793	12625
All variables, restricted survey area, **only linear, quadratic and product feature types**	-6278	39	793	12638
All variables **except aspect**, restricted survey area	-6243	70	793	12639
All variables, restricted survey area, all feature types, **bias layer**	-6245	80	793	12668
All variables **except bare ground**, restricted survey area, all feature types	-6240	88	793	12678
No vegetation variables but others included, restricted survey area, all feature types	-6256	78	793	12685
All variables, restricted survey area, **only linear features**	-6350	8	793	12716
All variables, restricted survey area, **only hinge features**	-6258	92	793	12724

The selected model was run using clusters of points in a 100 m buffer around Whinchat occurrence locations to depict territories and habitat use. A model just using Whinchat occurrence locations was also run to test for any substantial difference in the final model. The influence of the environmental variables of the two models on habitat suitability, and the relative contribution of each environmental variable to predicted suitability, was the same for both models. The main difference was that the model using the clusters of points to represent Whinchat territories was more conservative, representing a more gradual change in habitat suitability, compared to the model using just the Whinchat occurrence locations. The more conservative cluster model was chosen for the analysis as the clusters of points were thought to represent Whinchat habitat use better. Using the suitability categories defined earlier, 9% of the area (15.9 km^2) is highly suitable, 40% (70.6 km^2) is moderately suitable and 51% (91.5 km^2) is unsuitable (Figure 4.2).

Maxent measures the permutated importance of each variable. This is calculated by randomly permutating values of the variable among the data used to fit the model, and measuring the resultant decrease in model fit. A large decrease shows the model depends heavily on that variable (Phillips *et al.* 2007). These values are then normalised to give a percentage (Table 4.3). Altitude made the most informative contribution to predicting suitability; it contributed 43.4% to the model prediction (Table 4.3). Slope was the next most informative predictor contributing 19.6%. These two variables were the most important predictors of suitable habitat in the model and contained most of the information used to create the model prediction.

There is a strong trend for higher predicted habitat suitability at low altitudes (Figure 4.3) and in areas with moderately steep slopes. None of the other variables have such a strong influence on the predicted habitat suitability. Other trends were for higher predicted habitat suitability in areas with less scrub cover, less bare ground and a very slight trend for higher suitability with higher percentage cover of MG1 and CG3d, a more westerly aspect and a larger perimeter of CG3d.

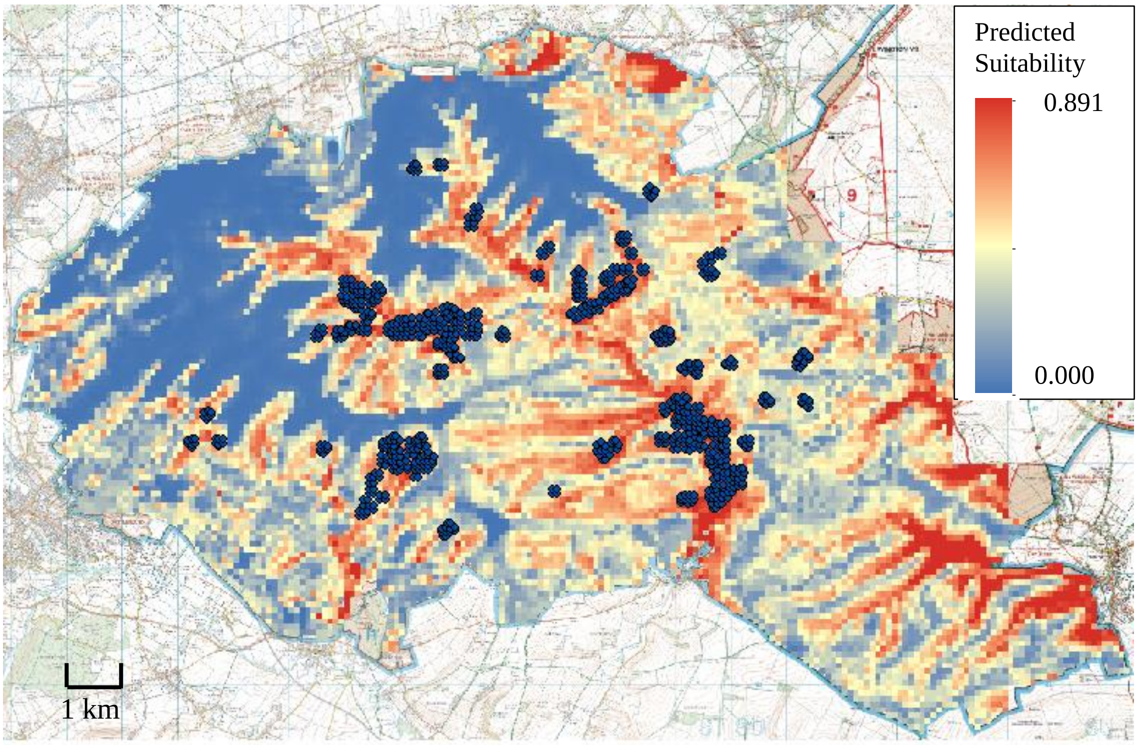
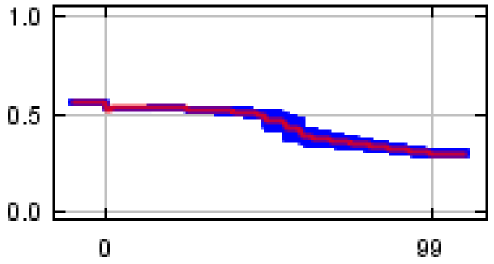


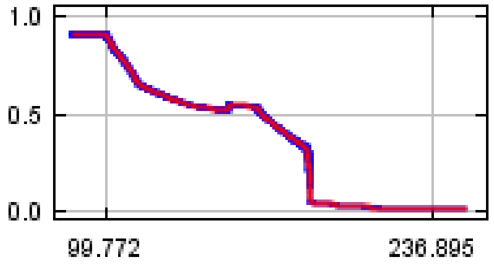
Figure 4.2. The Maxent projected predictions for Whinchat occurrence using clusters of occurrence points within a 100 m buffer around Whinchat sightings. The Whinchat presence occurrences clusters used to create the model are shown as blue dots. The map is based on [2011, Salisbury Plain – West, 1:25,000]. Map produced on behalf of The Controller of Her Majesty's Stationary Office © Crown Copyright. Lancaster University, Bailrigg, Lancaster, OS Licence No. 100028811.

Table 4.3. The permutated importance of the environmental variables used in the cross-validated Maxent prediction model. The permutated importance is calculated from randomly permutating the values of the variable among the data used to fit the model and measuring the resultant decrease in model fit. This value is then normalised to give a percentage. A high permutated importance shows the model depends heavily on that variable.

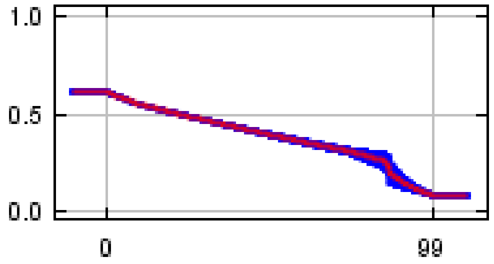
Variable	**Permutation importance**
Altitude	43.4
Slope	19.6
Area of CG3d vegetation	6.1
Percentage scrub cover	14.3
Area of MG1 vegetation	2.3
Eastness	4.9
Percentage bare ground	3.4
Perimeter of MG1 vegetation	2
Northness	3.2
Perimeter of CG3d vegetation	1



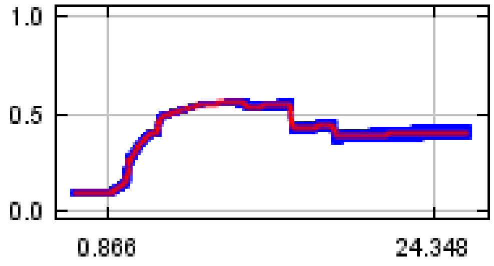
Percentage cover of bare ground (%)



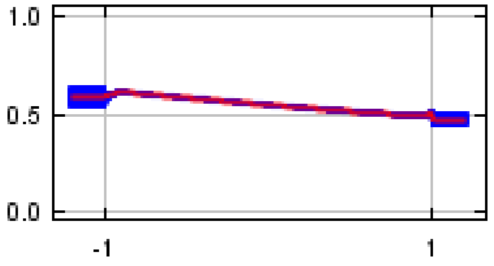
Altitude (meters above sea level)



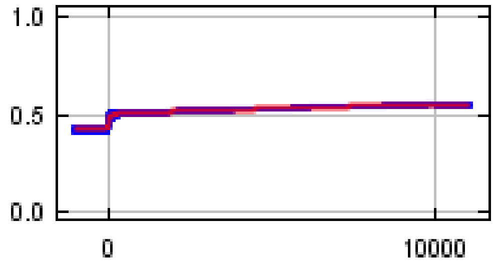
Percentage cover of scrub (%)



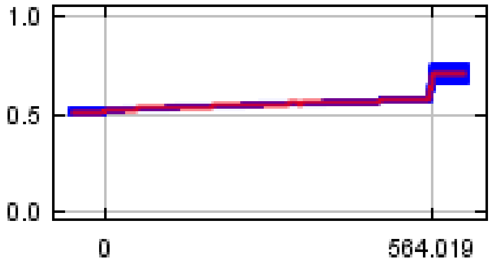
Slope (°)



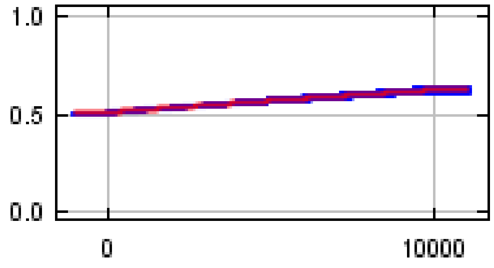
Eastness (˚)



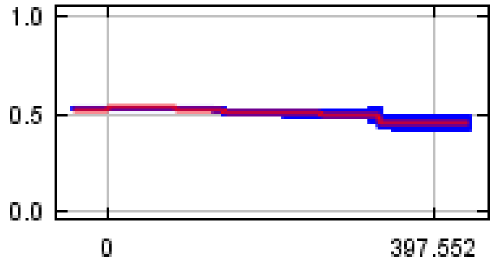
Area of CG3d type vegetation in a 100 m by 100 m cell (m^2)



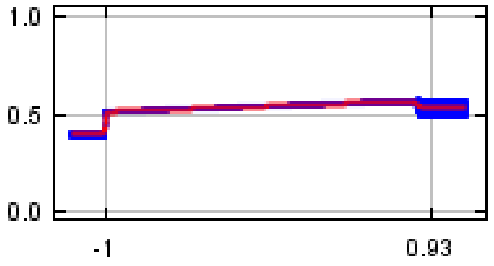
Perimeter of CG3d type vegetation in a 100 m by 100 m cell (m)



Area of MG1 type vegetation in a 100 m by 100 m cell (m^2)



Perimeter of MG1 type vegetation in a 100 m by 100 m square (m)



Northness (˚)

Figure 4.3. Response curves for the effect of each environmental variable on the Maxent model prediction. The curves show how the logistic predicted habitat suitability (y axis) changes as each environmental variable is varied keeping all other environmental variables at their average sample value, 0 = unsuitable habitat, 1 = highly suitable habitat. The curves show the mean (red) response from 10 crossfold validation +/- one standard deviation (blue).

4.4.2 Assessing model fit

Model fit was assessed using Whinchat sightings within 100 m of the survey point. Of 267 sampling points, Whinchats were present within a 100 m radius of 18 sampling points. Only one Whinchat was observed within a 100 m radius of a point where the habitat was predicted to be unsuitable. The mean predicted suitability for points where Whinchats were present within 100 m was 0.562 +/- 0.037 (SE), compared to the maximum suitability predicted for any of the survey points which was 0.77, and the mean suitability predicted for highly suitable squares which was 0.650 +/- 0.006. From the Maxent prediction map, 11.2% of the area has a predicted suitability of 0.562 or above which translates into 20 km^2. Thirty of the 267 sampling points had Whinchats observed within 250 m. The results of the analysis using Whinchat sightings within 250 m of the sampling point was qualitatively similar and therefore is not presented here for brevity. Figure 4.4 displays the sampling points plotted on a map of the Maxent predicted habitat suitability.

Observing a Whinchat was significantly more likely at a sampling point with a higher predicted suitability (GLM: Est = 5.41 +/- 1.66 (SE), p = 0.001, n = 267). The Maxent model accurately predicted areas where Whinchats were more likely to be present. Figure 4.5 displays the fitted values for the model of the relationship between predicted habitat suitability and the probability of observing a Whinchat within 100 m of the survey point. As so few Whinchats were sighted at survey points the probability of seeing a Whinchat only reaches about 30%, even when the predicted habitat suitability is 0.80.

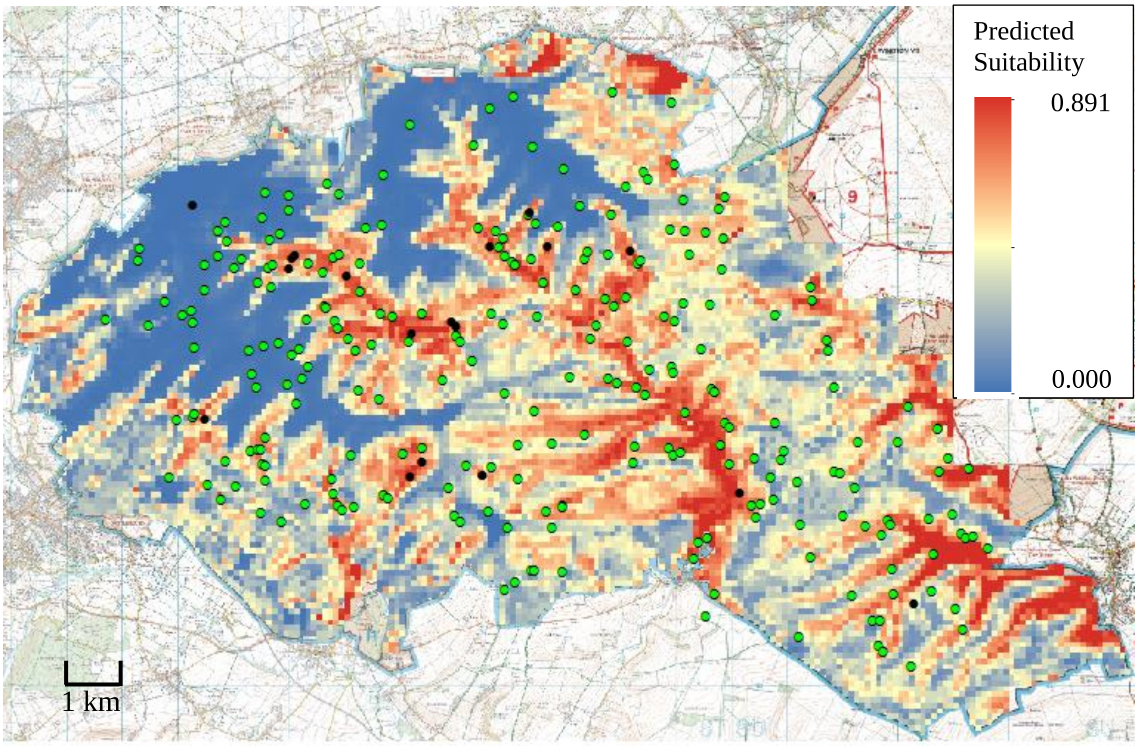


Figure 4.4. The random survey points plotted on a map of the Maxent projected predictions for Whinchat occurrence using the 100 m buffer cluster of points around Whinchat sightings as occurrence data. The green spots are survey points where no Whinchats were seen, the black spots are points where Whinchats were seen within 100 m of the survey point. The map is based on [2011, Salisbury Plain – West, 1:25,000]. Map produced on behalf of The Controller of Her Majesty's Stationary Office © Crown Copyright. Lancaster University, Bailrigg, Lancaster, OS Licence No. 100028811.

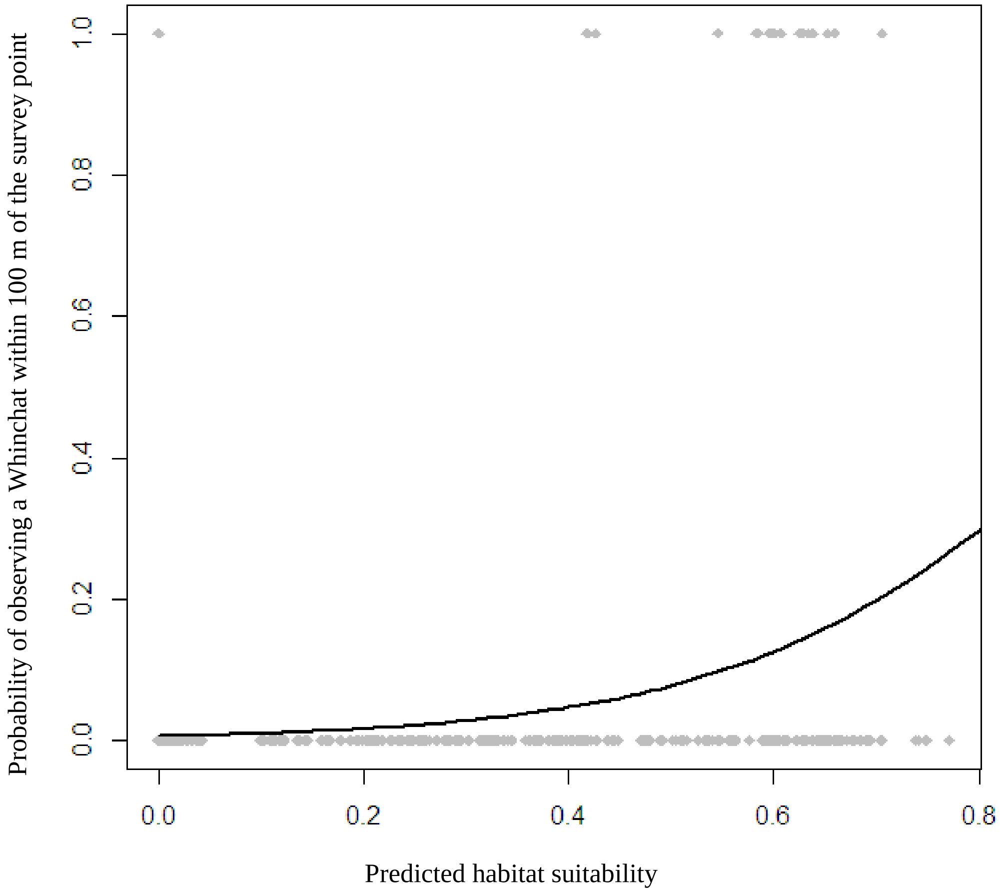


Figure 4.5. The fitted values (solid line) for the relationship between predicted habitat suitability at a sample point and the probability of observing a Whinchat within 100 m of the sampling point (n = 267). The dots are the observed values. The model is a binomial GLM with a logit link.

4.4.3 Effect of fragmentation

There was a significant effect of the predicted suitability of the surrounding 150 m and 250 m of habitat on Whinchat occurrence for moderately suitable sampling points (Table 4.4): if the predicted suitability of the surrounding 150 m and 250 m of habitat was higher there was a significantly higher probability of observing a Whinchat ($p = 0.012$ and 0.019 respectively). The predicted suitability of the surrounding 150 m and 250 m of habitat was not significantly correlated to the probability of observing a Whinchat at sampling points in highly suitable habitat. The predicted suitability of the surrounding 500 m of habitat had no significant effect on the probability of Whinchat occurrence for either habitat category. Results from the unsuitable habitat category are not included because a Whinchat was observed at only one out of 106 sampling points and therefore a reliable model could not be fitted.

The significant correlation between higher suitability of surrounding habitat at moderately suitable habitat points, and the probability of observing a Whinchat could simply be a spurious correlation affect. The average predicted habitat suitability value for Whinchat occupied points in moderately suitable habitat was 0.544 +/- 0.027 (SE), whereas the average predicted habitat suitability for all moderately suitable points was 0.464 +/- 0.013. The Whinchats were observed at the moderately suitable sampling points with higher suitability values, and higher suitability of a point is correlated with higher suitability in the surrounding 150 m and the surrounding 250 m of habitat (PPMCC = 0.656 and 0.522 respectively). Therefore this does not provide strong evidence of an effect of the surrounding habitat on Whinchat occurrence.

The distance to highly suitable, unsuitable and moderately suitable habitat did not significantly affect the chances of observing a Whinchat ($p > 0.05$; Table 4.4). The area of the habitat fragment a survey point was in also did not significantly affect the probability of observing a Whinchat. In general, the predicted suitability of the surrounding habitat, fragment area and distance to other habitat types appears to have had little effect on the probability of Whinchat occurrence (Table 4.4).

Table 4.4: GLM binomial models with a logit link for survey points in each category of predicted habitat type (moderately suitable: 0.3 < = suitability < 0.6, n = 104, highly suitable: suitability > = 0.6, n = 57). Results from the unsuitable habitat category are not included as a Whinchat was observed at only one out of 106 sampling points and therefore a reliable model could not be fitted. The dependent variable in each case was Whinchat occurrence in a 100 m radius from the survey point. The explanatory variables are listed on the left. The parameter estimate +/- 1 standard error and p value for the explanatory variable in each model are presented. An asterisk is used to denote p values below 0.05.

Variables	Just predicted suitable habitat survey points	Just predicted moderately suitable habitat survey points
Predicted suitability of surrounding 150 m radius of habitat	Est = -2.16 +/- 5.33, p = 0.685	Est = 12.41 +/- 4.95, p = 0.012*
Predicted suitability of surrounding 250 m radius of habitat	Est = -4.23 +/- 4.51, p = 0.348	Est = 11.34 +/- 4.82, p = 0.019*
Predicted suitability of surrounding 500 m radius of habitat	Est = -6.50 +/- 4.05, p = 0.109	Est = 7.52 +/- 4.76, p = 0.114
Distance to nearest predicted suitable habitat	NA	Est = -0.002 +/- 0.002, p = 0.248
Distance to nearest predicted moderately suitable habitat	Est = -0.012 +/- 0.016, p = 0.461	NA
Distance to nearest predicted unsuitable habitat	Est = -0.000 +/- 0.004, p = 0.923	Est = 0.174 +/- 0.092, p = 0.059[1].
Area of fragment the survey point is in	Fisher's exact test: p = 0.757	Fisher's exact test: p = 0.382

1. variable was square-root transformed to make it conform to an approximately normal distribution

4.4.4 Proportion of suitable habitat occupied

Far fewer Whinchats were observed at survey points in the moderately suitable and highly suitable habitat categories than would be expected based on the Maxent model predictions of habitat suitability and the number of survey spots in each habitat category (Figure 4.6; see methods for a reminder of how these expected counts were calculated). When allowing for sightings within a 100 m radius, Whinchats were only observed at 24.3% of the highly suitable survey points predicted to have Whinchats, and 16.6% of the moderately suitable points predicted to have them. The results using Whinchat sightings within 250 m of the sampling point were qualitatively similar and therefore are not presented here. This suggests that there is a large area of unoccupied, yet suitable, breeding habitat for Whinchats on Salisbury Plain.

It is possible that Whinchats did use an area within 100 m of a survey point during the season but were not seen on the surveys. Each point was only surveyed once; therefore Whinchats that failed early and moved away or that moved into the area after failure elsewhere may have been missed depending on the date of the survey. Nine of the 267 sampling points were within 100 m of known nests during 2014. Of these points Whinchats were sighted within 250 m of six of the points and within 100 m of five of the points. It is possible to account for this uncertainty by assuming the worst case scenario, that Whinchats were missed at 44% of points where they were present. The adjusted estimates of expected number of Whinchats in each habitat taking into account possible missed Whinchats are also plotted in Figure 4.6. The observed number of Whinchats is still below what would have been expected even accounting for the possibility of a high rate of missed observations, with Whinchats observed at only 43.3% of suitable habitat points and 29.6% of moderately suitable habitat points where they would have been expected.

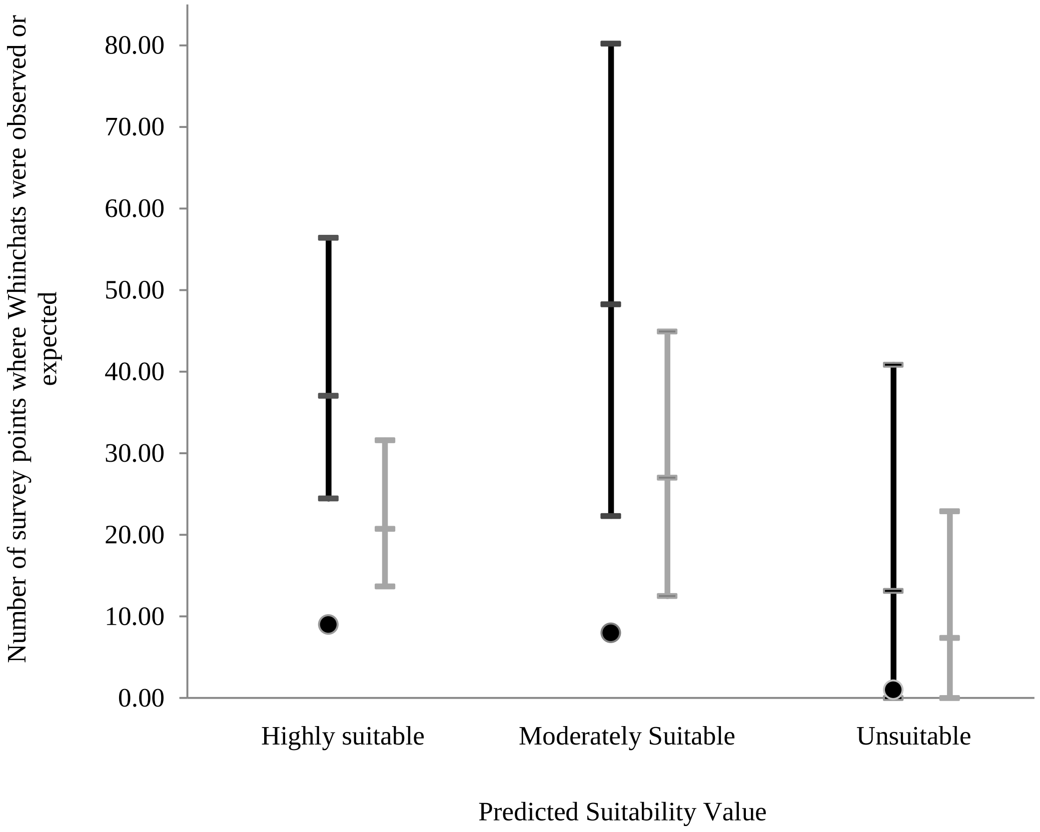


Figure 4.6. A comparison of Whinchat expected and observed occurrence in relation to habitat quality. The spots show the number of sample points where Whinchats were observed within a 100 m radius. The black bars show the mean, minimum and maximum expected number of survey points with Whinchats, as predicted by the habitat suitability model. Expected counts are calculated in proportion to the number of points sampled in each habitat category (Highly Suitable (predicted suitability > = 0.6), n = 57, Moderately Suitable (0.3 < = predicted suitability < 0.6), n = 104, Unsuitable (predicted suitability < 0.3), n = 106). The grey bars are adjustments of these estimates to account for the possibility of missing Whinchats at 44% of the points where they were expected.

4.5 Discussion

The Maxent prediction model, using large scale general habitat data based on NVC classifications, aerial maps and topography, successfully predicted areas where the random point survey showed that breeding Whinchats were more likely to be observed (Figure 4.5). However, only relatively few Whinchats were sighted, meaning the predicted probability of observing a Whinchat was low even in the most suitable habitats. Whinchats were more likely to be observed in moderately suitable habitats if the surrounding habitat suitability was higher but this may be a spurious correlation effect. There were no other indications of sensitivity to fragmentation at the level present in Salisbury Plain. The number of Whinchats sighted was far below the value expected in highly suitable and moderately suitable habitats, even when accounting for the possibility of false negatives, with Whinchats not observed at 56.6% of highly suitable points where they were predicted to be (Figure 4.6). This suggests that a large proportion of apparently suitable habitat was unoccupied on Salisbury Plain.

Detailed vegetation data were unavailable on the scale needed for an environmental predictor variable; the only vegetation data available at a 100 m by 100 m pixel scale for the entire study area were NVC classifications from 1996. This means some features such as long, dense, structural diverse vegetation, which we know are important for breeding Whinchats (Chapter 3), could not be directly included in the model. Future studies could also use Light Detecting and Ranging (LiDAR) data to get more fine grain information on vegetation structure, as Buchanan *et al.* (2005) did. Additionally, the vegetation may have changed since 1996. Care is needed, therefore, when drawing biological inferences on the influence of the selected variables on habitat suitability (Tinoco *et al.* 2009). However, to increase our confidence in this model, it is useful to compare the habitat preferences seen here with the results of Chapter 3, which looks at Whinchat habitat preferences in more detail, over a smaller scale.

Altitude and, to a lesser extent, slope were the two most important variables in predicting suitable habitat; with higher predicted suitability values occurring at low altitudes on moderately steep slopes. This suggests, as found in Chapter 3, that valleys are important breeding habitat. However, slope did not differ significantly between areas with Whinchats and areas without in Chapter 3 (5.2 +/-0.5 to 5.2 +/-0.2 Chapter 3, Table 3.6) and actually varied more for areas with Whinchats. If the middle range was preferred, as seen in the Maxent model, we would expect the standard error to be smaller for Whinchat occupied areas. The slope variable may be correlated with something else that was not included in the Maxent model, such as less waterlogged ground conditions, as slopes facilitate faster run off of rain than flat ground. Higher predicted suitability values were also associated with lower amounts of bare ground and lower scrub cover. The same trends in bare ground and scrub cover with Whinchat occurrence were observed in Chapter 3. Bare ground from the aerial maps used in the Maxent analysis generally refers to military roads and tank tracks, areas with large amounts of bare ground which are unsuitable for nesting, as Whinchats need long dense structurally diverse vegetation (Chapter 3; Fischer *et al.* 2013; Richter & Düttmann 2004; Broyer *et. al* 2012). Areas with a high percentage of scrub cover, as defined by the aerial map used in this analysis, are actually generally blocks of trees planted for military training exercises. Fischer *et al.* (2013) found Whinchats preferred to nest further away from forests and suggested that this was due to predator avoidance. Extensive scrub cover may block the view of an approaching predator (Götmark *et al.* 1995) and provide lookout points for avian predators to spot a nest from (Berg *et al.* 1992; Andersson *et al.* 2009). There was a slight trend for higher suitability values with increasing cover of CG3d (rank tussocky chalk grassland) and MG1 (reverting arable grassland). This reflects findings from other studies that Whinchats are commonly associated with abandoned farmland and unimproved grassland (Fischer *et al.* 2013; Orlowski 2004; Frankiewicz 2008). Generally there is a high degree of congruence between the predicted trends in the environmental features from the Maxent model in this chapter and the empirical habitat preference data in Chapter 3. I therefore conclude that the Maxent model predicts the habitat preferences of Whinchats with a high degree of certainty.

The average suitability of points Whinchats were sighted at was 15% lower than the average suitability of highly suitable points. This suggests Whinchats are not just selecting the most suitable breeding habitat according the environmental variables included in the model, something else must be determining which areas they select to breed in. It is possible that an important variable is missing from the model, as mentioned above the vegetation data available were not highly detailed and was from 1996, but due to the limited management allowed on Salisbury Plain (Ash *et al.* 2011) habitat change should be minimised. Broadscale comparisons with a smaller scale NVC survey conducted in 2004 (pers. comm. Redhead, J.) suggest little change in NVC classifications between 1996 and 2004. Another possibility is that Whinchats are undervaluing highly suitable habitat, relying on rapidly assessed cues that fail to fully represent habitat quality, or are being deterred by changes in habitat appearance despite no change in quality (Gilroy & Sutherland 2007). Alternatively Whinchats may be selecting breeding habitat based on other factors in addition to habitat quality. Often a species behaviour and life history influence its occupation of habitat, not just the habitat suitability. For example, many territorial species are thought to show conspecific attraction, clustering despite the presence of nearby suitable habitat (Stamps 1988). This could benefit the species by improving the chances of finding a mate, providing enhanced detection and early warning of predators, or providing cues of habitat suitability (Stamps 1988). Ward and Schlossberg (2004) experimentally demonstrated conspecific attraction, showing that Black-Capped Vireos established territories in previously unoccupied areas if tapes of their song were played. Site fidelity (Lane *et al.* 2001) and assessments of conspecifics breeding success (Doligez *et al.* 2002) have also been found to play a role in breeding habitat selection. Thus these behavioural influences on habitat selection are very important aspects to consider in conservation management as it means that the current distribution of Whinchats may have been influenced by the prior distribution, and also suggests a poor capacity to colonise newly created areas of suitable habitat (Muller *et al.* 1997; Lane *et al.* 2001; Ahlering & Faaborg 2006).

In the moderately suitable habitats, Whinchat presence was associated with significantly higher values of predicted suitability in the surrounding habitat (Table 4.4). This could suggest that when habitat suitability is at the lower end of the habitable range, territories need to be bigger to compensate, and therefore having surrounding habitat with similar or higher habitat suitability values becomes more important. This theory is supported by Calladine & Bray (2012) who found that Whinchat territories at higher altitudes were larger and suggested it was due to reduced food availability compared to lower altitudes. However, it is also possible that, in this study, the Whinchats were just selecting habitat based on the high predicted suitability at the survey point and the fact that these points also had higher predicted suitability in the surrounding habitat was irrelevant. In general the predicted suitability of surrounding habitat had little effect on the probability of Whinchat occurrence; with 10 out of 12 models (Table 4.4) suggesting Whinchats were not sensitive to fragmentation at the level present in the study site. However, it is important to note that in this study there were not large changes in predicted suitability between neighbouring 100m by 100m squares, and the patch definition was restricted by the size of the raster cell used in delineation (Girvetz & Greco 2007). In areas with more stark changes in habitat type, such as intensive agricultural land, Whinchats may be more susceptible to fragmentation and patch isolation. Horch & Birrer (2011) looked at Whinchat occupancy in un-grazed plots of 9000 m^2 and 1000 m^2 within cattle grazed fields. They found that these plots needed to be at least 10,000 m^2 and represent at least 10% of the area of favourable grassland to have an effect on Whinchat territory establishment. Orlowski (2004) found that the smallest field occupied by a Whinchat pair was 9000 m^2. Therefore any of the 100 m by 100 m squares produced by the Maxent prediction model with a high enough predicted suitability would be sufficient for territory establishment. It may be necessary to study territory establishment on an even smaller scale to determine any effect of fragmentation on

Whinchats. It is also important to consider that breeding success of the pairs in different habitat suitabilities was not assessed in this analysis (discussed in Winter *et al.* 2006). It is possible that Whinchats breeding in more isolated fragments have lower nest success, as has been found for various grassland prairie birds (Herkert *et al.* 2003).

Far fewer Whinchats were observed at suitable and moderately suitable survey points than would be expected from the model if breeding habitat was limited (Figure 4.6). Even when accounting for the model accuracy and using the minimum predicted habitat suitability value for the category, only 36.8% of highly suitable points from the minimum expected actually had Whinchats. This suggests there is a lot of suitable breeding habitat that is unoccupied (approximately 64%). It is possible that Whinchats were present at some of the points and not observed, though the surveys were conducted in good weather at the times of day when the birds were most active, and in the middle of the breeding season when most pairs had eggs or chicks, and were alarm calling loudly, which should minimise this problem. As all points were only surveyed once in order to maximise the number of points that could be sampled, it is also possible that for some points Whinchats may not have been occupying the area when the point was surveyed but were there at a different point in the season and either, left early due to early failure, or moved into the area later due to failure elsewhere. If we allow for the possibility of a high rate of false negatives and assume 44% of whinchat were missed, still far fewer Whinchats were observed than would be expected (Figure 4.6), suggesting that the Salisbury Plain Whinchat population is below carrying capacity. Possible reasons for a site being below carrying capacity may be that it is small and isolated or that there are not enough Whinchats to fill it (Newton 1998). Salisbury Plain is the largest area of continuous grassland in Northwest Europe (Ash *et al.* 2011) and habitat patches are generally not isolated. However, Whinchats have declined in abundance by an estimated 67% in Europe since 1980 (EBCC 2012), which does suggest there may not be enough birds to fill the habitat. This implies that for the Salisbury Plain population at least, demographic parameters are currently limiting the population, rather than lack of suitable breeding habitat.

The Maxent model was able to reliably predict suitable Whinchat habitat, demonstrating that it is possible to create an accurate habitat suitability map even if spatial data are not available for all the relevant environmental variables. This opens up opportunities for rapid creation of habitat suitability maps for many other species using citizen science collected occurrence data (for example from birdtrack: http://www.bto.org/volunteer-surveys/birdtrack/taking-part/birdtrack-apps), and selecting the most relevant existing spatial data available for the area of interest. Citizen scientists can also be used to test the model’s performance, allowing us to have confidence in its predictive power. Habitat suitability maps can be used to direct conservation planning and research efforts towards conserving areas of key habitats, and thereby reduce population declines associated with habitat loss and fragmentation (Yost *et al.* 2008; Tittensor *et al.* 2009; Irvin *et al.* 2013).

Chapter 5: Limitations to breeding success in a declining grassland migrant bird

A predated Whinchat nest.

5.1 Abstract

Population growth and expansion may be limited by low reproductive success or low adult survival and low recruitment. Previous chapters have established that the preferred breeding habitat of Whinchats is not apparently limiting the population on Salisbury Plain. Here, the causes of breeding failure and potential limitations to Whinchat breeding success are identified. Productivity was low compared to other populations of Whinchats in similar habitat. Nocturnal predation was the main cause of breeding failure and nestling starvation was very rare. Clutch sizes and hatching success were similar between years and to other studies elsewhere in Europe, suggesting that parental condition was not a key limitation to breeding output. Egg daily survival rates were lower in territories with moderate amounts of bare ground cover, and nestling survival rates were higher in territories with medium vegetation height and a high abundance of invertebrates, if the perch abundance was low. Grazing by livestock during the breeding season had a negative influence on daily nestling survival rates. In general, the low proportion of variance explained by all the models suggests that predation risk may vary within and between years, independently of any of the measured vegetation, food, weather or temporal variables. This study illustrates that predation has the potential to limit breeding success in ground nesting grassland birds.

5.2 Introduction

Reproduction requires a large energy input for gamete production and parental care (Martin 1987). The amount of food available to the parents before egg laying can determine their subsequent investment in the offspring, with parents in poor condition generally exhibiting reduced clutch sizes (Martin 1987; Slagsvold & Lifjeld 1988; Konarzewski 1993; Devries *et al*. 2008), lower hatching success (Martin 1987; Jamieson 2004; Serrano *et al.* 2005) and reduced parental care (Martin 1987; Slagsvold & Lifjeld 1988). In years when conditions on the over-wintering grounds, or on arrival at the breeding grounds, are favourable, with abundant food and mild weather conditions, the intra-population variation in body condition is reduced (Newton 1998; Newton 2008); however, when resources are limiting, subordinate individuals will be out-competed and forced into sub-optimal habitats, leading to a subsequent decline in their condition (Marra & Holberton 1998; Marra *et al.* 1998; Marra & Holmes 2001). Higher variability in clutch sizes, hatching success and brood sizes can, therefore, suggest a lack of good quality overwintering habitat or poor spring food supplies at breeding sites (Högstedt 1980; Martin 1987; Forbes 1991).

Causes of partial or complete nest contents loss in breeding birds include predation (Martin 1993; Vickery *et al.* 1992; Patterson & Best 1996; Donald *et al.* 2002; Zanette *et al.* 2006a; Bellebaum & Bock 2009), adverse weather (Rotenberry & Wiens 1989, 1991; Chase *et al.* 2005; McDonald *et al.* 2004; Elkins 2010), food shortage (Wiklund 1984; Martin 1987; Siikamaki 1998; Britschgi *et al.* 2006; Lu *et al*. 2011), disturbance (Phillips & Alldredge 2000; Steidl & Anthony 2000; reviewed in Frid & Dill 2002 and Price 2008) and agricultural activity (Baines 1990; Green *et al.* 1997; Müller *et al.* 2005; Perlut *et al*. 2006; Posadas-Leal *et al.* 2010; Grüebler *et al.* 2012; Fischer *et al.* 2013). On Salisbury Plain, with the lack of agricultural activity and limited access allowed, predation or lack of food would be expected to be the main cause of breeding failure. Adverse weather can also cause direct clutch or brood loss (i.e. via flooding nests (Gray 1974; Frankiewicz 2008), or chilling nestlings (McDonald *et al*. 2004; Elkins 2010)). However, extreme weather events resulting in widespread egg or nesting mortality are relatively rare (Newton 1998) so weather usually exerts its effect through interactions with food availability (Rottenberry & Wiens 1991; Rodriguez & Bustamante 2003) or predation risk (e.g. Morrison & Bolger 2002; Chase *et al.* 2005).

In ground nesting grassland birds, predation is commonly cited as the primary cause of nest failure (e.g. Best *et al.* 1997; Winter 1999; Koford 1999; Frankiewicz 2008; Ludlow *et al.* 2014), therefore we would expect parent birds to be under strong selection pressure to choose breeding habitats which reduced the risk from predators (Martin 1993). Generally, for grassland bird species, higher nest concealment and denser vegetation are associated with reduced predation risk (Winter 1999; Davis *et al.* 2005; Winter *et al.* 2005; Knutson *et al.* 2007; studies reviewed in Wilson *et al*. 2005). Denser vegetation makes predator movement more difficult and provides better nest site cover, and the relatively homogenous habitat dilutes the chances of a predator actually finding the nest site (Martin 1993). Many previous studies, however, have found weak and inconsistent correlations between breeding success and vegetative cover for grassland birds (Davis 2005; Winter *et al.* 2005; Jones & Dieni 2007; review by Chalfoun & Schmidt 2012; Vickery *et al.* 1992; Koford 1999). Chalfoun & Schmidt (2012) suggested several hypotheses for these apparent discrepancies, including anthropogenic, methodological, ecological and evolutionary explanations. Two of the more commonly cited reasons are a diverse predator community (Filliater *et al.* 1994, Pietz & Granfors 2000, Davis 2005) and conflicting habitat requirements for the birds themselves, i.e. the safest nesting sites may not coincide with the best foraging habitats (Wilson *et al*. 2005; Lima 2009; Vickery & Arlettaz 2012; Götmark *et al.* 1995).

The effects of food limitation on breeding success may act more subtly than the effects of predation. Rather than causing complete breeding failure, food limitation may increase within-brood variability in nestling condition and incidences of partial brood mortality (Piper *et al.* 2012; Davies *et al.* 2014). Lack of food can also act indirectly to make nestlings more vulnerable to predation. Hungry nestlings will beg more frequently and more loudly which may attract predators (Cotton *et al.* 1996; Diego *et al.* 2012), or a lack of food may increase parental foraging time and distance (Tremblay *et al.* 2005; Britschgi *et al.* 2006). The parents spend less time guarding the eggs or nestlings (Martin 1987), or make more trips to the nest, which increases the chances of revealing its location (Martin *et al.* 2000). Parents may be able to compensate for reduced food availability by increasing their provisioning rate or food load sizes (e.g. Siikamaki *et al.* 1998; Martin 1987) and, therefore, the effect of food availability on breeding success may only be noticeable when shortages are particularly acute (Tremblay *et al.* 2003, 2005). It is also important to note that food availability does not just depend on the raw abundance and calorie content of the food source; it is also affected by access to food resources determined by vegetation structure (e.g. Whittingham & Evans 2004; Atkinson *et al.* 2005; Wilson *et al*. 2005; Hoste-Danylow *et al*. 2010; Vickery & Arlettaz 2012). In the case of Whinchats, the availability of tall herbaceous plants are important for access to food because they act as observation perches for the visually foraging birds (Opperman 1990; Oppermann 1992; Bastian & Bastian 1994; Richter & Düttmann 2004).

In this chapter I aim to determine the factors limiting Whinchat reproductive success on the Salisbury Plain. Reproductive output can be limited either through poor parental condition, resulting in reduced clutch sizes and hatching success, or via losses of eggs or nestlings - which on Salisbury Plain is mainly due to starvation or predation. The potential limiting effect of parent condition will be explored by comparing variation in clutch size and hatching success both within the site between years, and to other studies in Europe. Causes of breeding failure will be examined via regular nest monitoring and measures of food availability and habitat quality for individual territories.

Low clutch sizes and hatching rates, and more variability within the population, would suggest low parent condition, probably linked to harsh over wintering conditions or harsh conditions on arrival at breeding sites. High partial brood mortality, along with high mortality from diurnal predators attracted to begging nestlings, would suggest a limiting food supply and should be reflected in the measurements of food availability per territory. Links between successful breeding and vegetation or topographical features would suggest that variations in habitat quality were mediating predation risk and may also reflect variations in food availability. It would be predicted that Whinchats in territories with denser cover and with a higher availability of invertebrates would have a higher breeding success due to increased food availability and increased cover from predators. Due to the high quality habitat on Salisbury Plain (section 2.2), breeding success would be expected to be higher here compared to other populations from farmed areas.

5.3 Methods

5.3.1 Study area

The study area was a section of Salisbury Plain, Wiltshire, in southwest England. Initially, four valleys with high Whinchat populations were selected for intensive survey work in 2012 (West Hill, Berril, K-crossing and Imber). An extra site, Southdown Track, was added part-way through the 2012 season, although vegetation and invertebrate data were not collected for this site in 2012. In 2013 and 2014, due to a reduced number of breeding pairs in the study areas already established, an additional site, Ic valley, was used and vegetation and invertebrate data were collected as for all other sites (section 2.2 for more details and a map of the sites).

5.3.2 Habitat sampling

Vegetation quadrats and invertebrate samples were taken at the nests and at points 20, 40, 60 and 80 m north of nests and the same distances to the west. These distances were chosen because the average size of a Whinchat territory in a natural meadow is 0.015 – 0.018 km^2 (Bastian & Bastian 1996), which gives a radius of approximately 76 m. Additionally, provisioning parents on Salisbury Plain remained within 100 m of the nest 99.4% of the time (pers. obs). In 2012, sampling was conducted between the 10th – 21st July, which is towards the end of the breeding season, and consequently only final nesting attempts for each pair were sampled. As the abundance of invertebrates towards the end of the breeding season may not accurately reflect the availability of insects to the Whinchats during reproduction, and the vegetation may differ, sampling was performed either in the week before a nest was due to hatch or in the week after a nest hatched in 2013 and 2014. Territories were sampled for all nesting attempts to capture variations in territories through the season that may influence nest success. In 2013, the sample at the nest for successful nests was taken after the nest had finished to avoid excessive disturbance. However, this meant that one of the samples for each successful nest in 2013 was taken 1-3 weeks later than the other samples, and therefore it was decided to exclude all samples taken over the nests in 2013 to avoid biasing the data and instead derive the average vegetation and insect variables from the other eight samples for each territory. In 2014, it was decided that on balance any disturbance from sampling over an active nest was unlikely to have any more effect than a general nest visit to measure nestlings. For 2012 and 2014, all nine samples were used to calculate a mean value for each invertebrate and vegetation variable.

Vegetation was recorded from 1 m^2 quadrats at each sampling point. Table 5.1 defines each of the vegetation variables measured. Vegetation variables were selected based on findings from other studies about which habitat variables are important for breeding Whinchats (Britschgi *et al.* 2006; Bastian *et al.* 1994; Bastian & Bastian 1996; Opperman 1990; Oppermann 1992; Orlowski 2004; Richter & Düttmann 2004; Müller *et al.* 2005; Frankiewicz 2008; Broyer 2009; Grüebler *et al*. 2012; Fischer *et al.* 2013). All of the vegetation data were collected by the same observer in order to minimise any inter-observer variability in sampling techniques. Invertebrates were sampled with a sweep net (37 cm diameter by 82 cm) with ten sweeps of equal depth and intensity at 1 m intervals heading away from the nest, and starting at each sampling point. Invertebrate data in 2012 were collected via a different method which was found to be inappropriate for sampling the Whinchats' diet and therefore only the 2013 and 2014 invertebrate data were used in this analysis (section 2.5.2 for details). Invertebrates were sampled between 09:30 and 18:00 on days when the grass was dry and the wind speed was less than 12 mph (Beaufort scale 0-3). The invertebrate sampling data were summarised in three measures: overall abundance, order richness and inferred biomass (section 2.5.2). Invertebrate order richness and invertebrate abundance were highly positively correlated and therefore only invertebrate abundance was used in the analysis.

UK Ordnance Survey coordinates were recorded for each nest site in 2012 and for each of the nine sampling point in 2013 and 2014 using a hand held GPS device (Garmin eTrex). These coordinates were used to calculate altitude, aspect and slope from the Digital Elevation Model in ArcView (DEM; NERC Earth Observation Data Centre 2007; Redhead, J. pers. comm.; ESRI 2010). To aid interpretation, aspect was converted to a two level factor of 'northeast' for 0°-135° and 316° – 360° and 'southwest' for 136° – 315°.

Grazing data acquired from the Ministry of Defence (MOD) (Defence Estates, Tilshead, pers. comm.) were marked out on an ArcGIS map on a monthly basis between January 2011 and June 2014. The data were categorised based on how recent the grazing activity was (Table 5.2). For all nests, a 100 m radius buffer was drawn around the nest site using ArcGIS 10.0 (ESRI 2010) and the most recent grazing activity that overlapped with the buffer was taken as the grazing category for that nest. Grazing is by sheep and cattle and is limited to 10-14 days on areas of 8.2 ha or when the sward height reaches 5 cm (Ash & Toynton 2000).

Table 5.1. Vegetation variables measured for each 1 m^2 quadrat in 2012, 2013 and 2014. Measurements were observed by eye. Other vegetation variables were also measured but were not included in the analysis to avoid high correlations between variables (grass:herb ratio, standard deviation in vegetation height, maximum perch height, percentage of ground cover at 20cm height - see section 3.3.3 for definitions).

Variable	Definition
Plant species richness	Number of plant species observed when viewed from above
% Cover ground level	Percentage of ground covered with vegetation when viewed from above
Vegetation height (cm)	The mean of 5 measurements taken (one in each corner of the quadrat and one in the centre). A plastic sward disk (weight 135 g, diameter = 20 cm) was dropped from a height of 1 m with a bamboo cane though the centre
Perch abundance	Number of perches in quadrat. A perch is any projection above the height of the general vegetation that could support approximately 16 g (the mean weight of a Whinchat)
Perch height (cm)	The height of the smallest perch in the quadrat measured from the ground
% Cover tussocks	Percentage of quadrat area covered by tussocks when viewed from above. A tussock is defined as a clump of grass

Table 5.2. Grazing categories based on monthly grazing data from cattle and sheep grazing for the west of Salisbury Plain provided by the MOD (Defence Estates, Tilshead, pers. comm.) from 2011 to 2014.

Category	Description
0	Un-grazed the previous year
1	Grazed January-August of previous year
2	Grazed September-April before breeding season
3	Grazed during the breeding season while the nest was active

5.3.3 Nest success

Over the three-year study period, extensive searches resulted in 199 nests being found: 17% were found at the laying stage, 70% of nests were found during the incubation stage; and 13% were found after hatching. Nest locations were recorded to the nearest 1 m, using a handheld GPS unit (Garmin eTrex). Subject to access restrictions, nests were monitored every one to five days (mean 2.85 +/- 0.02 days) until failure or fledging. To monitor dates and times of predation events accurately, a Thermochron© iButton© (DS1921G-F5) temperature sensor was placed into 90 nests. These sensors record the temperature of the nest cup every 30 minutes, and so reveal when the contents are taken or when the parents cease brooding or incubation. In some cases the parents removed the iButtons and some nests with iButtons were successful or were abandoned; therefore, the actual sample size of iButton data from nests that failed due to predation is 47. For nests which failed, but were without iButtons, the end date was estimated as the mid-point between the last visit when the nest was active and the final visit when failure was detected. A nest was considered to have failed through predation if its contents had disappeared, and was considered abandoned if the parents were not present in the territory on three consecutive visits and the eggs were cold or the nestlings were dead in the nest. A nest was considered successful if it produced at least one fledgling. In 2014, an experiment to assess the impact of the researcher on nest success was conducted. Some nests were not visited but instead the nest activity was confirmed by remote observation of the parents in the nest vicinity (section 6.3.2).

Where adult Whinchats were colour-ringed it was possible to identify the breeding adults and whether a nest was a first or second attempt. Where the parent birds were not ringed, a nest was assumed to be a relay if a second clutch was laid within two weeks of a failed nest within the same territory.

Nine days after hatching, all nestlings were weighed and had their tarsi measured (section 2.4.1), although due to occasional access restrictions, this occurred a day either side in a minority of cases. The hatching date was accurate to within 1.5 days for nests found at the egg stage. For the small proportion of nests found later, hatching date was estimated based on a growth curve created from weight and tarsus measurements from known age nestlings, and based on physical characteristics such as feather growth and eye opening status (see section 2.4.2). An index of body condition was calculated by regressing an individual's weight (g) against their size (measured by tarsus (mm)) and extracting the residuals for use in the analysis

(Davies *et al.* 2014). Body condition was normally distributed. The necessary assumptions that mass and tarsus length were linearly related (LM: Est = 0.567 +/- 0.057, $p < 0.0001$, $n = 301$) and that condition was independent of tarsus length (Pearson's Product Moment Correlation Coefficient (PMCC) =5.35×10^{-18}, df = 299, $p = 1$) were upheld (Green 2001). Body condition at day nine was used as the majority of nestling growth had occurred by this stage (section 2.4.2) and therefore effects on nestling condition due to a lack of food should be most evident.

5.4 Data analysis

5.4.1 General breeding statistics

Mayfield estimates of Daily Survival Rate and nest survival for all nests and all years were calculated with standard errors for both the egg and nestling stages (Mayfield 1975; Johnson 1979). Daily Survival Rate (DSR) is the probability of a nest surviving from one day to the next, whereas nest survival is the probability of a nest successfully fledging at least one chick, and is calculated by raising the mean DSR to the power of the length of the breeding cycle (Mayfield 1975). Nest survival can also be separately calculated for the laying, incubation and nestling rearing periods. The laying period was taken to be four days, the incubation period 13 days and the nestling period 12 days (Cramp 1988); therefore, for nests that survived the nestling phase the end date was taken to be 12 days after the nestlings hatched and the end of the egg phase was the day of hatching. The final nesting attempt of each pair was used in these estimates to measure the overall seasonal productivity. The Mayfield method is more meaningful than apparent breeding success estimates (from raw percentages of successful versus failed nests), because it accounts for the positive bias from nests that are found at a later stage and therefore are more likely to be successful as they have already survived for part of the breeding cycle (Mayfield 1975). In addition, clutch size, hatching success and fledging success were compared between years. As nests were found at different stages and some nests were not checked between the laying and incubation stages in 2014 (for an experiment Chapter 6), the sample size of nests for these calculations varies.

5.4.2 Modelling Daily Survival Rates

The effect of vegetation, invertebrate fauna, topography and grazing on nest success were explored using logistic-exposure models (Shaffer 2004). These models are similar to a typical generalized linear binomial model, except the link function contains an additional exponent of 1/observation interval (the number of days between successive nest visits) in the numerator and denominator. This accounts for the fact that the probability of a nest surviving an observation interval depends on its length. This method has advantages over the Mayfield method in that temporal influences on nest survival can be included rather than assuming constant nest survival for a set nest stage (i.e. incubation and nestling rearing), and continuous predictors can be modelled (Shaffer 2004). As with the Mayfield method, the logistic exposure models give Daily Survival Rates (DSR) and the two methods give almost identical results on the same dataset (Lloyd & Tewksbury 2007). For this analysis, nest survival was split into two models looking separately at egg stage survival and nestling stage survival, as it was thought that different factors were likely to be operating at the two stages. The incubation and laying stages were analysed together, due to the small sample size of nests found at the laying stage and the consideration that the effect of the predictors would be unlikely to vary to any great extent between these two periods. Two nests were run over by tanks rather than predated or abandoned: these nests were removed from the analysis.

5.4.3 Variable selection and model building

The data were analysed in the R statistical package (R Development Core Team 2014). All variables were tested for normality and transformed where necessary (Table 5.3). Vegetation and topography features were analysed separately to invertebrate features because the invertebrate data were unavailable for 2012 (section 2.5.2). Due to the large number of variables, it was not possible to reliably analyse all the vegetation and invertebrate variables in one model just for 2013 and 2014; the number of predictors would exceed the 10:1 subjects to predictors rule (Harrell, 2001) and result in over-fitting. Instead, invertebrate variables were analysed with perch vegetation variables (*perch abundance* and *perch height*) as these were most likely to be connected to foraging efficiency (Oppermann 1990; Opperman 1992; Bastian & Bastian 1994; Richter & Düttmann 2004). The effect of grazing was also modelled separately because it was measured on a different scale, and also used up degrees of freedom meaning fuller models would not converge.

Temporal variables were included in all full models to account for any variation due to first egg date, nest age or year (Dinsmore *et al.* 2002; Nur *et al.* 2004; Grant *et al.* 2005). *First egg date* was calculated in April days, with the 1st April for each year set to 1, and first egg date derived as number of days since this date. *First egg date* was either known for nests found during laying, or estimated by back-calculation for nests found during incubation or after (mean accuracy over all nests = +/- 0.89 days, minimum accuracy = +/- 6 days for two nests). Mean *nest age*, which is the number of days a nest has been active, was calculated from the first egg date for each observation interval of a nest.

Following the suggestion of Burham & Andersson (2002) regarding the need to have apriori hypotheses for all terms before including them in the global model, squared terms were only included for *vegetation height*, *percentage bare ground*, *first egg date* and *nest age*, because these were variables where prior knowledge of the study species and studies on similar species suggested possible quadratic relationships with the DSR (Pearce-Higgins & Grant 2006, Hood & Dinsmore 2007; Grant *et al.* 2005; Davis 2005). A quadratic term for *nest age* was included for egg phase models only, to account for any difference in the effects of *nest age* within the laying and incubation phases (Grant *et al.* 2005). Only interactions which made biological sense were considered, which included: a *slope* and *aspect* interaction (Calladine & Bray 2012), an interaction between *perch abundance*, and *invertebrate abundance* and *biomass*, because of their potential link in foraging, and an interaction between *first egg date* and *grazing*.

For the egg stage, 31 nests were relays and for the nestling stage, 3 were relays. It is problematic to use random effect models for survival analysis as the data are left truncated, nests that fail early may be missed, this therefore violates the assumption that the random effect is normally distributed with a mean of zero (Heisey *et al.* 2007 & Rotella *et al.* 2007). However, clutch size, hatching success and fledgling success for colour ringed individuals were not significantly correlated between and within years (Kruskal Wallis Test: $p > 0.44$). This suggests a random effect for 'individual parent' is unnecessary and nesting attempts can be treated as independent events despite sharing some parents. Similar conclusions were reached in a study on Alpine Accentors (Hartley *et al.* 1995; Davies *et al.* 1995). The residuals of the global models plotted against site showed no relationship, suggesting a 'site' random effect was unnecessary.

In addition to the models of DSR, the relationship between variation in nestling condition at day nine and food availability was assessed, since it is reasonable to assume that chick condition is maintained by food supply. The variables used to represent food availability were: invertebrate biomass, perch abundance and perch height, and these were tested against mean brood nestling condition at day nine and its standard deviation. Temporal variables could not be included as the sample size was small for this analysis (n = 35) which meant only a maximum of three variables could be included in the model to avoid over-fitting.

Global models were created for each analysis and the residuals assessed visually to ensure a good fit. The dredge function from the MuMIn package (Bartón 2014) was then used to evaluate all possible models derived from the global model and rank them based on the small sample variant of the Akaike Information Criterion (AICc; Burnham & Anderson 2002). Smaller values of AICc indicate models which explain the most variance while limiting the number of parameters (Sugiura 1978). Model averaging was used where there was no single best model with a weight > 0.9 (Grueber *et al.* 2011). Models within 2 AICc of the top model were averaged to give parameter estimates and unconditional standard errors which incorporate the model selection uncertainty (Burnham & Anderson 2002). There are two types of model averaging possible: the ‘natural average method’ and the ‘zero method’ (Burnham & Anderson 2002; Grueber *et al.* 2011). The natural average method estimates each predictor only over the models in which it appears in the set and weights it by the summed weights of these models. The zero method substitutes a parameter estimate and error of zero into models where the given parameter is absent and then averages over all the models in the set. The natural average method is recommended where the main predictors may have weak effects relative to other covariates (Nakagawa & Freckleton 2011), and as preliminary analysis suggested relatively weak effects of habitat variables compared to temporal variables the natural average method was chosen. The global model parameters were standardized to a mean of zero and a standard deviation of 0.5 to ensure the model averaged parameters were interpretable relative to each other (Grueber *et al.* 2011) using the R package ‘arm’ (Gelman 2008, 2014). Following Shaffer & Thompson (2007), any effects where the 95% confidence intervals did not include zero are displayed graphically.

Table 5.3. Transformations used to make variables conform to a normal distribution. After transformation all variables were approximately normally distributed. See Table 5.1 for definitions of the variables.

Variables	Transformations
% Ground cover: once transformed = % bare ground	Log (101 - % ground cover)
Perch abundance	Sqrt (perch abundance)
Invertebrate abundance	Sqrt (invertebrate abundance)
Invertebrate biomass (mg)	Sqrt (invertebrate biomass)

5.5 Results

5.5.1 General breeding statistics

Nest survival estimates for the egg and nestling stages were not significantly different: 44.7% (95% CI: 35.1% – 56.8%) for eggs and 54.4% (95% CI: 45.2% – 65.3%) for nestlings. The overall nest survival rate, taken over all years, was 24.2% (95% CI: 20.7% - 28.3%, n = 207, DSR = 95.2%). Clutch sizes, hatching success and other nest productivity measures are summarised in Table 5.4. Partial brood mortality was rare in the Salisbury Plain study population, as was abandonment (Table 5.4), so nearly all nestlings that hatched, and were not predated, subsequently fledged. Out of the 199 monitored nests, 69.4% failed to fledge any young. The majority of nests failures were attributable to predation (89.1%), desertion at the egg (7.25%), or nestling stages (2.17%), and 1.45% were run over by military vehicles. Over 2012 – 2014 a mean number of 1.6 +/- 0.22 nestlings fledged per nesting attempt and 2.18 +/- 0.23 nestlings fledged per pair.

Data from temperature sensors (iButtons) in 47 failed nests showed that 81% were predated between sunset and sunrise. A Chi-squared test assuming equal probabilities of a nest being predated in darkness or light in proportion to the amount of light available, found that nests were significantly more likely to be predated at night ($\chi^2 = 32.4$, df = 1, $p < 0.0001$).

Studies on other Whinchat populations in Europe have found similar mean clutch sizes and hatching success (Robinson 2005; Britschgi *et al.* 2006; Frankiewicz 2008; Grüebler *et al.* 2012). However, the number of fledglings per pair for Salisbury Plain (2.18 +/- 0.23) is low compared to other studies on comparable habitat types such as late mown meadows (3.3 +/- 0.3) in Germany (Fischer *et al.* 2013) and abandoned fields in Poland (4.17 +/- 0.24; Frankiewicz 2008) and Russia (3.77 +/- 3.07; Shitikov *et al.* 2015), though the Russian estimates vary widely by year. The overall nest survival rate is also unexpectedly low, 24.2% (CI: 20.7% - 28.3%), compared to the mean nest survival estimate over nine years from abandoned fields in Russia (35%, CI: 23.1 – 46.5; Shitikov *et al.* 2015) and late mown meadow estimates from Slovenia (41%, CI: 27.4% - 55.7%) (Tome, D. & Denac, D., pers. comm.) and Switzerland (55.7%, Grüebler, M. pers. comm.), but higher than estimates from early mown meadows in Switzerland: 12.2%. All nest survival estimates were calculated using a 29 day breeding cycle from the DSR.

Table 5.4. Breeding statistics for the Salisbury Plain Whinchats each year, 2012, 2013 and 2014. The variables are listed on the left. Hatching success refers to the percentage of laid eggs that hatch excluding predation and abandonment. The total sample size for the year is included in brackets next to the relevant result, these refer to the number of eggs for hatching success and to the number of nests for all other measures. The Daily Survival Rates (DSR) are calculated using Mayfield estimates and only include the final nesting attempt for each pair to calculate the overall productivity for the season.

	2012	2013	2014
Mean clutch size	5.53 +/- 0.13 (59)	5.56 +/- 0.13 (68)	5.51 +/- 0.14 (57)
Hatching success	95.3% (172)	89.4% (151)	92.8% (166)
Percentage of nests abandoned as eggs	6.35% (63)	1.59% (63)	6.85% (73)
Percentage of nests abandoned as nestlings	3.17% (63)	1.59% (63)	0% (73)
Percentage of nests where partial predation occurred	0% (63)	6.35% (63)	0% (73)
Fledglings Per Nesting Attempt (including predation)	2.05 (63)	1.41 (63)	1.38 (73)
Fledglings Per Pair (including predation)	2.63 (49)	1.89 (47)	2.02 (50)
Daily Survival Rate (DSR)	95.8 +/- 0.82 (51)	95.1 +/- 0.88 (53)	94.6 +/- 0.94 (50)

5.5.2 Means and ranges for variables used in logistic exposure models

The means +/- 1 standard error and the range for the predictor variables used in the logistic exposure models are presented in Table 5.5.

Table 5.5. The mean +/- 1 standard error and the range, calculated over all Whinchat nests, for the predictor variables used in the logistic exposure models. For each nest, eight or nine 1 m^2 vegetation quadrats and invertebrate sweep net samples (of 10 sweeps) are averaged to give a mean value. See Table 1 for definitions of the variables.

Variables	Mean +/- SE	Range
Plant species richness	7.55 +/- 0.14	3.88 – 13.1
% Bare ground	6.16 +/- 0.33	1.56 - 28.8
Vegetation height (m)	15.5 +/- 0.32	4.95 – 24.4
Perch abundance	2.18 +/- 0.15	0.00 – 7.33
Perch height (cm)	58.2 +/- 1.37	0.00 – 122
% Tussock cover	56.6 +/- 1.69	5.00 – 95.6
Altitude (m abs)	128 +/- 1.40	104 – 170
Slope (˚)	5.73 +/- 0.26	0.00 – 15.7
Aspect	SE	NA
Invertebrate abundance	25.3 +/- 1.32	4.00 – 117
Invertebrate biomass (mg)	62.1 +/- 3.80	5.00 – 190
First egg date	5th June	5th May – 3rd July

5.5.2 Vegetation and topography influences on breeding success

Vegetation and topographical influences were evaluated for 162 nests monitored during 2012 – 2014. The highest weight for any one model was 0.24 for the egg phase and 0.07 for the nestling phase, indicating that no one model was highly supported (Table 5.6). The model averaged standardized parameter estimates for the best supported models (within < 2ΔAICc of the top model), together with their unconditional standard errors and the variable importance of each predictor, are presented in Table 5.7. The variable importance weights a term by how many of the models in the < 2ΔAICc subset it appears in - if the term is present in all models its variable importance will be 1 (Burham & Anderson 2002). All models had low R-squared values (< 0.1; Table 5.6), indicating that a large proportion of the variation in breeding success was not explained by the influence of vegetation, topography or temporal effects.

The best models for egg stage survival found a strong quadratic relationship between *percentage cover of bare ground* and the DSR (Table 5.7; Figure 5.1), with survival rates highest at low (1.6%) and high (20 %) percentage cover of bare ground, and lowest at intermediate (7.4 %) percentage cover of bare ground. *Nest age* also had an effect, with the egg phase DSR highest for nests early in the breeding cycle then declining as the number of days of exposure increased (Table 5.7; Figure 5.1).

The best models for nestling stage survival found a strong quadratic relationship between the *vegetation height* and nestling stage DSR (Table 5.7; Figure 5.2). Nestling stage DSR was highest at intermediate vegetation heights (approximately 15 cm) and lowest at low vegetation heights (5 cm) (Figure 5.2). The daily survival rates for the nestling phase also differed between years with mean survival in 2014 lower than 2012: nestling phase DSR in 2012 was 0.97 (CI: 0.94 – 0.99), when mean values are taken for all other parameters, as opposed to 0.93 (CI: 0.889 – 0.96) in 2014. There was also evidence of a non-significant effect of (*first egg date*)^2 on nestling DSR (Table 5.7), which suggests a trend for higher survival for nestlings from clutches laid in the middle of the breeding season rather than the beginning or end.

There was no strong evidence for effects of any other parameters on egg phase or nestling phase DSR (the 95% confidence intervals contained zero). However, the variable importance values indicated that *first egg date* in the egg phase and *slope*, *first egg date* and *nest age* in the nestling phase, were common parameters in the top models. This suggests that although they may not have had strong effects on the DSR these predictors do help to explain some of the variation (Table 5.7).

Table 5.6. Model statistics for the best supported subset of models (within ΔAICc < 2 of the top model) for the effect of vegetation, topographical and temporal influences on a) the Daily Survival Rate (DSR) for the egg phase of the Whinchat's breeding cycle and b) the DSR for the nestling phase of the Whinchats breeding cycle (as there were 25 models within ΔAICc < 2 of the best model only the first 10 are shown). The model's weight and ΔAICc compared to the other models in the set are included. The R-squared (Rsq) values for all models ranged between a) Rsq= 0.035 – 0.042, for the egg phase and b) Rsq= 0.0342 – 0 .070 for the nestling phase.

a) Model - Egg Phase	Delta	Weight
Nest age + First egg date + % Bare ground + % Bare ground^2	0.00	0.24
Nest age + % Bare ground + % Bare ground^2	0.53	0.18
Nest age + First egg date + % Bare ground + % Bare ground^2+ Slope	1.66	0.10
Nest age + First egg date + % Bare ground + % Bare ground^2 + Species richness	1.77	0.10
Aspect + Nest age + First egg date + % Bare ground + % Bare ground^2	1.81	0.10
Nest age + First egg date + First egg date^2 + % Bare ground + % Bare ground^2	1.82	0.10
Vegetation height + Nest age + First egg date + % Bare ground + % Bare ground^2	1.97	0.09
Nest age + % Bare ground + % Bare ground^2 + Slope	1.99	0.09

b) Model – Nestling Phase	Delta	Weight
Vegetation height + Vegetation height^2 + Nest age + First egg date + Slope + Year	0.00	0.07
Vegetation height + Vegetation height^2 + First egg date + Slope + Year	0.11	0.07
Nest age + First egg date + First egg date^2 + Slope + Year	0.71	0.05
Vegetation height + Vegetation height^2 + Nest age + First egg date + Slope + Plant species richness + Year	0.84	0.05
Vegetation height + Vegetation height^2 + First egg date + Slope + Plant species richness + Year	0.86	0.05
Vegetation height + Vegetation height^2 + Nest age + Slope + Year	0.89	0.05
Nest age + First egg date + First egg date^2 + Year	0.94	0.04
First egg date + First egg date^2 + Slope + Year	0.98	0.04
Vegetation height + Vegetation height^2 + Nest age + First egg date + Year	1.24	0.04
Nest Age + Slope + Year	1.27	0.04

Table 5.7. The model averaged parameter estimates and +/- the unconditional standard error, for the best supported models (within < 2 ΔAICc of the top model) for the relationship between the DSR for the egg phase and the nestling phase of the Whinchat breeding cycle and vegetation, topography and temporal variables. The number of observation intervals = 421 for eggs, 302 for nestlings. The parameter estimates have been standardized to a mean of zero and a standard deviation of 0.5 to make the effect sizes comparable. Asterisks indicate model parameters where the 95% confidence intervals did not include zero, indicating strong evidence for an effect. Dots indicate parameters where the 95% confidence intervals only just included zero, indicating a weak effect. Dashes indicate predictor variables that were not included in any of the best models. The variable importance for each predictor in the model set is also included.

	Egg Stage		Nestling Stage	
Predictor	Parameter Estimate	Variable Importance	Parameter Estimate	Variable Importance
First egg date	-0.27 +/- 0.92	0.73	1.31 +/- 2.93	0.83
First egg date^2	-1.06 +/- 2.17	0.10	-4.32 +/- 2.73•	0.35
Vegetation height	-0.09 +/- 0.31	0.09	4.63 +/- 1.99*	0.62
Vegetation height^2	-	-	-4.58 +/- 1.92*	0.62
Plant species richness	0.16 +/- 0.29	0.10	0.57+/- 0.45	0.18
% Bare ground	-5.13 +/- 1.92*	1.00	0.32 +/- 0.46	0.06
% Bare ground^2	4.92 +/- 1.93*	1.00	-	-
% Tussock cover	-	-	0.21 +/- 0.49	0.03
Altitude	-	-	-0.62 +/- 0.42	0.09
Slope	-0.18 +/- 0.26	0.19	-0.58 +/- 0.32	0.74
Aspect (SW)	0.13 +/- 0.27	0.10	-0.14 +/- 0.35	0.03
Slope : Aspect	-	-	-	-
Year 2013	-	-	-0.53 +/- 0.57	0.87
Year 2014	-	-	-1.01 +/- 0.48*	0.87
Nest age	-0.75 +/- 0.29 *	1.00	0.54 +/- 0.35	0.72
Nest age^2	-	-	NA	NA

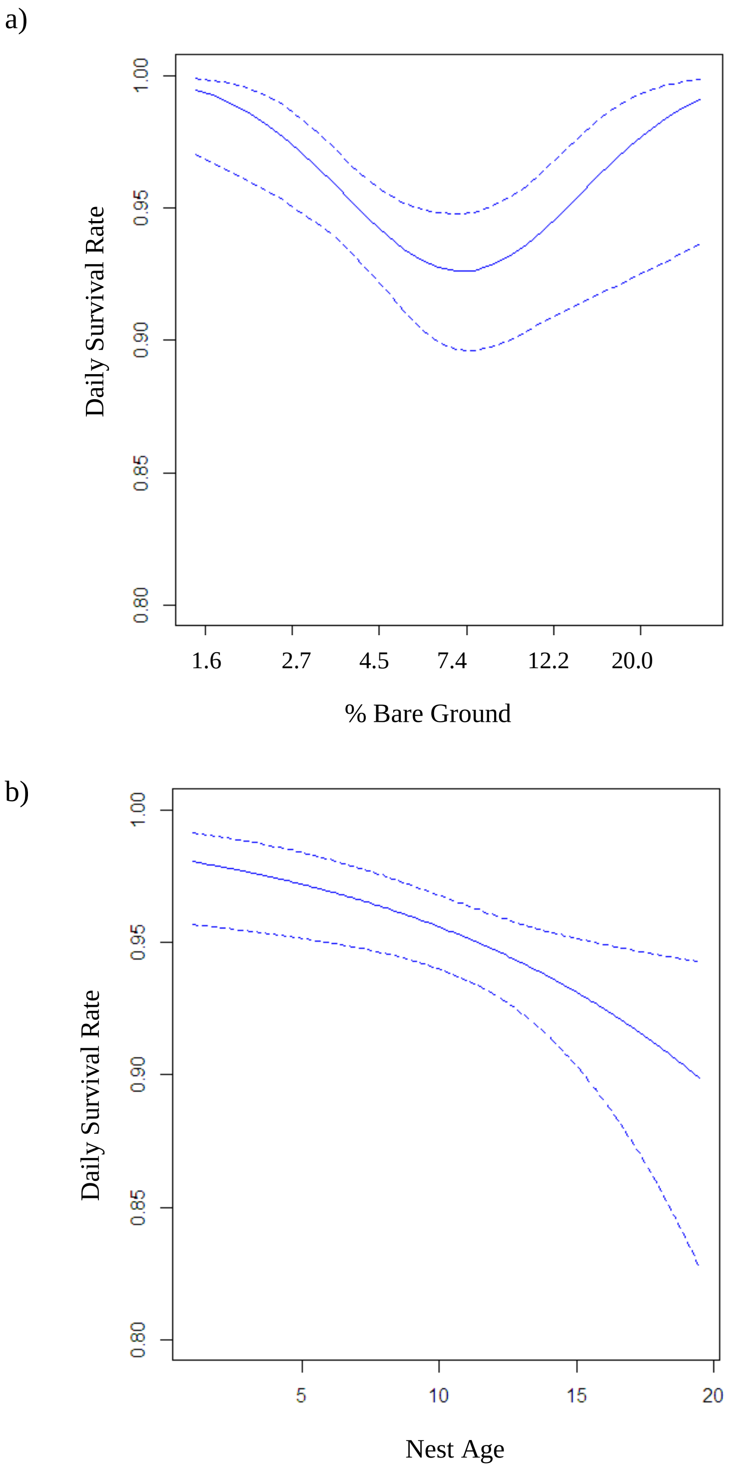


Figure 5.1. The predicted effect (solid line) of a) *percentage of bare ground* and b) *nest age*, on the DSR for the egg stage using the model averaged parameters from the best supported models (within < 2 ΔAICc of the top model) and setting all parameters other than a) *percentage bare ground* and b) *nest age* to their mean values, *aspect* was set to southwest. See Table 5.5 for the mean values of the variables. *Percentage bare ground* was on a log scale but the values have been back transformed to make the axis more interpretable. The dotted lines are the 95% confidence intervals for the prediction which are asymmetric around the estimate after back-transformation from the logit scale.

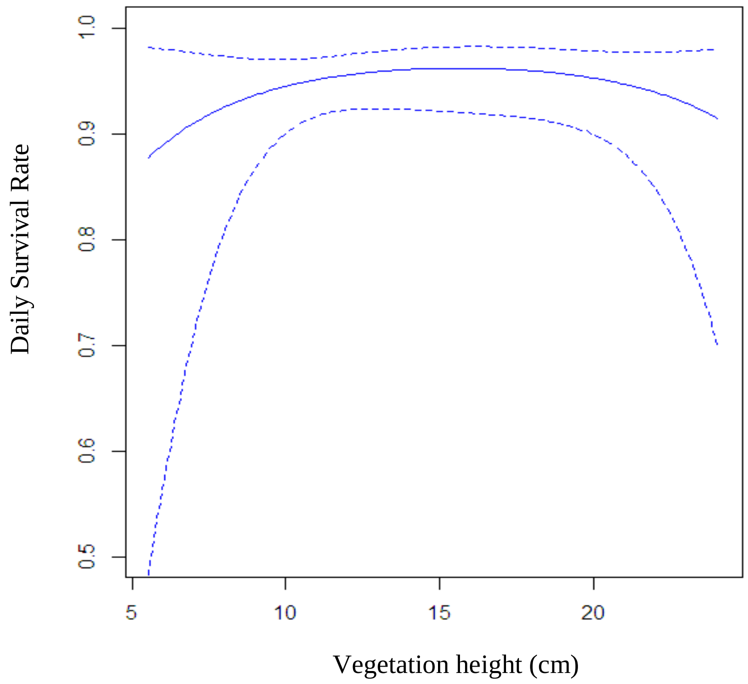


Figure 5.2. The predicted nestling phase DSR (solid line) with changing *vegetation height*. The prediction uses the model averaged parameters from the best supported models (within < 2 ΔAICc of the top model) where all parameters other than *vegetation height* are set to their mean values, *aspect* was set to southwest, *year* was set to 2013. The dotted lines are the 95% confidence intervals for the prediction which are asymmetric around the predicted DSR after back-transformation from the logit scale.

5.5.3 Effect of grazing on breeding success

The effect of *grazing* was evaluated for 162 nests. Model averaging was used (Table 5.9) because no one model was highly supported (Table 5.8). Again, all models had low R-squared values (< 0.1; Table 5.8), indicating that a large proportion of the variation in breeding success was not explained by the influence of grazing or temporal variables. Only *nest age* had a strong effect on the DSR for the egg phase, as already found in the previous model (Table 5.7, Figure 5.1). The variable importance was low for all other predictors (< 0.6) indicating that none of them were favoured in the top models (Table 5.8). However, there was also evidence that *year* had a weak effect on egg phase DSR (the 95% confidence intervals just included zero), with DSR lower in 2014 compared 2012 (Table 5.9). This effect was not apparent in the previous model, suggesting it might be related to difference in the vegetation at nest sites in 2014, probably due to the extensive flooding of the study site in April of this year (pers. obs.).

A strong negative effect of *grazing* was evident on the DSR for the nestling phase. The DSR for nests where *grazing* occurred within 100 m during the breeding season was 0.85 (CI: 0.69 – 0.94) compared to a DSR of 0.97 (CI: 0.94 – 0.99) for nests with no *grazing* within the previous year (Table 5.9; Figure 5.3). However, DSRs were similar for grazing categories 0 – 2 (Table 5.2), suggesting that grazing before the start of the breeding season does not influence survival for the nestling phase. There was no evidence of an interaction between *grazing* and *first egg date*, but that is consistent with only within-season grazing affected the DSR. As in the previous model, there was evidence of weak effect of (*first egg date*)^2 on nestling DSR (Table 5.9). There was no strong evidence of other temporal effects on nestling stage DSR (the 95% confidence intervals contained zero): the effect of *year* was no longer evident, suggesting that the *year* effect observed in the previous model (Table 5.7) may actually represent a difference in the extent of category 3 grazing between 2014 and 2012. However, the variable importance values indicated that *first egg date* and *nest age* were common parameters in the top models, as was found for the previous model (Table 5.6). This suggests additional temporal variation in the nestling phase DSR that was not due to variation in grazing regime, vegetation and topography.

Table 5.8. Model statistics for the best supported subset of models (ΔAICc < 2 of the top model) of the effect of grazing category and temporal influences on the DSR for a) the egg phase and b) the nestling phase of the Whinchat's breeding cycle. The predictor variables included in each model are displayed along with the model's weight and ΔAICc compared to the other models in the set. Rsq values range between a) 0.014 – 0.026 b) 0.041 – 0.064. : = interaction.

a) Model: Egg Phase	ΔAICc	Weight
Nest age	0.00	0.30
Nest age + First egg date	0.53	0.23
Nest age + Year	0.71	0.21
Nest age + Year + First egg date	1.23	0.16
Nest age + First egg date + First egg date^2	1.93	0.11
b) Model: Nestling Phase		
Grazing + Nest age	0.00	0.22
Grazing + Nest age + First egg date + First egg date^2	0.04	0.22
Grazing + First egg date + First egg date^2	0.44	0.18
Grazing + Nest age + First egg date	0.78	0.15
Grazing	1.17	0.13
Grazing + First egg date	1.69	0.10

Table 5.9. The model averaged parameter estimates +/- the unconditional standard error, for the best supported models (within < 2 ΔAICc of the top model) for the relationship between the DSR for the egg phase and the nestling phase of the Whinchat breeding cycle, grazing category and temporal variables. The number of observation intervals = 421 for eggs, 302 for nestlings. The parameter estimates have been standardized to a mean of zero and a standard deviation of 0.5 to make the effect sizes comparable. Asterisks indicate model parameters where the 95% confidence intervals did not include zero, indicating strong evidence for an effect. Dots indicate parameters where the 95% confidence intervals only just included zero, indicating a weak effect. Dashes indicate predictor variables that were not included in any of the best models, : = interaction. The variable importance for each predictor in the model set is also included.

	Egg Phase		Nestling Phase	
Predictor	Parameter Estimates	Variable Importance	Parameter Estimates	Variable Importance
Grazing 1	-	-	-0.08 +/- 0.70	1.00
Grazing 2	-	-	-0.49 +/- 0.43	1.00
Grazing 3	-	-	-1.65 +/- 0.51*	1.00
First egg date	0.08 +/- 1.30	0.50	2.39 +/- 2.97	0.65
First egg date^2	-1.76 +/- 2.17	0.11	-4.43 +/- 2.49•	0.40
Grazing : First egg date	-	-	-	-
Year 2013	-0.48 +/- 0.39	0.37	-	-
Year 2014	-0.66 +/- 0.38•	0.37	-	-
Nest age	-0.71 +/- 0.29*	1.00	0.57 +/- 0.35	0.60
Nest age^2	-	-	NA	NA

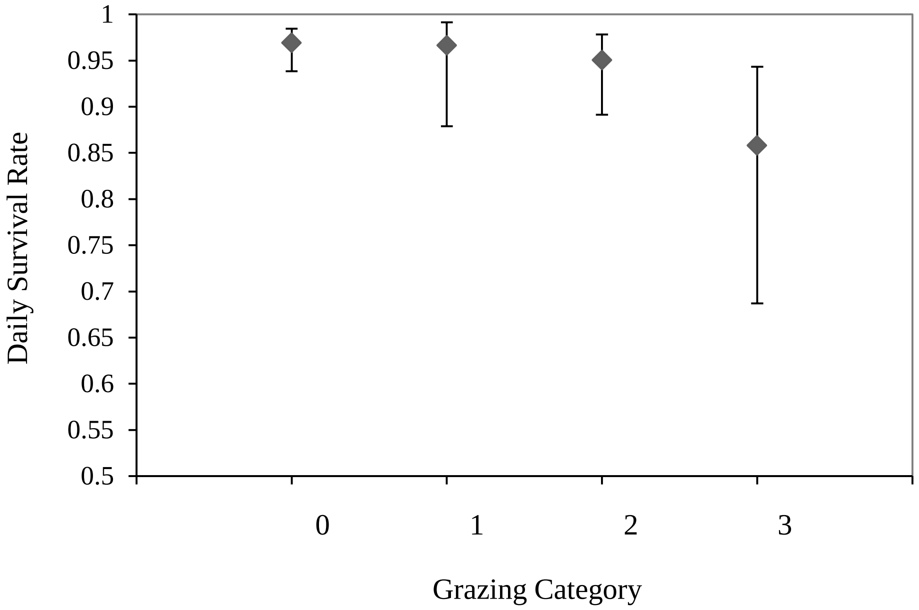


Figure 5.3. Predicted Daily Survival Rates (DSR) for the nestling phase (dots) with 95% confidence intervals (bars) for the different grazing categories: 0 = un-grazed for the last 2 years; 1 = grazed January-August of the previous year; 2 = grazed September-April before the breeding season; 3 = grazed during the breeding season while the nest was active; the other parameters were set to their mean values. Confidence intervals are asymmetric around the predicted DSR after back-transformation from the logit scale.

5.5.4 Effect of food availability on breeding success

The influence of food availability was evaluated for 123 nests monitored between 2013 – 2014. No single model was strongly supported (Table 5.10), therefore model averaging was used (Table 5.11).

Egg phase DSR declined with increasing *nest age* (as seen in the previous 2 models: Tables 5.7 and 5.9), but there was no evidence of an effect of food availability from the variables measured. However, for nestling phase DSR there was strong evidence for an interaction effect between *invertebrate abundance* and the *perch abundance* (Table 5.11). Where perch availability was low, higher *invertebrate abundance* was associated with a higher DSR, whereas at higher levels of *perch abundance* the abundance of invertebrates did not have an effect on the model output (Figure 5.4a), suggesting more efficient prey capture by parents. There was also strong evidence that nestling DSR was highest mid-way through the season and lower for late season nests (Table 5.11; Figure 5.4b). The same trend was observed in the models using years 2012-2014 but the effect was weaker there (-4.32 +/- 2.73 as opposed to -6.37 +/- 2.65). *Year* also had a strong effect, showing the same trend observed in Table 5.7, which was thought to be due to increased grazing within the season in 2014. Seasonality (*first egg date*) had a stronger effect on nestling phase DSR than *invertebrate abundance* and *perch abundance* but there was also more variability in the relationship (-6.37 +/- 2.65 as opposed to -4.17 +/- 1.42). There were only two best models for the nestling phase (Table 5.11), and the R-squared values were the highest out of all the models in this chapter (0.104, 0.105), though still low, suggesting a lot of additional unexplained variation in breeding success. A PPMCC test was used to assess the correlation between perches and other vegetation variables to ensure the apparent effect of perch availability on nestling phase DSR was not spurious, caused by a correlation between perch abundance and other vegetation variables. *Perch abundance* and *perch height* did not show a correlation higher than 0.4 with any vegetation or topographical variable, giving confidence that the model reflects a real relationship. *Invertebrate abundance* and *invertebrate biomass* also did not show strong correlations with any habitat variables, the strongest relationship being a correlation of 0.46 of *invertebrate abundance* with the *vegetation height*.

One nest in 2014 had particular high values for *invertebrate abundance* compared to the others. This was a real value and the invertebrate data were square-rooted to reduce the skewing effect of variable. To ascertain that the relationship between daily nestling survival rate and *invertebrate abundance* was not just caused by this large value the analysis was re-run deleting this value. The results were qualitatively similar.

Table 5.10. Model statistics for the best supported subset of models (within ΔAICc < 2 of the top model) of the effect of food availability and temporal variables on the DSR for the a) egg phase and b) nestling phase of the Whinchat's breeding cycle. The predictor variables included in each model and the model's weight and ΔAICc compared to the other models in the set are included. The Rsq values for all models ranged between a) 0.019 – 0.020 for egg phase, b) 0.104 – 0.105 for nestling phase. : = interaction.

a) Model: Egg Phase	ΔAICc	Weight
Nest age	0.00	0.42
Nest age + Perch height	1.50	0.20
Nest age + Invertebrate abundance	1.53	0.20
Nest age + Year	1.67	0.18
b) Model: Nestling Phase		
Year + First egg date + First egg date^2 + Invertebrate abundance : Perch abundance	0.00	0.72
Year + Nest age + First egg date + First egg date^2 + Invertebrate abundance : Perch abundance	1.84	0.29

Table 5.11. The model averaged parameter estimates +/- the unconditional standard error, for the best supported subset of models (within < 2 ΔAICc of the top model) for the relationship between the DSR for the egg phase and the nestling phase of the Whinchat breeding cycle, food availability and temporal variables. The number of observation intervals = 327 for eggs, 205 for nestlings. The parameter estimates have been standardized to a mean of zero and a standard deviation of 0.5 to make the effect sizes comparable. Asterisks indicate model parameters where the 95% confidence intervals did not include zero, indicating strong evidence for an effect. Dots indicate parameters where the 95% confidence intervals only just included zero, indicating a weak effect. Dashes indicate predictor variables that were not included in any of the best models, : = interaction. The variable importance for each predictor in the model set is also included.

	Egg Stage		Nestling Stage	
Predictor	Parameter Estimate	Variable Importance	Parameter Estimate	Variable Importance
First egg date^2	-	-	-6.37 +/- 2.65*	1.00
First egg date	-	-	5.71 +/- 2.72*	1.00
Invertebrate abundance	0.20 +/- 0.30	0.20	2.40 +/- 0.77*	1.00
Invertebrate biomass	-	-	-	-
Invertebrate abundance : Perch abundance	-	-	-4.17 +/- 1.42*	1.00
Invertebrate biomass : Perch abundance	-	-	-	-
Perch height	-0.20 +/- 0.28	0.20	-	-
Perch abundance	-	-	0.11 +/- 0.58	1.00
Year 2014	-0.18 +/- 0.29	0.18	-1.54 +/- 0.61*	1.00
Nest age	-0.76 +/- 0.31*	1.00	0.21 +/- 0.38	0.28
Nest age^2	-	-	NA	NA

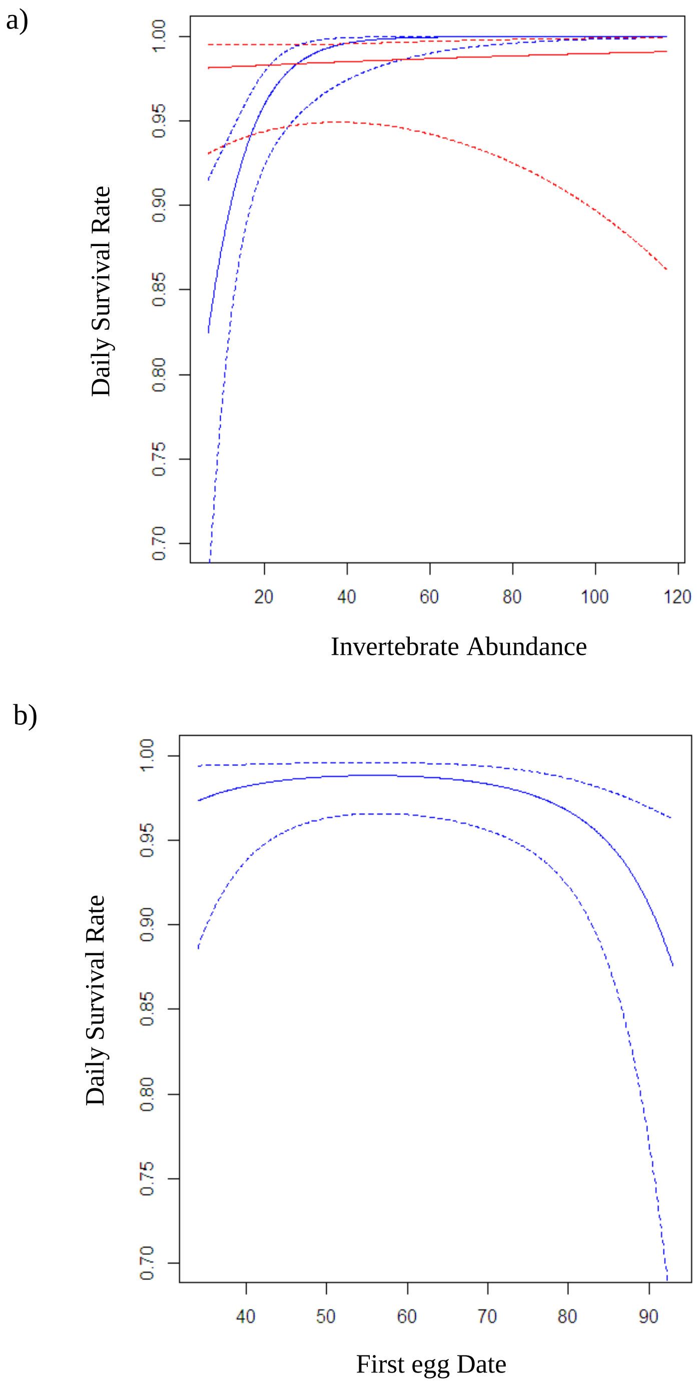


Figure 5.4. The predicted nestling phase DSR (solid line) for a) varying *invertebrate abundance* in areas with low *perch abundance* (lower quartile = 0.802, blue) and high *perch abundance* (upper quartile = 4.33, red) and for b) varying laid dates (in April days), using the model averaged parameters from the best supported subset of models (within < 2 ΔAICc of the top model) and setting all parameters other than a) *invertebrate abundance* and *perch abundance* and b*) first egg date* to their mean values, *year* was set to 2013. The dotted lines depict the 95% confidence intervals for the prediction, which are asymmetric around the predicted DSR after back-transformation from the logit scale.

The relationship between nestling condition and food availability was also assessed for the 35 nests which survived until day nine after hatching. The best model averaged model contained only invertebrate biomass, and the 95% confidence intervals for this parameter estimate contained zero indicating no evidence for an effect on mean nestling condition. The variability in nestling condition also showed no strong effects with any of the variables.

5.6 Discussion

The possible limitations to reproductive output considered here were: poor parental condition, a shortage of food for nestlings, and predation of nest contents. Clutch sizes and hatching rates were comparable to other studies (Britschgi *et al.* 2006; Frankiewicz 2008; Grüebler *et al.* 2012), suggesting that parent condition is not the main limitation to reproductive output (Martin 1987). However, without actually measuring the body condition of adults prior to breeding it is not possible to discount an impact of parent condition on breeding success. The strongest source of mortality for nest contents was predation (Table 5.4), as has also been found for other Whinchat populations from un-farmed areas (Frankiewicz 2008; Tome & Denac 2012; Shitikov *et al.* 2015). Whilst I was unable to directly identify the nest predators, there was little evidence of nestlings starving to death in the nest and abandonment was also relatively low (Table 5.4). Further, most nests were predated at night, which suggests that diurnal predators were not attracted to the nests by the vocal begging of hungry nestlings (Diego *et al.* 2012). The logistic exposure models suggested the daily survival rate in the egg phase was lowest at moderate levels of bare ground and reduced with increasing nest age (Table 5.7). Grazing during the breeding season had a significant negative effect on nestling phase survival and there was weak evidence that nestling phase survival was highest in the middle of the breeding season (Table 5.9). Nestling phase survival was also higher at moderate vegetation heights (Table 5.7) and in areas with a higher abundance of invertebrates if the perch abundance was low (Table 5.11). However, the condition of nestlings was not related to either the abundance of invertebrates or their biomass within breeding pairs' territories. Temporal effects of year were only present in some models, indicating that they probably represented differences in the grazing regime or weather related variation in vegetation. The R-squared values for all models were low indicating that although there was strong evidence for some habitat influences, there was still a large proportion of variation in DSR for both the egg and nestling phases not explained by the measured vegetation, invertebrate, topographical and temporal variables.

5.6.1 Predation risk

As most nest losses were due to predation, rather than a shortage of food, relationships between habitat, temporal variables and daily survival rates presumably reflect mediations in predation risk. During the egg phase, survival was highest for territories with low and high percentage cover of bare ground, and nestling phase survival was highest at intermediate vegetation heights. Moderate vegetative height and low amounts of bare ground may both improve concealment of nests from visually searching predators (Martin 1993; Winter 1999; Rangen *et al.* 1999; Davis 2005; Stauffer *et al*. 2011) and dilute the transmission of auditory and olfactory cues (Martin 1993). Additionally more vegetation and taller vegetation is harder for predators to walk through and therefore may serve to reduce predation rates by impeding the predator's progress or by deterring them to search in other areas (Lariviere & Meisser 1998). Intermediate vegetation heights, rather than the tallest vegetation, are likely preferred due to the balance necessary between concealment and not obstructing the view for the parents of approaching predators while they provision nestlings (Whittingham & Evans 2004; Whittingham *et al.* 2004; Wilson *et al.* 2005). Very tall vegetation would also reduce foraging efficiency by making it harder to see and capture prey items (Whittingham & Evans 2004; Butler & Gillings 2004; Wilson *et al.* 2005; Vickery & Arlettaz 2012) and might lead to the parents leaving the nest unguarded for longer as their foraging trips took longer. A current study found that Whinchats were less likely to forage in areas of tall vegetation (Murray *et al., in prep*). The negative relationship of intermediate levels of bare ground with egg phase daily survival is harder to explain. It is possible areas with intermediate levels of bare ground attract small mammalian predators such as mice, stoats and weasels, as some vegetation provides cover from larger mammalian predators such as foxes (Jacob & Brown 2000; With 1994; Davis 2005) and the patches of bare ground may allow easy foraging opportunities; however, this scenario remains to be explicitly studied in detail.

Grazing was found to have a negative effect on nestling phase daily survival rates, similar to findings from many other studies on grassland birds (Gray 1974; Fondell & Ball 2004; Müller *et al.* 2005; Sutter & Ritchison 2005; Rahmig *et al.* 2009; Fischer *et al.* 2013). No trampling of nests occurred in this study, therefore the negative effect of grazing is likely to be mediated via an increase in predation risk. Grazing removes the concealing and obstructing vegetation, making nests more visible (Sutter & Ritchison 2005; Fondell & Ball 2004) and easier to access (Lariviere & Meisser 1998). In this study, the visual difference in concealment between nests in currently grazed and un-grazed areas was striking, with nests in actively grazed areas 100% visible from above as opposed to an average of 21% in non-grazed areas (pers. obs.). The interesting aspect to note in this study is that only grazing during the breeding season had a negative effect, not grazing the winter before, or anytime up to a year before. This may explain why grazing during the egg phase did not have a strong affect on daily survival rates, as the grazing was introduced part way through the egg phase. At the low levels of grazing allowed on Salisbury Plain (a maximum of 120 cattle per 8 ha for 2 weeks once every 2 – 3 years; Ash & Toynton 2000), the vegetation appears to be able to recover to a level suitable for Whinchat nesting within one year. As Whinchats have higher breeding success in areas with moderate vegetation heights rather than the tallest vegetation, infrequent grazing may even be beneficial for them, and it is certainly beneficial for the invertebrate fauna which compromises their prey (Jerrentrup *et al.* 2014). A recent study has actually found evidence to suggest that selective grazing may help to maintain suitable foraging habitat for Whinchats (Murray *et al. in prep*). Thus, so long as grazing is kept to a low level and the main core sites for the Whinchats are left un-grazed in the breeding season, it is unlikely to have a negative impact on breeding success.

Daily survival during the egg phase reduced with increasing nest age. Shitikov *et al.* (2015) found the opposite pattern in nesting Whinchats in abandoned fields in Russia, which they suggested was due to changing activity patterns of groups of predators along with variation in nest susceptibility. However, Grant *et al.* (2005) also found DSR decreased with nest age during the incubation phase in a study of Clay-coloured sparrows and Vesper sparrows. He suggested this was probably due to the additive exposure risk, where the longer a nest is active, the more likely it is to loose individual eggs due to predation or poor weather, which increases the cumulative probability of total failure. However partial predation was very rare on Salisbury Plain (Table 5.4). He also found parent nest visits increased in frequency through incubation which could increase the probability of parents disclosing the nest location to predators (Martin *et al.* 2000; Pietz & Granfors 2000). However, this argument would suggest the nestling phase DSR also should decrease with increasing nest age. In Grant *et al.* (2005) the opposite pattern occurs, with DSR increasing through the nestling phase, which he suggests may be due to increasing parental defence and reducing nestling vulnerability. On Salisbury Plain, the parameter estimate for nest age effects during the nestling phase was positive in all models, but there was no evidence of a strong effect. There was also weak evidence for nestling phase survival to be highest in the middle of the season and lowest at the end of the season. This may be because there is a higher density of all species' nests during the middle of the season (pers. obs.) and therefore the chance of any one being predated is reduced. The higher predation risk at the end of the season could reflect the initial increase in the predator population directly after their breeding cycle. The same pattern was found for the Russian Whinchat population (Shitikov *et al.* 2015); however, studies on different species in America have found the opposite pattern (e.g. Dinsmore *et al.* 2002; Knuston *et al.* 2007; Stauffer *et al.* 2011). In general, it appears the effect of temporal influences on DSR may vary widely between species, and even between populations of the same species in different geographic regions. Temporal influences are likely to reflect a variety of different unmeasured variables, such as weather, variations in parental behaviour and variations in predator behaviour and abundance (Dinsmore *et al.* 2002; Nur *et al.* 2004; Grant *et al*. 2005; Shitikov *et al*. 2015). Therefore, caution should be exercised when attempting to generalise or draw biological inferences from relations between DSR and temporal influences.

5.6.2 Food availability

In the absence of nestling death through starvation, food supply and the likelihood of nest failure may still be linked if nestling hunger increases their begging intensity (Cotton *et al.* 1996), and so their detection by potential predators (Diego *et al.* 2012). In this case, however, nest failure was mainly attributable to nocturnal predation, probably from badgers, foxes, stoats and other mammals, which would occur independently of chick begging behaviour. The absence of a relationship between the condition index of nestlings at nine days old and the availability of food provides additional support for the lack of a food shortage, though Davies *et al.* (2014) noted that due to the correlation between nestling condition and parent condition it may be difficult to detect links between nestling condition and habitat variables. However, the positive correlation between nestling phase daily survival rates and invertebrate abundance when the availability of perches was low, but not when they were plentiful, conversely suggests food availability does still have a role in determining breeding success. It is possible that these results reflect an interaction between territory quality and the effectiveness of parental defence behaviours. Birds in better condition generally arrive on the breeding grounds first and select the best territories (Newton 1998; Kokko 1999), which we would assume to be the territories that have higher food availability. Various studies have found that dominant parents that are in better condition defend their nests more vigorously (e.g. Rufous Bush Chats – Alvarez & Sanchez 2003; Great Tits – Quesada & Carlos Senar 2007) and more vigorous defence behaviours often result in a higher probability of nest success (Andersson *et al.* 1980; Greig-Smith 1980; Knight & Temple 1986; Montgomerie & Weatherhead 1988). There is a large amount of inter-specific variation in nest defence behaviour and in a small passerine bird such as a Whinchat, it is likely to encompass distraction behaviours such as alarm calling, flying around the predator and attempting to lead it away from the nest rather than direct attacks on the predator (Simmons 1952; Greig-Smith 1980). Additionally, with higher food availability parents can forage more efficiently and therefore spend a shorter time foraging and consequently increase their nest attentiveness (Martin 1987). It is also possible that the predators' behaviour varied indirectly in relation to variation in insect abundances as invertebrate abundance is generally higher in thicker and taller vegetation (Whittingham & Evans 2004;Woodcock *et al.* 2009) , and this type of vegetation would impede predator passage (Lariviere & Meisser 1998). However, no strong correlations were found between the measured invertebrate and vegetation variables.

5.6.3 Parental condition

The consistency of clutch size and hatching success within the population and compared to other populations in Europe, suggests that adult condition is not the main factor limiting breeding success in the Salisbury Plain Whinchats (Högstedt 1980; Martin 1987; Forbes 1991). However, as clutch size and hatching success were only monitored for three years and body condition was not measured in the adults prior to breeding it is not possible to discount a limiting effect of parental condition on breeding success. It is possible that clutch size is consistent because it is evolutionarily constrained in Whinchats and therefore cannot exhibit much variability, or that Whinchats in all the compared studies are in poor condition. Further study is needed for reassurance that parental condition is not limiting.

5.6.4 Conclusions

Whinchat breeding success was lower than expected considering that the habitat is largely unimproved from an agricultural perspective (Frankiewicz 2008; Fischer *et al*. 2013; Shitikov *et al.* 2015; pers. comm. Grüebler, M.; pers. comm Tome, D. & Denac, D.). The main cause of nest failure was nocturnal predation, suggesting Salisbury Plain may have a particularly large predator population relative to other comparable grassland sites. This is possibly due to the large area of the site (the largest grassland in northwest Europe; Ash *et al*. 2011) and the lack of agricultural activity, or regulated predator control, encouraging a large and diverse population of predators (Gibbons *et al.* 2007). Similar scenarios have been found on other high quality sites – for example, Misenhelter & Rotenberry (2000) found lower breeding success in undisturbed areas compared to more highly disturbed areas, which they suggested may be because predatory snakes were deterred from the disturbed areas. High predation rates are also problematic for other species of ground nesting birds (Langgemach & Bellebaum 2005): increases in predation associated with changes in land-use are considered the main reason for declines in meadow birds in Europe over the last forty years (Malpas *et al.* 2013a; Roodbergen *et al.* 2012) and a contributing factor in the decline of grassland birds in America (Brennan & Kuvlesky 2005).

In general the low proportion of variance explained by all the models presented here suggests that predation risk may vary within and between years independently of any of the measured vegetation, topographical, food or temporal variables. Many other studies looking at correlations between vegetation and nest success have also failed to find strong conclusive links (Vickery *et al.* 1992; Davis 2005; Winter *et al.* 2006 and see a review on the topic by Chalfoun & Schmidt 2012). For ground nesting birds it has been suggested that predation is generally by incidental opportunists rather and a coevolved specialist (Vickery *et al.* 1992; Schmidt *et al.* 2001), and the resulting broad range of nest predators with different search methods mean no one habitat type is favourable (Filliater *et al.* 1994, Pietz & Granfors 2000, Davis 2005). Streby *et al.* (2014) however, suggest that failures to find strong links between nest success and habitat variables occur because the habitat best for overall season productivity, including post fledging survival, may be different to what is best for nest success. However, it is still useful to look at relationships between habitat and nest success because, as demonstrated here, some effects are apparent, and this understanding can be used to guide conservation efforts better than no knowledge at all would. It is possible to find factors which can be altered to improve nest success (Knutson *et al.* 2007), such as reducing grazing in the breeding season and ensuring more habitat with moderately tall vegetation and a high invertebrate abundance. It also helps us to understand factors influencing nest success which are outside human control (Knutson *et al.* 2007).

Chapter 6: Nest monitoring does not appear to affect Whinchat nesting success

A Whinchat mother feeding her nestlings

6.1 Abstract

It is important to assess the affect that research activities may have on breeding success to ensure estimates are not biased. Some studies have suggested that nest monitoring can increase the chances of nest failure due to predation, while others suggest that human nest visits may actually deter mammalian predators. Nest monitoring visits can also influence breeding success more indirectly by altering parental provisioning behaviour. Here, the influence of monitoring activities on nest success was examined. First, during the egg phase, a sample of nests were not visited between the initial finding event and the estimated hatching date; instead the nest status was assessed from afar. Daily Survival Rates (DSR) for these nests were compared to nests visited every two days. Second, during the nestling phase, the effects of observer nest visits on parental provisioning behaviour were determined. Nest visits were found not to significantly affect egg DSR. Parental provisioning was disrupted for a maximum of 20 minutes (0.52% of the nestling period) following an observer visit, but a temporary increase in parental provisioning rate following this disturbance compensated for missed feeds.

6.2 Introduction

The increasing use of rural areas by humans enjoying recreational activities, and the associated increase in infrastructure such as roads, has led to concern that human activities adversely affect breeding birds (Hill *et al.* 1997). Empirical studies have shown that human disturbance increases the risk of nest failure due to predation (Götmark 1992) or desertion (Tremblay & Ellison 1979; Piatt *et al.* 1990; Beale & Monaghan 2004). Animals are likely to respond to human disturbance as though it was a potential predation event (Frid & Dill 2002; Beale & Monaghan 2004; Price 2008), though the level of the response may vary (Tilgar *et al.* 2011; Reimers & Eftestøl 2012). Disturbance may also have non-lethal detrimental effects (Cresswell 2008; Martin & Briskie 2009; Lima 2009) such as temporarily interrupting nestling provisioning (e.g. Ghalambor & Martin 2002; Zhao 2005; Ghalambor *et al.* 2013), and altering incubation behaviours (e.g. Ghalambor & Martin 2002; Chalfoun & Martin 2010; Kovarik & Pavel 2011; Zanette *et al.* 2011; Ibanez-Alamo & Soler 2012). Such changes in parental behaviours have been shown to lead to lower brood sizes and offspring masses prior to fledging (Coslovsky & Richner 2011; Zanette *et al.* 2011) and premature fledging, which probably results in a higher risk of post-fledging predation (Cole 1910; Pietz & Granfors 2000). Long term and intense disturbance can even cause population declines (Frid & Dill 2002) through reduced body condition (e.g. Madsen 1995) and breeding success (e.g. Phillips & Alldredge 2000), especially when combined with unfavourable environmental conditions (Madsen 1995).

Disturbance by researchers during nest monitoring activities can potentially influence the outcome of a nest either directly, by encouraging nest desertion (e.g. Tremblay & Ellison 1979; Piatt *et al.* 1990), or indirectly. Indirect effects include increasing the risk of predation through flushing parents and thereby leaving nests unguarded (e.g. Strang 1980), creating olfactory or visual trails leading to a nest (Whelan *et al.* 1994), and eliciting conspicuous parental defence behaviours such as alarm calling that could alert predators to the presence of the nest (Major 1990; Weidinger 2008; Jacobson *et al.* 2011). A review by Götmark (1992) found researcher activities had reduced nesting success in 49% of studies but Mayer-Gross *et al.* (1997) suggested that many of these studies had incidences of nest disturbance far greater than that usually inflicted by a trained nest observer following the British Trust of Ornithology's guidelines (Ferguson-Lees *et al.* 2011). A more recent meta-analysis on 25 species from six orders found that researcher visits did not affect the probability of nest predation (Ibanez-Alamo *et al.* 2012). In fact, nest visits by observers may actually have reduced the risk of predation for passerines and ground nesting birds, as the presence of humans may deter mammalian predators (Macivor *et al.* 1990; Ibanez-Alamo & Soler 2010; Ibanez-Alamo *et al.* 2012, but see Skagen *et al.* 1999). The effects of researcher visits to nests were found to vary widely among species, sometimes even within the same habitat (Weidinger 2008; Ibanez-Alamo *et al.* 2012): it is therefore important to quantify the magnitude of the effect researcher disturbance has on breeding success.

Due to the fact that birds interpret human disturbance as a predation threat (Frid & Dill 2002; Beale & Monaghan 2004; Price 2008), nest monitoring visits also can affect breeding success by altering the parents' behaviour, for example, by causing a temporary suspension of nestling provisioning (Wheelwright & Dorsey 1991; Michl *et al.* 2000; Zhao 2005; studies reviewed in Lima 2009; Tilgar *et al.* 2011; Paclik *et al*. 2012; Ghalambor *et al.* 2013; Mutzel *et al.* 2013; Vitousek *et al*. 2014; but see Hakkarainen *et al.* 2002) and an increase in vigilance, nest guarding and nest defence behaviours (Montgomerie & Weatherhead 1988; Wheelwright & Dorsey 1991; reviewed in Frid & Dill 2002 and Price 2008; Caro 2005; Mutzel *et al*. 2013). This behaviour is adaptive, as the risk of the predator finding the nest is reduced (Eggers *et al*. 2005, 2008), the parent can invest more time and energy in nest defence (Montgomerie & Weatherhead 1988) and the parents' survival chances may also be increased (Lima 2009), but there is a trade-off of reduced food supply to the nestlings, which can reduce offspring condition and possibly their future survival chances and reproductive output (Trivers 1972; Clark & Ydenberg 1990; Dale *et al.* 1996; Michl *et al.* 2000; Frid & Dill 2002; Price 2008;

Martin & Briskie 2009; Lima 2009). When disturbance is repeated and frequent, the temporary suspension of feeding has the potential to cause harmful cumulative consequences, with young fledging at smaller sizes (Scheuerlein & Gwinner 2006; Thomson *et al.* 2006; Tilgar *et al.* 2011). Some studies found that parents will compensate by provisioning at a higher rate after a predation threat (Paclik *et al.* 2012; Mutzel *et al.* 2013 but see Tilgar *et al.* 2011) and by provisioning larger load sizes (Eggers *et al.* 2008; Lima 2009). However, there is limited scope for compensation as a nestling's digestive system can only process a certain quantity of food within a given time period (Eggers *et al.* 2005).

The response of the parents to a perceived 'predation threat' will vary depending on the balance between the potential 'value' of the nestlings and on the perceived risk to the parents (Trivers 1972; Montgomerie & Weatherhead 1988; Clark & Ydenberg 1990). The potential 'value' of the nestlings depends on nestling age (Dale *et al.* 1996; Michl *et al.* 2000; Pavel & Bures 2001; Zhao 2005), brood size (Tilgar & Kikas 2009), nestling condition (e.g. Michl *et al.* 2000), the parent's investment so far (e.g. Dale *et al*. 1996; Pavel & Bures 2001) and the potential for re-nesting (reviewed by Martin 1987; Michl *et al.* 2000). For example, parents may risk more and resume feeding earlier for larger broods (Tilgar & Kikas 2009) or nestlings in better condition (Michl *et al.* 2000) and female parents may take more risks than male parents for younger nestlings if they have invested more in the nestlings up to this stage (Michl *et al*. 2000; Pavel & Bures 2001; Dale *et al*. 1996). The perceived risk to each parent may depend on the type of predator (Bures & Pavel 2003; Martin & Briskie 2009; Tilgar *et al.* 2011; Ippi *et al.* 2013), the sex, size, condition and experience of the parent (Martindale 1982; Montgomerie & Weatherhead 1988; Lima 2009), and the protection offered by the surrounding nesting habitat (Eggers *et al.* 2008; Lima *et al*. 2009; Martin & Briskie 2009). For example, parents may be more risk-averse if the predator is perceived as a threat to both the nestlings and the adults themselves (Tilgar *et al.* 2011) and if the nest site is more exposed (Eggers *et al.* 2008). For situations where a species can actively defend its nest against a predator, parents may remain close to the nest following a predation threat, and restrict their foraging range (Marzluff 1985; Martindale 1982; Hakkarainen *et al.* 2002; reviewed in Lima 2009). The parent that is most effective at defending the nest often remains closer to the nest than their partner (e.g. Gila Woodpecker, Martindale 1982). In species where neither parent is actively able to defend the nest contents against predators, the optimal strategy is likely to be nest crypsis and the minimisation of parental activity (Burhans 2000; Bures & Pavel 2003).

In this chapter, I aim to explore the potential effects of visiting Whinchat nests to monitor reproductive success. Daily survival rates during the egg phase are compared between nests which received visits every two days, and those that were visited only once. Previous studies suggest that where the main predators are mammalian, as appears to be the case in this study (Chapter 5), the nest predation rates may be reduced by more frequent monitoring visits. Additionally, I quantify the provisioning behaviour of parents in relation to researcher nest visits. Nests were visited and the parental behaviour then observed for an hour following the visit. It is predicted that the Whinchat parents will reduce nestling provisioning until the perceived threat has diminished to avoid disclosing the nest location and to allow more time to be allocated to nest guarding and vigilance behaviours. To this end, it is also predicted that parents are likely to remain in the vicinity of the nest immediately after a predation threat, to enable earlier nest predator detection, and will avoid long foraging trips until the perceived threat has diminished.

6.3 Methods

6.3.1 Study area

The study area was a section of Salisbury Plain, Wiltshire, in southwest England. Six valleys with high Whinchat populations were selected as study sites (see section 2.2 for details and a map of the study sites).

6.3.2 Nest visit experiment during egg phase

Nests were found for all known breeding pairs within the six study sites. The location of all nests was recorded using a Geographical Position System (GPS) reading at the nest site. Nests were also marked in the field using an unobtrusive bamboo cane near to the nest. In 2014, nests were paired in the order of finding, with alternate nests being designated as ‘visit’ nests and ‘distance-visit’ nests. Daily watches of breeding adults early in the season and recording of behaviour and nest building activity enabled hatching date to be estimated to within two days. Visit nests were visited every two days and distance-visit nests were not visited after the initial nest finding event, until the estimated hatching date. Distance-visit nests were assessed from a distance every two days, to determine whether they were still active, either by observing the female leaving the nest and returning to incubate, or, in time constrained situations, via alarm calling parents on the territory when the researcher was in the vicinity. After the initial nest finding, the observer never went closer than 20 m to the distance-visit nests and, in general, stayed at least 80 m away. This experiment was only conducted for the egg phase of the breeding cycle.

6.3.3 Disturbance experiment during nestling provisioning

Thirty-nine monitored nests were included in the experiment: 20 in 2013 and 19 in 2014. The researcher approached the nest and set up a video camera on a tripod, pointing at the nest, one metre away. Marker canes were placed into the ground at 20, 40, 60 and 80 m from the nest, to enable distance estimation. The observer then retreated to at least 80 m to watch the parents during their subsequent provisioning activities. The video camera recorded provisioning visits by the parents, and the observer recorded the parents' distances from the nest once every minute for the hour following the disturbance event. Pilot studies in 2012 recorded provisioning rates to nestlings at different ages, using a mixture of direct observation and video recording. Data from 16 nests for nestlings aged 5 – 8 days (day 0 = hatch day) revealed variable provisioning rates (mean: 1.35 feeds per 5 minutes, 95% CI: 0.98 – 1.73 feeds per 5 minutes, n = 16). The experiment was, therefore, conducted on each nest three times, when the nestlings were 6, 7 and 8 days old; the period of maximum provisioning rate. Provisioning watches were conducted between 9 am to 6 pm, which avoided times when feeding rates may be particularly high or when the need to feed nestlings would be more urgent. Watches were not conducted in moderate to heavy rain. Due to weather conditions, access restrictions and predation of nests, there were some cases where it was not possible to undertake all three replicates (25 nests with 3 days of data, 8 nests with 2 days of data and 4 nests with 1 day of data). Provisioning data from two nests were excluded: one because of technical problems with the camera and one because the local topography prevented observations without disturbing the birds and therefore resulted in a complete lack of provisioning visits.

6.3.4 Nestling condition

Body condition was calculated as the residual body mass from a linear regression of a nestling’s weight (g) against tarsus length (mm) at six days after hatching (section 5.3.3). Nestling body condition was then averaged for nestlings within a nest to produce a mean value per nest.

6.4 Data analysis

The data were analysed using the R statistical package version 2.3.1 (R Development Core Team 2014). A logistic exposure model (see Shaffer 2004 and section 5.4.2), with ‘visit’ or ‘distance-visit’ as a factor, was used to assess the influence of nest visits on the Daily Survival Rate (DSR) for the egg phase of the breeding cycle. Only first broods were included in the analysis to avoid pseudo-replication. The trends in the disturbance experiment data were investigated using GAMMs (Generalised Additive Mixed Models) and plots of mean values for each time period. The time since the disturbance event was split into 12 five-minute periods, with the number of feeds calculated for each observation period and then averaged over the three replicates for each nest. Occasionally these data were missing for some observation periods, but once averaged over the 1 – 3 observation periods per nest there were no gaps in the provisioning data. Based on pilot data from 2012, five minutes was selected as long enough to allow provisioning events to occur, but short enough to detect the gradual pattern of change in provisioning rate after a predation event. The sex of the provisioning parent was determined in 98% of feeds. The number of feeds per five-minute period was positively skewed and therefore was square-root transformed for use in the analysis. An asymptotic, Non-linear Least Squares (NLS) model was used to produce an equation for the relationship between time since disturbance and parental provisioning rate, and to determine the disruption time for provisioning. However, it is not possible to add additional covariates to an asymptotic model with currently available frequentist R packages, therefore GAMMs were used to examine the variation in number of feeds with parental sex, brood size and nestling condition.

Linear Mixed Models (LMM) were used to assess the time until the first feed after nest disturbance (latency to feed), and how this varied due to parental sex, brood size and chick condition, with nest as the random effect. The latency to feed was positively skewed and therefore was square-root transformed to an approximately normal distribution. The global model, which included two interaction effects of parental sex and brood size and parental sex and nestling condition, was simplified via backwards stepwise deletion using the drop1 command in R (Chambers 1992; see section 3.4.2 for more details on drop1). For each nest, the mean latency to feed for both parents was calculated over the 1 – 3 observation periods. To determine if parents attempted to compensate for lost feeds by provisioning at a higher rate for a short period, the maximum value for the mean number of feeds in a five minute period was compared to the mean number of feeds in the last five minutes of each observation period (55 - 60 minutes) using a paired t-test.

The percentage of time spent 20 m or less from the nest was investigated in the same way as the number of feeds: the data were split into 12 five-minute blocks of time. For each block the number of distance observations where a parent was 20 m or less from the nest was divided by the total number of distance observations for that parent within the five minute block. This percentage was then averaged for each 5 minute block over the 1-3 observation periods per nest. The percentage of time spent 20 m or less from the nests was selected because within 20 m was considered a distance that the parents could still see the nest, and any approaching predator from, well before the predator got close enough to attack, therefore suggesting a preference for nest guarding and vigilance. The percentage of time spent 20 m for less from the nest was positively skewed. However, transformation did not improve the distribution, and the final model residuals did not reflect any problems despite the skew.

6.5 Results

6.5.1 Effect of nest visits on egg survival

There was no significant difference in the Daily Survival Rates of visit and distance-visit nests (Figure 6.1).

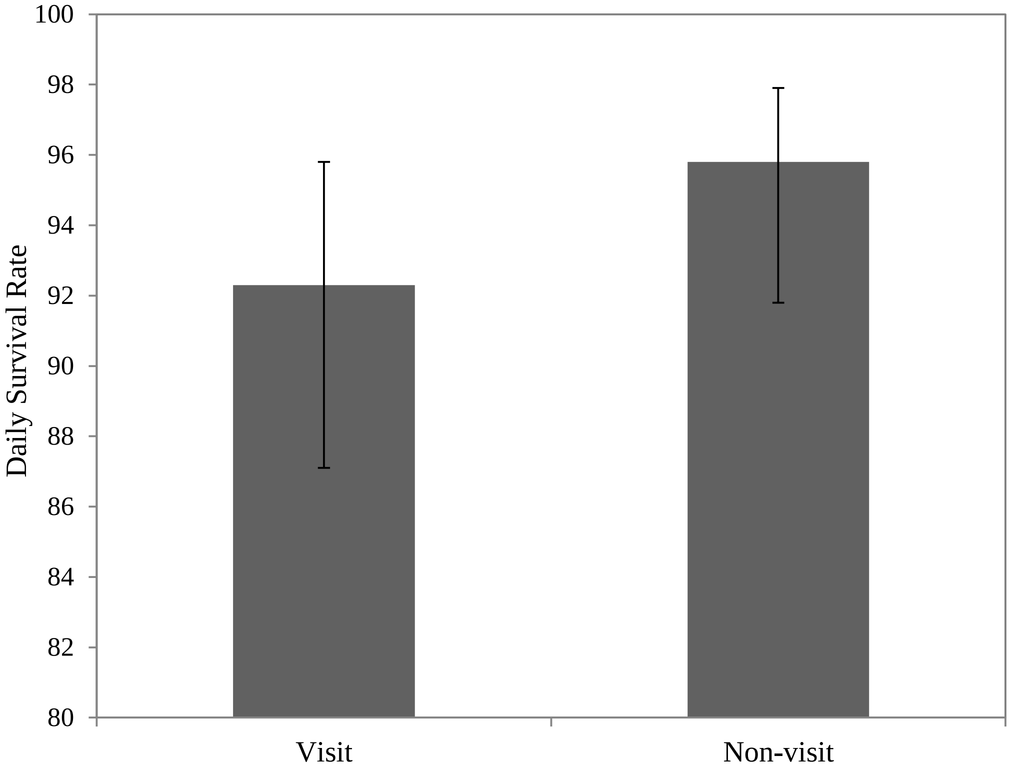


Figure 6.1. The Daily Survival Rates (DSR) for the egg phase for visit and distance-visit nests, using only first broods. The bars are the 95% confidence intervals (visit nests: n = 17, distance-visit nests: n = 18). There was no significant difference in the Daily Survival Rate for the egg phase for visit and distance-visit nests (Logistic-exposure GLM: ANOVA, p = 0.569, df = 122, n = 124 observation intervals).

6.5.2 Effect of nest visits on parental provisioning behaviour

Figure 6.2 displays the mean provisioning rates, over all nests, for each five minute block. From visual examination of these data it was decided that an asymptotic, Non-linear Least Squares (NLS), model of the form: Asymptote/(1 + exp((midpoint – time since nest disturbance) / slope)), would be appropriate. The starting values for the NLS model were chosen based on Figure 6.2.

To account for the repeated measures of the 12 five minute blocks for each nest, a global model with a random effect of nest was used (AIC = 618); this had a lower AIC than the global model with nest and year random effects (AIC = 620) and the global model without a random effect (AIC = 695). The model parameters are displayed in Table 6.1. Residual plots confirmed the model was a good fit. After a nest disturbance event, the parental provisioning rate increased up to a maximum level at around 20 minutes where it levelled off (Figure 6.3). This asymptote translates to 1.12 feeds (95% CI: 1.11 – 1.14) in five minutes.

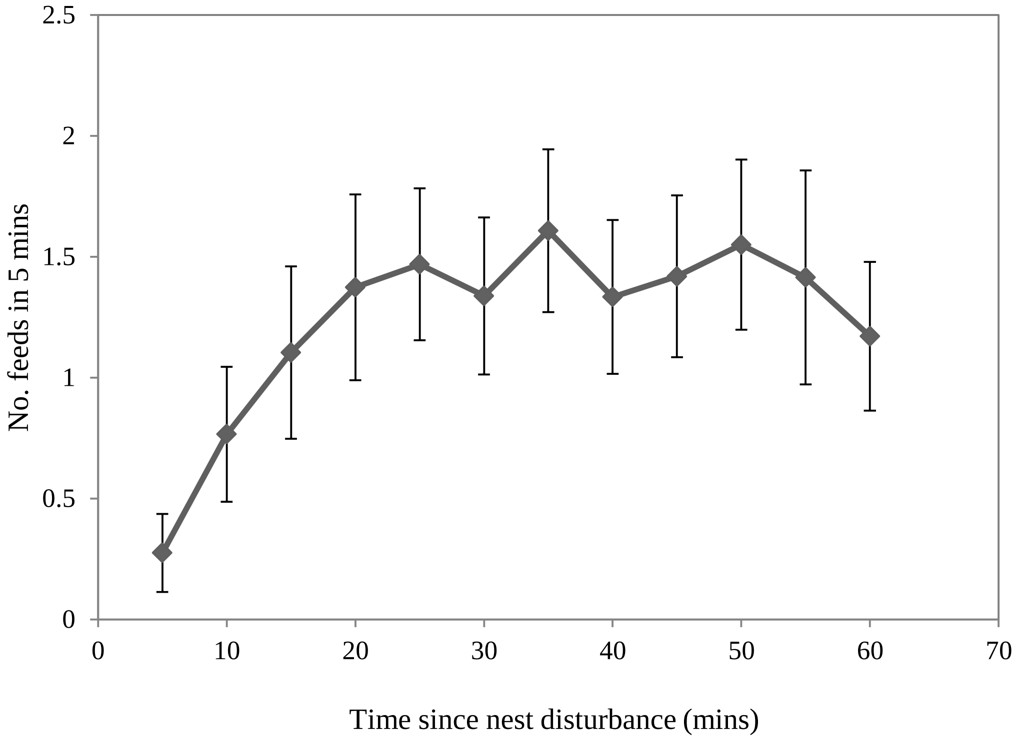


Figure 6.2. The mean number of feeds over all nests in each 5 minute period since the nest disturbance event up to 60 minutes (n = 37 nests). The bars display the 95% confidence intervals.

Table 6.1. An NLS model of the change in square-rooted provisioning rate per five minute block, with time since a nest disturbance event. Nest was a random effect, there were 37 groups with a total of 444 observations. The model log-likehlihood = -304.1, deviance = 608, residual df = 439, the standard deviation of the random asymptote for each territory is 0.298. The model equation: square-rooted number of feeds in 5 minutes = 1.06/(1+exp((8.12-time since nest disturbance)/3.45)).

	Parameters estimates
Asymptote	1.06 +/- 0.004
Midpoint	8.12 +/- 0.004
Slope	3.45 +/- 0.004

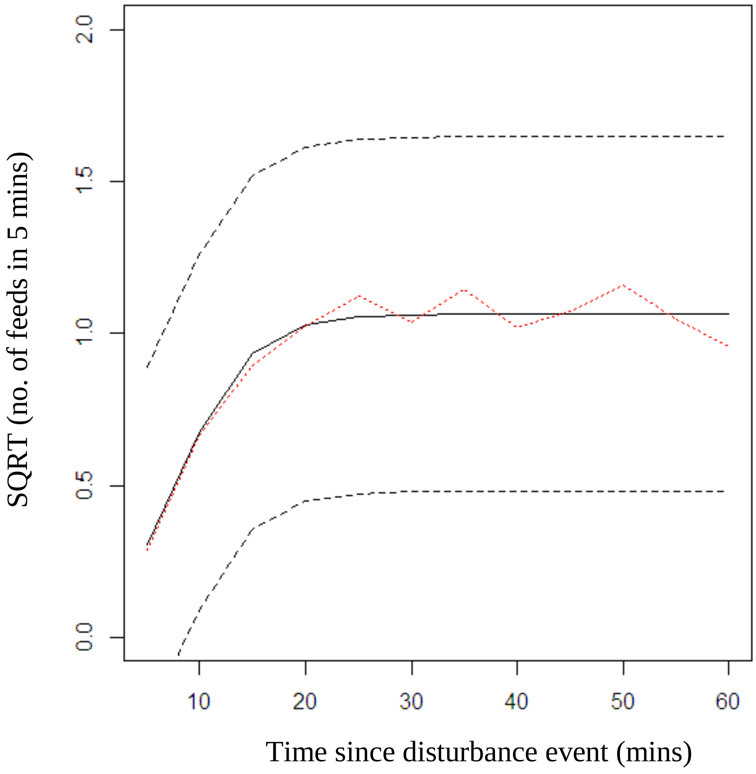


Figure 6.3. An asymptotic random effects NLS model of the change in provisioning rate per five minute block with time since a nest disturbance event, the solid line is the value for an average nest, 95% of nests are within the dotted lines (n= 444 in 37 groups). The red line is the square-rooted mean provisioning rates per 5 minutes block from the raw data.

6.5.3 Variations in parental response to disturbance due to parental sex and nestling condition

The global model allowed different smoothing slopes for the provisioning rates for each parental sex and included a parental sex and condition interaction and a brood size term. A model allowing the smoothing slope to change with nestling condition was too complex to fit with the data available: separately evaluating this model without the other variables indicated that there was not a significant change in slope with condition. A global model with a random effect of nest had an AIC of 1042, as opposed to a global model with year and nest as random effects, AIC = 1044, and a global model without random effects, AIC =1190. Therefore only a random effect of nest was used. The best model had a smoothed term for time since disturbance, and included parental sex and brood size terms (Table 6.2). Brood size did not have a significant effect on the provisioning rate (GAMM: $p > 0.223$) but it was included in all models as a control for variations in brood sizes between nests.

There was a marginally significant difference in the response of males and females, with males provisioning generally at a higher rate: (GAMM: Est = 0.0709 +/- 0.0292, $p = 0.0152$, $n = 852$ observations from 37 groups, Figure 6.4) but, as GAMMs rely on approximation, only probabilities less than 0.01 provide strong evidence of an effect (Zuur *et al.* 2009). The smoothed term is highly significant ($p < 1 \times 10^{-16}$), and the model AIC without the smoothed term is much higher (Table 6.2), indicating the smoothed term is necessary. Residual plots confirmed the global model and end model were both good fits for the data.

Table 6.2. Model selection for a GAMM looking at the variation in response to nest disturbance through provisioning rate, due to differences of parental sex or in average nestling condition at 6 days old. Brood size was included in all models to control for any effect of variation in brood size between nests (3 nests of 3, 7 nests of 4, 8 nests of 5 and 19 nests of 6) on the provisioning rate. Nest was included as a random effect to account for repeated measures of provisioning rate, which was calculated for 12 five minute periods for each nest. Time = time since nest disturbance by the researcher, condition = average nestling condition for a nest when the nestlings were 6 days old, S = a smoother term, sex = male or female parent, : = interaction effect. N = 852 observations from 37 nests.

Model	AIC
S(time) + sex + brood size	1038
S(time) + sex + condition + brood size	1040
S(time) +sex : condition + brood size	1042
S(time) + brood.size	1042
S(time : sex) + sex : condition + brood size	1052
Time + sex + brood size	1089
Sex + brood size	1139

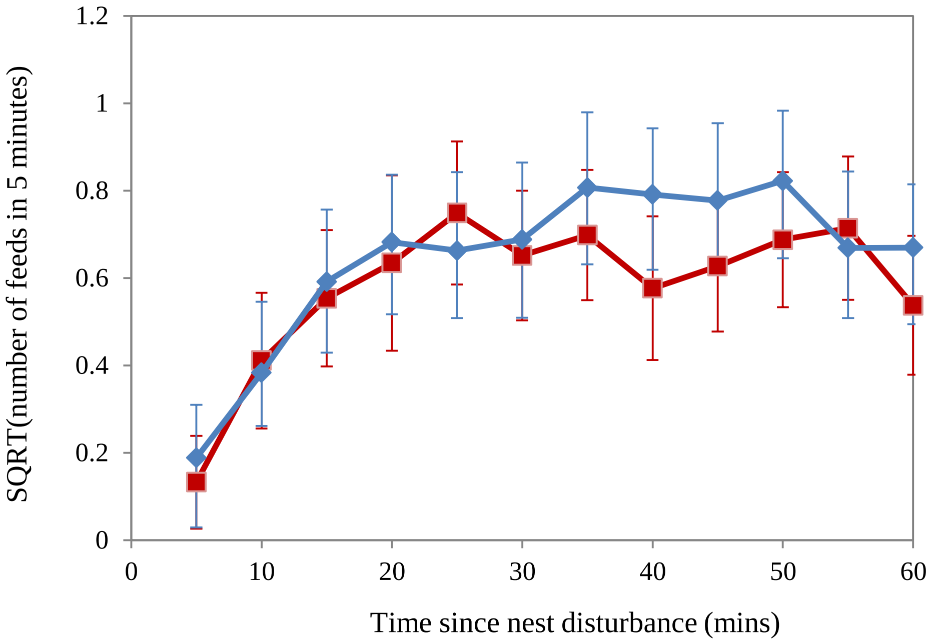


Figure 6.4. The square-rooted mean number of feeds for males (blue) and females (red) over all nests in each 5 minute period since the nest disturbance event up to 60 minutes (n = 36 females, n = 35 males, but from 37 different nests as one nest only had a male parent and two only had female parents). The bars display the 95% confidence intervals.

6.5.4 Latency to feed

The global model had a brood size and parental sex interaction and a nestling condition and parental sex interaction. A random effect of nest did not change the AIC value (both equalled 236), suggesting the variation between pairs was as great as the variation within pairs, but a linear mixed model was used anyway to give a conservative model. None of the variables had a significant effect on latency to feed and all dropped out of the model in backwards stepwise deletion.

Table 6.3. Model selection for the relationship between square-rooted latency to feed, the sex of the provisioning parent, the brood size and the nestling condition. The global model is sqrt(latency to feed) = sex : condition + sex : brood size. In each round of selection each term is sequentially dropped from the model and the change in residual deviance (LRT) calculated and compared to a Chi distribution to give a p value. The AIC of the new model and the LRT and significance of removing the term are reported. The model is a LMM (n= 71 in 37 groups). : = an interaction effect.

Variables	DF	AIC	LRT	P value
Sex : condition	1	228	0.019	0.889
Sex : brood size	1	227	0.192	0.661
Sex	1	225	0.047	0.828
Brood size	1	223	0.770	0.380
Condition	1	223	1.82	0.177

6.5.5 Compensatory increase in provisioning rate

The maximum provisioning rate is significantly higher than the end provisioning rate in the last 55 – 60 minutes of an observation period (Paired t-test: t = 9.39, df = 36, p < 0.001, Figure 6.5).

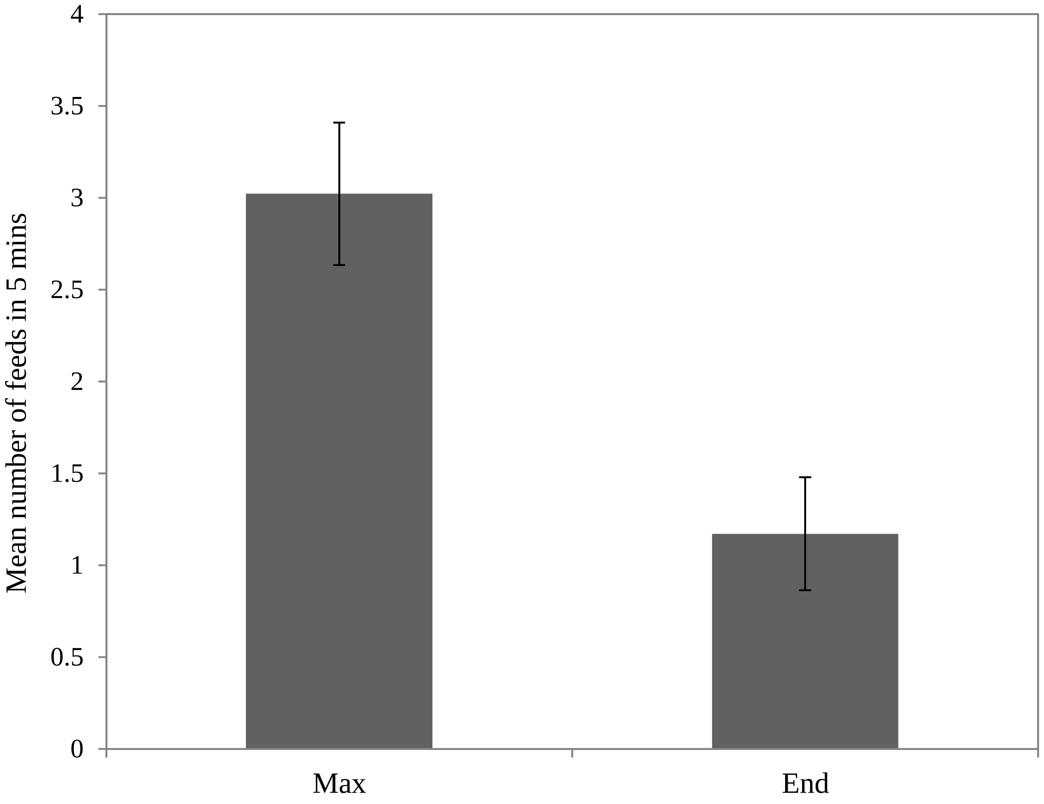


Figure 6.5. Comparing the mean maximum number of feeds in a 5 minute period and the mean number of feeds 55 – 60 minutes after a nest disturbance event. The bars display the 95% confidence intervals (n = 37).

6.5.6 Parental distance from the nest with time after a predation threat

Initially the pattern in the data was explored by plotting the mean percentage of time each parent spent within 20 m of the nest for each five minute block (Figure 6.6) and via a GAMM. A GLMM (Generalised Linear Mixed Model) was considered suitable as the effective degrees of freedom (edf) from the GAMM was 1, which indicates the data follow a linear trend. Ideally a binomial model should be used as the dependent variable is in the form of a proportion and therefore bounded between 0 and 1. However, a binomial model gave warning messages due to the lack of variability in the data. Therefore, a Gaussian model was also fitted to confirm the results. For both models, the end results were qualitatively similar, therefore only the results of the Gaussian GLMM are reported.

The AIC was lower for a global GLMM model just with nest as a random effect as opposed to territory and year (-132 as opposed to -130), both random effect models were better than a GLM without random effects (AIC = -9.74). The AIC reduced when the sex and time since disturbance interaction was removed (AIC = -145 as opposed to -131). The amount of time that the parents spent within 20 m of the nest did not change significantly with increasing time since the nest disturbance event (GLMM: Est = 0.000446 +/- 0.000408, df = 0.0844, t = 1.09, p = 0.275, n = 885 observations in 39 groups). Males spent significantly less time within 20 m of the nest than females (GLMM: Est = -0.0550 +/- 0.0143, df = 0.0855, t = -3.85, p = 0.000125, n = 885 observations in 39 groups). However, the magnitude of the difference was small, with males spending about 5% less time within 20 m of the nest than females. The variance of the random intercept for nest was 0.0149.

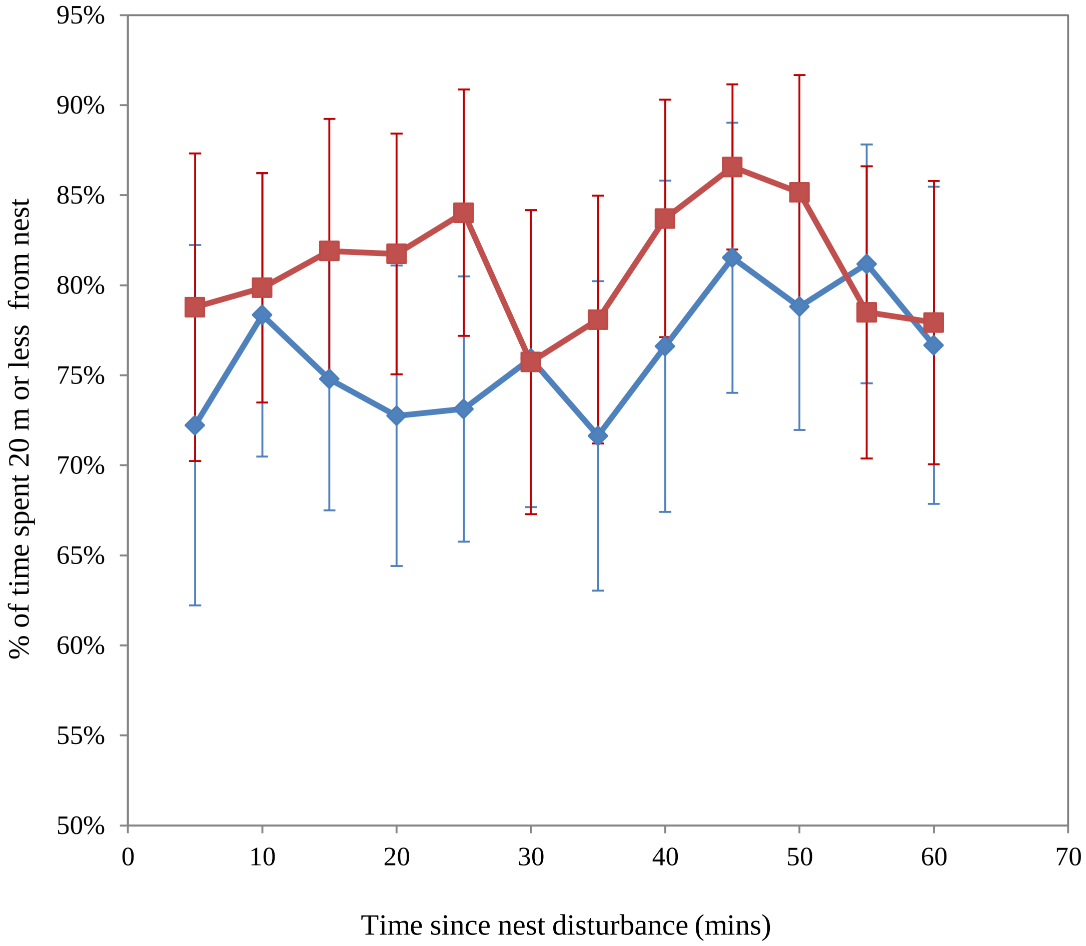


Figure 6.6. The mean percentage of time spent within 20 m of the nest for males (blue), and females (red), with increasing time since a nest disturbance event. The bars display the 95% confidence intervals (n = 885 observations in 39 groups).

6.6 Discussion

The main findings of this chapter were that nest monitoring visits did not have a significant negative effect on nest survival during incubation (Figure 6.1), and though parental provisioning rates were reduced for about 20 minutes following the disturbance (Figures 6.2 and 6.3), this equates to only 0.52% of the available foraging time during the nestling phase and therefore is unlikely to have a severe impact on nestling development. This is reassuring as it suggests that routine monitoring activities did not affect the outcome of nesting attempts. Though male parents appeared to provision nestlings at a higher rate than female parents, this difference was not significant (Figure 6.4) and there was no effect of brood size or nestling condition on the provisioning rate. Latency to feed also did not vary significantly with brood size, parental sex or nestling condition (Table 6.3). Comparing the maximum provisioning rate during a one hour observation period to the provisioning rate at 55 – 60 minutes provides evidence that parents compensate for missed feeds by temporarily increasing their provisioning rate (Figure 6.5). The time parents spent 20 m or closer to the nest did not appear to be affected by nest disturbance (Figure 6.6), though on average females spent significantly more time closer to the nest than males.

Despite the study site consisting largely of unmanaged grassland, where researcher trails may be more obvious compared to sites with shorter vegetation, monitoring visits to nests did not significantly increase the chances of nest failure. This supports the findings from similar studies of ground-nesting grassland birds (Cotter & Gratto 1995; O’Grady *et al.* 1996; Lloyd *et al.* 2000; Jacobson *et al.* 2011). Salisbury Plain supports large populations of other species of ground nesting birds including Meadow Pipits, Skylarks, Yellowhammers, Whitethroats and Reed Buntings (Stanbury *et al.* 2002, 2005) and there were many other trails in the vegetation from related work on Whinchats and from other people such as soldiers training, farmers, security forces and other researchers, therefore the predators may not have learned to associate trails with nests (Hannon *et al.* 1993; O’Grady *et al.* 1996; Weidinger 2008). The main predators of nests on Salisbury Plain were found to be nocturnal, which suggests mammalian predators (Chapter 5). Various other studies have found that mammalian predators are deterred by human scent trails and therefore visited nests are actually less likely to be predated (Macivor *et al.* 1990; Ibanez-Alamo & Soler 2010; Ibanez-Alamo *et al.* 2012). However, this pattern was not observed on Salisbury Plain. The lack of organised predator control on Salisbury Plain, along with the random nature of scent trails discussed above, could explain the lack of deterrence of mammals to human scent trails. Alternatively, different predators may vary in their response to human scents, for example with foxes deterred but stoats attracted, so thereby leading to no overall effect (Jacobson *et al.* 2011).

Nest disturbance temporarily reduced the provisioning rate of parents; similar effects of disturbance have been found in other studies (e.g. Delaney *et al.* 1999; Steidl & Anthony 2000; Verhulst *et al.* 2001). This parental response is considered an adaptation to: reduce the risk of revealing the nest location, allow more time to be invested in defence and vigilance behaviours, and reduce adult predation risk (reviewed in Martin & Briskie 2009 and Lima 2009). However, parental response to a perceived predation risk can have real consequences on breeding success: Zanette *et al.* (2011) found perceived predation risk reduced song sparrow offspring production by 40%.

It took approximately 20 minutes for the provisioning rate to recover, assuming the asymptote of the NLS model (Table 6.1) represents the undisturbed provisioning rate. The mean provisioning rate recorded for undisturbed nests of nestlings in approximately the same age range (5 – 8 days old), from pilot data in 2012, was 1.35 feeds (95% CI: 0.983 – 1.73, n = 16 nests) in five minutes. The asymptote provisioning rate of 1.12 is within this range, therefore supporting this assumption. In an average summer day there are 16 hours of daylight, which is 960 minutes, therefore 2.08% of the day's provisioning is affected by disturbance from a nest visit during the day. When not conducting the disturbance experiment, nests were visited three times in the 12 – 13 days of the nestling period, which is 60 minutes of reduced provisioning out of 11520 minutes (0.52% of the nestling period). The Whinchat parents may have reacted more strongly to disturbance in this experiment due to the presence of the camera and tripod at their nest in addition to the researcher visit. Therefore, this disturbance estimate is conservative and the true disturbance level is likely to be even lower. These findings provide relatively strong evidence that disturbance, at the level usually undertaken by researchers during the nestling phase in this project, does not adversely affect offspring fitness. It also appears that Whinchat parents compensate with increased provisioning for a short time after being disturbed (Figure 6.5) as has been found for various other species (e.g. Paclik *et al.* 2012; Mutzel *et al.* 2013).

Unlike results reported elsewhere, the change in the provisioning rate after disturbance and the latency to return to feed did not vary significantly with parent sex (Dale *et al.* 1996; Michl *et al.*

2000; Pavel & Bures 2001; Zhao 2005), brood size (e.g. Tilgar & Kikas 2009) or nestling condition (Michl *et al.* 2000). It is possible that this was due to the age of the nestlings used in the experiment. In Whinchats, parental care is female biased, with only females incubating the eggs and brooding the nestlings, though both sexes feed the nestlings (Cramp 1988), therefore nestlings may have more reproductive value to the female early in life than the male. The pilot data from 2012 suggested that the males' proportional investment in the nestlings (reflected in his provisioning behaviour) increased as they aged. Therefore by 6 – 9 days old the nestlings are probably equally valuable to both parents (as also suggested by Tilgar & Kikas (2009)). The lack of an effect of nestling condition and brood size on the provisioning rate and latency to feed may be due to a lack of variation in nestling condition on Salisbury Plain. As demonstrated in earlier chapters (Chapters 3 and 5), food does not appear to be limiting on Salisbury Plain and nestling condition did not show much variation. If this study was conducted on a site with larger variations in nestling condition, a difference in risk taking for different quality broods (e.g. Michl *et al.* 2000; Tilgar & Kikas 2009) may have been apparent, though Dale *et al.* (1996) also failed to find significant brood size and nestling condition effects in pied flycatchers.

The percentage of time the parents spent 20 m or closer to the nest did not vary significantly with time since the nest disturbance event. Parents generally always spent a high percentage of their time (70 – 80%) within 20 m of the nest (Figure 6.6). Preliminary analysis using the actual distances of parents from the nest, rather than the percentage of time parents spent within 20 m, also found no change in the mean distance over time. As food appears to be relatively abundant on Salisbury Plain, the parents may not need to travel far from the nest to forage (Andersson 1981), allowing them to spend most of their time close to the nest and thereby be able to guard the nest more effectively (Marzluff 1985; Martindale 1982; Hakkarainen *et al.* 2002; reviewed in Lima 2009). Whinchats cannot aggressively defend their nests from approaching humans, or other predators, by attacking. However, they do use alarm calling and perching in close proximity to the approaching individual to quiet their young and as distraction techniques (Montgomerie & Weatherhead 1988; Caro 2005; Lima 2009). The change in provisioning pattern suggests Whinchats did spend a larger proportion of their time exhibiting nest guarding or vigilance behaviours immediately after a nest disturbance event, rather than foraging to provision nestlings, and then this reduced over time leading to an increased provisioning rate (reviewed in Frid & Dill 2002, Price 2008 and Lima 2009).

From this study we have found that visiting nests every two to three days does not significantly affect the egg phase Daily Survival Rate and visiting three times during the nestling period is unlikely to have a detrimental effect on nestling condition from interrupted provisioning as only 0.52% of the provisioning period would be disrupted. However, despite no evidence of a significant damaging effect of nest monitoring on nest success, it is still important to take precautions to minimise any potential impact (Jacobson *et al.* 2011; Reynolds & Schoech 2012) and follow guidelines for nest monitoring (Martin & Geupel 1993; Ferguson-Lees *et al.* 2011). Depending on the research aims, it may be possible to use temperatures sensors placed in nest cups to monitor clutch and brood survival, reducing the number of visits necessary (Hartman & Oring 2006; Weidinger 2006; Jacobson *et al.* 2011; Mougeot *et al.* 2014), or to monitor using micro-nest cameras which has the added advantage of identifying the nest predators (Pietz & Granfors 2000).

Chapter 7: Estimating survival and determining settlement patterns in a declining Afro-Palearctic migrant bird

A colour-ringed adult male Whinchat

7.1 Abstract

Wintering ecology is poorly studied for most Afro-Palearctic migrants. It is possible to account for the effects of over-winter survival by determining annual survival estimates. These estimates can then be studied in conjunction with values for productivity, to identify the demographic mechanisms causing a decline. Survival estimates can also be compared between populations and species with the aim of uncovering external population limitations. Here, variation in survival, site fidelity and settlement patterns depending on age and sex are investigated to determine the influence of non-breeding season conditions on population stability. Survival estimates are compared to those from other studies on Whinchats and other Palearctic migrants to identify potential external limiting factors. Adult (older than first breeding year) survival rates were comparable to those of other Palearctic migrants but first-year (in first breeding year) apparent survival rates were low. This may be partly attributable to higher natal dispersal compared to breeding dispersal. Breeding dispersal distances did not differ significantly between males and females, or with the success of breeding attempts in the previous breeding season. The population exhibited protandry, with males arriving back on the breeding grounds six days before the adult females, who in turn arrived on the breeding grounds twelve days before first-year females. There was a significant positive correlation between territory occupancy order by females in successive years and also by males and females within each individual breeding season suggesting the first occupied territories are consistently preferred.

7.2 Introduction

For many Afro-Palearctic migrants, research has focused disproportionately on their breeding ecology and only relatively recently has there been a shift in focus towards factors such as anthropogenic habitat degradation and drought within the non-breeding range (Vickery *et al.* 2014). By estimating annual survival rates it is possible to, atleast partially, account for the unknown influences acting on a population during the non-breeding season. Survival rates are often lower for niave birds in their first breeding year than adults (Siriwardena *et al.* 1998; Clark & Martin 2007) and may be lower for females than males (Donald *et al*. 2007). Therefore, survival estimates should be calculated separately for these different groups. Estimates of annual survival rates for different sex and age categories, along with data on breeding success, can then be used to identify the demographic mechanisms causing a decline using population models (see Chapter 8; Green *et al.* 1999). Once the demographic mechanisms behind a decline are understood, it is much easier to determine which external causes are likely to be responsible, and thereby to adopt appropriate conservation action (Green *et al*. 1999). Therefore, estimating annual survival rates, the variation in these rates with time, and the variation in survival rates between adults and niave birds in their first breeding year is very useful.

Calculations of survival suffer from the problem of correctly identifying whether birds are lost due to mortality or to permanent emigration (Lebreton *et al.* 1992). The estimated survival rate and how close it is to the true survival rate will therefore depend on the level of site fidelity, natal philopatry and the effort used or needed to detect returning birds. This means that, when measuring overwinter survival, it is also important to quantify breeding and natal dispersal distances and to examine how they are affected by factors such as age, sex or breeding habitat quality. Natal dispersal is defined as the dispersal of an individual from their birth site to their breeding site the following year, whereas breeding dispersal refers to dispersal of an individual from their breeding site one year to their breeding site the following year (Greenwood & Harvey 1982). Natal dispersal distances are generally higher than breeding dispersal distances (Greenwood & Harvey 1982; Weatherhead & Forbes 1994; Lemon *et al.* 1996; Sedgwick 2004; Shitikov *et al.* 2012). This is thought to be because first-year birds seeking their first breeding territories are outcompeted for the best territories by adult birds that are already at the breeding site, or the result of selection pressure due to high net costs of inbreeding (Greenwood & Harvey 1982; Lozano & Lemon 1999; Sedgwick 2004). Weatherhead & Forbes (1994) and Paradis *et al.* (1998) found that migrants had higher natal dispersal distances than resident birds, probably because migratory birds have to disperse anyway to migrate, and therefore pay the cost of leaving familiar natal areas, whereas resident species can avoid this by not dispersing. There is also evidence of higher dispersal distances in females as opposed to males in territorial birds (Greenwood & Harvey 1982; Bensch & Hasselquist 1991; Payne & Payne 1993; Lemon *et al.* 1996; Murphy 1996, Paton & Edwards 1996; Norman & Peach 2013; but see Clarke *et al.* 1997; Sedgwick 2004). This is thought to be due to familiarity with a territory being advantageous in defence (Hinde 1956; Greenwood 1980; Paton & Edwards 1996; Schjorring *et al.* 2000). However, it may also be due to limited territory availability for arriving females, as rather than choosing from any vacant territory they can only choose from territories already occupied by males (Arlt & Pärt 2008). Many studies have found that dispersal distance depends on the breeding success in the previous season (Greenwood & Harvey 1982; Paton & Edwards 1996; Murphy 1996; Haas 1998; Doligez *et al.* 1999; Hoover 2003; Sedgwick 2004; Pasinelli *et al.* 2007; Shitikov *et al.* 2012; Shitikov *et al.* 2015), with unsuccessful breeders dispersing greater distances than successful breeders. However, this pattern may also depend on breeding site quality (Bollinger & Gavin 1989; Bensch & Hasselquist 1991; Holmes *et al.* 1996; Doligez *et al.* 1999), and the effect is often stronger in females than males (Greenwood & Harvey 1982; Murphy 1996; Paton & Edwards 1996; Sedgwick 2004, though not always: Payne & Payne 1993), and in first-years compared to older birds (Holmes *et al.* 1996). Again, this is thought to be due to the advantages of defending a known territory for males, whereas females are freer to explore and find a new, better territory (Greenwood & Harvey 1982). Dispersal distances can also vary due to large scale habitat structure and configuration; for example a study on Whinchats in Russia found very low natal philopatry and site fidelity (Shitikov *et al.* 2015) compared to other studies in Europe (Schmidt & Hantge 1954; Müller *et al.* 2005), which was thought to be caused by habitat fragmentation.

As well as influencing survival, conditions in wintering grounds and on migration may also influence the arrival time of birds on the breeding grounds and this can affect their breeding success. In migratory birds, males generally arrive before females (protandry), and adults before first-years (Darwin 1871; Francis & Cooke 1986; Bench & Hasselquist 1991; Holmes *et al.* 1996; Morbey & Ydenbery 2001; Currie *et al.* 2000; Cooper *et al.* 2009; Saino *et al.* 2010). Various hypotheses may explain the occurrence of protandry (Morbey & Ydenbery 2001; Kokko *et al.* 2006; Saino *et al.* 2010) but the evidence is inconsistent depending on the set of species studied and methods used. The main advantages suggested for males are: access to superior territories, access to more receptive females which increases potential mating opportunities (favoured by Kokko *et al.* 2006; supported by Rubolini *et al.* 2004 and Coppack *et al.* 2006), and sexual selection advantages where females use earlier arrival as a measure of quality (supported by Saino *et al.* 2010). The hypotheses put forward to explain why adults arrive before first-years are less equivocal. Adult birds have greater experience of the migration route and are generally better able to judge energy needs and orient themselves (Baldaccini & Bezzi 1989; Woodrey 2000; Wiltschko & Wilschko 2003). Moreover, they are usually in better physical condition than first-years (Francis & Cooke 1986; Møller 1994) due to being able to acquire winter territories in those areas that confer better foraging (Stutchbury 1994; Marra 2000), and are therefore able to arrive earlier on the breeding grounds through a combination of earlier and faster migration (Rguibi-Idrissi *et al.* 2003; Smith & Moore 2005; Cooper *et al.* 2009). Earlier arrival on the breeding grounds is commonly associated with individuals acquiring better quality territories (Aebischer *et al.* 1996; Hasselquist 1998; Currie *et al.* 2000) and having higher reproductive success (Møller 1994; Bensch & Hasselquist 1991; Tryjanowski *et al.* 2004; Norris *et al.* 2004; Saino *et al.* 2004a; Smith & Moore 2005; Moore *et al.* 2005; Newton 2006, 2008; Møller *et al.* 2009; Reudink *et al.* 2009; Cooper *et al.* 2011). Earlier arrival can, however, also incur costs, for example the increased risk of inclement weather on passage, or at the breeding grounds, due to the late arrival of spring in temperate regions (Whitmore *et al.* 1977; Møller 1994; Brown & Brown 1998, 1999 and 2000; Smith & Moore 2005; Newton 2006, 2007).

Both breeding season conditions and non-breeding season conditions are implicated as potential causes of population change in Whinchats in the UK over the last 20 years (Balmer *et al.* 2013; Henderson *et al.* 2014). Breeding habitat extent, quality and breeding productivity were investigated in earlier chapters (Chapters 4 & 5). In this chapter, I quantify breeding season return rates as an estimate of non-breeding season survival and compare these values to other sites and with respect to values for productivity, to allow a relative assessment of the balance between productivity and survival. In this way, I aim to identify potential external demographic limiting factors, in spite of the Salisbury Plain breeding population's relative stability (section 2.2.1). Variations in site fidelity in adults and first-years, and with respect to breeding success the previous year, will also be quantified to improve our understanding of the accuracy of the survival estimates. Additionally the indirect effect of over-winter conditions, due to their influence on arrival time and the effect this has on breeding success will be analysed; regular surveys will establish the pattern of arrival and territory settlement and regular nest monitoring will determine subsequent breeding success. If survival in this population is predominantly related to the quality of the breeding habitat, then it would be predicted that survival would be relatively high, given the availability of apparently suitable breeding habitat on Salisbury plain (Chapter 4) and the indication of a plentiful food supply (Chapters 3 & 5). If survival predominantly reflects non-breeding habitat conditions then it should be consistent with estimates from other Whinchat populations and other Afro-Palearctic migrant species, assuming the birds winter in similar locations. Based on previous studies, I would expect natal dispersal distances to be greater than breeding dispersal distances and breeding dispersal to be greater after breeding failure. Adult males would be expected to arrive first on the breeding sites to secure the best territories, gaining sexual selection advantages and overall higher breeding success; whereas sub-dominant first-year females would be expected to arrive last as they are likely to be outcompeted for breeding territories and therefore have the least to gain by risking earlier arrival.

7.3 Methods

7.3.1 Study area

The study area was a section of Salisbury Plain, Wiltshire, in southwest England. Details of the study sites within this area used each year between 2010 – 2014, and a map of the sites can be found in section 2.2.

7.3.2 Trapping and marking adult birds

During the 2010-2013 breeding seasons, as many adults as possible that bred within the study sites were caught, biometrics were taken and individuals were marked with individual combinations of colour rings and a numbered metal BTO ring (section 2.4). Nine days after hatching, nestlings were colour ringed with site and year combinations which were not individually identifiable: individual combinations were assigned the following year if the birds were re-caught. In total, 74 adult males, 66 adult females and 292 nestlings were ringed.

7.3.3 Whinchat surveys

Surveys were conducted using standardised Common Bird Census techniques (Bibby 2000), ensuring the entire site was covered in a comprehensive manner but focusing on the study sites where ringing had occurred the years before. In 2011, the three initial study sites (see section 2.2) were surveyed once a week, from the last week in April to the end of July. Additionally, a sample of selected valleys (as surveyed in 2000 and 2005; Stanbury *et al*. 2000 & 2005), were surveyed between the last week April until mid-May. In 2012, the survey coverage was more intensive. Four study sites (Imber, West Hill, Berril and K-crossing- see section 2.2) were repeatedly surveyed every three days. Surveys in 2013 – 2014 aimed to establish the arrival dates of individual Whinchats and to establish the pattern of territory settlement, as well as to detect returning colour ringed birds. Daily systematic surveys were conducted from mid-April until mid-May, with six sites surveyed (Imber, West Hill, Berril and K-crossing, Ic Valley and Southdown Track). Each site was repeatedly surveyed every 1 – 2 days. Sampling aimed to be exhaustive: in all surveys at least one hour was spent at each site. This was considered to be sufficient because a cumulative percentage frequency curve suggested that the first Whinchat was always spotted within 45 minutes of arriving at a site (Figure 7.1). From mid-May, when the Whinchats had settled into territories, work was focused more on individual pairs. However, all sites were still visited every 1 – 3 days. For all observed Whinchats, I recorded the colour-ring combination if present, time, sex, activity and coordinates of the location, using a handheld GPS unit (Garmin exTrex). Surveys were usually completed during 06:00-11:00 and 16:30-20:30, when the birds were most active. During busy periods, when large numbers of new Whinchats arrived, the surveys took place all day, and the order of site visits was rotated to ensure an equal coverage at peak times. Valleys surrounding the core sites were also surveyed on an *ad hoc* basis as time allowed. In addition, as part of data collection for chapters 3 and 4, 32 one kilometre by one kilometre grid squares were surveyed for Whinchats during 2012 and 2013 (Chapter 3), and 267 random points were surveyed in 2014 (Chapter 4).

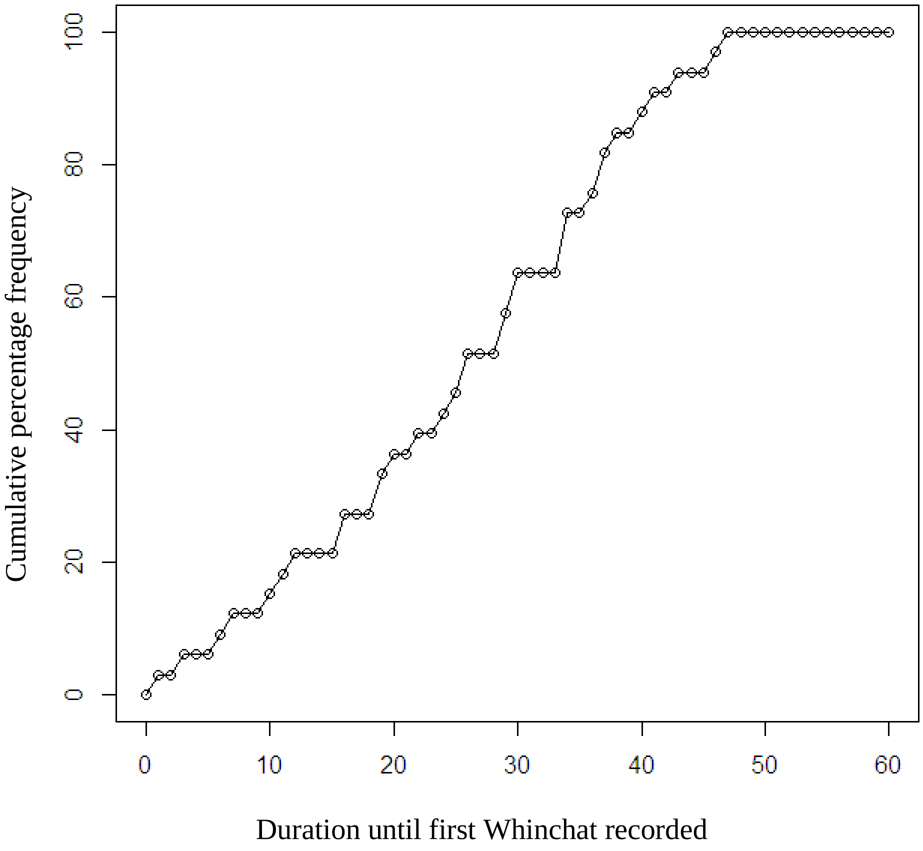


Figure 7.1. A cumulative percentage frequency plot of the time taken to first observe a whinchat on arrival at a survey site. The first Whinchat at a site was always spotted within 45 minutes of beginning the survey, which suggests that ensuring each site is surveyed for at least an hour should avoid false negatives. The data are from 33 survey visits to study sites in 2013.

7.3.4 Breeding success

First and subsequent nests were found for every pair observed within the six study sites between 2012 – 2014, and for as many pairs as possible with the reduced sampling effort available in 2010 and 2011. These nests were then checked generally every two days, or once a week for 2010 and 2011, until either the nest failed or the nestlings fledged (section 2.3 and 5.3.3). Body condition of nestlings at day nine was calculated for use as an additional measure of breeding success (section 5.3.3 for details).

7.3.5 Breeding and natal dispersal distances

Natal and breeding dispersal distances were calculated for colour-ringed birds, using the UK Ordnance Survey coordinates of the nests or, in the case of birds re-sighted outside the main study sites, the location at which they were first recorded. Between year inter-nest distances were calculated in ArcGIS 10.0 (ESRI 2010).

7.3.6 Territory settlement

A Whinchat was classed as having settled on a territory if it was sighted there on three consecutive occasions: the first occasion was then recorded as the settlement date. Territory settlement dates were included for un-ringed Whinchats on the assumption that the same individual occupied the territory during a season. This approach is justified because for colour-ringed birds classed as settled, individuals recorded on the first occasion were always the same as those subsequently recorded on the second and third occasions. Ringed Whinchats were very rarely seen away from their territory once settled (only 2 occasions in 3 years and then only about 500 m away) and never changed territory unless their nest failed. In 2014, it was not possible to access one study site, Imber, between 5th and 11th May, due to military operations, therefore the accuracy of arrival dates for this site during this period was lower.

7.4 Data analysis

Apparent survival is the probability that an individual both survives from one year to the next and also does not permanently emigrate from the population during this time (Lebreton *et al.* 1992). Apparent survival rates were estimated using Cormack-Jolly-Seber models (Lebreton *et al*. 1992) using MARK version 6.1 (McClintock & White 2012). These models also estimate the recapture probability, which is the probability of recording a ringed bird in the study area if it is alive and present.

I was unable to assign sex to the nestlings at the time of ringing and so two separate data sets were used. Data from Whinchats ringed either as adults or nestlings were analysed to examine differences in first-year survival, and data from Whinchats ringed as adults only were used to assess any influence of sex on survival. Nestlings were fitted with colour rings that identified the year and site of hatching but not individuals, so for example, there were a few occasions when it was not possible to determine if a returning female, which was a first-year the previous year, was the same individual that had been sighted in the area the previous year. This may have affected eight observations so models were run both assuming returning birds of the same sex with the same colour combination were the same, and assuming that they were not.

The Cormack-Jolly-Seber model relies on four assumptions: first, the recapture probability is the same for every Whinchat in the study population, second, every marked animal has the same probability of surviving until the next recapture event, third, marks are not lost and fourth, they are released immediately after recapture (Cooch & White 2014). Assumptions three and four were met but assumptions one and two are more difficult to test. There are many possible causes of violations which cannot easily be known. For example, some Whinchats may temporarily leave the study area (for further details and examples see Cooch & White 2014). To test that these assumptions are met, the global models were assessed for goodness of fit using the three methods available in MARK: median c-hat, bootstrapped re-samples and the program RELEASE (Burham *et al.* 1987). These tests allow estimation of the amount of ‘extra binomial noise’, also called over-dispersion, present in the global model, and thereby measures the lack of fit (Cooch & White 2014). This measure of over-dispersion is described by the variance inflation factor, called c-hat. Ideally, when there is no over-dispersion, c-hat should be one. However, values less than three can still be considered as an acceptable fit (Lebreton *et al.* 1992). For values of c-hat that differ from 1, but are within this acceptable range, the global model can be adjusted to correct for this over-dispersion by changing the value of c-hat for the model from 1 to the value obtained using one of the above tests, which has the effect of increasing the variance estimates to accommodate the extra ‘noise’ (Cooch & White 2014). The AICc scores for candidate models are then adjusted for over-dispersion and converted to QAICc: the log likelihood divided by c-hat, the over-dispersion parameter (Burham & Andersson 2002; Cooch & White 2014). This is a more conservative test and simpler models, with fewer parameters, tend to be favoured increasingly as c-hat increases.

For the analysis presented here, the program RELEASE had problems running for the sample size of data available; the other two methods both gave similar estimations for c-hat. The highest, and, therefore, the most conservative estimation of c-hat, was used (Cooch & White 2014). The global model for the adult and first-year data assumed survival varied over years and in the first-year of life, but was constant within a year for adults (older than first breeding year). The recapture probability was assumed to be constant within a year for adults and first-years, as it was considered unlikely that first-years that return to the study site would be harder to re-sight than adults, but was allowed to vary between years. Tests of fit for the global model for first-year and adult survival indicated the most conservative estimate of c-hat = 1.34 and the global model was adjusted to this value of c-hat. The global model for just adult data assumed the survival and recapture probabilities both varied with sex and year. In this case, the recapture probability was allowed to differ for the separate sexes as females are less conspicuous than males. Tests of fit for this global model indicated that the most conservative estimate of c-hat = 1.52, the global model was adjusted to this value. As c-hat was adjusted for both global models the candidate models were compared using QAICc. The analysis was also run with c-hat = 1 to check that changing c-hat did not change the overall outcome; the apparent survival estimates, recapture estimate and top models (ΔAICc < 2) were exactly the same and the same parameters were significant in the model; the only difference was that the standard errors when c-hat = 1 were slightly smaller.

The rest of the analysis was performed in the R statistical package version 2.3.1 (R Development Core Team 2014). All mean values throughout the analysis are presented with +/- 1 standard error.

7.5 Results

7.5.1 Differences in apparent survival with age

The best survival model showed that apparent survival was lower for returning first-year birds than for returning adults (Table 7.1). Reassuringly, the qualitative model output remained unchanged when first-years that could not be individually identified were assumed to be the same bird, or if they were assumed to be two different birds, as described in the methods. For brevity, therefore, I present only the models that assumed the returning birds with the same sex and ring combinations were the same individuals. The best model had a ΔQAICc > 4 compared to the next best model, therefore model averaging was not used (Table 7.1). The best model only contained an effect of age on the apparent survival parameter and a constant recapture probability. Apparent survival of first-years was significantly lower than for adults (Table 7.2; Figure 7.2).

Table 7.1. Model selection results using Cormack-Jolly-Seber models to estimate apparent survival and recapture probabilities for adults (older than first breeding year) and first-years (in first breeding year). C-hat was adjusted to 1.34. φ = survival probability, P = recapture probability, K = number of parameters, n = 396.

Model	QAICc	ΔQAICc	AICc Weights	Model Likelihood	K	QDeviance
φ(age)P(constant)	380	0.000	0.450	1.000	3	37.7
φ(age)P(year)	384	4.04	0.060	0.133	6	35.6
φ(age + year)P(constant)	385	5.76	0.025	0.056	6	37.3
φ(age : year) P(constant)	388	8.01	0.008	0.018	9	33.3
φ (age + year)P(year)	388	8.72	0.006	0.013	9	34.0
φ(age : year)P(year)	391	11.4	0.002	0.003	12	30.4
φ(constant)P(constant)	397	17.2	0.000	0.000	2	56.9
φ(year)P(constant)	402	22.1	0.000	0.000	5	55.6
φ(constant)P(year)	402	22.1	0.000	0.000	5	55.7
φ(year)P(year)	406	26.2	0.000	0.000	8	53.6

Table 7.2. Back-transformed apparent survival estimates (φ) for adults (older than first breeding year) and first-years (in first breeding year), along with the recapture probability (P) from the best MARK model selected based on QAICc, (φ(age)P(constant)). The 95% confidence intervals are shown in brackets.

	Estimate
First-year survival	0.200 (0.129 – 0.298)
Adult survival	0.520 (0.396 – 0.641)
Recapture	0.537 (0.365 – 0.700)

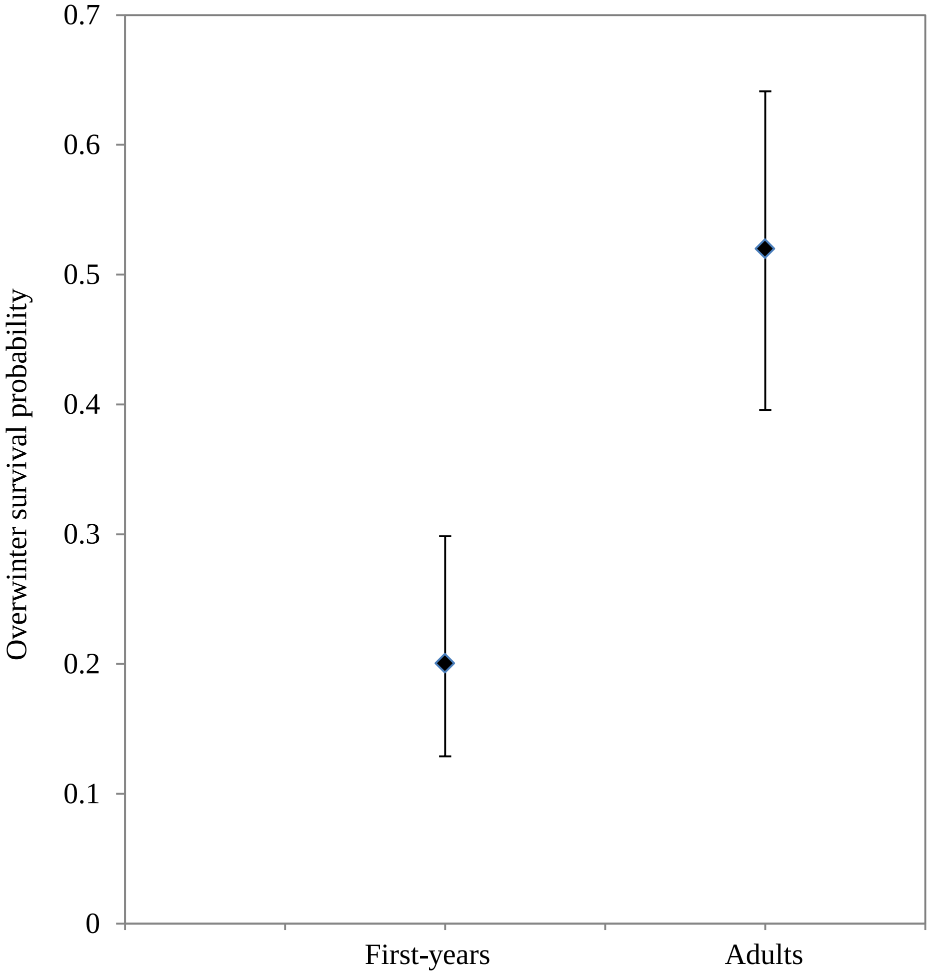


Figure 7.2. MARK estimated apparent survival probabilities for adults and first-years (n= 396), from the best model ($^{\varphi}$(age)P(constant)), selected by QAICc. The dots are the apparent survival estimates for each group and the bars display the 95% confidence intervals.

7.5.2 Differences in apparent survival with sex

Three models were within 2 ΔQAICc of the best model, which assumed constant apparent survival for both sexes and constant recapture probability (Table 7.3). The other two models both had the same number of parameters, with one including only an effect of sex on the recapture probability, and the other an effect of sex on the apparent survival probability, but for both models these effects were not significant. As the best three models all contained different parameters, model averaging was not used. The results presented are from the model including an effect of sex on apparent survival as this was the parameter of interest. There was no significant difference in apparent survival estimates between the sexes, the beta parameter for sex included zero in its 95% confidence intervals, (β = 0.629, 95% CI: -0.357 – 1.62). However, there is some evidence of a non-significant trend for higher survival in adult males compared to adult females (Figure 7.3). The recapture probability was within the range of the recapture probability for the model with adults and first-years (0.537 (0.365 – 0.700) compared to 0.622 (0.343 – 0.838): Table 7.2 and Table 7.4).

Table 7.3. Model selection results using Cormack-Jolly-Seber models to estimate apparent survival and recapture probabilities for adult males and adult females. C-hat was adjusted to 1.52 $^{\varphi}$ = survival, P = re-sighting probability, K = number of parameters, n = 105, : denotes an interaction.

Model	QAICc	ΔQAICc	AICc Weights	Model Likelihood	K	QDeviance
φ (constant)P(constant)	133	0.00	0.259	1.000	2	24.6
φ (sex)P(constant)	134	0.51	0.201	0.776	3	23.0
φ (constant)P(sex)	134	0.55	0.196	0.759	3	23.1
φ (sex)P(sex)	136	2.42	0.077	0.299	4	22.8
φ (year)P(constant)	137	3.31	0.050	0.191	5	21.5
φ (constant)P(year)	137	3.61	0.043	0.165	5	21.8
φ (year)P(sex)	137	4.10	0.033	0.129	6	20.1
φ (sex)P(year)	137	4.14	0.033	0.126	6	20.2
φ (year + sex)P(constant)	138	4.26	0.031	0.119	6	20.3
φ (constant)P(year + sex)	138	4.67	0.025	0.097	6	20.7
φ (year + sex)P(sex)	139	6.19	0.012	0.045	7	20.0
φ (sex)P(year + sex)	140	6.28	0.011	0.043	7	20.1
φ (year)P(year)	140	6.53	0.010	0.038	7	20.3
φ (year)P(year + sex)	141	7.26	0.007	0.027	8	18.8
φ (year + sex)P(year)	141	7.43	0.006	0.024	8	19.0
φ (sex)P(year : sex)	141	7.93	0.005	0.019	8	19.5
φ (year + sex)P(year + sex)	143	9.48	0.002	0.009	9	18.7
φ (year)P(year : sex)	147	14.1	0.000	0.001	11	18.6
φ (year + sex)P(year : sex)	150	16.3	0.000	0.000	12	18.4
φ (year : sex)P(year + sex)	150	16.5	0.000	0.000	12	18.6
φ (year : sex)P(year : sex)	154	20.7	0.000	0.000	14	17.7

Table 7.4. Back-transformed apparent survival estimates ($^{\varphi}$) for adult (older than first breeding year) males and adult females, along with the recapture probability (P) from the second best MARK model selected based on QAICc, ($^{\varphi}$(sex)P(constant)). The 95% confidence intervals are shown in brackets.

	Estimate
Male survival	0.512 (0.335 – 0.686)
Female survival	0.359 (0.189 – 0.573)
Recapture	0.622 (0.343 – 0.838)

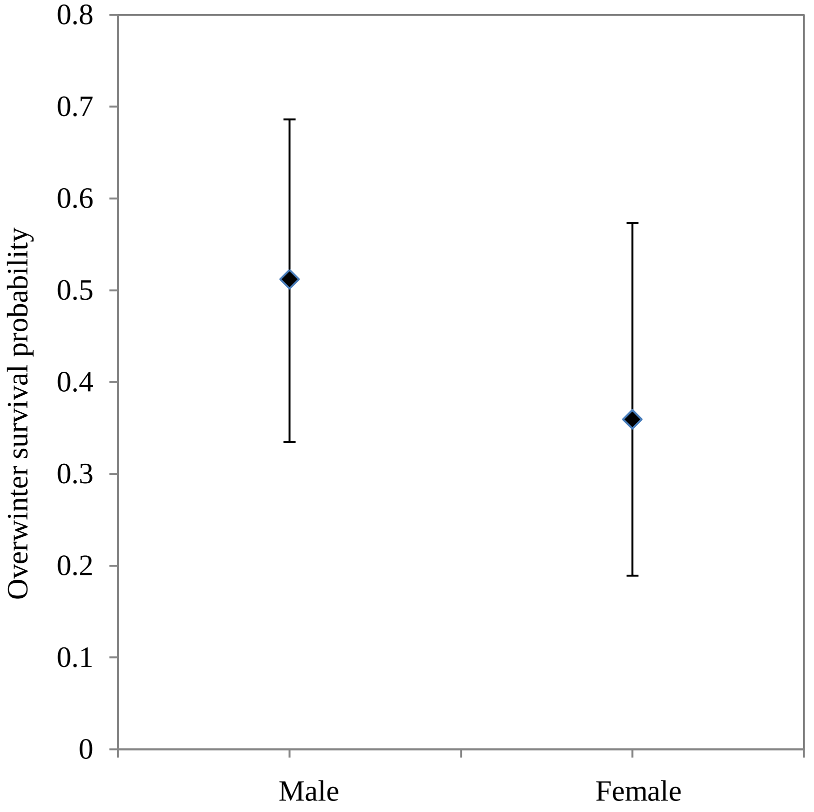


Figure 7.3. The MARK estimated apparent survival probabilities for adult males and adult female adults (n = 105), from the second best model ($^{\varphi}$(sex)P(constant)), selected by QAICc. The dots are the apparent survival estimates for each group and the bars display the 95% confidence intervals.

7.5.3 Comparisons to other studies using MARK apparent survival estimates

The apparent annual survival estimates of adult Whinchats from Salisbury Plain are slightly higher than estimates from Russia and Switzerland, and at the top end of estimates from other comparable Palearctic migrant species, especially when just considering adult male survival (Table 7.5). The adult female apparent survival rate is especially low in Switzerland. Survival of a fledgling into the first breeding year is comparable to results from Switzerland but low relative to mean estimates for other open-nesting migrant species (Table 7.5).

Table 7.5. Table of MARK calculated apparent annual survival estimates (+/- SE) from this study and studies from other countries in Europe, for first-year breeders (mixed sexes), and for older males and females (classified here as Adults) ([1]Whinchats on Salisbury Plain, [2] Whinchats on fragmented abandoned fields - Shitikov *et al*. 2015, [3] Whinchats on a farmed area - Müller *et al.* 2005, [4] Nine other open-nesting, Palearctic migrant passerines – Lesser Whitethroat, Swallow, Sedge Warbler, Whitethroat, Blackcap, Willow Warbler, Garden Warbler, Yellow Wagtail - (Boddy 1993, 1994 and Siriwardena *et al.* 1998).

	Salisbury Plain[1]	Russia[2]	Switzerland[3]	Mean for open nesting Palearctic migrants[4]
Adults (mixed sexes)	0.52 +/- 0.06	0.27 +/- 0.06	-	0.25 – 0.53
Adult Females	0.36 +/- 0.10	-	0.21 +/- 0.06	-
Adult Males	0.51 +/- 0.09	-	0.48 +/- 0.05	
First Years (mixed sexes)	0.20 +/- 0.04	-	0.17 +/- 0.03	0.24 – 0.48

7.5.4 Comparisons to other studies using annual return rates

In Table 7.6 the Salisbury Plain return rates are compared to those from another site in the UK, Geltsdale (Cumbria) and from sites in Europe (Germany). Return rates from Salisbury Plain are comparable to those from other sites. Generally adult male return rates are higher than those of adult females, and first-year return rates are lowest.

On Salisbury Plain in 2012 and 2014, more adults than first-years occupied the territories in the core study sites: in 2012 76.9% of territories were occupied by adults and only 23.1% by first-years and in 2014 the ratio of adults to first-years occupying territories was 69.7%:30.3%. However, in 2013 this pattern was reversed with 70.2% of territories occupied by first-year breeders and 29.8% of territories occupied by adults. This is reflected in the higher first-year return rate and lower adult return rate in 2013 compared to other years.

Table 7.6. The percentage of returning colour-ringed adult male, adult female and first-year Whinchats by year for Salisbury Plain (estimates are not adjusted by MARK). The number in brackets is the number of ringed Whinchats in each category present the year before. Ringed Whinchats that were not seen one year, but were recorded the year after, were included in the missed year as they were known to have been alive during that time. Also included are return rates from other studies from the UK (Geltsdale in Cumbria, pers. comm Westerberg, S.) and Germany for comparison ([1]Schmidt & Hangte 1954, [2]Bezzel & Stiel 1977, [3]Bastian 1992).

		Adult Females	Adult Males	First-years
2011	Salisbury Plain	28.6% (7)	43.8% (16)	11.4% (35)
2012	Salisbury Plain	35.7% (14)	45.0% (20)	10.3% (39)
2013	Salisbury Plain	25.9% (27)	32.3% (31)	14.0% (129)
2014	Salisbury Plain	19.0% (42)	41.7% (48)	9.0% (89)
Other studies from Europe				
2012 – 2014	Geltsdale (UK)	28.3%	38.8%	21.5%
1949 - 1951	Heidelberg[1]	27%	47%	6.5%
1974 - 1976	Bavarian Alps[2]	41.8%	39.2%	11%
Before 1992	Radolfzell,Helogland, Hiddensee & Sempach[3]	25.1%	43.8%	7.9%

7.5.5 Dispersal

The data on dispersal distances were positively skewed and were, therefore, analysed using non-parametric tests. First-year birds that were re-sighted, but not re-caught to enable individual identification, were not included as the exact dispersal distances could not be calculated. When looking at the effect of breeding success the previous year on dispersal distances for Whinchats which were first-years the previous year, age was determined using the methods described in section 2.4.1. In all other cases first-years refers to Whinchats which were ringed as nestlings.

Natal dispersal was significantly greater than breeding dispersal (Figure 7.4); with median natal dispersal distances of 1.21 km (IQR: 2.03 km) compared to median breeding dispersal distances of 0.21 km (IQR: 0.46 km). Adult males (median: 0.22 km, IQR: 0.34 km) dispersed further than adult females (median: 0.17 km, IQR: 0.52 km), but not significantly so (Figure 7.5). However, there was a stronger trend for first-year males to disperse further from their birth site to their breeding site than first-year females (a median dispersal distance of 2.07 km, IQR: 2.30 km, compared to 0.76 km, IQR: 0.83 km; Figure 7.5), the differences between the median values for these estimates suggests the lack of a significant effect may have been due to the small sample size (n = 16). Dispersal distances were not significantly higher after failing to breed during the previous season compared to Whinchats which bred successfully (Figure 7.6). However, there was more variability in dispersal distances after failing to breed successfully during the previous season, especially when only considering birds which bred for the first time the previous year (Figure 7.6c) or when only considering females (Figure 7.6d). It appears that after breeding failure Whinchats are more likely to show higher breeding dispersal than after successful breeding but not all failed breeders choose to disperse further.

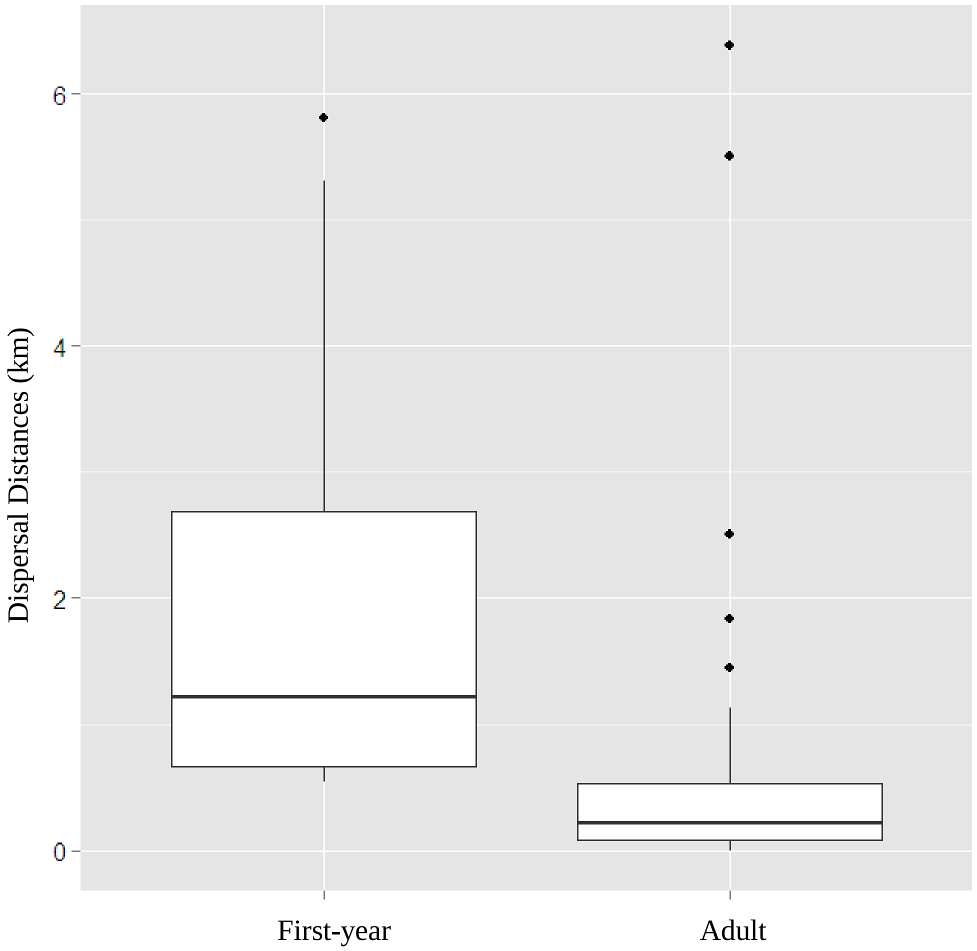


Figure 7.4. A boxplot of the distribution of natal dispersal and breeding dispersal distances for first-years and adults respectively. The box shows the Interquartile Range (IQR), the lines extending from the box are 1.5*IQR, the central line represents the median of the distribution (first-year: n = 16, adult: n = 41). Breeding dispersal was significantly greater than natal dispersal (Mann-Whitney: W = 570, p = 0.0001, n = 57).

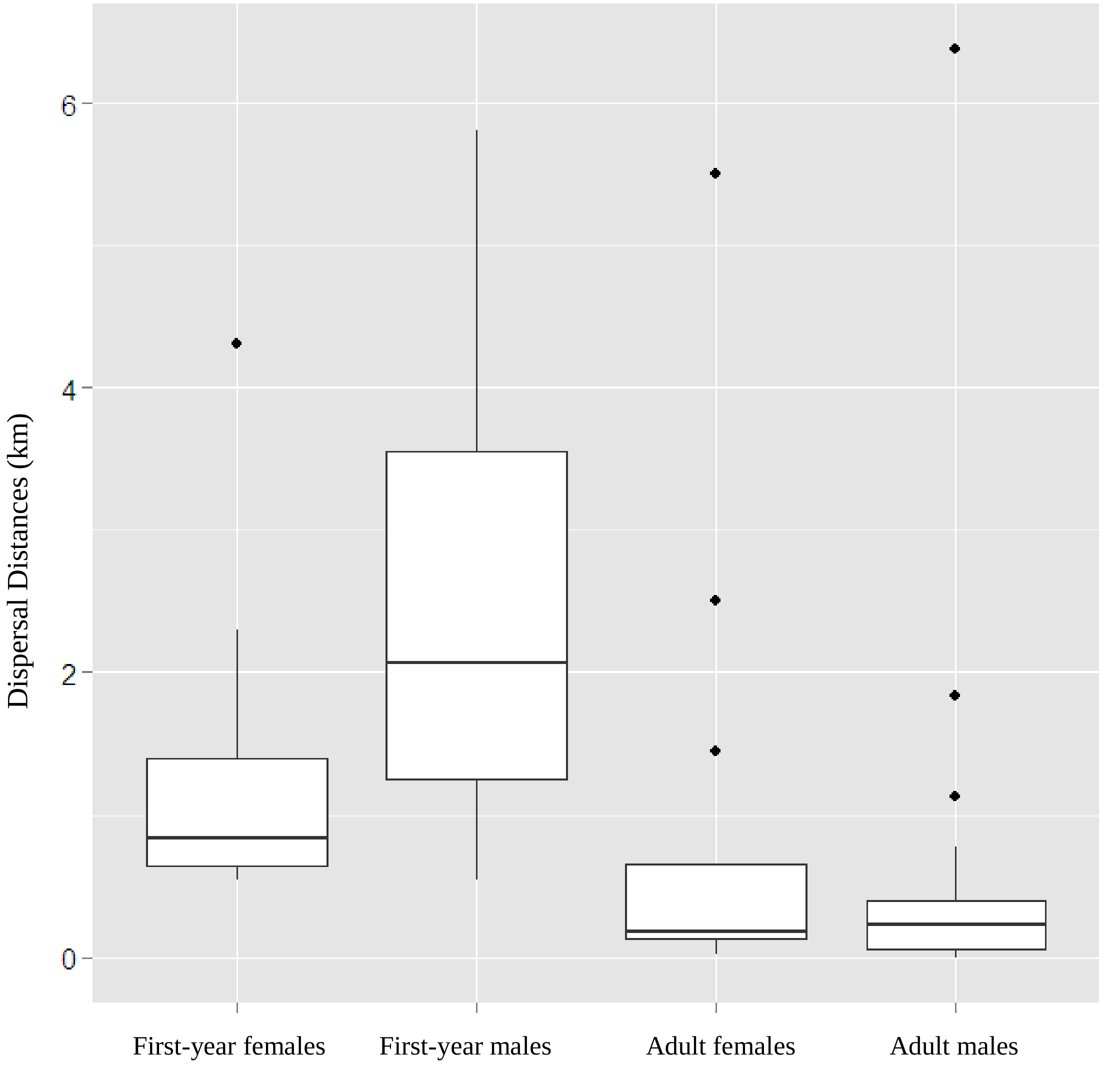


Figure 7.5. A boxplot of the distribution of natal dispersal distances and breeding dispersal distances for males and females. The box shows the Interquartile Range (IQR), the lines extending from the box are 1.5*IQR, the central line represents the median of the distribution (first-year females: n = 8, first-year males: n = 8, adult females: n = 15, adult males: n = 26). There was no significant different in natal dispersal distances in first-year males and females (Mann-Whitney: W = 16, p = 0.11, n = 16), or in breeding dispersal distances between adult males and females (Mann-Whitney test: W = 150, p = 1.00, n= 41).

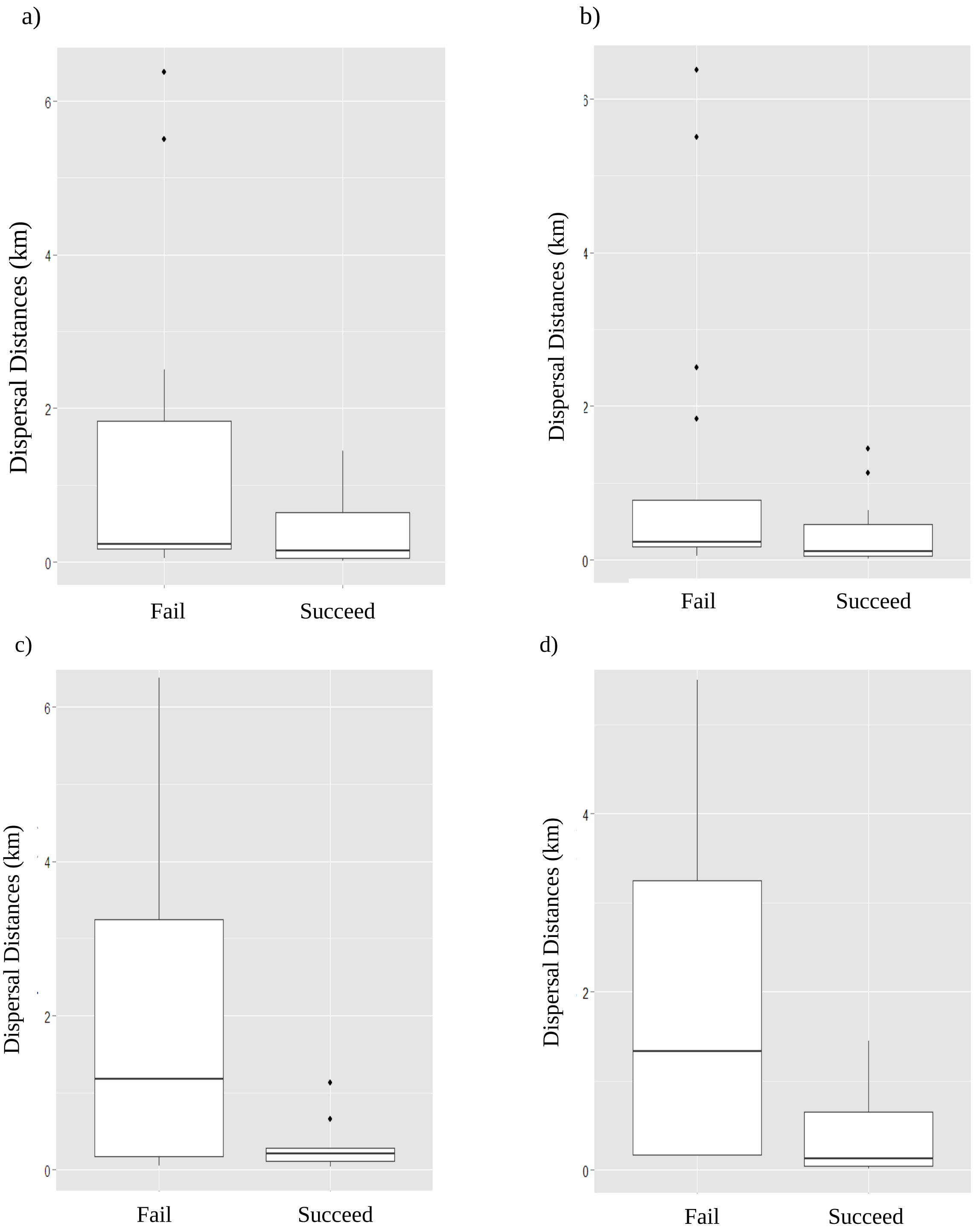


Figure 7.6. A boxplot of the distribution of breeding dispersal distances in adults based on their breeding success of the previous year for a) using the breeding success over the whole season (Mann-Whitney: W = 220, p = 0.092, n = 15 fail, 22 succeed), b) using breeding success of first attempts (Mann-Whitney: W = 229, p = 0.063, n = 21 fail, 16 succeed), c) using breeding success over the whole season but only including males and females which were first-yearsduring their previous years breeding attempt (Mann Whitney: W = 51, p = 0.167, n = 8 fail, 9 succeed), d) using breeding success of the whole season but only including females (Mann Whitney: W = 34, p = 0.138, n = 4 fail, 11 succeed). The box shows the Interquartile Range (IQR), the lines extending from the box are 1.5*IQR, the central line represents the median of the distribution.

7.5.6 Variation in arrival date

Variation in arrival date with age and sex was assessed. Whinchats recorded outside the core study sites were excluded from the analysis, as these areas were not surveyed regularly. Whinchats recorded after May were also not included, as they were assumed to have moved into the area following a failed breeding attempt elsewhere.

Males arrive significantly earlier than females (Figure 7.7); males arrived, on average, six days before adult females, and 18 days before first-year females. Adults also arrived significantly earlier than first-years but there was an interaction between age and sex due to later arrival of first-year females compared to adults of both sexes and first-year males (Figure 7.7).

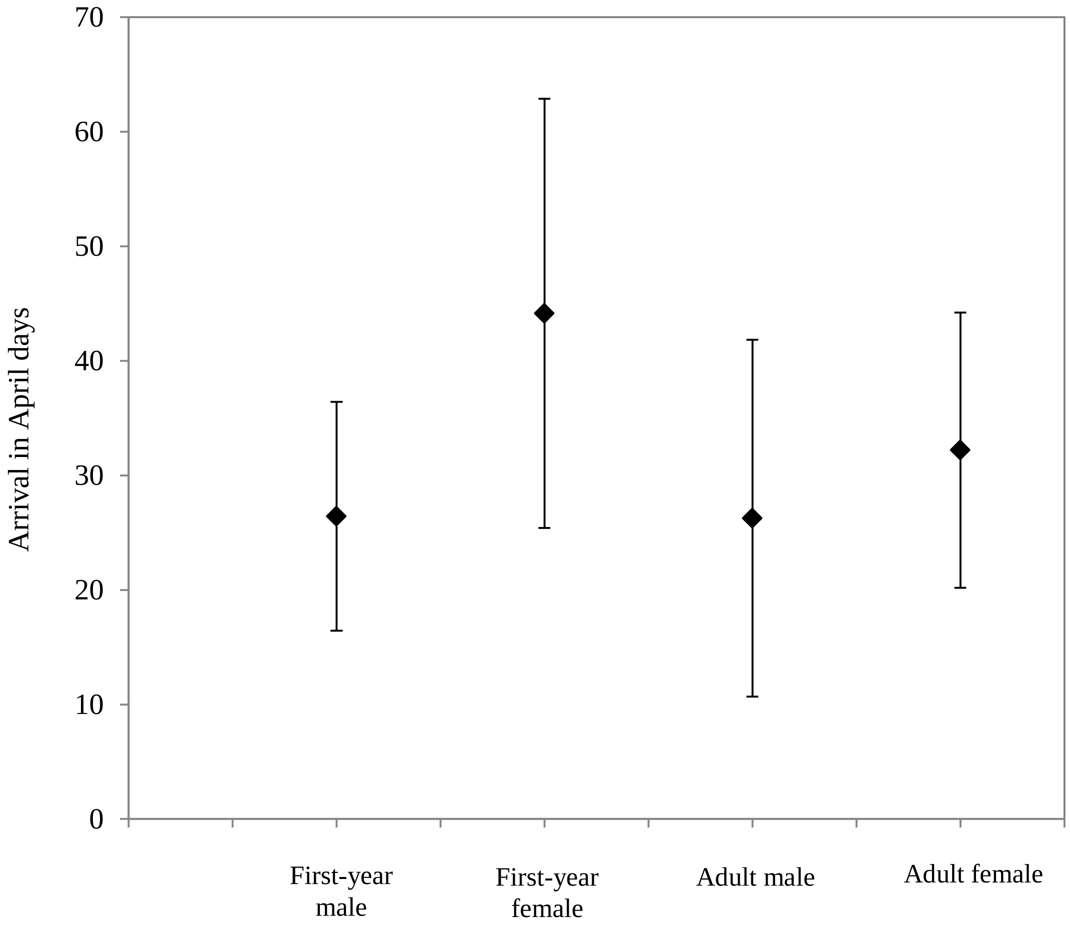


Figure 7.7. The mean arrival dates, in April days (1^{st} April = 1), of male and female, adult and first-year Whinchats. The dots are the mean values, the bars represent the 95% confidence intervals. Males arrived significantly earlier than females (ANOVA: F = 22.5, df = 1, n = 48, p < 0.0001) and adults arrived earlier than first-years (ANOVA: F = 4.25, n = 48, p = 0.045). There was also a significant interaction effect between sex and age (ANOVA: F = 6.03, df = 1, n = 48, p = 0.018).

7.5.7 Effect of territory settlement order on success

To investigate whether the same territories were occupied first in successive years, nests from 2014 were matched to the nearest first breeding attempt nest from 2013 and the rank order of settlement was compared using a tied-corrected Spearman's rank correlation test (Hollander & Wolfe 1973; Best & Roberts 1975). Binomial GLMs were then used to investigate the relationship between breeding success and territory settlement date. As breeding cannot start until the female is present, and the females always arrived either with or after the males (pers. obs.), the date of female territory occupancy was used for the analysis.

The order of female territory occupancy was significantly, positively correlated with order of male territory occupancy (Spearman's rank: rho = 0.353, p = 0.005, n = 61). There was a significant positive correlation in the order of territory occupancy by females for 2013 and 2014 (Spearman's rank: rho = 0.436, p = 0.014, n = 31), but not for males (Spearman's rank: rho = -0.008, p = 0.967, n = 31). There is also a significant positive correlation between first egg date and both male and female territory settlement date (Spearmans's rank: rho = 0.369 and 0.359, p = 0.003 and 0.004 respectively, n = 61). However, the first occupied territories were not necessarily the most successful, and there was no significant correlation between breeding success and territory settlement date (Figure 7.8), or between nestling condition for successful nests and territory settlement date (LM: Est = 0.029 +/- 0.021, n = 23, p = 0.195).

To assess if the first selected territories were chosen on the basis of habitat features, two Linear Regression Models (LM) were run to assess the relationship between female settlement date and the key invertebrate and vegetation features of the territory (Chapter 5). There was no relationship between the (*percentage of bare ground*)^2 or the (*mean vegetation height*)^2 and female settlement date (LM: $p > 0.05$ for all variables). However, there was a marginally significant interaction between *perch abundance* and *invertebrate abundance*, where territories with higher invertebrate abundance were favoured when perches were scarce, but when perches were plentiful, female settlement date was unrelated to invertebrate abundance (Table 7.7).

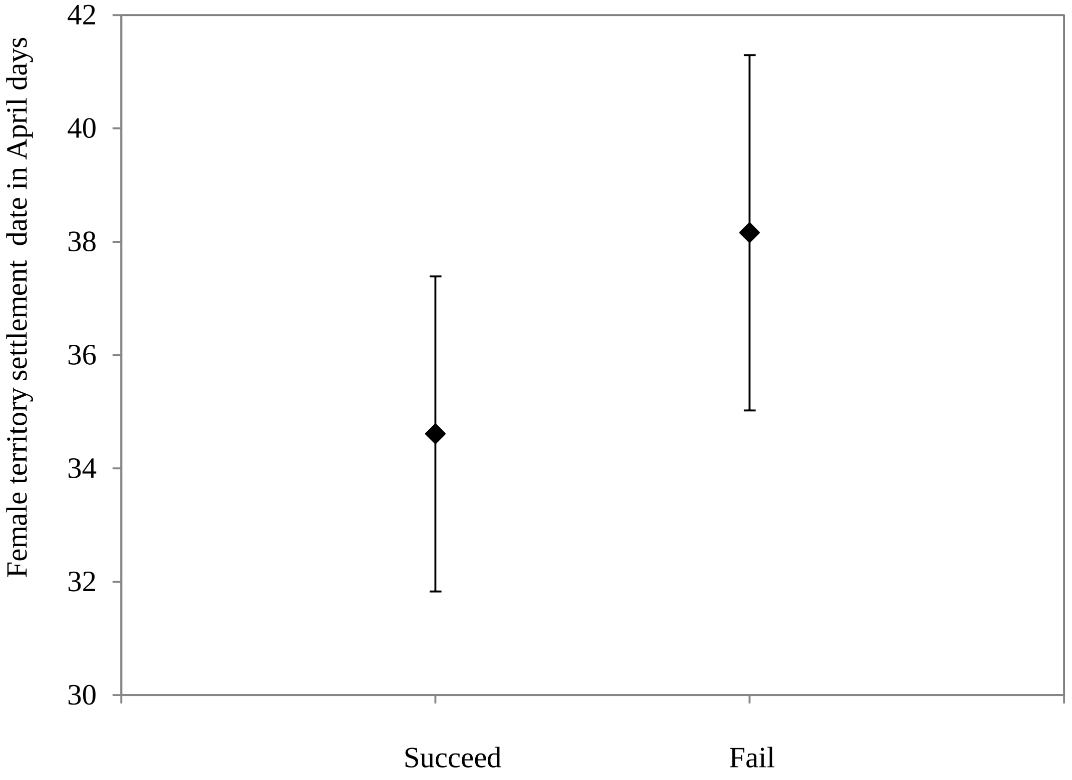


Figure 7.8. The mean territory settlement dates for females that bred successfully over the course of the season and that failed to breed (shown by the dots), the bars represent the 95% confidence intervals (n = 23 succeeded, n = 38 failed). There was no significant correlation between breeding success (taken as 0 = no fledglings, 1 = at least 1 fledgling) and territory settlement date (GLM: Est = -0.0472 +/- 0.0317, n = 61, p = 0.136).

Table 7.7. A Linear Regression Model (LM) of the effect of perch abundance and invertebrate abundance on female territory settlement date (n = 60). Invertebrate abundance and perch abundance were both square-root transformed prior to analysis to make them conform to a normal distribution.

	Estimate	t-value	P-value
Intercept	56.3 +/- 8.02	7.02	<0.001
Invertebrate abundance	-5.21 +/- 1.90	-2.74	0.008
Perch abundance	-7.44 +/- 4.99	-1.49	0.142
Invertebrate abundance : Perch abundance	2.15 +/- 1.09	1.98	0.053

7.6 Discussion

Adult apparent survival estimates for Salisbury Plain were higher than estimates for other Whinchat populations in Europe and at the high end of mean estimates for nine other open nesting, passerine, Palearctic migrant species, but first-year apparent survival estimates were lower than would be expected (Table 7.5). The apparent survival estimates for males and females did not differ significantly. However, the mean female survival rate was 15 percentage points lower than the mean male survival rate. Mean first-year apparent survival was significantly lower, by 32 percentage points, than the mean survival estimate for older Whinchats, however, natal dispersal distances were also significantly greater than breeding dispersal distances (Figure 7.4), suggesting that the difference in apparent survival may be partly due to a higher proportion of first-years permanently emigrating from the study site. Breeding dispersal distances did not differ significantly between males and females (Figure 7.5), nor were they significantly higher after breeding failure the previous season; however, dispersal behaviour after breeding failure was more variable, whereas after breeding success all breeding dispersal distances were small (Figure 7.6). The population exhibited a degree of protandry, with males arriving back on the breeding grounds on average six days before adult females who, in turn, arrived on average twelve days before first-year females. There was a significant positive correlation between territory occupancy order by females in successive years and also by males and females within each individual breeding season. This suggests the first occupied territories are preferable in some way. First occupied territories were not significantly more likely to contain successful breeders or have nestlings in better condition (Figure 7.8). However, they did have earlier first egg dates and tended to have a higher abundance of invertebrates if perch availability was low (Table 7.7), suggesting food availability plays an important role in territory selection.

7.6.1 High adult survival

Adult apparent survival estimates were at the top end of estimates for other open nesting, passerine, Palearctic migrants and also high compared to estimates from a Whinchat study in Russia (Table 7.5), but annual apparent survival rates and return rates were comparable to other Whinchat studies in the UK, Germany and Switzerland (Table 7.5; Table 7.6) and survival estimates from a study in Africa (0.52- 0.54: Blackburn & Cresswell 2015a).The relatively high adult survival estimates compared to other Palearctic migrant passerines could suggest high site fidelity in Whinchats. However, site fidelity is not a uniform trait; at one site in Russia, site fidelity was much lower in the local Whinchat population than the local Yellow Wagtail population, which was thought to be due to the patchy fragmented nature of the habitat (Shitikov *et al.* 2012). High adult apparent survival rates may also reflect true high survival rates, the comparable species all winter in approximately the same area but they differ in their habitat requirements and may vary in their ability to exploit the habitat. Whinchats are generalist insect feeders (Britschgi *et al*. 2006; section 2.5.2) and have been found to adapt well to the current levels of anthropogenic change in Nigeria (Hulme & Cresswell 2012; Blackburn & Cresswell 2015b) and show high wintering survival in this area (Blackburn & Cresswell 2015a) though wintering habitats and population trends over a wider area remains to be studied.

Female apparent survival on Salisbury Plain was higher than apparent survival estimates for female Whinchats from a mown area in Switzerland (Müller *et al.* 2005). Mowing during the breeding season has been found to cause high female mortality with brooding or incubating females more vulnerable than the males (Grüebler *et al.* 2008), but on Salisbury Plain no mowing occurs during the breeding season (Ash & Toynton 2000). Moreover, as only two dead females were found at nest sites during the course of the study, and all ringed individuals were regularly re-sighted throughout the season, it is likely that the values for survival represent non-breeding season survival. It is also possible the lower apparent female survival in Switzerland was due to higher dispersal in females which failed to breed successfully, as has been observed in a Whinchat population in Russia (Shitikov *et al.* 2015); breeding success was very low in some years at the Swiss site (Müller *et al.* 2005).

In general, these findings provide evidence that non-breeding season survival is not particularly low for adult Whinchats compared to other migrants. Therefore, it seems unlikely that the large scale population declines seen in Whinchats over the last 50 years are only due to poor overwinter adult survival. However, this study only examines one Whinchat population in detail for a relatively short time frame: we need to be cautious when applying these findings to other Whinchat populations in other time periods.

7.6.2 Lower female survival compared to males

Mean adult apparent survival was lower for females than for males. It is possible that this difference could be due to lower detectability of females compared to males; the top three models included one with an effect of sex on the recapture probability (Table 7.3). However, this effect was not significant, and for all nests in the core study sites both the male and female were recorded. Other reasons for a trend in lower female apparent survival could be higher breeding dispersal, which was not supported in this study (Figure 7.6), or genuine higher mortality in females. Passerine birds commonly show a trend for lower female apparent survival estimates compared to males, probably due to a lower competitive ability compared to males and increases in metabolic costs and predation risk during incubation (Breitwisch 1989; Payevsky *et al.* 1997; Siriwardena *et al.* 1998; Donald 2007). However, in these studies, as on Salisbury Plain, the difference in mortality between the sexes is often not significant.

Contrary to the prediction, dispersal distances were not greater for females than for males (for Whinchats: Bezzel & Stiel 1977, Bastian 1992, for other species: Greenwood & Harvey 1982; Payne & Payne 1993; Lemon *et al.* 1996; Murphy *et al.* 1996, Paton & Edwards 1996; Norman & Peach 2013). However, adult dispersal distances can depend on interacting factors such as: habitat composition (Shitikov *et al.* 2012; Shitikov *et al.* 2015), territory quality and dominance (Weatherhead & Boak 1986; Holmes *et al.* 1996), population density (Greenwood & Harvey 1982), age and experience (Lemon *et al.* 1996; Sedgwick *et al.* 2004), presence of previous mate (Payne & Payne 1993; Murphy 1996) and previous breeding experience (Weatherhead & Boak 1986; Lemon *et al.* 1996; Hoover *et al.* 2003), meaning that clear patterns of higher female dispersal distances may not always arise. In fact, a review by Clarke *et al.* (1997) found no gender bias towards longer dispersal distances in 33% of species, a female bias in 53% and a male bias in 15%.

Breeding dispersal distances were also not significantly higher after nesting failure of a first attempt or failure over the whole season, counter to the results of many studies (Greenwood & Harvey 1982; Bensch & Hasselquist 1991; Paton & Edwards 1996; Murphy 1996; Haas 1998; Doligez *et al.* 1999; Hoover 2003; Sedgwick 2004; Pasinelli *et al.* 2007; Shitikov *et al.* 2012; Shitikov *et al.* 2015). However, breeding dispersal distances were more variable for failed breeders, and also showed a trend towards greater distances for failed breeders when just considering birds which had bred for the first time (Holmes *et al.* 1996) or females alone (Greenwood & Harvey 1982; Murphy 1996; Paton & Edwards 1996; Sedgwick *et al.* 2004) (Figure 7.6). It should also be considered that some territories may change in quality between years due to grazing, flooding and military activity, making them less attractive to settling Whinchats, regardless of their breeding success the previous year.

7.6.3 Low first-year survival

First-year apparent survival was much lower than adult survival, and lower than would have been expected from comparisons of MARK apparent survival estimates from other studies of open-nesting passerine Palearctic migrant species, but were comparable with estimates from other Whinchat studies (Tables 7.5 and 7.6). Over-winter survival is commonly lower in first-year birds compared to adults (Johnson 1973; Mead 1979; Breitwisch 1989; Siriwardena *et al.* 1998; Sedgewick 2004; Menu *et al.* 2005; Newton 2006; Clark & Martin 2007; Calvertt *et al.* 2009) due to their lack of experience and lower competitive ability (Baldaccini & Bezzi 1989; Stutchbury 1994; Yong *et al.* 1998; Woodrey 2000; Marra 2000; Wiltschko & Wilschko 2003; Calvertt *et al.* 2009). It is also important to remember that estimates of first-year survival usually include post-fledging survival, which is a period of higher vulnerability (Tome & Denac 2012; Dybala *et al.* 2013) and is associated with high mortality (Tome & Denac 2012; Cox *et al.* 2014; Grüebler *et al.* 2014). A recent study on Whinchats at one site in Africa, where site fidelity is very high (Blackburn & Cresswell 2015c) suggested most first-year mortality must either be during the post-fledging period or on the first migration, as after this stage survival was found not to differ between first-years and adults (Blackburn *&* Cresswell 2015a). Part of the low first-year apparent survival for Salisbury Plain is probably due to a high proportion of first-years permanently emigrating from the study site: median natal dispersal distances were five times higher than median breeding dispersal distances. However, it is unlikely that first-years are dispersing into the immediate area surrounding the core study sites, surveys in these surrounding areas only found two first-years out of the total of 30 that returned. An additional, albeit brief, survey on the east section of Salisbury Plain also did not find any colour-ringed Whinchats. This suggests that either the first-years were dispersing longer distances from their natal site to other sites or first-year survival is especially low. Salisbury Plain is a large area of suitable Whinchat habitat surrounded by a matrix of towns and intensive farmland- far less suitable habitat. It is relatively isolated from other areas of suitable habitat and therefore, the probability of any individual returning naïve first-year Whinchats missing Salisbury Plain and returning elsewhere may be relatively high.

Natal dispersal was higher than breeding dispersal on Salisbury Plain, as is consistent with many other studies (Greenwood & Harvey 1982; Weatherhead & Forbes 1994; Lemon *et al.* 1996; Sedgwick 2004; Shitikov *et al.* 2012), including several on Whinchats (Schmidt & Hantge 1954; Bezzel & Stiel 1982; Rebstock & Maulbetsch 1988; Bastian 1992). Clues as to the reason for high natal dispersal can be found from examining the annual return rates and the ratio of adult to first-year territory holders. In 2013, when adult male return rates were particularly low, a much higher proportion of territories (72% as opposed to 30%) in the core study sites were occupied by first-years than adults compared to the other years. Therefore, it appears that higher natal dispersal is probably due to competition for territories, (e.g. Lanyon & Thompson 1986; Sherry & Holmes 1989; Lozano & lemon 1999), rather than an adaptation to promote out-breeding (Greenwood & Harvey 1982; Weatherhead & Forbes 1994; Wheelwright & Mauck 1998). Sherry & Holmes (1989) found similar results in a Redstart removal experiment, where a higher proportion of first-years re-colonised the removal sites than would be expected from the ratio of first-years to adults in the population. The large potenital pool of first-year recruits evident on Salisbury Plain also suggest that true first-year survival is not as low as it appears (Shitikov *et al*. 2014).

7.6.4 Arrival patterns and implications for breeding success

Males arrived on the breeding grounds first, then adult females on average six days later, and lastly, first-year females, a further 12 days after that. Protandry is commonly observed in territorial migrants (Morbey & Ydenberg 2001; Kokko *et al.* 2006) and has previously been observed in Whinchats (e.g. Frankiewicz 2008). Suggested causes of the differences in arrival times for different sex and age groups are: wintering at different latitudes, different morphological capabilities, differences in physical condition and flight speeds, and different sensitivity to migratory cues leading to different departure times (Coppack & Pulido 2009). For Whinchats, there is not a big difference in size between males and females (section 2.4.1) and different ages and sexes have been observed wintering in the same areas (pers. comm. Blackburn, E.), so the first two options seem unlikely to apply. Work in Nigeria on wintering Whinchats found no significant differences in body condition, territory quality, or wintering location between the different sex and age categories. However, they did find that males departed on average eight days before females, although age was not a significant determinant of departure dates (Risley *et al.* 2015). Therefore it seems possible that males exhibit a lower threshold of response to photoperiod cues (Coppack & Pulido 2009), which has so far been demonstrated under laboratory conditions for Dark-eyed Juncos (Ketterson & Nolan 1985), *Sylvia* Warblers (Terrill & Berthold 1990; Widmer 1999), Pied Flycatchers and Redstarts (Coppack & Pulido 2009), or that earlier migration in males may have an innate endogenous basis (e.g. Maggini & Bairlein 2012).

In other studies of migrant birds, the earlier arrival on the breeding grounds is associated with higher reproductive success (Møller 1994; Bensch & Hasselquist 1991; Tryjanowski *et al.*

2004; Norris *et al.* 2004; Saino *et al.* 2004; Moore *et al.* 2005; Smith & Moore 2005; Newton 2006, 2008; Møller *et al.* 2009; Reudink *et al.* 2009; Cooper *et al.* 2011). On Salisbury Plain, there were no significant reproductive advantages from settling in a territory earlier. Females who bred successfully did, on average, arrive earlier than those that did not breed successfully, but there was a high amount of overlap in the 95% confidence intervals (Figure 7.8). However, analysis of vegetation and invertebrate features of territories known to be important for breeding success (Chapter 5) found a marginally significant perch availability and invertebrate abundance interaction effect, which suggests food availability may be important (Table 7.7). In Chapter 5 the same interaction effect was observed in association with higher nestling daily survival rates. Therefore, it appears that Whinchats favour territories with higher food availability, but, it is likely that the stochastic nature of nest predation (Chapter 5) obscures any measured benefits to productivity from arriving earlier and selecting such territories. Earlier territory settlement was associated with earlier first egg dates, and thereby the potential for a longer breeding season, enabling more nesting attempts, and in particular, it may allow fledglings plenty of time to improve their foraging skills before leaving on their migratory journey, which is likely to increase their survival rates (Møller 1994; Siikamaki 1998; Visser & Verboven 1999; Naef-Daenzer *et al*. 2001). However, earlier arrival can also be costly, due to increased likelihood of harsh weather conditions during migration (Whitmore *et al.* 1977; Brown & Brown 1998, 1999 & 2000; Newton 2007), and on the breeding grounds (Møller 1994, Newton 2006: Tables 4 & 5), and reduced food availability (e.g. Nolan 1978). For example, from around 10th March to 10th April in 2013, the UK experienced prolonged cold weather and strong easterly winds that also affected northwestern Europe (www.metoffice.gov.uk) and in this year adult male return rates were lower than for other years (Table 7.6). First-year females would have avoided the worst of this weather by migrating later.

Protandry is thought to have evolved due to separate selection pressures operating on males and females, with earlier arriving males usually benefiting from superior territories, more mating opportunities and a sexual selection advantage that females do not accrue through early arrival (Morbey & Ydenbery 2001; Kokko *et al.* 2006; Saino *et al.* 2010). However, it is also interesting to consider why first-year females arrived so much later than adult females, despite leaving the wintering grounds at the same time (Risley *et al.* 2015), whilst male first-years arrived back the same time as adult males. In this Whinchat population, females appear to be the limiting resource because some unpaired males were present at sites whereas unpaired females were never seen (pers. obs.). A recent review found that male biased adult sex ratios are common in birds, especially in declining species such as Whinchats (Donald 2007). Therefore, females appear to be guaranteed a mate regardless of arrival time. First-year females will probably be outcompeted by older females for the best breeding sites and therefore might as well migrate slowly, feeding up at stopover sites and arrive in good condition, when the climate at the breeding site is more hospitable, and the aggressive battle for territories is over, rather than risking adverse conditions and using more energy and reserves to arrive earlier (Stewart *et al.* 2002; Copper *et al.* 2009).

7.6.5 Consequences for the Salisbury Plain Whinchat population

This analysis shows that adult survival is relatively high for the Salisbury Plain population and comparable to other Whinchat populations, which therefore suggests low adult non-breeding season survival is not the main factor causing the Whinchat population decline. However, first-year apparent survival was low compared to other migrant species. If this is due to high mortality, rather than purely high natal dispersal, it will lead to a slow decline in the population as the adults die and are not replaced. The Salisbury Plain population appeared stable between 2002-2013 compared to the UK as a whole (section 2.2.1), which suggests it is being buffered from the declining trend affecting the rest of the UK (Baillie *et al.* 2014), either by high reproductive output or immigration. From Chapter 5 it is evident that reproductive output in the Salisbury Plain population is not particularly high, in fact with current levels of productivity at approximately two fledglings per breeding pair and apparent first-year survival of only 20%, it would take approximately five years for an adult Whinchat to replace itself. As Whinchats generally only live for two years (Robinson 2005) it is evident that the population is not self-sustaining and therefore must be relying on immigration. This assertion is supported by data on the percentage of first-year breeders which were hatched at the site, only 24.8%, meaning 75.2% of first-year breeders immigrated into the population. Additional support for high levels of immigration comes from the high proportion of first-year breeders occupying territories in years when adult return rates were low, which suggests a large pool of potential recruits, probably drawn by the high availability of suitable breeding habitat (Chapter 4), apparently good food supplies (Chapter 5), and large existing Whinchat population at the site (Stamps 1988; Stanbury *et al.* 2005). Salisbury Plain presents a large area of suitable habitat and is relatively close to the Southern coast. Therefore, Salisbury Plain may be relatively readily settled in by immigrant Whinchats due to the broad front migration of the much larger UK population of Whinchats over the south of England en route to the upland population centres. However, with the declining trend in the UK population as a whole, the size of this recruitment pool will be decreasing and therefore a decline in future years is expected.

7.6.6 Conclusions

In general the findings in this chapter indicate that low adult survival is not limiting the Whinchat population but low first-year survival might be. A large potential pool of first-year recruits and high natal dispersal distances both suggest first-year survival is not as low as it appears. However, it is not possible from this study to determine how low true first-year survival really is. Blackburn & Cresswell's (2015a) study found evidence to suggest that most first-year mortality occurs either on the breeding grounds post-fledging or during the first migration. However, there is currently a lack of research in this area. On Salisbury Plain, adult Whinchats generally exhibited low breeding dispersal, but this trait is not true of all Whinchat populations (e.g. Shitikov *et al.* 2015) and therefore site fidelity should always be measured when estimating survival. When returning to breeding sites Whinchats show protandry, which appears to be caused by females leaving wintering areas later and first-year females migrating more slowly. It was also discovered that Whinchats show a preference for settling in territories with high invertebrate availability. This sort of information could be useful in guiding conservation management aimed at increasing Whinchat recruitment in an area.

Chapter 8: General Discussion

The signing of a resolution to petition governments to protect Whinchats at the European Whinchat symposium, Helmbrechts, Germany, May 2015

8.1 Introduction

This thesis aimed to quantify the key demographic parameters driving Whinchat population change, with a focus on the influence of factors such as predation risk, and availability of nesting and foraging habitat. From this knowledge it is possible to determine which factors are currently limiting the population, and provide insight into what the most effective conservation action might be (Caswell 2000, 2001). For example, the main difference between Salisbury Plain and other Whinchat habitats is the large area of natural grassland and the lack of agricultural intensification. As the most commonly cited cause of the current Whinchat population decline is agricultural intensification on the breeding grounds (Grötenhuis & Van 1986; Bastian 1989; Richter & Düttmann 2004; Grüebler *et al.* 2008; Broyer *et al.* 2009; Fischer *et al.* 2013), studying population trends and limitations in an area where this factor is largely absent is particularly interesting.

8.1.1 Summary of overall results

In Chapter 3, I established the habitat requirements for breeding Whinchats in agriculturally unimproved grassland. This is similar to the pre-decline habitat and therefore should avoid the possibility of a favoured habitat feature being rare or absent due to habitat change (Anteau *et al.* 2012). Whinchat breeding habitat requirements were, specifically: sheltered valleys with long, structurally diverse grass; a high density of tussocks for nesting in; and an abundance of perches to forage from. This habitat was thought to increase concealment and reduce thermoregulatory stress for both incubating females and the brood or clutch, but still minimise visual obstruction and allow easy access to food, thereby reducing predation risk while increasing foraging efficiency (Martin 1992, 1993; Davis 2005; Kim & Monaghan 2005; Whittingham & Evans 2004; Wilson *et al*. 2005; Fischer *et al.* 2013). On Salisbury Plain, the mean invertebrate abundance, biomass and order richness did not differ significantly between areas occupied and unoccupied by Whinchats, which suggests a uniformly sufficient food supply over the whole area. Using this information on habitat preferences and data on bird sightings, I was able to model the availability of suitable breeding habitat for Whinchats on Salisbury Plain. The conclusion was that breeding habitat did not appear to be limiting and that Whinchats did not appear to be vulnerable to the current degree of habitat fragmentation in the study area (Chapter 4).

As the Salisbury Plain Whinchat population did not occupy over half of the apparently suitable breeding habitat available (Chapter 4), something other than habitat availability must be limiting population expansion. To identify the life history stage at which population limitation was occurring, I quantified the key demographic parameters of productivity (Chapter 5) and survival (Chapter 7), and compared them to other studies of Whinchats. Variation in clutch size, hatching success and brood size was small within this study and similar to other studies, which suggests that parent condition was not limiting reproductive output (Högstedt 1980; Martin 1987; Forbes 1991). However, without directly measuring parental condition prior to breeding this theory cannot be verified. Surprisingly the nest survival rate and number of fledglings per pair was lower on Salisbury Plain than for other studies in similar habitat. By far the biggest cause of nest failure in this study was nocturnal predation, probably by mammals such as badgers, stoats or foxes. Meanwhile, partial brood mortality was very rare and nestling starvation appeared to be negligible. Within territories, lower breeding success was linked to the presence of moderate amounts of bare ground and grazing during the breeding season, whereas higher breeding success was linked to moderate vegetation heights, areas with greater vegetation cover or larger patches of bare ground, and higher perch abundance when invertebrate abundance was low. Additionally, territory settlement patterns of arriving Whinchats showed a marginally significant trend for females to preferentially select territories with a high abundance of perches in areas where invertebrate abundance was lower (Chapter 7). These features probably reflect enhanced nest concealment and structural obstruction from predators (Martin 1993; Winter 1999; Rangen *et al.* 1999; Lariviere & Meisser 1998; Davis 2005; Stauffer *et al*. 2011), and enable increased foraging efficiency (Oppermann 1992; Whittingham & Evans 2004; Whittingham *et al*. 2004). The effect of researcher disturbance on nest success was also explored and found not to have a significant effect on nest success in the egg phase and to cause minimal disruption to the provisioning of nestlings (Chapter 6).

Apparent survival rates of adult (older than first breeding year) and first-year (in first breeding year) Whinchats on Salisbury Plain were similar to those found in other European studies, although female survival was lower at a meadow site in Switzerland, due to agricultural mowing (Chapter 7; Müller *et al.* 2005). Compared to other studies on open nesting Palearctic migrant passerines, adult survival was high but first-year apparent survival was low (Boddy 1993, 1994 and Siriwardena *et al.* 1998). Part of this low survival may be explained by natal dispersal into areas outside the main study sites but it may also be due to genuinely higher mortality (reviewed in Newton 2006 and Calvertt *et al.* 2009): unfortunately it was not possible to separate these factors in this study.

In summary, it would appear that low breeding success due to predation and low first-year survival are the main factors limiting Whinchat population expansion on Salisbury Plain. It also appears that at current rates of productivity and first-year survival, combined with adult survival of only two years on average, the population is not self-sustaining. However, as demonstrated in section 2.2.1, the population appears to have remained stable in contrast to the UK general decline. This suggests the population is being maintained by immigration, and Whinchats from elsewhere are being drawn to the large availability of suitable breeding habitat and apparently ample food supplies.

8.1.2 Population modelling

This sort of detailed information on limiting factors and quantification of demographic parameters can be used to create a population model. Such a model can then project the population trend and determine which demographic parameters the population growth rate is most sensitive to via a ‘prospective analysis’, and which have caused most of the past variation in population growth rate via a ‘retrospective analysis’ (Caswell 2001; Fletcher *et al*. 2006; Wright *et al*. 2009; Sim *et al.* 2011; Hastings & Gross 2012; Grüebler *et al.* 2014). Interpreting the model output, alongside the other information on limiting environmental factors and comparisons to other populations, can help to guide conservation management decisions (Kroon *et al.* 2000; Caswell 2001; Hoekmann *et al* 2006; Klok *et al.* 2009; de Sim *et al.* 2011). Here, I end the thesis by bringing together information from the previous chapters to aid in the building and interpretation of a population model for the Whinchats on Salisbury Plain. This model will predict the future population trend in the Salisbury Plain Whinchat population based on the demographic rates of breeding success, adult survival and first-year survival from 2011 to 2014. Observed population trends from 2011 to 2014 will be compared to the predicted population trends for each year to assess the accuracy of the model and the influence of outside factors, such as immigration. The sensitivity of the projected population growth rate to relative change in each demographic rate will be explored in a ‘prospective analysis’. A’ retrospective analysis’ will also be conducted to determine how much past temporal variaition in each demographic rate has contributed to temporal variaition in the population growth rate (Caswell 2000). Based on the results of the previous chapters, I predict that the population growth rate will be less than one, indicating a declining population. I would also predict that the predicted population decline will be greater than the observed population decline due to a high influx of immigrants.

8.2 Methods

8.2.1 Study site, population census, breeding success and survival

Details of the study site are given in section 2.2. The study area was regularly surveyed from 2010 to 2014 (section 7.3.3). As the size of the study area varied between years, the density of breeding pairs was calculated annually and used to give an estimate of the population size for each year. Details on nest monitoring are given in section 2.3 and section 5.3.3. For the purposes of the population model, the mean number of fledglings per pair over the whole season (for 2012 – 2014) was used as a measure of productivity. If a pair moved outside the study area for a re-nesting attempt this would not have been included, but Grüebler *et al.* (2015) found that parents rarely exhibit within season dispersal if the habitat surrounding the nest remained unchanged (i.e. not grazed or mown). In this study, the habitat surrounding nests remained unchanged in the vast majority of cases which suggests that changing territories within a season to re-nest is a rare event. Details on the estimates of survival for each age class are given in section 7.5.

8.3 Data analysis

8.3.1 Observed and expected population growth rate

There are two type of population growth commonly reported: the realised population growth (λ_r) and the projected population growth (λ).

For the realised population growth rate: $\lambda_r = \frac{N_{t+1}}{N_t}$ *(eqn 1)*

where N_t = the population size at the beginning of the breeding season in year *t* (Cooch & White 2014).

The observed population size was compared to the population size predicted from the survival and breeding success rates the previous year *(eqn 2).*

$$N_{t+1} = N_t \times ((P_{juv} \times F) + P_{ad}) \qquad \textit{(eqn 2)}$$

where N_t = the population size in year *t*, P_{juv} = first-year survival from year *t* to year *t +1*, P_{ad} = adult survival from year *t* to year *t+1* and F = breeding success measured as the number of fledglings per individual breeding Whinchat per breeding season, calculated as 0.5 × the number of fledglings per pair per season (adapted from a population model in Sim *et al.* 2011). The adult and first-year survival rates did not vary significantly between years and therefore remain the same despite the value of *t*. This model does not include immigration into the population but permanent emigration from the population should be accounted for in the MARK survival estimate (Lebreton *et al.* 1992). Any discrepancies between predicted and actual values for population growth rate will be due to stochastic variation in the demographic parameters and immigration into the population.

8.3.2 Projected population growth rate

The projected population growth rate is a measure of the 'per capita growth rate' that is eventually reached, assuming the same yearly demographic parameters for survival of each stage class and for breeding success. It is used to project what will happen to the population in the future (Hastings & Gross 2012). Within each stage class, in this case Whinchats in their first-year of life and adults (older than their first year), there is assumed to be little variation in the probability of surviving and reproducing (Akçakaya 2000). Only two stage classes were used here due to the limited data available and the relatively short life span of Whinchats. The projected population growth rate is calculated as the dominant eigenvalue *(eqn 3)* of the projection matrix, a stage structured matrix of the population demographic parameters representing the life cycle of an individual in the population (Figure 8.1; Benton & Grant 1999; Caswell 2001).

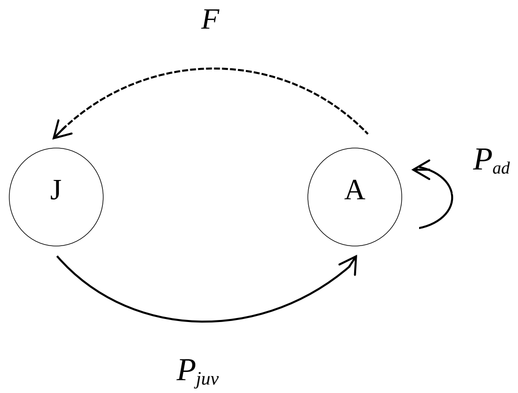


Figure 8.1. The circles represent the stage classes, J = First-year of life, A = Adults. P_{juv} is the probability of a fledgling surviving through to its first breeding year, P_{ad} is the probability of an adult (older than first breeding year) surviving. *F* is the breeding success, the number of fledglings produced per adult from one breeding season. The arrows represent the contribution of an average individual in one class to the number of individuals in the class one time step later- either through surviving or reproducing (Hastings & Gross 2012).

This life cycle translates to give the following matrix of demographic parameters, where the columns represent all contributions by an average individual to the population (Hastings & Gross 2012). For adults, this is their survival and breeding success and for fledglings, this is just their survival, as they will not reproduce until they are approximately one year old (Cramp 1988). The rows represent all the contributions towards the numbers of individuals in a particular class after one age step, so breeding success represents the contribution towards fledglings, and adult and first-year survival represent the contributions towards the adult stage (Hastings & Gross 2012).

$$A = \begin{bmatrix} 0 & F \\ P_{juv} & P_{ad} \end{bmatrix}$$

The dominant eigenvalue (λ) for this population matrix was calculated by solving the following equation:

$Ax = \lambda x$ *(eqn 3)*

With the steps below*:*

$$\begin{bmatrix} 0 & F \\ P_{juv} & P_{ad} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} \lambda x_1 \\ \lambda x_2 \end{bmatrix}$$

Is solved to give 2 simultaneous equations:

$\lambda x_1 = F x_2$ *(1)*

$\lambda x_2 = P_{juv} x_1 + P_{ad} x_1$ *(2)*

Which can then be solved for λ as follows:

$\lambda^2 - P_{ad} - P_{juv} = 0$

$$\lambda = \frac{P_{ad} \pm \sqrt{{P_{ad}}^2 + 4P_{juv}}}{2}$$

The 95% confidence intervals for λ were calculated from 1000 bootstrap resamples of the projection matrix, assuming a normal distribution for each demographic parameter based on the means and variances from the observed data, and calculating λ for each of these matrices. The 95% confidence intervals were the 2.5% and 97.5% quantiles from the distribution of λ.

8.3.3 Basic and integrated elasticities

To determine which demographic parameter λ is most sensitive to, the elasticities for the population matrix were calculated using the 'popbio tool' (Stubben & Milligan 2007) in R version 2.3.1 (R Development Core Team 2014). The elasticity calculates the proportional change in the population growth rate when one demographic rate is altered but the others are held constant (de Kroon *et al.* 1986; de Kroon *et al.* 2000; Caswell 2001). Elasticites for each demographic rate in the projection matrix will sum to one (de Kroon *et al.* 1986; Messerton-Gibbons 1993). The elasticity for an element of the matrix, $a_{ij,}$ is given by:

$$\frac{\partial \, log \, \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \; \frac{\partial \lambda}{\partial a_{ij}} \qquad \textit{(eqn 4)}$$

where ∂ is the partial differential (Caswell *et al.* 1984; de Kroon *et al.* 1986).

The integrated elasticities (IE) (*eqn 5*) are an extension of basic elasticities, they quantify the total effect of a specific demographic rate on λ, including direct and indirect effects, by accounting for covariance between demographic parameters (van Tienderen 1995). Integrated elasticities (IE) ensure the population consequences of variation in a demographic rate are predicted accurately (van Tienderen 1995; Saether & Bakke 2000; Reid *et al.* 2004; Coulson *et al*. 2005; Sim *et al*. 2011), as co-variation between demographic parameters is very common (Caswell 2000). The integrated elasticities are calculated by the following equation:

$$\mathrm{IE}_i = \sum_j r_{ij} \times e_j \times \frac{CV_j}{CV_i} \qquad \textit{(eqn 5)}$$

(van Tienderen 1995; Saether & Bakke 2000), where *e* = elasticity, CV = coefficient of variation for a demographic rate and r_{ij} is the correlation coefficient between the time series of two demographic parameters, matrix elements *i* and *j*. Integrated elasticities can be positive or negative, a negative value means that any positive effect of the demographic rate on population growth is counteracted by negative correlations with the other demographic parameters (van Tienderen 1995).

With only four years of data for all the necessary demographic parameters (Tables 8.1 and 8.2), the integrated elasticity calculations may not be very reliable for this study. Additionally, breeding success (Chapter 5) and apparent survival rates for adults and first-years did not vary significantly between years (Chapter 7). This meant MARK calculated survival rates were the same for all years. Forcing MARK to give different yearly survival estimates by including year in the model gave estimates with large overlapping confidence intervals for each year and the pattern of change over years from these estimates did not match the observed pattern of change from the percentage of returning colour ringed Whinchats (Chapter 7). Therefore, the proportions of returning colour-ringed adults and first-years, out of the number known to be alive the previous year (return rate) were used for calculating the integrated elasticities to get an idea of the effect of correlations between demographic parameters and determine how robust the conclusions based on the basic elasticities were likely to be (Sim *et al.* 2011). The correlation between breeding success from 2010 – 2013 and adult and first-year return rates from 2011 – 2014 was used, as it was expected that the number of fledglings produced would affect survival the following year (Sim *et al.* 2011). For correlations in survival rates, the correlation between adult return rates from 2011 – 2014 and first year return rates from 2011 – 2014 was used. Using return rates, rather than MARK estimated apparent survival rates, will underestimate the survival rates, as the recapture probability is not accounted for. However, the recapture probability did not vary significantly between years in this study and survey effort was relatively high and constant in all years (Chapter 7). Therefore, variation in return rates should still reflect temporal variation in adult survival. Despite this, the results of the integrated elasticities need to be interpreted cautiously as the four years of data from this study were not sufficient to accurately predict temporal variation in survival.

Predicting the projected population growth rate and how sensitive it is to change in a demographic rate (the elasticities) is called '*prospective analysis'* and is useful for determining how a population may respond to a proposed conservation management action or environmental change (e.g. Jenouvrier *et al*. 2005; Fletcher *et al*. 2006). These predictions are independent of observed previous variation in demographic parameters (Caswell 2000). The contribution of temporal variation in each demographic rate to temporal variation in the realised population growth rate was also calculated using equations 6 and 7. This is called the '*retrospective analysis'* and is useful for determining causes of past variations in the population growth rate (Caswell 2000).

Just accounting for direct effects, the variation in the realised population growth rate is:

$$\mathrm{Var}\,(\lambda) = \sum_x e_x^2\ CV_x^2 \qquad \textit{(eqn 6a)}$$

Or, when accounting for direct and indirect effects:

$$\mathrm{Var}\,(\lambda) = \sum_x IE_x^2\ CV_x^2 \qquad \textit{(eqn 6b)}$$

So the proportional contribution of each matrix element to the total variation in the realised population growth rate is:

$$X_x = e_x^2 CV_x^2 / \mathrm{Var}\,(\lambda) \qquad \textit{(eqn 7a)}$$

or

$$X_x = IE_x^2 CV_x^2 / \mathrm{Var}\,(\lambda) \qquad \textit{(eqn 7b)}$$

(Horvitz *et al.* 1997; Caswell 2001; Sim *et al*. 2011).

8.4 Results

8.4.1 Comparisons of vital rates between years and to other studies

Clutch size, brood size, daily nest survival rate (DSR) and number of fledglings per pair did not differ significantly between years (Table 8.1, ANOVA: $p > 0.05$, for DSR see Chapter 5). Annual estimates of apparent survival for adults and first-years also did not differ significantly between years (Table 8.2 and section 7.5).

Table 8.1. Yearly estimates for mean clutch size, brood size and Daily Survival Rate of final attempt nests (DSR) using the Mayfield method (Mayfield 1975), with +/- one standard error (SE) (Johnson 1979), from breeding pairs of Whinchat on Salisbury Plain. The sample sizes for each year are shown in brackets after the date. Overall estimates using data from the years 2012 – 2014, when nest monitoring effort was most intensive (section 5.3.3), are also included.

Year	Clutch Size	Brood Size	DSR	Fledglings per pair
2010	5.80 +/- 0.20 (5)	5.00 +/- 0.52 (6)	95.50 +/- 1.97 (11)	2.73 +/- 0.83 (11)
2011	5.75 +/- 0.25(4)	5.33 +/- 0.33 (9)	96.57 +/- 1.38 (15)	3.20 +/- 0.73 (15)
2012	5.53 +/- 0.13 (59)	5.38 +/- 0.18 (24)	95.81 +/- 0.82 (51)	2.63 +/- 0.38 (49)
2013	5.56 +/- 0.13 (68)	4.94 +/- 0.26 (18)	95.14 +/- 0.88 (53)	1.89 +/- 0.39 (47)
2014	5.51 +/- 0.14 (57)	5.32 +/- 0.75 (19)	94.62 +/- 0.94 (50)	2.02 +/- 0.38 (50)
Overall using (2012-2014)	**5.53 +/- 0.08**	**5.19 +/- 0.12**	**95.23 +/- 0.50**	**2.18 +/- 0.22**

Table 8.2. Yearly apparent survival estimates +/- 1 SE for adult (older than first breeding year) and first-year (in first breeding year) Whinchats (n = 396), with the percentages of returning colour-ringed birds for each year. The sample sizes for the return rates are in brackets next to the value for each year. See Chapter 7 for more details.

Year	Adult apparent survival	First-year apparent survival	Proportion returning colour-ringed adults	Proportion returning colour-ringed first-years
2010	NA	NA	NA	NA
2011	0.52 +/- 0.06	0.20 +/- 0.04	0.39 (23)	0.11 (35)
2012	0.52 +/- 0.06	0.20 +/- 0.04	0.41 (34)	0.10 (39)
2013	0.52 +/- 0.06	0.20 +/- 0.04	0.29 (58)	0.14 (129)
2014	0.52 +/- 0.06	0.20 +/- 0.04	0.31 (90)	0.09 (89)
Overall	**0.52 +/- 0.06**	**0.20 +/- 0.04**	**0.35 +/- 0.029**	**0.11 +/- 0.011**

8.4.2 Observed and predicted population growth rate

The observed population trend closely matched the predicted population trend for the years 2011 – 2013 but in 2014 it was significantly higher than expected (Figure 8.2). From 2010 to 2014, the observed population trend showed a decline of about 30% while the predicted population trend suggested a decline of approximately 50% from 2011 to 2014. It appears, therefore, that the population decline is buffered to some extent by immigration into the population.

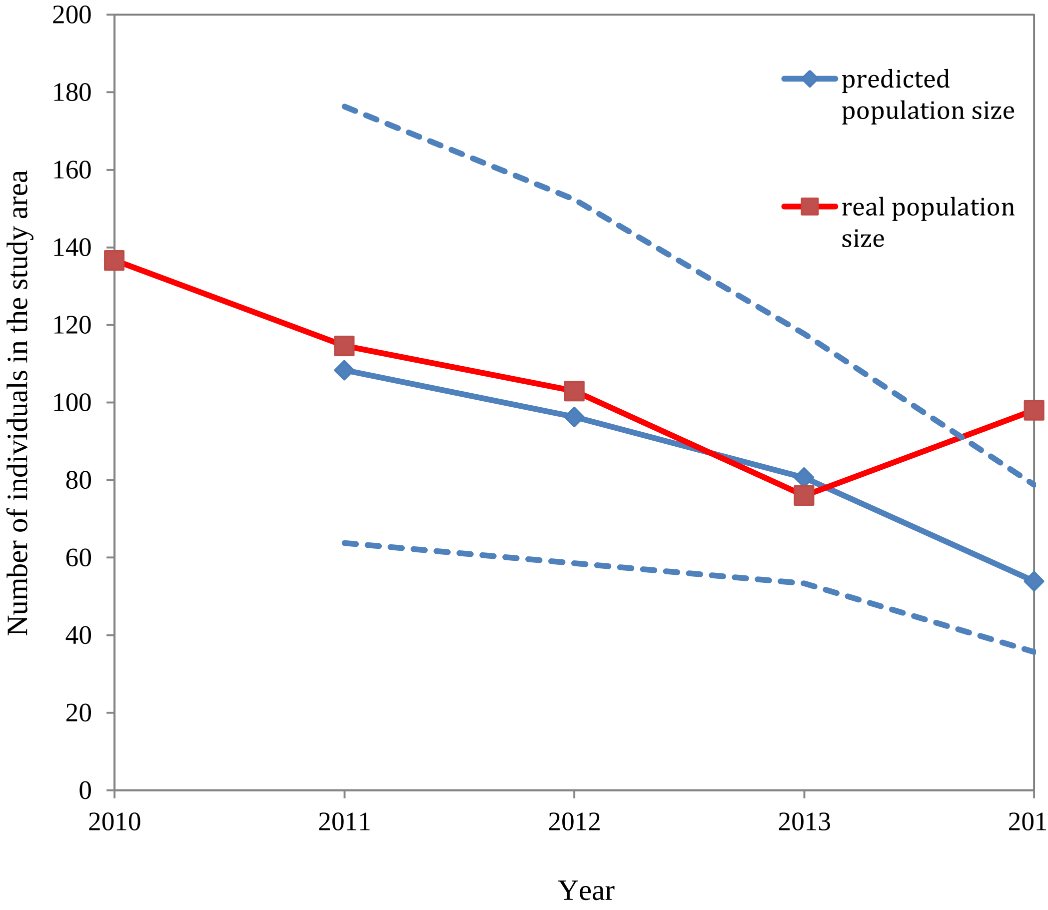


Figure 8.2. The observed population trend between 2010 – 2014 (red line) and the predicted trend (blue solid line) using the equation: $N_{t+1} = N_t \times ((P_{juv} \times F) + P_{ad})$, where N_t = the population size in year t , P_{juv} = first-year survival from year t to year $t+1$, P_{ad} = adult survival in year t to year $t+1$ and F = the number of fledglings per breeding individual in year t. The dotted blue lines are the 95% confidence intervals for the estimate, using the lower 95% confidence interval for each demographic rate for the lower line and the upper 95% confidence interval for each demographic rate for the upper line.

8.4.3 Prospective and retrospective analysis

The projection matrix (Caswell 2001) is:

$$A = \begin{bmatrix} 0 & F \\ P_{juv} & P_{ad} \end{bmatrix} = \begin{bmatrix} 0 & 1.09 \\ 0.20 & 0.52 \end{bmatrix}$$

Where, P_{juv} = first-year apparent survival, P_{ad} = adult apparent survival and F = the mean number of fledglings per individual breeding Whinchat between 2012 – 2014.

This gives the dominant eigenvalue of λ = 0.794 (95% CI: 0.655 – 0.918), meaning that under time invariance the mean population is projected to decline by 20.6% per year. The projected population growth rate (λ) was almost twice as sensitive to change in adult survival than to changes in first-year survival and breeding success (Table 8.3). To deliver a stable population ($\lambda = 1$), breeding success or first-year apparent survival would have to more than double, or adult survival would need to be approximately 1.5 times higher. To reverse the current population decline, these parameters would need to increase to even higher values.

Breeding success was positively correlated to adult and first-year return rates the following year, and adult return rates were negatively correlated to first year return rates from the same year (Table 8.4). Using return rates for adults and first-years, as opposed to apparent survival estimates, did not change the qualitative pattern of the elasticities. When accounting for indirect effects (via IE), the projected population growth rate was still most sensitive to changes in adult return rates. However, it was more sensitive to changes in breeding success than changes in first-year return rates. The projected population growth rate was 11% less sensitive to changes in breeding success compared to adult return rates and 55% less sensitive to changes in first year return rates than adult return rates.

When examining only direct effects through elasticities, most of the temporal variation in the projected population growth rate was explained by temporal variation in the adult return rates, closely followed by breeding success (Table 8.4). These variables together explained almost 80% of temporal variation, with the remainder explained by variation in first-year return rates. However, when incorporating indirect effects due to correlations between the demographic parameters, the majority of variance in the projected population growth rate was explained by variance in breeding success, with less than 10% explained by variance in first-year return rate.

Table 8.3. For each matrix demographic rate: the mean values (+/- 1 SE), the elasticities using these mean values and the value necessary for λ to equal 1 if all other demographic parameters of the projection matrix stayed the same.

Variable	Mean	e	Mean for $\lambda = 1$
Breeding Success (F)	1.09 +/- 0.22	0.257	2.40
Adult survival (P_{ad})	0.52 +/- 0.04	0.487	0.79
First-year survival (P_{juv})	0.20 +/- 0.04	0.257	0.44

Table 8.4. The correlation matrix, mean values, standard deviation (SD), coefficient of variance (CV) and integrated elasticities (IE) for each demographic parameter and the temporal variation in the population growth rate (λ) explained by each parameter including direct effects only (e^2CV^2) as a proportion of the total temporal variation in growth rate (Xe) and direct and indirect effects (IE^2CV^2 and as a proportion = X_{IE}). The proportion of annually returning colour-ringed adults and first-year Whinchats, out of the number of colour ringed Whinchats known to be in the population the previous year (return rate), was used to examine temporal correlations, rather than apparent survival estimates. F = breeding success (number of fledglings per individual), A_r = proportion of returning colour ringed adults, J_r = proportion of returning colour ringed first-years.

	Correlation matrix											
	F	A_r	J_r	Mean	SD	CV	e	e^2CV^2	X_e	IE	IE^2CV^2	X_{IE}
F	1	0.72	0.33	1.25	0.54	0.22	0.285	0.0050	0.38	0.566	0.020	0.58
A_r	0.72	1	-0.33	0.35	0.06	0.17	0.430	0.0051	0.39	0.631	0.011	0.33
J_r	0.33	-0.33	1	0.11	0.02	0.19	0.285	0.0029	0.23	0.284	0.003	0.09

8.5 Discussion

At current levels of breeding success, adult apparent survival and first-year apparent survival, and assuming no change in these values in future years, the Salisbury Plain Whinchat population is predicted to decline by approximately 20% per annum. Prospective analysis suggests that improving adult survival would have the most benefit on the population growth rate (Table 8.3), although considering the currently high adult survival compared to similar species (Chapter 7), this may not be possible. When indirect effects of vital rates are accounted for, breeding success is the second most influential parameter (Table 8.4), which suggests this life history phase may be a better target for the implementation of management actions. Despite the low level of first-year survival compared to other open nesting Palearctic migrants (Boddy 1993, 1994; Siriwardena *et al.* 1998), the projected population growth rate is least sensitive to variations in this demographic rate, therefore management actions focused on improving first-year survival are likely to be less effective in the long term (Caswell 2000; Caswell 2001). With so few years of data, it is not possible to be certain which demographic rate was responsible for most of the observed temporal variation in the realised population growth rate. However, the analysis suggests that variation in breeding success and adult return rates are likely to have caused the majority of variation in the population growth rate, with first-year return rates having the least influence. From 2010 to 2014, the observed population trend for the study area showed a decline of about 30%. The predicted population size, based on yearly values for demographic parameters, closely matched the observed population size for all years except 2014 (Figure 8.2). This suggests that emigration from the study sites matched immigration into the study sites for 2011-2013, but in 2014, net immigration was greater than in previous years, thereby partly buffering against the projected decline. However, with the decline in the UK Whinchat population as a whole (Baillie *et al*. 2014), it is unlikely that immigration will be able to buffer the Salisbury Plain population from further decline in the future and therefore an accelerating decline is expected over the next decade.

8.5.1 Population trend

The deviation in the observed and predicted Whinchat study population size in 2014 implies immigration is buffering against the declining population trend. Field observations found that there was immigration into the population in the other years too, but there was also some emigration to areas outside the core study sites. These emigrants would not have been included in the breeding pair census but were included for calculating apparent survival (section 7.3.3). Additionally, MARK apparent survival estimates account for any missed birds in study areas and for non-permanent emigration to areas outside the survey area via the recapture probability, and incorporate this into the apparent survival estimate (Lebreton *et al.* 1992). Therefore, in the previous years it appears that emigration, probably to nearby surrounding areas, approximately balanced immigration into the population but in 2014, net immigration was higher.

At current levels of breeding success, adult survival and first-year survival, the Whinchat study population is not self-sustaining, and has declined by 30% over the last four years. The strength of this decline has been partly buffered by immigration, and this probably also explains the apparent lack of a significant population decline in the Salisbury Plain Whinchat population as a whole from 2002 to 2012 (section 2.2.1). Salisbury Plain is the largest area of unimproved grassland in northwest Europe (Ash & Toynton 2000) and, as found in previous Chapters, there appears to be plentiful suitable breeding habitat (Chapter 4) and food (Chapter 3 & Chapter 5). These factors are likely to have made Salisbury Plain an attractive location for immigrants. Additionally, the large population of Whinchats on Salisbury Plain may have attracted immigrants through conspecific attraction (Stamps 1988; Chapter 4). The relative stability of the Salisbury Plain population could also be explained by the UK population as a whole contracting to concentrate in the core breeding sites, as often happens in declining populations, probably due to stochastic extinction and lack of re-colonisation in sites with less prevalent populations (Donald & Greenwood 2001). The dispersal behaviour of whinchats on the study site would suggest the immigrants are mostly first-year Whinchats, as adult breeding dispersal distances were much smaller than natal dispersal distances, and breeding failure did not significantly affect dispersal distance (Chapter 7). Of the known first-years occupying territories in the study site, 75.2% were immigrants (pers. obs.). However, the boundaries of the study sites were based on logistics, and form part of a larger area of habitat and a larger population of Whinchats (section 2.1). Immigration and dispersal will also depend, to an extent, on the size of the study area: in a larger study area, more of the suitable habitat will be encompassed and, therefore, dispersal and immigration will appear lower (Lambrechts *et al*. 2000; Schaub *et al*. 2013).

Salisbury Plain appears to be a ‘sink’ population (Müller *et al.* 2005; Pulliam 1988, 1996), which relies on immigration to be maintained. There are various other examples of populations maintaining stability through immigration (Fletcher *et al*. 2006; Wilson & Arcese 2008; Schaub *et al.* 2010, 2012, 2013) but in declining species, the supply of immigrants will eventually run out and these sink populations will also decline in the long term. The fact that even an apparently high quality habitat, without agricultural intensification, can act as a sink has implications for conservation management more widely. The high quality habitat at Salisbury Plain probably helps to attract immigrants into the population, but the same high quality habitat is also probably the reason for the high predation rates, as the site is also able to support a large abundance and diversity of predators (Imber Conservation Group pers. comm.). Other studies have also found lower breeding success in apparently high quality sites, compared to more degraded areas, due to higher predation in the high quality sites (e.g. for California Towhees, Purcell & Verner 1998 and Sage Sparrows, Misenhelter & Rotenberry 2000). This shows the importance of detailed population studies, including assessments of nest survival, and the danger of relying purely on census counts as an indication for population stability (Green 1995; Winter *et al.* 2006).

8.5.2 Adult survival may not be the best target for conservation management

As the population growth rate is most sensitive to changes in adult survival, conservation management plans purely based on the prospective analysis should target factors that affect adult survival (Caswell 2001). This interpretation, however, should also consider the constraints on each demographic parameter as well as the potential for management action to change them (de Kroon *et al.* 2000; Hoekman *et al.* 2006; Clark & Martin 2007; Klok *et al.* 2009; Norris & McCulloch 2003; Ehrlén *et al.* 2001; Wemmer *et al.* 2001; Calvert *et al.* 2009). The annual adult apparent survival rate for the Salisbury Plain Whinchats would need to be 0.79 (Table 8.3) to achieve population stability in the absence of change in the other demographic parameters. This level is outside the range of survival estimates for 31 farmland and grassland passerine species (Siriwardena *et al.* 1998) and outside the range of apparent survival estimates for other open nesting Palearctic migrants (Boddy 1993, 1994 & Siriwardena *et al.* 1998) and, therefore, unlikely to be achievable through management. For migrant birds, it is currently thought that most adult mortality occurs during migration (Sillett & Holmes 2002; Newton 2006; Calvert *et al.* 2009; Klaassen *et al.* 2014; Blackburn & Cresswell 2015a), especially during poor weather events (Whitmore 1977; Newton 2007), and with large numbers also lost to anthropogenic causes such as hunting and collisions with man-made structures (reviewed in Newton 2007, 2008 and Vickery *et al.* 2014). However, data are currently lacking for this phase of the life-cycle (Newton 2006, 2007, 2008; Calvert *et al.* 2009; Vickery *et al.* 2014), which makes implementing effective conservation action difficult. In the case of Salisbury Plain, breeding season mortality was considered to be low as most colour-ringed Whinchats were re-sighted throughout the season.

Comparative studies, covering a wide variety of migrants, have also found population growth to be most sensitive to adult survival (Pfister 1998; Saether & Bakke 2000; reviewed in Calvertt *et al.* 2009). Generally, adult survival is the most influential parameter affecting growth rate for species with high adult survival and low reproductive rates, whereas for species with low adult survival and high reproductive rates, breeding success is most important (Saether & Bakke 2000; Heppell *et al.* 2000; Stahl & Oli 2006; Clark & Martin 2007). Long distance migrants have been found to produce fewer eggs per year than similar sized short-distance migrants and residents (Brudere & Salewski 2009), which suggests a selection pressure to compensate for low or unpredictable reproductive output by increasing survival and consequently the number of reproductive attempts through life (Roff 1992; Clark & Martin 2007). It appears, therefore, that adult survival is an important consideration in trying the halt declines in migrants. For some populations it may be possible to increase adult survival, for example, by introducing legislation to reduce hunting (Newton 2004a, 2008), or changing the mowing regime to avoid killing incubating females (e.g. Green *et al.* 1997; Grüebler *et al.* 2008). However, as seen here with Whinchats and in other studies (e.g. for waders - Klok *et al.* 2009; Seychelles Magpie Robins - Norris & McCulloch 2003, Willow Tits – Lampila *et al.* 2006), it may not always be possible to increase adult survival and in these cases we need to instead focus on a parameter we can increase, while ensuring no management or environmental changes that will increase adult mortality.

8.5.3 Targeting breeding success may be more effective

Conservation management action would probably be most effective if it concentrated on increasing breeding success. By far the largest cause of nest loss on Salisbury Plain is nocturnal predation (Chapter 5). There is evidence that populations of some predators, such as foxes and crows, have increased over the last few decades (Andren 1992; Panek & Bresinski 2002; Newton 2004b; Langgemach & Bellebaum 2005) and this increase is thought to be a key contributor to declines in ground nesting meadow birds in Europe (Roodbergen *et al*. 2012; Malpas *et al.* 2013a). Possible ways to reduce predation risk include management action to encourage the preferred vegetation structure to reduce potential predation (Martin 1993; Lariviere & Meisser 1998; Winter 1999; Rangen *et al.* 1999; Davis 2005; Stauffer *et al*. 2011;), and enhance foraging efficiency (Chapter 5; Martin 1987; Butler & Gillings 2004; Whittingham & Evans 2004; Whittingham *et al.* 2004). This would mainly revolve around a suitable grazing regime, which avoids excessive defoliation in the breeding season (Lariviere & Meisser 1998; Fondell & Ball 2004; Sutter & Ritchison 2005), but which promotes structural diversity for foraging (Murray *et al.* in prep). On Salisbury Plain, moderate disturbance by military training activity also serves this function.

It may also be worth considering more drastic action to improve nest success in some areas, such as regular predator control. Predator control was successfully implemented on part of Salisbury Plain, from 1984 to 1990, to increase grey partridge numbers (Tapper *et al.* 1996). However, results can be mixed depending on the main predator, the species of concern and the time frame of the experiment (Gibbons *et al.* 2007). A review in Newton (1998), and updated by Nordström (2003), found 15 out of 25 studies implementing predator control increased numbers of breeders the following year (Gibbons *et al.* 2007). Many studies, however, have found that it was not effective in the long term, especially for declining populations (Côté & Sutherland 1997; Gibbons *et al.* 2007) and, when predator control ceased, the predator population quickly returned to former levels (Newton 1998). Another option that could be implemented if the Whinchat population declined to critical levels is predator exclusion, using fences or cages to exclude mammalian predators, while allowing free movement of parents and fledglings (Patterson 1977; Rimmer & Deblinger 1992; Jackson 2001; Johnson & Oring 2002; Murphy *et al.* 2003a; Isaksson *et al.* 2007; reviewed in Gibbons *et al.* 2007; Malpas *et al.* 2013b). Predator exclusion measures are usually effective (Patterson 1967; Rimmer & Deblinger 1992; Johnson & Oring 2002; Jackson 2001; Murphy *et al.* 2003a, 2003b; Isaksson *et al.* 2007; Boschert 2008; Malpas *et al.* 2013b; but see Mabee & Estelle 2000; Pearson *et al.* 2012) but there is some risk of increased predation of incubating adults (Johnson & Oring 2002; Murphy *et al.* 2003b; Isaksson *et al.* 2007) and it would not be possible to implement this measure on more than a local scale. On Salisbury Plain, nests would have to be individually protected, as large scale fences would interfere with army training. A small scale trial of this method to assess its effectiveness would be necessary before wider implementation.

For long distance migrants, improving breeding success is often a more feasible option than improving adult or first year survival, as breeding success is easier to monitor directly and experimentally assess potential limitations than survival (Sillett & Holmes 2002; Calvertt *et al.* 2009). For example there are various studies assessing environmental influences on breeding success: for the effects of food limitation see studies reviewed in Martin (1987), for predation see Tapper *et al.* (1996), for a combination of food limitation and predation see Zanette *et al.* (2006ab), for agricultural activity see Sutter & Ritchison (2005) and Grüebler *et al.* (2015). Reproductive success is, however, often one of the most variable and least sensitive parameters for the population growth rate in birds (Pfister 1998; Saether & Bakke 2000), especially in species with high adult survival and low reproductive rates (Stahl & Oli 2006; Clark & Martin 2007). Increased reproductive success may be offset by increased density dependent mortality at stopover sites on the wintering grounds and may not actually translate into and an increased breeding population the following year (Newton 2004a; 2008). Population demography models can help to predict the potential impact of increasing a demographic rate (Caswell 2001) but well-designed monitoring and evaluation is critical to assess how effective newly implemented conservation action is. For example Kentie *et al*. (2015) found that paying farmers to leave unmown patches of up to 5 m diameter around nests in mown fields did not improve nest success compared to mowing the whole field as usual and therefore payments for later mowing would be a better use of resources.

8.5.4 Low first-year survival

First-year apparent survival had the smallest effect on the projected population growth rate when accounting for indirect effects due to correlations between demographic parameters. This measure is actually an amalgamation of several different life-history phases: post-fledging survival, survival during the first autumn migration, survival on the wintering grounds, survival on the first spring migration and natal philopatry. As reported in Chapter 7, natal philopatry is lower than breeding site fidelity, so actual first year survival may be higher than estimated in this study. Separating out these influences is logistically very difficult to achieve, but would be useful to improve our understanding of Whinchat population dynamics to ensure the most effective conservation actions are implemented (Newton 2008; Calvert *et al*. 2009; Sim *et al.* 2011; Grüebler *et al.* 2014). A recent paper by Blackburn & Cresswell (2015a) measured annual survival in Whinchats from September, and found no significant difference in survival rates between adults and first-years, which suggests that any true low first-year survival must be due to mortality in the post-fledging period or on the first migration.

The post-fledging period is a time of high mortality due to the inexperience of fledglings and their ineffective predator escape strategies (Krementz *et al.* 1989; Sullivan 1989; Anders *et al.* 1997; Sillett & Holmes 2002; Tome & Denac 2012; Cox *et al.* 2014; Grüebler *et al.* 2014). On Salisbury Plain, a pilot study in 2014 aimed to measure post-fledging mortality through colour ring re-sighting, and found 53% of fledglings were known to be alive seven days after fledgling (Atkinson *et al.* 2015); however, this study was limited by an inability to determine if an unseen fledgling was actually dead or just ‘out of sight’ in the long vegetation. Although not without its own problems (Kershner *et al.* 2004; Mattson *et al.* 2006; Fisher *et al*. 2010; Barron *et al*. 2010), radio-tracking could be a useful to investigate the post-fledging period. So far, only one study has radio-tracked fledgling Whinchats. Tome & Denac (2012) found the probability of surviving for a month after fledging to be 0.52, dropping to 0.35 when extrapolating to the beginning of the autumn migration. If post-fledging survival is similar on Salisbury Plain, it would suggest that first-year migratory and over-winter survival was equal to, or even higher, than adults. However, in Tome & Denac's study some mortality was due to mowing, which does not occur on Salisbury Plain (Ash *et al*. 2011), but which can be avoided elsewhere by delaying mowing activity (Tome & Denac 2012; Broyer 2007, 2009; Strebel *et al.* 2015). On Salisbury Plain, it seems likely that most post-fledging mortality is due to predation (Atkinson *et al.* 2015) and therefore predator control may be able to reduce post-fledging mortality (Keedwell 2003; Gibbons *et al*. 2007).

Survival is generally thought to be lower in first-years than in adults during migration (Sillett & Holmes 2002; Calvertt *et al.* 2009) due to lack of experience (Baldaccini & Bezzi 1989; Woodrey 2000; Wiltschko & Wilschko 2003) and reduced competitive ability, compared to adults, at stopover sites (Yong *et al.* 1998; Woodrey 2000). These factors also make them more vulnerable to human induced changes in habitat or climate which reduce food availability and increase predation pressure (Newton 2006, 2008). However, conservation management action targeting the migratory route or the wintering grounds is more difficult to implement than changes during the breeding season. Difficulties include lack of knowledge on locations of wintering birds and migratory routes, but also potential conflicts with residents and businesses in developing countries (Mabogunje 1995; Newmark & Houge 2000; Sanderson *et al*. 2006; Newton 2004a, 2008; Calvert *et al*. 2009; Vickery *et al*. 2014). Limitations on these two life history phases are currently poorly understood, with only one main study group working on wintering Whinchats in part of their range in Nigeria (Blackburn, E. pers. comm.), and only one study published so far on Whinchats at a migratory stopover site (Koce & Denac 2010). Geolocators were fitted to individuals from one population of Whinchats wintering in Nigeria (Blackburn, E. pers. comm.) but for the majority of the population the migratory route is not yet known (Vickery *et al*. 2014).

In general, the first-year of life is a period of high mortality for all migrants (Johnson 1973; Mead 1979; Breitwisch 1989; Siriwardena *et al.* 1998; Sedgewick 2004; Menu *et al.* 2005; Newton 2006; Clark & Martin 2007; Calvertt *et al.* 2009), but despite the potential importance of this life history phase, detailed knowledge on limitations to first-year survival, or even whether factors on the breeding or wintering grounds have the most impact, are lacking for many species (Tarof *et al*. 2011; Redmond & Murphy 2012; Sim *et al.* 2013; Grüebler *et al*. 2014). Where studies have quantified these components of first year survival the results differ, with some finding that most first-year mortality occurs in the post-fledging period (e.g. Grüebler *et al.* 2014), and others that most mortality occurs during migration (e.g. Tarof *et al.* 2011), which indicates that generalisation across species and populations is not reliable. The problem is further compounded by the fact that first-year migrants in general show higher dispersal distances than adults (Greenwood & Harvey 1982; Weatherhead & Forbes 1994; Lemon *et al.* 1996; Sedgwick 2004; Shitikov *et al.* 2012) making it difficult to determine how low their true survival actually is (Lebreton *et al.* 1992). However, advances in technology mean it is increasingly becoming possible to track migrant birds year round (Bridge *et al.* 2011), therefore knowledge of limitations to first-year survival will hopefully improve over the next decade.

8.5.5 Habitat quality and quantity

In this study, I found that Whinchats prefer breeding territories in sheltered valleys with long, structurally diverse grass, a high density of tussocks for nesting in and an abundance of perches protruding from the surrounding vegetation, from which to forage (Chapter 3). Some of these results are similar to findings from other studies on Whinchats (Oppermann 1990, 1992, Bastian & Bastian 1994; Ritcher & Duttmann 2004; Fischer *et al*. 2013; Pearce-Higgins & Grant 2006; Broyer *et al.* 2012) and grassland birds in general (e.g. Davis 2005). However, the preference for valleys and tussocks has not been noted before. Valleys were thought to be particularly important on Salisbury Plain due to the exposed nature of the site, meaning they offered a milder microclimate. In future work it would be interesting to test this prediction using sensors to measure the difference in exposure between valleys and hilltops. Tussock density does not appear to have been specifically measured in other Whinchat studies, but its importance is probably habitat dependent, where tussocks are rare or absent bracken is commonly used instead as a sheltered, concealed nest location (Pearce- Higgins & Grant 2006; Westerberg *et al.* 2015). Mean invertebrate abundance, biomass and order richness did not appear to be important for territory selection on Salisbury Plain (Chapter 3). However, in intensively farmed areas, where invertebrate abundance and biomass are more limited, these variables do affect settlement decisions (Bastian *et al.* 1994; Opperman 1999).

Suitable breeding habitat was not limiting on Salisbury Plain and Whinchats did not appear to be sensitive to fragmentation at the level present in the study area. However, there are indications from other studies that more extreme fragmentation, such as grassland patches interspersed with forest, may reduce return rates of both adults and first-years (Shitikov *et al*. 2015). It would also be useful to look at the effect of fragmentation on nesting Whinchats in pockets of suitable grassland within farmed areas. Horch & Birrer (2011) found plots of suitable habitat needed to be at least 10,000 m^2 for Whinchats to establish territories, which can be used as a guide for management implementation. As yet, however, no work has explicitly examined whether breeding success is lower for Whinchats in these grassland patches fragmented by more intensively farmed areas, which is an important pre-requisite before implementing ‘set aside’ conservation measures.

The main breeding ground cause of declines in migrants is considered to be habitat loss and fragmentation (Vickery *et al.* 2014). Agri-environment schemes may go some way towards creating or protecting the features important for breeding Whinchats (e.g. Reuter & Jacob 2015) and other open nesting migrants, by increasing structural heterogeneity and thereby creating more of the combination habitat types needed to meet foraging and nesting requirements (Benton *et al.* 2003; Wilson *et al.* 2005; Vickery & Arlettaz 2012). For example Conservation Headlands improve invertebrate food supplies by reducing pesticide and herbicide use, and combining this with grassy field margins this will also provide nesting cover (Aebischer *et al.* 2000). Another highly beneficial measure is increasing the percentage of low intensity meadows on farms (e.g. OFAG 2010), which provides more resources for foraging and nesting, and reduces nest losses by delaying mowing (Grüebler *et al.* 2008; Grüebler *et al.* 2012; Kentie *et al.* 2015), but also leads to an increase in the invertebrate populations in surrounding fields (Albrecht *et al.* 2010).

8.5.6 Elasticities and Integrated Elasticities

This study only had four years of data on demographic rates and therefore cannot reflect the longer term temporal variability in the population. However, elasticities are robust to large changes in the matrix demographic parameters (de Kroon 2000; Caswell 2000, 2001; Ehrlén *et al.* 2001), and will give good predictions of future responses despite environmental stochasticity, unless the environment is extremely variable or catastrophic events are common (Benton &Grant 1999).

In this analysis, the integrated elasticities should be interpreted with care as they were calculated using return rates, rather than adult survival estimates, and the correlations between rates were based on only four years of data. The projected population growth rate was still most sensitive to adult survival after accounting for indirect effects but breeding success was more influential than first-year survival. It would, however, make more sense to focus conservation efforts on breeding success, because, as discussed above, it is easier to alter with conservation management action than first-year survival or adult survival.

Determining population limitations for any species is complex due to interactions and correlations between different environmental factors and demographic parameters which may be difficult to detect (Newton 1998). For migrants, who by definition inhabit different areas at different times of the year, this is especially difficult as year round study is usually not possible (Newton 2004a, 2008). It is, therefore, important to continue to study a population after conservation management has been implemented to assess how effective the management action is and determine whether to implement it more widely.

8.5.7 Opportunities for further research

The findings from this study raise several interesting questions which warrant further study. The very high predation rate despite the high habitat quality was unexpected. It would be interesting to investigate the predation rates in other grassland, ground nesting birds on Salisbury Plain, to determine if these were equally high. It would also be interesting to assess whether proximity to the surrounding agricultural habitat at the edge of Salisbury Plain is related to the predation rate. If the Plain supports a large predator population because of the high habitat quality, lower predation rates might be expected for nests closer to the edge. However, if the high predator density is due to a ‘honey-pot’ effect, with predators drawn to the high food supplies on Salisbury Plain, predation rates may actually be higher for birds closer to the edge of the area. It would be interesting to determine if valleys do offer a more suitable microclimate for nesting, using sensors to measure the difference in exposure between valleys and hilltops. It would also be very useful to unpick the different factors affecting first-year survival. Radio tags could be used to estimate postfledging survival, and an intensive mist netting effort in September could also be used as an additional assessment. The ratio of adults to juveniles in the population could be calculated (Green *et al*. 1999) and this measure then compared to the productivity estimated from nest monitoring until fledging. In general it would also be useful to understand more about the non-breeding period, including the variability in migratory routes and wintering grounds.

The one study that has so far attached geolocators to Whinchats found they had no overall effect on return rates (though the use of a tied harnesses for attatchment was detrimental), which suggests this practise could be implemented more widely with appropriate caution (Blackburn, E. pers. comm.).

8.5.8 Overall conclusions and wider applications

The results from this study suggest that the Whinchat population on Salisbury Plain is limited by low breeding success and low first-year apparent survival, and that breeding success is probably the best demographic parameter to target with conservation management action. Nest protection or predator control measures may be successful in raising breeding success. Low first-year apparent survival was also notable in other Whinchat populations, and could reflect limitations on migration or at wintering grounds; however, it may also be caused by high post-fledging mortality on the breeding grounds, or just reflect high natal dsipersal. More studies need to be done on post-fledging survival in Whinchats in different habitats and on over-winter survival to try to separate out these factors. This study also shows that it is important to ensure adult survival remains high because the population growth rate is most sensitive to change in this parameter and therefore a relatively small reduction in the adult survival rate may have a substantial negative effect on the population growth. The Whinchat population on Salisbury Plain appeared stable relative to the UK population as a whole between 2002 – 2012 (section 2.2.1), but the recent observed population trends in the study population show a decline which is likely to accelerate in the future due to a reduction in immigration as the UK population continues to decline (Baillie *et al*. 2014). In the past, it is likely that the large area of the site, with a large existing Whinchat population, and apparently plentiful supplies of food and suitable nesting habitat, attracted immigrants into the population to buffer against decline. However, the large area and high quality habitat also attracts high densities of generalist predators (pers. comm. Imber Conservation Group), and the resultant low productivity combined with low first-year survival means the imbalance between productivity and survival is too low to sustain population growth for long term stability.

The key difference between Salisbury Plain and other areas where Whinchats have been studied is the lack of breeding habitat change from farming and the large size of the area (Ash & Toynton 2000; Ash *et al*. 2011). Up to now most studies have cited breeding ground habitat change as the main reason for Whinchat declines (Grötenhuis & Van 1986; Bastian 1989; Richter & Düttmann 2004; Grüebler *et al.* 2008; Broyer *et al.* 2009; Fischer *et al.* 2013). The fact that the Salisbury Plain population is still projected to decline in the long term is particularly interesting and suggests that though agri-environment schemes may help to improve breeding success in other Whinchat populations (e.g. Grüebler *et al*. 2012), the story is not that simple, and other factors such as nest predation and first year survival also need to be considered. Whinchats are becoming increasingly well studied across Europe (e.g. Müller *et al.* 2005; Frankiewicz 2008; Grüebler *et al.* 2008, 2012, 2015; Broyer 2009; Tome & Denac 2012; Fischer *et al.* 2013; Shitikov *et al.* 2015), comparing variations in key demographic parameters between these different study populations and relating these differences to differences in habitat quality or resource availability will drastically improve our understanding of Whinchat population dynamics and ideally enable effective conservation action tailored to different study populations depending on their needs.

The populations of many long-distance migrants have shown severe declines over the last 30 years, (Newton 2004a, 2008; Sanderson *et al.* 2006; Heldbjerg & Fox 2008; Vickery *et al*. 2014). To enable positive conservation management action to try to halt these declines we need to understand why they are happening. This study demonstrates one way to achieve this aim, through detailed studies of a sample population, quantifying all the key demographic parameters and the associated environmental factors that may affect them. Data gained from these type of studies allow us to identify the most vulnerable life history stages and the most limiting environmental factors (Caswell 2001; Robinson *et al.* 2004; Fletcher *et al*. 2006; Wright *et al*. 2009; Calvert *et al*. 2009; Sim *et al.* 2011; Hastings & Gross 2012; Grüebler *et al.* 2014). Knowledge gained from studying one migrant species may also ‘provide insights’ into population limitations for other migrants, including poorly studied species (Calvert *et al*. 2009) with similar life histories and habitat requirements.

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Appendix: scientific names

Arctic Tern	*Sterna paradisaea*
Barn Swallow	*Hirundo rustica*
Bewick’s Swan	*Cygnus columbianus bewickii*
Blackcap	*Sylvia atricapilla*
Black-capped Vireo	*Vireo atricapilla*
California Towhees	*Pipilo crissalis*
Carrion Crow	*Corvus corone*
Clay-coloured Sparrow	*Spizella pallida*
Common Chiffchaff	*Phylloscopus collybita*
Common Whitethroat	*Sylvia communis*
Garden Warbler	*Sylvia borin*
Gila Woodpecker	*Melanerpes uropygialis*
Great Tit	*Parus major*
Grey Partridge	*Perdix perdix*
Lesser Kestrel	*Falco naumanni*
Lesser Whitethroat	*Sylvia curruca*
Meaddow Pipit	*Anthus pratensis*
Purple Heron	*Ardea purpurea*
Red Knot	*Calidris canutus*
Red-backed Shrike	*Lanius collurio*
Redstart	*Phoenicurus phoenicurus*
Red-winged blackbird	*Agelaius phoeniceus*
Reed Bunting	*Emberiza schoeniclus*
Rufous Bush Chat	*Cercotrichas galactotes*
Sage grouse	*Centrocercus urophasianus*
Sage Sparrows	*Amphispiza belli*
Sedge Warbler	*Acrocephalus schoenobaenus*
Seychelles Magpie Robin	*Copsychus sechellarum*
Skylark	*Alauda arvensis*
Stonechat	*Saxicola rubicola*
Vesper sparrow	*Pooecetes gramineus*
Western Sandpiper	*Calidris mauri*
Wheatear	*Oenanthe oenanthe*

Whinchat	*Saxicola rubetra*
White Stork	*Ciconia ciconia*
Willow Tit	*Poecile montanus*
Willow Warbler	*Phylloscopus trochilus*
Yellow Wagtail	*Motacilla flava*
Yellowhammer	*Emberiza citrinella*

Badgers	*Meles meles*
European Bison	*Bison bonasus*
Foxes	*Vulpes vulpes*
Stoats	*Mustela erminea*

False Oat-grass	*Arrhenatherum elatius*
Meadow Brome	*bromus erectus*
Red Fescue	*Festuca rubra*
Tall Fescue	*Festuca arundinacea*

Stony Corals	*Scleractinia*