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# **Factors Determining the Density and Distribution of Palearctic Migrants Wintering in Sub-Saharan Africa.**

By  
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Submitted for the degree of Doctor of Philosophy to the University of St  
Andrews



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## Abstract

The Sahel of West Africa is the major wintering area for a large number of Palearctic migrant birds, as well as supporting a distinct Afrotropical avifauna. Fluctuations in the European breeding populations of several migrant species have been linked to drought events in the Sahel. The arrival of large numbers of migrants into an area already occupied by a resident bird assemblage has been identified as having a high potential for competition between these two residency groups. Densities of warblers found in this study were generally comparable to those found previously in the Sahel. However, declines in several species associated with habitat loss were also apparent. A number of species associated with more arid habitats appeared to be increasingly common in the study region, presumably reflecting habitat loss further north. Palearctic species selected for winter habitats that are structurally similar to those used during breeding. The shrub species *Salvadora persica* was strongly selected for by the majority of Palearctic but not Afrotropical warbler species, which appears to be due to the formers' dependence upon fruit as fuel for pre-migratory fattening. A large degree of inter-specific variation in microhabitat selection and foraging behaviour resulted in no clear division of resources between residents and migrants at the group level. Several species-pairs were identified as having a high potential for inter-specific competition however, but no evidence for competitive exclusion was found. It is possible that during periods of limited resource availability, competition, and resulting competitive exclusion, may increase. Future work should focus upon establishing long term population and habitat monitoring, and the use of experiments in which potential competitors can be excluded and food availability controlled. This study highlights the critical importance of conservation in the Sahel in protecting Palearctic migrant passerines, but also emphasises the need for a greater understanding of the effects of habitat loss on Afrotropical species.

Declaration

I, Jared Wilson, hereby certify that this thesis, which is approximately 60,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in October 2001 and as a candidate for the degree of Doctor of Philosophy in October 2002; the higher study for which this is a record was carried out in the University of St Andrews between 2001 and 2004.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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## Chapter 1 Introduction

This thesis describes in detail for the first time the factors determining the density and distribution of Palearctic migrant warblers on their wintering grounds. The rationale for this study is to obtain baseline, primary data that will allow us to monitor future changes in populations on the wintering ground and describe initial habitat associations that can guide any future attempts at conservation management in the Sahel. The theoretical framework for this study is how migrants fit into the communities that they join for only a part of the year: do they compete for resources with residents and how does this vary seasonally and with habitat?

Migration at some scale has been described in all major animal groups, but is most apparent in more mobile groups such as marine mammals, fish, flying insects and birds. Definitions of migration differ widely across authors and subjects, but that given by Baker (1978): "the act of moving from one spatial unit to another", encompasses most. Many zoologists also agree that migration must involve some degree of a return to origin. The scale of any movement involved, the degree of separation between spatial units, and the extent to which individuals and populations return to their origin, however, varies considerably across taxa and populations. Migration can occur through both the horizontal and vertical planes, as exemplified in the marine environment. Across all systems temporal fluctuations in resource availability have been identified as the driving force behind migration. The degree to which species and populations undergo migratory movements may provide an indication of the level of resource fluctuation and competition within a particular environment.

### 1.1 Avian Migration

Migration is a relatively common phenomenon within birds, and has been described in all major avian taxonomic groups across both temperate and tropical zones (Berthold 1993). This frequency of occurrence of migration is presumably due to the cosmopolitan distribution of the taxa, their high degree of mobility, and an inability to hibernate (Berthold 1993; Moraes 1995; Prinzinger *et. al.* 1981).

It appears that migration has evolved independently on a number of occasions, and in a number of different geographic regions and taxa (Berthold 1993; Monkkonen 1992; Monkkonen *et. al.* 1992). Three major avian migration systems occur, the Palearctic-Afrotropical, Palearctic-Sunda (Asia), and the Nearctic-Neotropical. All three systems

consist of mass movement of birds between temperate breeding grounds and tropical wintering grounds. However, the origins of migrant species are thought to vary between regions. In the Nearctic system, migration is believed to have evolved in tropical species that utilised edge habitats and more ephemeral resources (Greenberg 1988; Monkkonen *et. al.* 1992). These species were therefore predisposed to seasonal movements, with the trait becoming more extreme and ultimately resulting in tropical-temperate migration (Chesser and Levey 1998; Price *et. al.* 2000). Within the Palearctic region by contrast, migration is likely to have originated within temperate regions, with ice age events forcing more northerly species to take refuge within the more accommodating climates of Africa and SE Asia (Monkkonen *et. al.* 1992; Newton 1995; Price *et. al.* 2000). The loss of forest habitats from temperate regions during these ice ages may also explain the predominance of Palearctic migrant passerines associated with secondary habitats, in contrast to their Nearctic counterparts (Monkkonen *et. al.* 1992). More recent changes in climate and land use have also resulted in changes in distributions and migratory patterns in a number of species, confirming that the origin of bird migrations is likely to be multiple and species specific (Berthold 1995; Mason 1995).

## **1.2 Migratory Fat Deposition, Potential Flight Ranges and Barrier Crossing**

Although avian migration origins, routes and patterns are varied there are some unifying factors that operate for all avian migrants to some degree: distance must be travelled frequently over barriers where feeding is not possible and this must be fuelled. Across the majority of taxa the major fuel for migration is fat, with reserves stored during periods of hyperphagia prior to the onset of migration. Fat is an ideal resource for migration due to its high energy : mass ratio, its storage not requiring the addition of water, and the relatively low energetic costs involved in its oxidation (Ramenofsky 1989). Food consumption in birds can increase 25-30% during fat deposition ( Bairlein 1990; King and Farner 1965), and birds may increase body mass by 60-100% through the deposition of fat reserves (Berthold 1993). Dietary switches may occur during this period, with fruit in particular being targeted due to its high fat content and high energetic value, the latter required in order for fat deposition to take place (Snow and Snow 1988; Stoate and Moreby 1995). Alongside the deposition of fat reserves, many migrants undergo changes in body composition, presumably in order to compensate for the increased load of fat deposits. Reductions in carbohydrate, protein and water

reserves (Child and Marshall 1972; Lindström 1993) as well as in organ size (Battley *et. al.* 2004; Karasov 2004; Piersma 1998) have all been recorded.

Deposited fat reserves are consumed during migration, which in passerines is generally carried out in stages over a period of several weeks to months (Alerstam 2001). Individuals pause during migration in order to rest, refuel and avoid unsuitable climatic conditions (Berthold 1993). The amount of fat deposited prior to each stage of migration has been shown to depend upon the distance to be travelled, or the width of any barriers to be crossed (Berthold 1993). Geographical features which may represent a barrier to migration include any areas that do not allow for rest or refuelling e.g. seas or desert regions. An alternative strategy to direct crossing of 'barriers' is to migrate around these hostile environments (Alerstam 2001). The avoidance of such barriers may involve a significant detour and increase the overall distance travelled, potentially increasing both time and energy costs (Berthold 1993). In cases where the costs associated with barrier avoidance are less than the risks associated with crossing the barrier, detours in migration may occur (Alerstam 2001).

Seasonal variation in weather conditions or habitats during migration periods may result in migrant species undertaking 'loop migrations' in order to avoid seasonally differential barriers (Alerstam 2001). This results in the two stages of annual migration being geographically offset from one another, with outward migration benefiting from benign conditions at different locations to those encountered on the return. Such loop migrations have been recorded in waders, wildfowl, and passerines (Alerstam 2001; Jones 1995; Moreau 1972; Pearson and Lack 1992; Williams *et. al.* 1977)

Estimates have been made of potential migratory flight ranges by incorporating energy reserves, bird air speed, energy consumption during flight, and prevailing wind conditions (Alerstam 2001; Bairlein 1992; Biebach 1992; Hjort *et. al.* 1996; Pennycuik 1989; Rayner 1988). Discrepancies between these estimated flight ranges and the distances apparently covered in a single flight have been attributed to errors in calculations, individuals foraging along the route (i.e. not carrying out uninterrupted crossings), and meteorological conditions en route (Biebach 1992; Rayner 1988). If these potential biases are taken into account, flight ranges greater than 4000km have been estimated for trans-Saharan migrants, sufficient for a non-stop crossing of the Sahara (Alerstam 2001; Biebach 1992; Hjort *et. al.* 1996). Observations of nocturnal migrants pausing during daylight hours in seemingly inhospitable desert habitats, without feeding and with apparently adequate fat reserves, suggests that some

individuals may pause during migration in order simply to rest, rather than to refuel (Bairlein 1992). It has been suggested that birds may rest during trans-Saharan migration due to the high thermoregulatory demands exerted during daylight (Bairlein 1992; Biebach 1992). That lean birds are more likely to rest at sites with greater foraging (and therefore re-fuelling) potential suggests that individual birds are selecting stopover sites according to body condition and re-fuelling requirements (Bairlein 1987; Biebach 1992). For a full review of the mechanisms of avian orientation, navigation and physiology of migration see Baker (1978) and Berthold (1993).

## 1.3 Seasonal Variaticn in Migrant Ecology

As discussed above, seasonally fluctuating resources may result in movements of animals between areas with varying resource levels, ultimately leading to the establishment of migration. The arrival or departure of large numbers of individuals at a site may have profound effects upon resident species or populations. Availability of resources may vary considerably between seasons, and may be further compounded by changing levels of inter and intra specific competition. One may therefore expect variation in foraging behaviour or habitat selection in order to reduce levels of competition, or capitalise on available resources. Distinguishing between these two possible causes of variation in behaviour may be problematic however.

### 1.3.1 Habitat Selection

Although by no means exclusive, a strong similarity has been found between breeding and wintering habitat requirements in both Nearctic and Palearctic species (Monkkonen *et. al.* 1992). Whether these similarities are due to species selecting for similar habitats, or competitive exclusion by resident species is unclear. Although relatively little seasonal variation in habitat selection occurs in either Palearctic or Nearctic migratory species, there are significant differences in habitat preferences between these two migratory systems.

In wintering grounds, Nearctic migrants are strongly associated with 'high forest' (Terborgh 1980), with up to 29% of migrant species using it as their primary habitat (Stotz *et. al.* 1996), with a similar pattern also occurring in the Sunda region (Wells 1986). This contrasts with just 1% of Palearctic migrants (e.g. Wood Warbler *Phylloscopus sibilatrix*, House Martin *Delichon urbica*, Honey Buzzard *Pernis apivorus*)

using high forest in African winter grounds (Jones 1998; Moreau 1972;). Within Africa the majority of Palearctic migrants are associated with seasonal savannah or light woodland (Grimmett 1979; Leisler 1992; Lovei 1989; Monkkonen *et. al.* 1992; Moreau 1972). As discussed above, the apparent origins of migrants differed between the Palearctic-Afrotropic and Neotropic-Nearctic, and this may have resulted in the habitat preferences observed today. However, the pattern in habitat associations of migratory species in the two systems is mirrored in their respective tropical counterparts. A total of 2820 (75%) Neotropical species use humid forest habitats, with 1017 (25%) using non-forest habitats (Leisler 1990; Stotz *et. al.* 1996; Tramer and Kemp 1980). Yet in contrast, within Africa only 409 (28%) of Afrotropical species are associated with forest habitats and 1072 (72%) with non-forest habitats (Moreau 1966; Owen and Black 1993). This suggests that differences in available habitat between the two tropical regions may also have resulted in some of the differences found today.

### 1.3.2 Foraging Behaviour

As one may expect, variation in resource availability between breeding and wintering sites can result in variation in the foraging behaviour of migrant species. Comparisons of American Redstart *Setophaga ruticilla* foraging behaviour between breeding and wintering sites (NE USA and S Central America respectively) showed a constant prey capture rate during both seasons (Lovette and Holmes 1995). However, the study found that birds were increasing their foraging speed at winter grounds to maintain this rate, presumably to compensate for reduced prey availability. A significant difference in foraging speed was also found between early and late winter, and this was thought to be due to declining prey availability at the onset of the dry season. In the same species, the amount of time spent foraging during the summer peaked at 65%, with similar values also found in the Dark-eyed Junco *Junco hyemalis* (Lovette and Holmes 1995; Weathers and Sullivan 1989). This contrasts with studies in the tropics where American Redstart (Lovette and Holmes 1995), Mangrove Swallow *Tachycineta albilinea* (Ricklefs 1971) and Chestnut-backed Antbirds *Mymeciza exsul* (Marcotullio and Gill 1985) were all observed spending more than 85% of their time foraging. It seems possible that low prey abundance and/or shorter day length in the tropics results in extended foraging periods, even in migratory species where demands from breeding activity are not present.

Alongside foraging rates, foraging method has also been found to vary between seasons. American Redstarts were consistent in types of attack manoeuvre during the

winter, but these differed significantly from those utilised during the summer (Lovette and Holmes 1995). Summer prey were dominated by large energy-rich caterpillars and tipulid flies (Omland and Sherry 1994) winter, by small Diptera, Hymenoptera, Homonoptera, and adult Lepidoptera (Lovette and Holmes 1995). Differences in foraging activity, with a reduction in aerial attack, glean, sally-hover and flutter chase manoeuvres during winter, were presumably due to these differences in diet. Similar switching of prey between summer and winter has been observed in Bay-breasted Warbler *Dendroica castanea* and Worm-eating Warbler *Helmitheros vermivorus* (Greenberg 1995). The Yellow Warbler *Dendroica petechia* however, maintained a consistent diet between summer and winter, perhaps due to prey availability in mangrove winter habitat being similar to that at breeding sites (Wiedenfeld 1992). Within-season changes in foraging behaviour to take advantage of temporary resources have also been described (Forstmeier *et. al.* 2001; Lovette and Holmes 1995; Nystrom 1991). It therefore appears that some species at least, switch prey between winter and summer habitats, presumably due to changes in availability. Alongside a reduction in prey abundance, a dependence upon smaller and less energy-rich prey may result in increased search time for a reduced energy gain. The majority of the studies discussed above are from the Nearctic-Neotropical system, and unfortunately there are virtually no equivalent studies from the Palearctic-Afrotropical system.

## 1.4 Foraging Behaviour and Avoidance of Competition

### 1.4.1 Behaviour of Migrants

As discussed above, observed seasonal variation in foraging behaviour and prey selection by individuals have been linked to fluctuating resources. However, intraspecific sexual divergence in foraging behaviour has also been observed in a number of species, and must be the result of other processes. Three explanations have been put forward for sexual differentiation in foraging strategy: i) males forage in more obvious locations for song and defence purposes, ii) morphological differences result in differentiation, and iii) differentiation has evolved to reduce intra-pair competition (Nystrom 1991). Outwith breeding grounds and with greatly reduced song rates, the first hypothesis is unlikely to apply on wintering grounds, particularly in non-territorial species. However, the latter two hypotheses may apply in either breeding or non-breeding areas. Male Willow Warblers, *Phylloscopus trochilus*, gleaned more and

hovered less than females, particularly when slow-moving aphids were available. The shorter wings and smaller bodies of females were better adapted to hovering and searching leaf undersides than males, which focused on larger prey items (Nystrom 1991). In Yellow Warblers (where females are shorter-winged than males) females again gleaned less and hovered more than males during the breeding season (Busby and Sealy 1979). In Hooded Warblers *Wilsonia citrina*, males are shorter winged and forage at greater heights than females, with this segregation of resource use between the sexes continuing during the winter (Lynch *et. al.* 1985).

Morphological differences between species may play an important role in explaining interspecific variation in foraging behaviour in migrants (Nystrom 1991; Parrish 1995a; Parrish 1995b; Robinson and Holmes 1984; Robinson and Holmes 1982; Whelan 1989). *Phylloscopus* warbler species that mainly forage by gleaning at low levels in dense vegetation are relatively short-winged with large feet, whereas those foraging by gleaning in open vegetation are long winged with wide bills, and small species that hover-gleaned have shorter wings and finer bills (Forstmeier and Kessler 2001; Price 1991). Smaller arboreal passerines, whether species or individuals, generally hover more, focusing on smaller (and more cryptic) prey in more peripheral vegetation that require extended search periods (Forstmeier and Kessler 2001; Gustafsson 1988; Marchetti *et. al.* 1998; Price 1991). It would therefore appear that birds prefer vegetation types they are morphologically suited to; however smaller species and individuals may be forced to peripheral vegetation through competitive exclusion, rather than through selection (Forstmeier and Kessler 2001).

#### **1.4.2 Migrant and Resident Behaviour**

Variation in foraging methods, and prey or habitat selection has profound implications for potential competition between species. Coexistence of similar species is possible if species i) feed in separate parts of the habitat, ii) take different prey from the same habitat, or iii) exploit superabundant prey or co-operate (Lack 1971). Several authors have concluded that migrant species utilise habitat peripheries, undertaking more rapid and frequent foraging movements, and capitalising on more unpredictable resources than resident counterparts (Greenberg 1981; Herrera 1998; Greenberg 1986; Lack 1986a; Leisler 1990; Leisler 1993; Winkler and Leisler 1992; Rabol 1987; Tramer and Kemp 1980). A pattern supporting this has been found in migrant breeding grounds in Europe, with resident temperate species occupying optimal niches (Lack 1986a). Within Africa, Pied Flycatchers *Ficedula hypoleuca* foraged in different habitat strata

and also took prey from different substrates to African flycatchers, with a greater frequency of pouncing and using a greater diversity of feeding substrates and techniques (Salewski 2000). Willow Warblers foraged higher and within open vegetation more than did resident Camaropteras, with more prey being taken from twigs. Willow Warblers also used wings more during foraging and moved around a greater diversity of substrates, though no variation was found in travel distance, food intake rate, or number of movements between Willow Warbler and resident warbler species (Salewski 2000).

A more generalist approach to foraging behaviour would allow migrants to utilise seasonally abundant resources. Diet switching to utilise seasonal food resources (such as large insects) has been found in migrant species both in wintering and breeding sites (Herrera 1998; Lack 1986b). Half of all resident insectivore birds in Tanzania were found to forage on the ground, with termites being the most common food source (Lack 1986b). The dependence of residents on more predictable and stable food resources (such as terrestrial insects) has been put forward as an explanation for their apparent higher degree of specialisation (Herrera 1998; Lack 1986b). However, whether migrant diets differ from those of residents is unclear, with some studies reporting no differences (Leisler 1990; Sherry and Holmes 1996) and others finding that residents take a wider diversity of prey than migrant species (Lack 1986a). It has been suggested that migrants will be able to exist only in habitats where food is abundant (Herrera 1998; Lack 1971). The ability to utilise seasonally fluctuating resources would increase the opportunities for migrant species to occupy particular habitats. This flexibility in resource use may in turn result in reduced costs of antagonistic interactions with specialist species which can dominate a single resource. The reduced level of neophobia exhibited by migrant species, and their apparent willingness to use 'novel' habitats, would support the idea that migrants are able to access fluctuating resources more readily than resident species (Greenberg 1983; Leisler 1992).

Differences in foraging behaviour between migrant and resident species have been attributed by some authors to differential morphological adaptations (Gaston 1974; Winkler and Leisler 1992, but see Keast 1980; Niemi 2004). Possibly reflecting the demands of a migratory strategy, relative primary projection, distal wing segment length, bill length, leg length, and femoral length were all longer in migrant than resident species. Within migratory species, migration distance has been shown to be positively correlated with wing length and primary projection, the latter directly relating to flight performance (Winkler and Leisler 1992). Other morphological adaptations

exhibited by migrants also appear to be related to differences in foraging methods. For example, migrant species have lower muscle mass and longer femoral length than residents, matching the formers' reduced use of legs for clinging, and preference of bipedal hopping for locomotion (Leisler *et. al.* 1989).

The inference often made from migrants' increased foraging speed and diversity of method, a propensity to forage along habitat edges, and reduced specialisation is that it permits avoidance of competition with resident species (Bilcke 1984; Lack 1971; Rabol 1987). It is difficult to separate cause and effect in such relationships (Rabol 1990; Lack 1986a), and a decline in evidence of competition over time may be predicted as energy expenditure 'wasted' is reduced (Mayr 1963).

### **1.4.3 The Impact of Competition in Wintering Grounds**

The sudden arrival of large numbers of migrants on wintering areas already occupied by resident species has been identified as having significant potential for competition (Greenberg 1986; Lack 1971; Leisler 1992; Moreau 1972). This competition is likely to be limited to food or shelter resources, due to migrant species not being involved in breeding activities. As described above, differences in foraging behaviour between migrant and resident species have been found in a number of studies, and potentially indicate past or present competition, or competitive exclusion. Seasonal shifts in the behaviour of resident species following the arrival of migrants are also thought to result from competitive exclusion by migrant species (Rabol 1987). However, it remains possible that migrants utilise niches that are vacated by resident species due to seasonal environmental change (Leisler 1992; Rabol 1990). The use of removal experiments would help to clarify the situation, but to date, no such studies have been carried out.

Up to 40% of West African land bird species are thought to undertake intra-Africa migration, often in association with seasonal rains (Elgood *et. al.* 1994; Jones 1998; Moreau 1972; Jones 1998). It has been suggested that seasonal movement of Afrotropical species away from the Sahelian environment may 'release' habitats and niches for Palearctic migrants, explaining 'Moreau's Paradox' in which migrant species select for the seemingly hostile semi-arid environment of the Sahel as it enters an extended dry season (Moreau 1972; Fry 1992). The movement of Afrotropical species away from areas experiencing a seasonal influx of Palearctic migrant species may in

part explain why, despite the great apparent potential for competition within migration systems, overt aggression between residents and migrants appears rare (Curry-Lindahl 1981; Rabol 1990; Salewski 2000). In the Ivory Coast neither inter- nor intra-specific aggression was observed in Willow Warblers, whilst 88% and 94% of aggression observed in Pied Flycatchers and Green-backed Eromemola *Eromemola canescens* respectively was intraspecific (Salewski 2000). This suggests that at this site at least, interspecific aggression is not important. Aggression was found to be more frequent in a study on wheatears *Oenanthe spp* and their African counterparts (Leisler 1992), perhaps due to the groups' more similar resource use. However, even in this study aggression was observed more frequently between Palearctic migrants than between migrants and residents, with resident species always dominant over migrant species, independent of relative size (Leisler 1992). Interspecific aggression was also frequent in temperate breeding grounds between migrants, and between migrant and resident species (Orians and Willson 1964; Sherry and Holmes 1988). A study in Nigeria found that species of resident sunbirds Nectariniidae and flycatchers Muscicapidae occupying their 'core' habitats were always dominant over other similar species, regardless of size (Edington and Edington 1983). However, the presence of aggression does not give a good indication of the level of interference competition, and equally the absence of obvious signs of aggression does not indicate a lack of competition. To resolve this question, detailed foraging observations in habitats where the prey abundance is known are required in order to assess the degree of competition present.

Observations of foraging and other behaviour provides little quantifiable information on the degree of competition occurring, or the effects this may be having upon individuals or populations. However, such observations can to identify systems or species pairs in which competition appears to be important. This information can then be used in targeting experimental methods to determine the effects of competition.

Competition may ultimately result in segregation of species, populations, or individuals either spatially or temporally and this may explain the lack of overt signs of aggression and competition in many systems. The geographic separation in winter distributions of certain Nearctic migrants has been attributed to historic competition (Greenberg 1986; Keast 1980). In order to assess the true potential for competition, the relative abundances of species involved must be known (Leisler 1992). These data are unavailable for the majority of tropical systems, as are even the most basic information on time-budgets and seasonal flexibility in resource use, making assessment of competition difficult.

## 1.5 Population Limitation in Migrants

The dependence of migratory species upon breeding, wintering and passage sites makes the group vulnerable to change over a large geographic area. The need for any effective conservation strategy to assess processes across the entire geographic range compounds the problems associated with conservation of migratory species, particularly if these include remote or relatively poorly known regions. An important factor determining the conditions experienced by migratory species is the degree of competition occurring on winter grounds, with high levels of competition having the potential to limit populations. In order to assess the potential for competition an assessment of relative abundance of a species and its potential competitors, habitat preferences, and foraging behaviour are required.

Populations of Nearctic migrant passerines have declined significantly over recent years, apparently due to changes in conditions at breeding sites (Latta and Baltz 1997; Rappole and McDonald 1994; Sherry and Holmes 1996; Temple 1996). Alongside direct habitat loss through deforestation, forest fragmentation has increased predation and brood parasitism rates through the edge effect (Paton 1994; Robinson *et. al.* 1995). It has been suggested that migrant species are affected more greatly than temperate residents in the Nearctic due to their open nest cups, later breeding dates, smaller body size, and lack of defence against the increasingly widespread brood parasite the Brown-headed Cowbird *Molothrus ater* (Gates and Gysel 1978; Greenberg 1980; Robinson *et. al.* 1995; Wilcove and Whitcomb 1983). Evidence of winter habitat destruction impacting upon Nearctic migrant breeding populations has been found in relatively few species (Terborgh 1989). However, the rapid rate of forest destruction in Central American wintering sites is likely to have an increasingly evident impact upon breeding populations of Nearctic migrants (Newton 2004).

In contrast with Nearctic migrants, declines in Palearctic migrant passerines have largely been linked with mortality in African wintering grounds (Baillie and Peach 1992; Marchant 1992). Annual precipitation in the Sahelian region has been found to show a strong positive correlation with subsequent breeding populations in Western Europe (Bryant and Jones 1995; Moller 1989; Peach *et. al.* 1991; Winstanley *et. al.* 1974). Breeding populations of Common Whitethroat declined by over 50% in Western and Central Europe following the severe droughts experienced in the Sahel between 1965 and 1970 (Winstanley *et. al.* 1974). In Britain and Ireland a population of 0.5- 0.7 million pairs crashed by 80% in 1969, recovering to 25% by 1973-82, and to 29% by 1987

(Baillie and Peach 1992) see Fig 1. Breeding densities also declined markedly with populations in Southern England declining from 27 pairs per km<sup>2</sup> in 1964-8, to 11 per km<sup>2</sup> in 1969-72, with current densities still well below earlier levels (Glantz 1977). Populations of Sedge Warbler *Acrocephalus schoenobaenus* and Sand Martins *Riparia riparia* showed similar declines following Sahelian drought (Baillie, Crick, *et. al.* 2002; Baillie and Peach 1992; Foppen *et. al.* 1999; Peach *et. al.* 1991; Siriwardena *et. al.* 1998; Szep 1995; Winstanley *et. al.* 1974 ). Alongside the effect of winter rainfall, rapidly increasing human populations have also been linked to winter mortality, with the associated increase in grazing pressure, fuel-wood consumption, conversion of woodland to intensive agriculture, and use of pesticides (Jones 1995; Mendelsohn and Paz 1977; Mullie and Keith 1993). The very strong association with secondary habitats demonstrated by the majority of Palearctic species, as opposed to rainforest, has resulted in deforestation of high forest within Africa impacting on very few migrant species, relative to the numbers of species affected by changes in the Sahelian region.

The effects of changes in habitat area upon populations have been well described (Fuller *et. al.* 1995). However, the role of density dependent responses to these changes is more complicated (Goss-Custard *et. al.* 1995). The situation for migrant species is further complicated as knowledge of these responses in both breeding and non-breeding areas is required in order to predict effects of any habitat change (Newton 2004). Density dependent winter loss has been found in several species of migrant passerine wintering in Africa (Baillie and Peach 1992; Jarvinen 1987; Newton 1998; Owen and Black 1993; Stenning *et. al.* 1988;) however, the exact mechanism for this effect has not always been identified ( Newton 1998; Newton 2004).

Selection of higher quality wintering sites and habitats on arrival has been shown in a number of migrant species (Brooke 1979; Leisler 1992; Lundberg *et. al.* 1981). Densities are more consistent over time in better habitats ( Rodenhouse *et. al.* 2003; Zimmerman 1982), and population growth occurs in better quality habitats first (Newton 1998). Individuals wintering in poorer habitats have been shown to be in poorer body condition and to arrive at breeding grounds later than those on good quality winter habitat ( Bearhop *et. al.* 2004; Marra *et. al.* 1998), with both factors associated with lower reproductive success (Aebischer *et. al.* 1996; Bensch and Hasselquist 1991; Brooke 1979; Lanyon and Thompson 1986; Lundberg *et. al.* 1981). The rapid reduction in available resources at passage sites following the arrival of migrants (Nolet and Drent 1998; Moore and Yong 1991), may force later migrants to remain longer at these sites in order to obtain the required body condition to continue migration (Bibby and

Green 1981), ultimately affecting individual survival (Pfister *et. al.* 1998) or the date of arrival at breeding or wintering sites. These 'buffer effects' therefore can act to restrain population growth, and habitat preferences at winter sites must be understood in order to begin to assess potential density dependent processes occurring.

Migrant species are therefore susceptible to changes in conditions in breeding, wintering and passage sites. The "multiple jeopardy" faced by this group makes them highly susceptible to habitat degradation and loss, whilst simultaneously confounding the identification of causes of population change (Newton 2004).

## 1.6 African Migration Systems

Approximately 25% of all European bird species winter in Africa, with entire populations of many species wintering within the continent. It has been estimated that 5000 million land birds carry out this migration each year (Moreau 1972). As mentioned previously, the majority of Palearctic migrants are associated with secondary habitats rather than high forest during the winter. The core area for numbers of species and individual Palearctic migrants is the Sahel zone just south of the Sahara, with relative importance for migrants declining as one moves south (Jones 1998; Moreau 1972). The strong association of migrants with these semi-arid environments is not merely a function of the availability of the habitat, as broadleaved savannas cover approximately twice the area of the Sahel; although rainforest and derived savanna habitats span half that area (Jones 1998).

The relatively low number of Palearctic migrant individuals and species utilising Southern Africa is likely to be due to the suitability and availability of more northerly habitats, the increased cost of the greater migration distances to Southern Africa, the potential unsuitability of more southerly habitats during the rains, and the presence of many potentially competing breeding Afrotropical species during the Austral summer (Jones 1998; Newton and Dale 1996). Palearctic species wintering in Southern Africa have more extensive breeding and wintering ranges, suggesting individuals may be 'forced' south by greater population densities further north (Newton and Dale 1996). Why the Guinea Savanna zone just south of the Sahel is so little utilised remains unclear.

Site fidelity within and between winter periods has been found in both Palearctic and Nearctic species (Chettri *et. al.* 2001; Kricher & Davis 1986; Sherry and Holmes 1996).

However, whereas Nearctic migrants are believed to migrate directly to wintering grounds, many species of Palearctic migrants undertake staggered migration or itinerancy within Africa (Dowsett-Lemaire and Dowsett 1989; Elgood *et. al.* 1994; Moreau 1972). Palearctic migrants adopt one of three broad wintering strategies in Africa: 1) remain at one site north of the equator for the entire winter, 2) move slowly south as conditions deteriorate with the onset of the dry season (itinerancy), and 3) stage at a northerly site before moving to a more southerly secondary wintering area (Jones 1998). Presumably the second and third strategies are in response to the relative instability of many habitats within Africa, with many migrants moving further south with the onset of the dry season (Jones 1998).

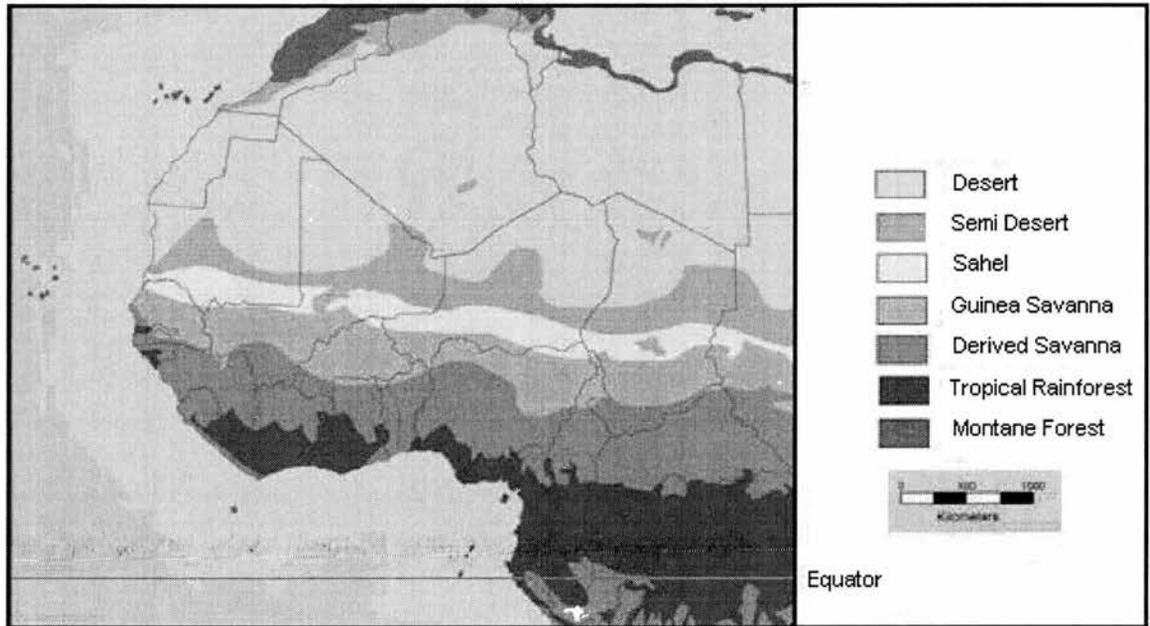
Autumn arrival of migrants in the Sahelian environment coincides with the start of the dry season and a period of increasing environmental hostility (Jones 1995; Jones 1998; Moreau 1972). Arthropod biomass declines 2-10 times, and foliage biomass, 60 times during the dry season (Jones 1998; Lack 1986b). The rapid feather moult found in a number of migrant species in the Sahel has been attributed to a capitalization on the limited period of greatest resource availability (Bensch *et. al.* 1991; Dowsett-Lemaire and Dowsett 1989; Fransson 2000; Hall and; Kaiser 1996; Waldenstrom and Ottosson 2002). By contrast, in East Africa the migrants' autumn arrival coincides with the rains and an associated peak in invertebrate abundance. However, the conditions experienced during the Sahelian dry season may be less inhospitable than initially assumed (Curry-Lindahl 1981; Jones 1995; Lack 1983; Morel 1973).

It has been estimated that the potential for interspecific competition exists between 10% of migrant species (Lack 1971), and that 28% of migrants are potential competitors with resident species (Moreau 1972). This compares with 10% of migrants in the Neotropics potentially competing with residents (Leisler 1992). However, in order to assess the true potential for competition, relative abundances of species involved must be known (Baillie and Peach 1992; Leisler 1992;). These data are unavailable for the vast majority of species in Africa.

## 1.7 The Sahel as a Habitat for Migrants

The Inter-Tropical Convergence Zone (ITCZ) and the rainfall it brings, dominates the climate and vegetation of West Africa. This low-pressure zone of warm and humid air is created by the convergence of the northeast and southeast trade winds. The rain produced as air rises and cools, in turn creates dry air at higher altitudes that move

north and south from the equator before descending to produce the Sahara and Kalahari deserts (Jones 1998). This results in tropical West Africa being dominated by a simple cline in precipitation and vegetation from the arid north to the humid equator, with this pattern mirrored south of the equator (Fig. 1). The resultant vegetation zones both north and south of the equator are similar in structure, though species composition does vary (Keay 1959).



**Fig. 1:** Major vegetation types in West Africa illustrating the decline in vegetation biomass and complexity as one moves north from the equator.

The Sahel region extends from 15-18 degrees north, with a small extension south to 13 degrees in the Lake Chad area. The single rainy season lasts for c. 3 months from June to August with 250-350mm of rain per year. Vegetation is dominated by *Acacia* and *Balanites* tree species and seasonal grassland. Small 'outliers' of isolated *Acacia* stands can occur as far north as 21 degrees (Morel and Morel 1992) where local topography produces increased precipitation, enabling remnants of historic distributions to persevere. As one moves south the Sahel grades into the Sudan and then Northern Guinea Savanna zones. The northern Guinea Savanna is similar in structure to the 'miombo' habitat found in east Africa (Jones 1998).

Expansion of the Sahara, with an associated southerly shift of the Sahel, was widely reported during the 1970's and early 1980's (Eckholm and Brown 1977; Ibrahim 1978) with expansion of 5km a year estimated (Charney *et. al.* 1975). However, tree-cutting for fuel wood (Eckholm and Brown 1977), conversion of savanna to agricultural land,

and overgrazing for pastoral agriculture (Glantz 1977) may all have been responsible for the observed changes in vegetation rather than it being due to desertification *per se* (Diouf and Lambin 2001; Hellden 1991; Lambin and Ehrlich 1997; Reynolds and Stafford Smith 2002; Thomas 1997). The widespread construction of bore holes in the region may exacerbate problems of habitat loss by focusing resource use into limited areas, resulting in severe habitat degradation at these sites (Hanan, *et. al.* 1991).

The large expanse of inhospitable land within the Sahara presents a significant barrier to Palearctic migrants. It was initially assumed that migrants crossed the Sahara as part of a single non-stop flight, crossing both the Sahara and the Mediterranean (c.5000km) in a single journey of 40-60 hours (Moreau 1972). However, recent work has indicated that at least some individuals pause at desert oases (Bairlein *et. al.* 1983; Bairlein 1992; Lindstrom 1995). The majority of individuals observed undertaking these pauses in migration had reasonable fat reserves and did not appear to require re-fuelling, a suggestion supported by the fact that these individuals were not observed to forage during the duration of their short stay of a single day. Lighter individuals apparently searched out larger areas of habitat to pause at, stayed for longer (up to 3 weeks), and actively foraging throughout their stay (Bairlein 1992). That resting birds are immobile during their stay, and therefore difficult to locate, may explain the apparent paucity of observations of migrants stopping over in the desert, and the general assumption that migrants did not break-up the trans-Saharan crossing. It has been suggested that individuals with high fat scores may break up their journey for thermoregulatory reasons (Biebach *et. al.* 1986; Biebach *et. al.* 1991; Biebach 1992), avoiding heat stress by resting during periods with the greatest temperatures.

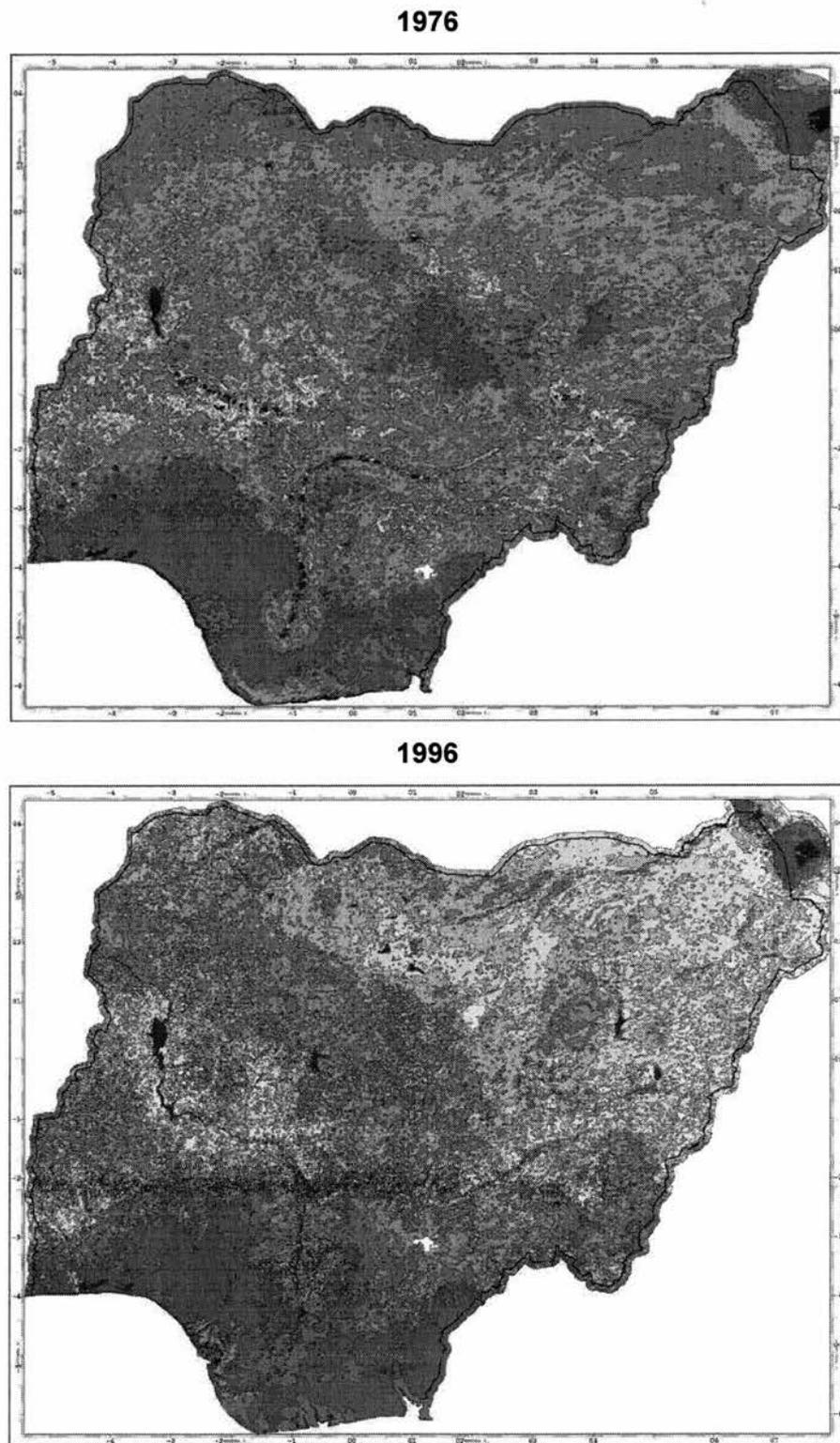
Increases in Sahara barrier width through desertification or habitat degradation potentially increase the proportion of birds requiring stop-over sites for re-fuelling, and may concurrently reduce the availability of these sites. It is possible that development of irrigation projects and boreholes across the region may help mitigate negative effects of habitat loss and degradation to some degree. Interspecific variations in migration strategy exist, and may expose species to varying degrees of stress. Spotted Flycatchers *Muscicapa striata* for example, deposit relatively small amounts of fat prior to the trans-Saharan crossing and are likely to stop to feed en-route. Loss of stop-over sites and increasing barrier width therefore increases their susceptibility to habitat loss (Bairlein 1992). Recent population declines in this species do not appear to be related to habitat loss (the species occurs in common and widespread secondary habitats in the Guinea Savanna and Derived Savanna Zones), and loss of migratory staging sites

may be implicated in the decline (Marchant 1992). It has been suggested that the spring trans-Saharan departure areas of Common Whitethroats *Sylvia communis* have recently shifted to the south compared with the 1960's, presumably due to loss of traditional departure areas further North (Ottoosson *et. al.* 2002). To understand the impacts of increases in barrier width on different species, further research is required into migratory strategies and foraging requirements.

## 1.8 Palearctic Migrants in the Sahel

### 1.8.1 Population Densities

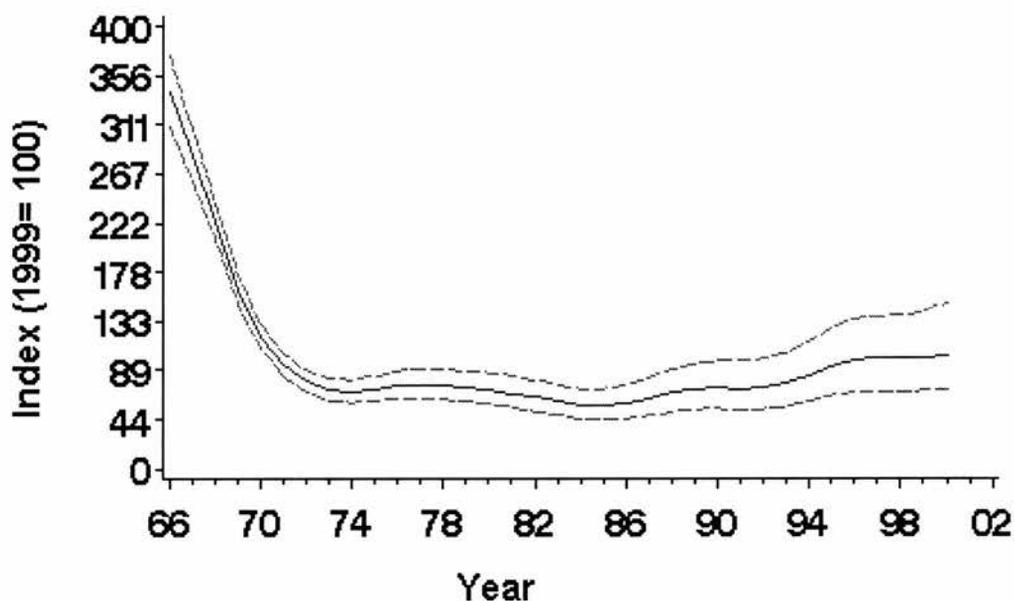
Despite the strong evidence linking breeding population declines of several species of Palearctic migrants with winter mortality in Africa, only limited information on winter distribution, densities and habitat requirements are available (Browne 1982; Jones *et. al.* 1996; Morel and Morel 1992; Stoate and Moreby 1995; Vickery *et. al.* 1999). Population densities of Palearctic *Sylvia* warblers wintering in riverine *Acacia nilotica* woodland in Senegal were found to be 2.7/ ha: up to ten times those found in thorn bush steppe in the same region (Morel and Morel 1992). There are reports of large numbers of species not normally associated with wetland habitats utilising this resource in the Sahel, for example 1000 Subalpine Warblers *Sylvia cantilans* reported in a single reed bed in Mali (Morel and Morel 1992). Away from wetland areas, densities of Palearctic migrants can be comparably high. Researchers in Nigeria found densities of *Sylvia* warblers ranging from 2.1 to 6.8/ha at five *Acacia* woodland sites in the northern Guinea savanna (Jones *et. al.* 1996).



**Fig. 2:** Changes in ground cover in Nigeria between 1976 and 1996. The increasing dominance of lighter shades, particularly in the NE, represents significant reductions in tree cover, and the increasing dominance of grasslands and bare ground (Geomatics International 1998).

Information on relative densities of Palearctic and Afrotropical species densities is even more limited (Jones *et. al.* 1996; Vickery *et. al.* 1999). Palearctic warblers were found to be twice as common as African counterparts in Northern Nigeria (Aidley and Wilkinson 1987; Jones *et. al.* 1996), and 5-10 times as common in the Senegal (Morel 1973). Away from West Africa results varied considerably, with Afrotropical warblers outnumbering Palearctic species in three studies (Jones 1998; Kelsey 1992; Rabol 1987) but being 1.5-3.5 times less common in a fourth (Lack 1986a). Whether this pattern is due to competitive exclusion of migrants by resident species (as suggested in the Neotropics) is unclear (Jones 1998). Densities of Palearctic and Afrotropical warbler species have been found to correlate significantly (Jones *et. al.* 1996), with the average density, biomass and number of species of migrants correlating broadly with vegetation complexity (Jones 1998; Lack 1983; Lack 1986a; Leisler 1992).

The loss of fruiting trees (particularly *Salvadora persica*), deforestation, and intensification of agriculture within the Sahel may be contributing to declines in populations of Palearctic migrants (Jones 1998). The extent of *A. nilotica* woodland declined by 90% between 1954-1986 in Senegal, with woodlands often destroyed because they provide shelter to pest bird species such as the *Quelea Quelea quelea* (Moller 1989). In Borno State in NE Nigeria a 14% decline in woodland occurred between 1976 and 1995 (Fig. 2) due to human clearance for fuel wood, grazing, and conversion to intensive agriculture (Geomatics International 1998). Habitat loss is likely to exacerbate the impact of future drought events upon populations (Marchant 1992). The ability of a migrant species to move within Africa will not necessarily negate any effects of habitat loss as resources prior to the northerly Sahara crossing will still be crucial (Newton and Dale 1996).



**Fig 3:** Breeding populations with 95% confidence limits of Common Whitethroat in the British Isles from 1966- 2002 derived from British Trust for Ornithology Common Bird Census data. From Baillie *et. al.* (2002).

### 1.8.2 Population Change: what we know in the Sahel

A review by Baillie and Peach (1992) found that analyses into the key factors influencing population limitation had been carried out for just three species of Palearctic migrant passerine: Common Redstart *Phoenicurus phoenicurus*, Barn Swallow *Hirundo rustica* and Pied Flycatcher. Despite this paucity of investigative analyses, winter loss has already been identified as a key factor in population declines in several Palearctic migrants (Baillie and Peach 1992; Marchant 1992; Winstanley *et. al.* 1974). In Germany, significant population declines were found in 60% of trans-Saharan migrants compared with 14% of non-migratory species (Newton 2004). As discussed above, although recent observed declines appear to be due to changes in wintering survival, and are relatively well documented, there are multiple aspects of migrant ecology which could be contributing to population declines e.g. barrier crossing, changes in competitive interactions and changes in rainfall. A surprising lack of investigative studies mean we know little about the relative importance of the various factors.

The impact of habitat loss, degradation and drought events within the Sahel upon Afrotropical species is entirely unknown. If as believed, these 'resident' species are

more highly specialised and less flexible than their migratory counterparts, one may expect Afrotropical species to be negatively effected to a greater degree than Palearctic. The majority of the 172 Afrotropical species classified as under threat are associated with forest habitats (Charney *et. al.* 1975) that make up less than one fifth of the continent (Jones 1998). It is therefore not surprising that the majority of conservation effort is directed at these forested habitats. Unlike the New World, conservation of African forest habitats will not result in the simultaneous conservation of migrant species wintering in the Afrotropics, let alone the non-forest African species. For example, the only globally threatened Palearctic migrant species (Aquatic Warbler *Acrocephalus paludicola*) is assumed to be dependent upon wetland sites within the Sahel zone during winter (Charney *et. al.* 1975), a habitat under increasing threat.

In comparison to their Nearctic counterparts, Palearctic migrants have been poorly studied on their wintering grounds, with the number of studies carried out in Africa half those in Latin America (Kelsey 1990; Leisler 1990). The deficiencies in research on wintering Palearctic migrants and research priorities in this area have been highlighted by various authors (Baillie and Peach 1992; Kelsey 1992; Leisler 1992;). Even basic knowledge on population limitation, distributions and habitat requirements of migrants in Afrotropical wintering grounds is still alarmingly limited. Without this information it is difficult to identify sources for reductions in population declines (Jones *et. al.* 1996; Jones 1998; Kelsey 1992), or assess the true degree or impact of competition within the system.

In this thesis I will present data on densities, distributions, habitat requirements and habitat use of a number of species of Palearctic migrant and Afrotropical passerines commonly occurring in the Sahel region of Nigeria. Comparison of any patterns present between migratory and resident species will be made, with particular reference to potential competition between and within groups. Predictive models will be employed to assess the potential effects of past and future habitat loss on populations over a wider geographical area. Finally an assessment of the implications of results upon conservation within the region will be addressed.

## Chapter 2 : Methodologies

### 2.1 Study Region

The Sahel is a semi-arid region within West Africa which borders the southern edge of the Sahara desert. In the majority of West Africa, it occurs between 15° and 18° N, with a southern extension in the Lake Chad Basin to c. 13° N. Annual rainfall of 250-600mm falls within a short wet season between May and September, with the amount of precipitation, and the length of the rainy season, declining with increasing latitude. Maximum temperatures range from 25-45°C, minimum from 5-30°C. Lowest temperatures are associated with strong, cool, dust-laden northerly Harmattan winds which dominate the region Dec-Feb, whilst temperature peaks occur just prior to the onset of the rains during May-July.

Within Nigeria the Sahel is restricted to the extreme NE of the country at c. 13° N, stretching from the shores of Lake Chad (13° E) west to Nguru (10° E). The entire area consists of dry sands with scattered poorly drained clays. Soils are generally very poor in organic content, acidic, and are highly susceptible to wind erosion and crust formation due to poor structure (Hiernaux 1999).

The region is dominated by *Acacia* tree species (*A. seyal*, *A. tortillis*, *A. nilotica* and *A. senegal* most common), *Salvadora persica* and *Balanites aegyptiaca*. Tree height does not exceed 8m, with a maximum height of 4-6m commonly found. Tree diversity is low with a maximum of 8 species per ha occurring, and single species stands common. Ground cover consists of seasonal grasses (*Cenchrus* sp., and *Aristida stipoides*), though for the majority of the year the ground is bare. South of the Sahel the habitat quickly grades into the Sudan zone, with tree species such as *Baobab* sp., *Combretum* sp., and *Guiera senegalensis* appearing, and vegetation complexity increasing.

## 2.2 Study Site Locations

Sixteen sites were used during this study, located across an area of 30,000 km<sup>2</sup> (320km by 100 km) between 10° E and 13° E, at approx. 13° N. This area was chosen because of a history of previous work carried out, and the relative ease of associated logistics. Two core study areas were used, the first near Alagarno (N 1308992° E 1333451°) in the extreme NE of Nigeria, the second Nguru (N 1251668° E 1026704°) in Northern central Nigeria. During the mid winter period of 2002/ 2003 4 additional sites were added at stratified longitudes along a W-E transect between Nguru and Alagarno in order to include sites at a broader range of longitudes and habitat types. Sites 1-12 were chosen as representative examples of the available habitats within these two study areas. Locations of study sites were recorded using decimal latitude and longitude co-ordinates on a Garmin™ 12 Geo Positioning System (GPS) handset using the World Geodetic System 1984 map datum, and are presented in Table 2.1.

**Table 2.1:** Study site numbers and locations.

Site	Site No	Degrees North	Degrees East
Reserve	1	13.040	13.376
Canal	2	13.097	13.340
Wat. FR	3	12.488	10.316
Nguru agric	4	12.533	10.267
Wat. Int Ag	5	12.537	10.336
Wat. Deg. Sav.	6	12.526	10.353
School	7	13.090	13.334
Bore	8	13.114	13.381
Prat	9	13.088	13.323
Commiphora	10	13.111	13.305
Quail	11	13.025	13.382
WofGashua	12	12.493	11.073
Geidam	13	12.490	11.474
EofDamasak	14	13.018	12.248
WofMalamfatori	15	13.289	13.005
Malam	16	13.369	13.204

## 2.3 Vegetation Sampling

Vegetation and habitat variables were recorded for use in habitat models, and to identify any temporal or seasonal changes in habitat parameters. A 25m radius vegetation plot (1963m<sup>2</sup>) was sampled at each bird point count location during the late morning or afternoon of the day of the point count. The centre of each plot was taken to be the point count location, with 25m radial distances measured from that point using a laser rangefinder. Plots were surveyed at least once, with repeat surveys carried out if the point count was repeated. The following variables were recorded for each plot:

- Date
- Latitude
- Longitude
- Tree species
- Tree height (0.5-3m, 3-5m, 5m+)
- % leaf for each sp
- flowering/ fruiting condition of each species
- Ground cover (relative proportion bare earth or grass)
- Degree of chopping (low, medium, high)
- Degree of browsing (low, medium, high)
- % agriculture

Tree species were identified using von Maydell (1986). Tree height was estimated with regular calibration checks of trees of known heights. An estimate of the tree species diversity in each vegetation plot was calculated using the Shannon-Weiner Index :

$$H' = \frac{n \log n - \sum f_i \log f_i}{n}$$

where  $n$  is the total number of individuals for all species and  $f$  is the number of individuals of each species present.

## 2.4 Study Site Habitat Descriptions

The species of woody perennial recorded across the study sites are presented in Table 2.2, and their mean heights in Fig 2.1. The vegetation present at each study site varied considerably (see Table 2.3), with tree density and mean height varying significantly between sites (see Fig 2.2). A significant difference in tree diversity (using the Shannon Wiener index) was also found across sites ( $p < 0.0001$ ,  $F_{15,725} = 8.5$ ).

**Table 2.2:** Woody perennial species recorded on study sites

Species	Shrub	Evergreen	Fruit Diameter (mm)
<i>Acacia albida</i>			
<i>Acacia nilotica</i>			
<i>Acacia pennata</i>			
<i>Acacia senegal</i>			
<i>Acacia seyal</i>			
<i>Acacia tortillis</i>			
<i>Balanites aegyptiaca</i>		E	30
<i>Bauhinia rufescens</i>			
<i>Boabab sp.</i>			
<i>Boscia senegalensis</i>	S	E	
<i>Calatropis procera</i>	S	E	100
<i>Cassia sieberiana</i>		E	
<i>Combretum sp.</i>			
<i>Commiphora africana</i>			10
<i>Euphorbia balsamifera</i>	S		
<i>Grewia sp.</i>	S		5
<i>Guiera senegalensis</i>	S	E	
<i>Leptadenia pyrotechnica</i>	S	E	
<i>Maerua crassifolia</i>		E	
<i>Mayetinus senegalensis</i>			7
<i>Mimosa pigra</i>	S		
<i>Mitragyna inermis</i>			
<i>Neem</i>			
<i>Parkia biglobosa</i>			
<i>Piliostigma reticulatum</i>	S	E	
<i>Prosopis juliflora</i>		E	
<i>Salvadora persica</i>	S	E	6
<i>Stereospernum kunthianum</i>			
<i>Tamarindus indica</i>			
<i>Zizyphus mauritiana</i>			15
<i>Zizyphus spina-christi</i>	S		20

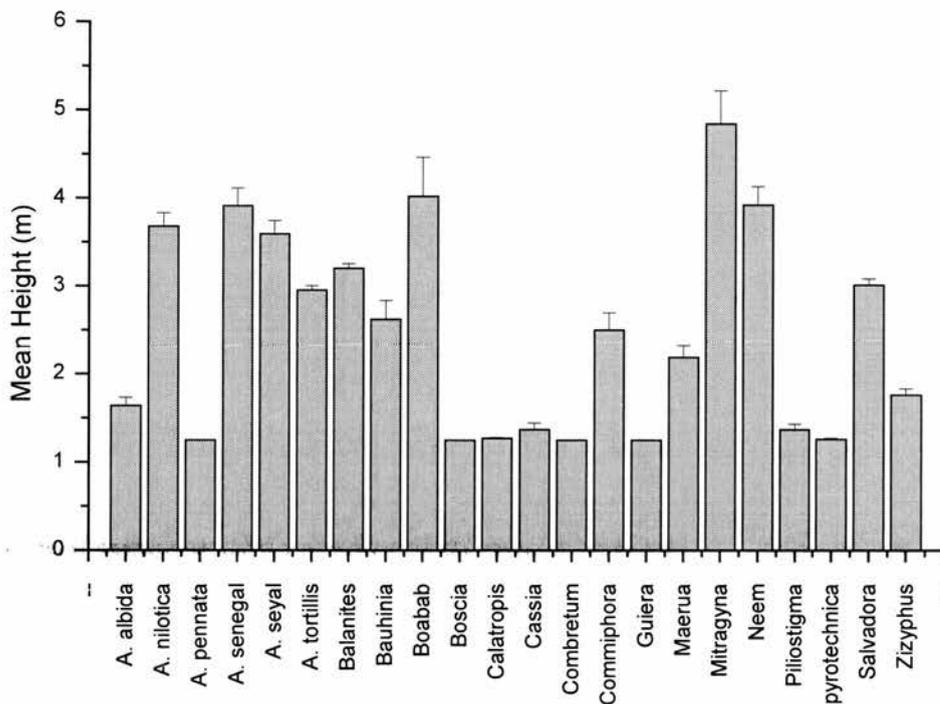
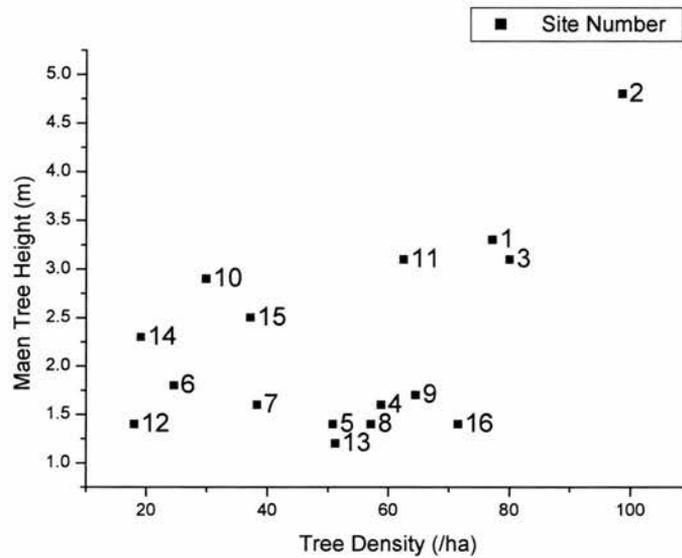


Fig. 2.1: Mean height ( $\pm$ SE) of tree species commonly occurring within the study sites.

Table 2.3: Study site habitat attributes, dominant tree species, tree diversity indices (Shannon-Wiener), habitat class, and percentage of agriculture. Habitat type are; W= woodland, S= open Savanna, A= Agriculture. Tree genus A.= *Acacia*.

Site	Site No	Acacia spp Density (ha)	Balanites Density (ha)	Salvadora Density (ha)	Tree Diversity (S-W)	Number Tree Species	Dominant Tree spp	Prop Dominance	Habitat Type	Percentage Agriculture
Reserve	1	34.3	25.3	12.2	0.6	3.6	<i>A. tortillis</i>	0.3	W	0
Canal	2	92.4	6.0	0.0	0.3	1.9	<i>A. tortillis</i>	0.9	W	0
Wat. FR	3	20.5	53.2	0.0	0.6	2.6	<i>Balanites</i>	0.7	W	0
Nguru agric	4	11.4	0.7	0.0	0.5	4.4	<i>Gueira</i>	0.2	A	87
Wat. Int Ag	5	15.7	1.1	0.0	0.5	2.9	<i>A. albida</i>	0.2	A	92
Wat. Deg. Sav.	6	3.1	19.9	0.0	0.3	1.6	<i>Balanites</i>	0.8	S	1
School	7	17.7	8.5	7.7	0.3	2.8	<i>A. tortillis</i>	0.4	S	12
Bore	8	7.1	0.2	0.0	0.2	2.7	<i>A. tortillis</i>	0.2	S	0
Prat	9	32.8	3.2	9.2	0.4	3.0	<i>A. tortillis</i>	0.4	S	0
Commiphora	10	8.5	2.4	8.6	0.3	3.3	<i>Salvadora</i>	0.4	S	0
Quail	11	43.6	10.8	0.7	0.6	3.3	<i>A. tortillis</i>	0.5	S	0
WofGashua	12	6.5	10.6	0.1	0.2	1.2	<i>Balanites</i>	0.4	S	0
Geidam	13	1.8	5.6	0.0	0.4	1.7	<i>Boscia</i>	0.5	W	34
EofDamasak	14	6.4	10.5	0.1	0.5	1.7	<i>Balanites</i>	0.4	S	0
WofMalamfatori	15	9.9	11.1	0.0	0.5	1.8	<i>Balanites</i>	0.4	S	3
Malam	16	0.2	1.4	39.4	0.6	2.2	<i>Salvadora</i>	0.5	W	13



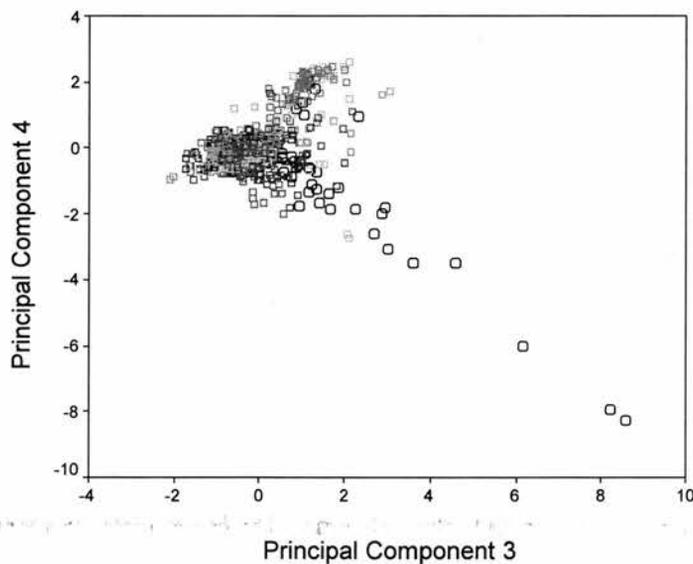
**Fig. 2.2:** Mean tree density and tree height across the 16 study sites. A significant difference in tree density ( $F_{15,725}=13.2$ ,  $p<0.0001$ ) and mean tree height ( $F_{15,725}=47.3$ ,  $p<0.0001$ ) was found across all sites.

### 2.3.1 Between-Site Variation in Habitats

In order to assess habitat differences between sites, a Principal Component Analysis (PCA) was carried out. Five principal components (PC's) derived from 9 key habitat attributes: densities of *Salvadora*, *Balanites*, *Calatropis*, all tree species, *Acacia* tree species and shrub species (excluding *Salvadora*), and mean tree height, tree diversity and percentage of agriculture were used (Table 2.4). Results from One-way ANOVAs of PC's indicated a significant difference in values occurred across sites and habitat classes. Principal components 3 and 4 were selected for use in comparisons across sites and habitat classes due to their relatively high F values. PC3 suggests that the greatest difference is found between sites with relatively high densities of *Salvadora*, all trees, and percentage of agriculture, and those with low *Balanites* density, and low mean tree height. In PC4 the greatest difference is apparent between sites with a high percentage of agriculture, and those with relatively low densities of *Salvadora*. Despite the highly significant differences in both PC3 and PC4 found across sites, a high degree of overlap was apparent (see Fig 2.3).

**Table 2.4:** Contribution of habitat variables to five principal components produced to examine variation of habitat across sites, habitats and between eastern and western study sites.

Variable	Principal Component				
	1	2	3	4	5
Salvadora Density (ha)	0.011	0.137	0.656	-0.648	0.169
Balanites Density (ha)	0.416	0.326	-0.319	-0.021	0.565
Tree Density (ha)	0.784	0.276	0.443	0.057	0.027
Acacia Density (ha)	0.742	0.184	0.156	0.185	-0.512
Shrub Density (ha) –excluding Salvadora	0.802	-0.554	-0.005	0.107	0.142
Calatropis Density (ha)	0.332	-0.848	-0.128	-0.111	0.229
Mean Tree Height (m)	0.357	0.461	-0.483	-0.057	-0.188
Tree Diversity	0.036	0.493	0.099	0.332	0.509
Percentage Agriculture	-0.295	-0.181	0.413	0.701	0.063
$F_{15, 725} =$	23.6	25.0	32.7	44.9	25.8
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001



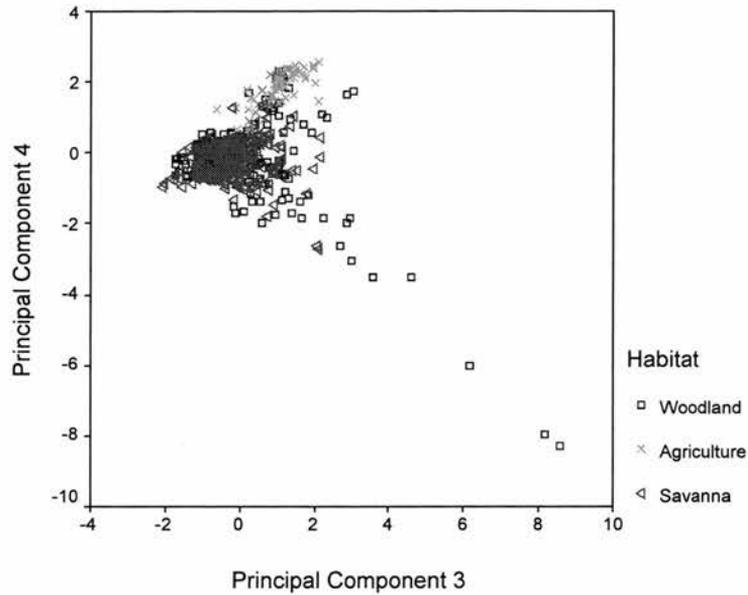
**Fig. 2.3:** Principal component 4 against principal component 3 from habitat PCA grouped by site (each site represented by unique symbols), illustrating the high degree of overlap between sites despite the significant differences across sites found for both PC 3 ( $F_{15,275}=32.7$ ,  $p<0.001$ ) and PC 4 ( $F_{15,275}=44.9$ ,  $p<0.001$ ).

### 2.3.2 Variation in Vegetation components between habitats

When the same PC's were used for comparisons of vegetation characteristics across the three habitat classes (Woodland, open Savanna and Agriculture) a significant difference was found (see Table 2.5). In PC3, this was mainly due to differences between sites with high *Salvadora* density, overall tree density and percentage agriculture, and low *Balanites* density and mean tree height. In PC4, differences between sites with low *Salvadora* density and those with a high percentage of agriculture explained much of the difference between habitat classes. As with between-site differences, a high degree of overlap was apparent between habitats (Figure 2.4).

**Table 2.5:** Between-habitat differences in vegetation Principal Component Analysis.

		Sum of Squares	df	Mean Square	F	P
<b>Principal Component 1</b>	Between Groups	57.715	2	28.858	31.2	<0.0001
	Within Groups	682.285	738	0.925		
	Total	740	740			
<b>Principal Component 2</b>	Between Groups	80.437	2	40.218	45.0	<0.0001
	Within Groups	659.563	738	0.894		
	Total	740	740			
<b>Principal Component 3</b>	Between Groups	100.33	2	50.165	57.9	<0.0001
	Within Groups	639.67	738	0.867		
	Total	740	740			
<b>Principal Component 4</b>	Between Groups	270.181	2	135.09	212.2	<0.0001
	Within Groups	469.819	738	0.637		
	Total	740	740			
<b>Principal Component 5</b>	Between Groups	4.341	2	2.171	2.2	0.114
	Within Groups	735.659	738	0.997		
	Total	740	740			



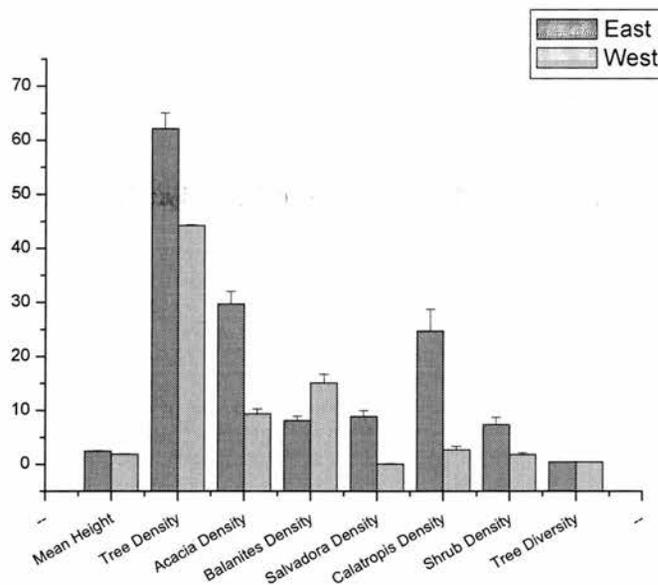
**Fig 2.4:** The variation in vegetation characteristics as described by principal components 3 and 4 between the three broad habitat classes. Both PC3 ( $F_{2,738}=57.9$ ,  $p<0.001$ ) and PC4 ( $F_{2,738}=212.2$ ,  $p<0.001$ ) showed significant differences between habitat classes. Post-hoc analysis indicated PC3 differed significantly between all three habitats, whilst PC4 differed between woodland and both savanna and agriculture ( $p>0.05$ ).

### 2.3.3 Variation in Vegetation components between Eastern and Western Sites

Habitat variables, as described by the three principal components shown in Table 2.4, showed significant variation between eastern and western sites in PC1 and PC3 (Table 2.6). However, in both of these PCs *Salvadora* was a significant factor in explaining these differences, due to its limited distribution in the NE of the study region. When *Salvadora* was excluded from the analyses, PC1 and PC3 still differed significantly between eastern and western sites. The results from PC1 indicated that the greatest difference between east and west was found when comparing sites with low overall tree diversity and high densities of shrubs, all trees and *Acacia* species. Greatest differences in PC3 were found between sites with low *Acacia* and all tree density with those with high densities of *Balanites*. It would therefore appear that habitats did vary significantly between east and western sites. Differences in vegetation parameters between eastern and western study sites are illustrated in Figure 2.5.

**Table 2.6:** Three principal components used for comparisons of habitat between eastern and western study sites, and three PCs when *Salvadora persica* is removed.

	Including <i>Salvadora</i>			Excluding <i>Salvadora</i>		
	1**	2	3**	1**	2	3**
<b>Balanites Density (ha)</b>	0.386	0.332	-0.307	0.386	0.344	0.653
<b>Tree Density (ha)</b>	0.792	0.341	0.358	0.793	0.317	-0.166
<b>Acacia Density (ha)</b>	0.744	0.235	0.059	0.744	0.239	-0.526
<b>Shrub Density (ha) —excluding <i>Salvadora</i></b>	0.837	-0.505	-0.055	0.837	-0.501	0.141
<b>Calatropis Density (ha)</b>	0.362	-0.843	-0.062	0.361	-0.844	0.281
<b>Salvadora Density (ha)</b>	-0.007	0.128	0.86			
<b>Mean Tree Height (m)</b>	0.308	0.45	-0.431	0.308	0.468	0.119
<b>Tree Diversity</b>	0.034	0.518	-0.058	0.034	0.519	0.396
<b>F<sub>1,739</sub> =</b>	41.3	0.1	23.0	41.5	0.7	21.3
<b>P</b>	<0.0001	0.731	<0.0001	<0.0001	0.411	0

**Fig 2.5:** Variation in habitat parameters between eastern and western study sites ( $\pm$ SE). Tree height (m), tree densities (per 25m radius plot), tree diversity (Shannon-Wiener Index). All variables showed significant differences ( $F_{1,739} > 17.0$ ,  $p < 0.01$ ) except Tree Diversity.

## 2.4 Study Bird Species Descriptions

Palaearctic warblers were selected for the main focus of this thesis as the groups is relatively common and widespread within the Sahel, with European breeding populations significantly affected by conditions within African wintering grounds (Baillie and Peach, 1992; Winstanley *et al* 1974; etc). Afrotropical warblers or their equivalents were also studied as they are presumably affected by many of the same factors as their Palaearctic counterparts, and are potential competitors for Palaearctic species during the Northern winter. Bird study species scientific names, body mass, residency class, breeding season, foraging guild and diet are presented in Table 2.7. Only the resident African race of Eastern Olivaceous Warbler *Hippolais pallida laeneni*, formerly considered conspecific with Western Olivaceous Warbler *Hippolais opaca* is considered here (Knox 2001).

## 2.5 Invertebrate Sampling

Invertebrates were sampled following the protocol established by Vickery *et al.* (1999). Dominant tree species were sampled at each site, with a minimum of 10 individuals of each species selected at random at each site during each study period. A 1m<sup>2</sup> beating tray was held under the tree 'canopy' and the foliage within 0.5m above this struck with a large stick 10 times. Invertebrates were identified to order and their length measured. Sampling was carried out during the 3 hour period following local sunrise. Unfortunately strong Haarmattan winds during Jan-March made sampling impractical during this period, with beating tray contents blowing on to the ground. Variables recorded were:

- Number of invertebrates
- No. within each invertebrate order
- Length of each invertebrate
- Tree species
- Tree height
- Canopy density (open, moderate, dense)
- Tree % leaf
- Flowering/ fruiting status
- Date
- Site
- Time
- Wind strength
- Dust level

Previous authors have excluded ants from analyses of invertebrate abundance due to their apparent unpalatability to birds (Jones *et al.* 1996; Morel and Morel 1992; Vickery *et al.* 1999), despite other studies finding ants are an important component of the diets of a number small insectivores both in the Sahel and on migration (Cramp 1992; Stoate and Moreby 1995). In this study analyses were carried out for abundance of all invertebrates and invertebrate abundance when ants were excluded. Results are presented in Chapter 5.

**Table 2.7:** Bird species included within analyses. **Residency:** A= Afrotropical 'resident', P= Palearctic migrant, AP= Afrotropical and/or Palearctic populations may be present. **Breeding Season:** R= Rains, D= Dry Season, N= Northern temperate summer. **Foraging Guild:** G=Gleaner, **Diet:** I= Insectivore, G= Granivore. O=Omnivore, C= Carnivore, F= Frugivore, N= Nectivore.

Common Name	Scientific Name	Body Mass (g)	Residency	Breeding Season	Foraging Guild	Diet
Brubru	<i>Nilaus afer</i>	22-25g	A	D	G	I
Cricket Warbler	<i>Spiloptila clamans</i>	6-8g	A	R	G	I
Northern Crombec	<i>Sylvietta brachyura</i>	6-8g	A	R	G	I
Yellow-bellied Eromemola	<i>Eremomela icteropygialis</i>	6-8g	A	R	G	I
Acacia Warbler	<i>Phylloscopus pulchella</i>	6g	A	R	G	I
Little Weaver	<i>Ploceus luteolus</i>	13g	A	R	G	IGF
Grey-backed Camaroptera	<i>Camaroptera brachyura</i>	9.5-11.5g	A	RD	G	I
Sennar Penduline Tit	<i>Anthoscopus punctifrons</i>	6-7g	A	U	G	I
Olivaceous Warbler	<i>Hippolais pallida</i>	8-13g	A	R	G	I
Pygmy Sunbird	<i>Anthreptes platurus</i>	5.2-7.2g	A	D	G	IN
Beautiful Sunbird	<i>Nectarinia pulchella</i>	6-8g	A	R	G	IN
Scarlet-chested Sunbird	<i>Nectarinia senegalensis</i>	7-12g	A	R	G	IN
Lesser Whitethroat	<i>Sylvia curruca</i>	10-14g	P	N	G	I
Common Whitethroat	<i>Sylvia communis</i>	13-18g	P	N	G	I
Subalpine Warbler	<i>Sylvia cantillans</i>	8-13g	P	N	G	I
Orphean Warbler	<i>Sylvia hortensis</i>	16-25g	P	N	G	I
Bonelli's Warbler	<i>Phylloscopus bonelli</i>	7-11g	P	N	G	I
Willow Warbler	<i>Phylloscopus trochilus</i>	7-12g	P	N	G	I
Wood Warbler	<i>Phylloscopus sibilatrix</i>	8-12g	P	N	G	I

## 2.6 Point Counts

### 2.6.1 Point Count Assumptions

Bird censuses were carried out using exact distance point counts. The assumptions of these counts are:

1. Birds at 0 m from the point are certain to be detected
2. Birds are detected at their initial location
3. Birds do not flee/ approach the observer
4. Birds moving into/ across the point during the count are not included
5. Individuals are not double counted
6. Birds (or defined flocks) behave independently of one another
7. Birds are correctly identified
8. Distances to birds are measured exactly.

(from Bibby *et al.* 2003; Buckland *et al.* 2001)

### 2.6.2 Point Count Periods

Point counts were carried out within defined seasonal study sessions in order to allow any temporal changes in avian densities to be identified. Count sessions comprised of six-week sessions, with the mid winter session centred on the winter solstice, taken to be Dec 22<sup>nd</sup>. These six-week sessions were deemed sufficiently broad to encompass distinct Palearctic migrant periods of passage and/or residency, whilst remaining narrow enough to identify potential changes in densities within autumn, winter and spring periods. Study sessions were:

- |                        |   |
|------------------------|---|
| 1. <i>mid autumn</i>   | <i>Sept 1<sup>st</sup> – Oct 14<sup>th</sup></i>    |
| 2. <i>late autumn</i>  | <i>Oct 15<sup>th</sup> – Nov 28<sup>th</sup></i>    |
| 3. <i>mid winter</i>   | <i>Nov 29<sup>th</sup> - Jan 12<sup>th</sup></i>    |
| 4. <i>early spring</i> | <i>Jan 13<sup>th</sup> - Feb 28<sup>th</sup></i>    |
| 5. <i>mid spring</i>   | <i>March 1<sup>st</sup> - April 22<sup>nd</sup></i> |

### **2.6.3 Point Count Transect Locations and Bearings**

The start point and bearing for each transect was established at random within each study area. Points were located at 110m intervals along each transect. At each point the latitude and longitude were logged using a Garmin 12 GPS. The 'Position Averaging Function' allowed an accuracy of 5m to be obtained. GPS locations were augmented with descriptions using compass bearings and distances to landmarks. On completion of each point count the observer continued along the transect line, using the GPS to give the distance to previous point, before stopping and repeating the count procedure at the required distance.

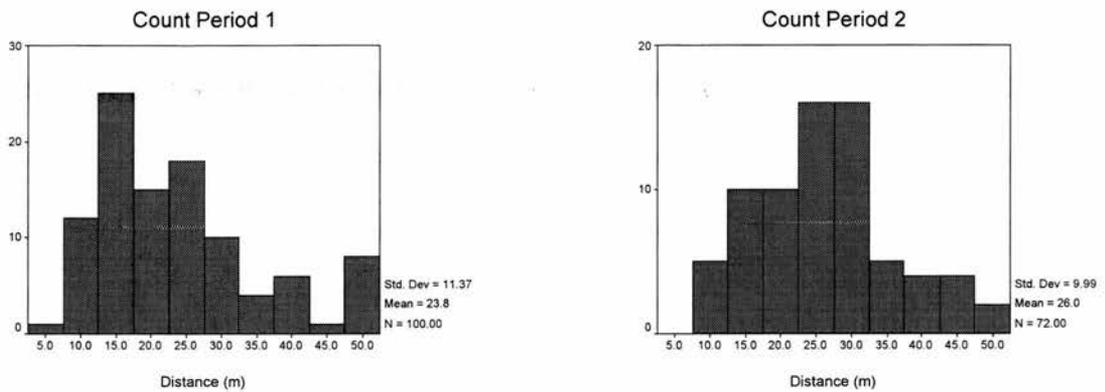
### **2.6.4 Count Length**

Point count methodologies incorporating a detectability function do not assume that all individuals present are found, only that those that are 0m from the observer are certain to be detected. Counts should aim to provide a 'snapshot' of individuals present, i.e. count length should be minimised as much as practical to limit the number of birds moving into or out of the count area, whilst at the same time ensuring the majority of individuals present are observed. A count period of 3 minutes gave sufficient time to provide a representative sample of birds present.

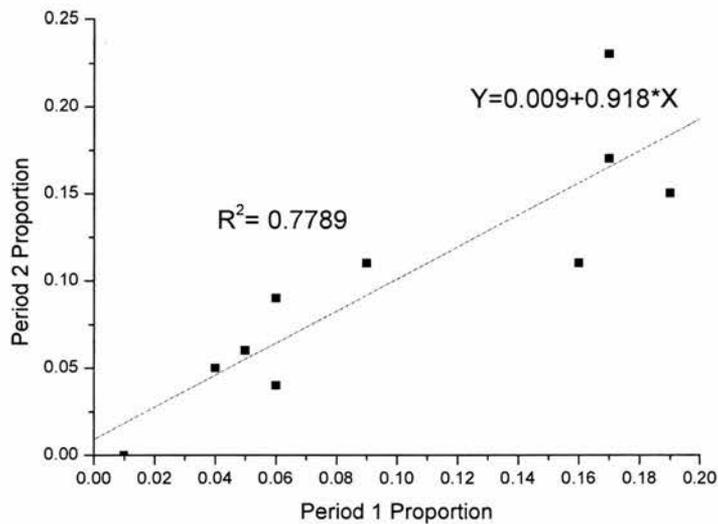
### **2.6.5 Count 'Settling' Period**

Frequently a 'settling' period prior to the initiation of a point count is used in order to allow any disturbance caused by the arrival of the observer to subside. The effect of such a settling period upon detection distance and the number of individuals observed was tested in this study. Seventeen point counts were carried out, with all observations within an initial 3 minutes separated from those occurring in a second 3 minutes period that immediately followed the first. Distances at which each individual bird was initially located for each count period did not differ significantly (Fig 2.6). The small peak in observations at 45-50m during count period 1 would suggest evasive movement from the observer was taking place. However, the overall peak in observations during count period 1 was closer to the observer than period 2. This would suggest that evasive movement during count period one does not occur and that a settling period prior to each count is unnecessary. This is supported by the significant correlation found in the

proportion of individuals observed within 10 distance categories between the two count periods (see Fig 2.7).



**Fig 2.6:** Histogram of distances from the observer at which warbler species were initially located during the initial and second 3 minute count periods. No significant difference was found between count periods (Kruskall Wallis  $\chi^2=3.679$ ,  $p=0.06$ ,  $df=1$ ) indicating that a settling period was not necessary.



**Fig 2.7:** The proportion of observations within 50m in 10 distance classes during two consecutive 3 minute count periods. A significant correlation was found between the two groups ( $F_{1,8}=15.7$ ,  $p=0.004$ ) indicating comparable detection distances between count periods.

The mean number of individuals observed within 50m of the observer during the first count period was 6.24, significantly greater than the 4.47 observed during count period 2 ( $p=0.014$ ,  $t=2.762$ ,  $df=16$ ). Examination of the count distributions indicated that a greater number of points contained no individuals in the second count period than the

first, rather than count periods generally holding fewer birds. This would suggest that birds are moving away from the observer during the initial 3-minute count period. Counts carried out during the second count period would therefore underestimate species abundance. The use of a longer settling period may allow these individuals to return, however the length of the period required may be prohibitively long. There was therefore insufficient evidence for the inclusion of a settling period prior to each point count. The exclusion of a settling period increased the number of counts it was possible to complete each morning by approximately 50%.

### 2.6.6 Detection by Sight or Call

Analyses of the proportion of all detections made by sound (i.e. individuals detected by call or song) indicated that variation in song and call rate did not differ significantly with season or site. However, analysis of the proportion of individuals located by call versus sight during each visit to each study site indicated that a significantly larger proportion of African warblers than Palearctic warblers were detected by call or song ( $F_{1,68}=4.4$ ,  $p<0.0001$ ), with relative proportions of 0.60 and 0.18 respectively. This is probably due to the highly vocal nature of one species of Afrotropical warbler, Olivaceous Warbler, which was located by call or song on a significantly greater proportion of occasions than the Afrotropical Warbler group ( $F_{1,79}=51.4$ ,  $p<0.0001$ ). Comparisons of the proportion of Palearctic, and Afrotropical warblers excluding Olivaceous warbler, located by call indicate that there was also a significant difference however ( $F_{1,90}=163.7$ ,  $p<0.0001$ ), with the proportion of individuals located by call 0.18 and 0.71 for Palearctic and Afrotropical species respectively. This would suggest that Palearctic species might be more visible than Afrotropical species, or occur in more open habitats. No significant seasonal difference in the proportion of individuals located by call was evident for Palearctic Warblers, Afrotropical Warblers, Not Olivaceous Warblers, or Olivaceous Warblers ( $F_{4,41}<1.0$ ,  $p>0.05$ ). The possibility that the inclusion of both visual and vocal detections may cause bias in the detection probability curve, due to the extended distance at which vocal detections could be made compared to visual detections, was considered. However, the lack of seasonal change in the calling rates of either Palearctic or Afrotropical species suggests that any such bias would remain constant within the study.

### 2.6.7 Effect of Time of Day

The proportions of Palearctic Warblers, Afrotropical Warblers and Not Olivaceous Warblers individuals located by call or song showed no significant linear, quadratic or cubic relationship with minutes after sunrise ( $p > 0.05$ ,  $df = 14$ ). It would therefore appear that call/ song rates do not decline with time of day at rates out of proportion to any declines in detection rates that may occur.

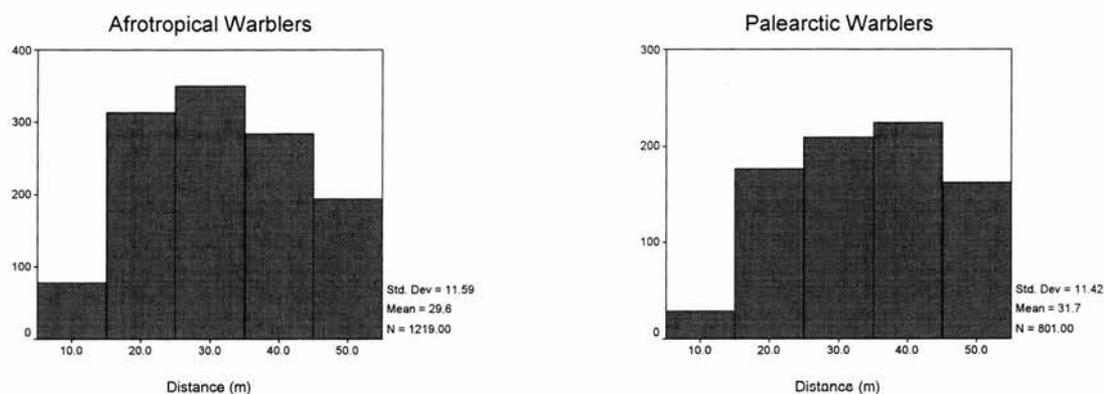
A decline in bird activity following a post-dawn peak was expected due to declining foraging activity and increasing temperatures. This was tested using a general linear model with raw count of warblers at each point as dependent variable and minutes after sunrise, residency, and the interaction between residency and minutes after sunrise as explanatory variables. The model assumed a Poisson distribution and a link function. Results indicated that the number of Palearctic individuals recorded declined significantly with minutes after sunrise, whilst no significant relationship was found in Afrotropical species (Table 2.8) It was possible that the lack of a significant effect of minutes after sunrise upon the number of Afrotropical warblers observed was due to the highly vocal nature of Olivaceous Warbler. This common Afrotropical warbler species sings throughout much of the day and therefore may have maintained a relatively consistent detection probability when compared to Palearctic species. The analysis was therefore repeated with Olivaceous Warbler and other Afrotropical warbler species separated from one another, with neither showing a significant relationship with minutes after sunrise. Comparisons of relative proportions of detections by sound and sight indicate no diurnal variation in either Palearctic or Afrotropical warbler species. It therefore appears that time of day effects Palearctic species but not Afrotropical. Point counts were therefore carried out during a 2.5 hour period following local sunrise (calculated using the GPS). Bird activity was extremely low during the late afternoon (pers obs) and no counts were carried out during this period. No significant difference was found in the time point counts were carried out and year, season, study site, or between eastern and western study sites ( $F_{1,739} < 2.0$ ,  $p > 0.05$ ).

**Table 2.8:** Results from the GLM assessing the effects of minutes after sunrise upon the detection of Afrotropical and Palearctic warbler species.  $P_{crit}=0.02$ , residual variance =6222.3147, residual df= 3725, residual variance/ residual df=1.6704,  $R^2=0.02$ . The estimate shows the direction and strength of relationships within the crossed design.

Source	DF	F	p		estimate
<b>Residency</b>	1, 3722	0.28	0.5971	<b>Afrotrop</b>	0.047
				<b>Palea</b>	0.000
<b>Minutes after sunrise</b>	1, 3722	12.5	0.0004		0.001
<b>Residency * Minutes after sunrise</b>	1, 3722	21.4	<0.0001	<b>Afrotrop</b>	0.000
				<b>Palea</b>	-0.005

### 2.6.8 Comparison of Detection Distance Between Afrotropical and Palearctic Warbler Species

Significant differences were present in the distribution of distances at which Afrotropical and Palearctic warblers were initially detected (see Fig 2.9). This appears to be due to a greater proportion of Palearctic species being detected at a greater distance (40m) than their Afrotropical counterparts (30m). A greater proportion of Olivaceous Warbler were located by call than both Palearctic Warbler Group and Not Olivaceous Warbler Group (see above). One would therefore have expected Afrotropical warblers to be located at greater distances than Palearctic if detection distance was purely a function of vocalisation behaviour. This suggests that the greater distance at which Palearctic Warbler Group were located may have been due to their greater visibility. To further explore the relationship between the detection distance of Palearctic and Afrotropical warbler, the mean distances at which individual birds were detected were compared between residency groups using One-way ANOVA. Results indicated that no significant difference occurred  $F_{1,170}=1.7$ ,  $p=0.196$ . This supports the assumption that detection distances were comparable between groups, and that the use of raw count data in some analyses would be appropriate. For estimation of densities of each species, Distance software allows detection probability curves to be produced for each species and therefore accounts for any interspecific variation in detection.



**Fig 2.9:** Histogram of distances from the observer at which Afrotropical (left) and Palearctic (right) warbler species were initially located. A significant difference was found between the two groups ( $\chi^2=16.025$ ,  $p<0.0001$ ,  $df=1$ ).

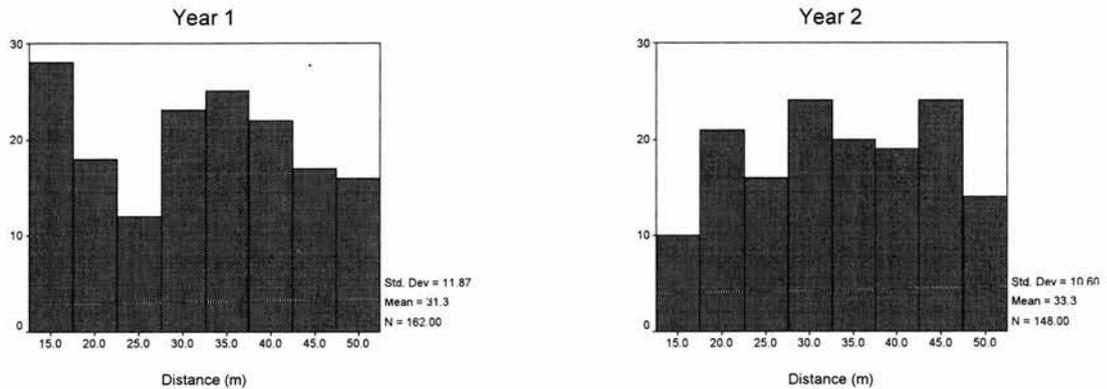
### 2.6.9 Between Year Variation in Detection Distance

Data from the two mid-winter periods were used to test for between year differences in detection distances. No significant differences were found between years in Afrotropical warblers ( $\chi^2=2.474$ ,  $df=1$ ,  $p=0.116$ ) or in Palearctic warbler detection distances (see Fig 2.10).

### 2.6.10 Point Count Protocols

Points were surveyed once during each count session, with individual points revisited during subsequent count sessions. In total, 1861 point counts were completed by three observers, 88% by Jared Wilson (JW), 7% by Ross McGregor (RM) and 5% by Paavo Salinen (PS) at sixteen study sites over five study periods (Table 2.9). Point count length (3 minutes) was timed using a digital watch with countdown alarm. Variables recorded at each point are given in Table 2.10. Point locations were recorded using a Garmin 12 GPS and using descriptions relative to landmarks, Haarmattan wind strength was estimated using the Beaufort scale, and dust levels were classed as low, moderate and high. Exact distances were measured using a Bushnell Yardage Pro™ laser rangefinder with a range of 10-700m and an accuracy of 1m. Distances less than 10m were estimated by eye, with regular calibration checks of estimated distances made using measured distances. Points were relocated using the GPS GOTO function and point descriptions. Any points which during subsequent visits had gained Fulani herdsman camps (a not unknown occurrence) were excluded until they had departed. Birds were identified to species by sight or call during each point count, with reference

to Borrow and Demey (2001), Svensson *et al.* (1999), or Roche (1996) made later if identification was uncertain.



**Fig 2.10:** Histogram of distances from the observer at which Palearctic warbler species were initially located between the two study years. No significant difference was found between the two years ( $\chi^2 = 2.026$ ,  $df=1$ ,  $p=0.155$ ).

**Table 2.9:** Number of Point Counts Completed at Each Site During Each Count Period (Round)

Site No	Location	Name	RND 1	RND 2	RND 3	RND 4	RND 5	RND 6	RND 7	TOTAL
			Nov-01	Dec/Jan-02	Feb/Mar-02	Apr-02	Oct-02	Nov-02	Dec-02	
1	Alagarno	Reserve	60	59	60	60	32	32	32	335
2	Alagarno	Canal	60	58	57	60	31	31	28	325
3	Nguru	Watucal FR		50	48	48			31	177
4	Nguru	Nguru Agric		50	50	50			26	176
5	Nguru	Watucal Agric		29						29
6	Nguru	Watucal Rd		28	28	28				84
7	Alagarno	School		44	29	29	29	29	29	189
8	Alagarno	Bore Hole		44	28		27	18	27	144
9	Alagarno	Pratincole		57						57
10	Alagarno	Commiphora		36	28					64
11	Alagarno	Quail		36						36
12	Transect	Gashua							49	49
13	Transect	Geidam							49	49
14	Transect	Damasak							48	48
15	Transect	WofMalam							50	50
16	Transect	Malafatori							49	49
		<b>TOTAL</b>	<b>120</b>	<b>491</b>	<b>328</b>	<b>275</b>	<b>119</b>	<b>110</b>	<b>418</b>	<b>1861</b>

**Table 2.10:** Variables recorded at each point count

<b>Prior to Count</b>	<b>During Count</b>
Date	Bird species
GPS Location	Distance to bird
Location Description	Number of individuals
Haarmattan wind strength	Substrate of bird (tree [species], ground, flight)
Haarmattan dust level	How bird initially located (sight, call, both)
Start time	
Minutes after local sunrise	

## 2.7 Distance Sampling Software Methodology

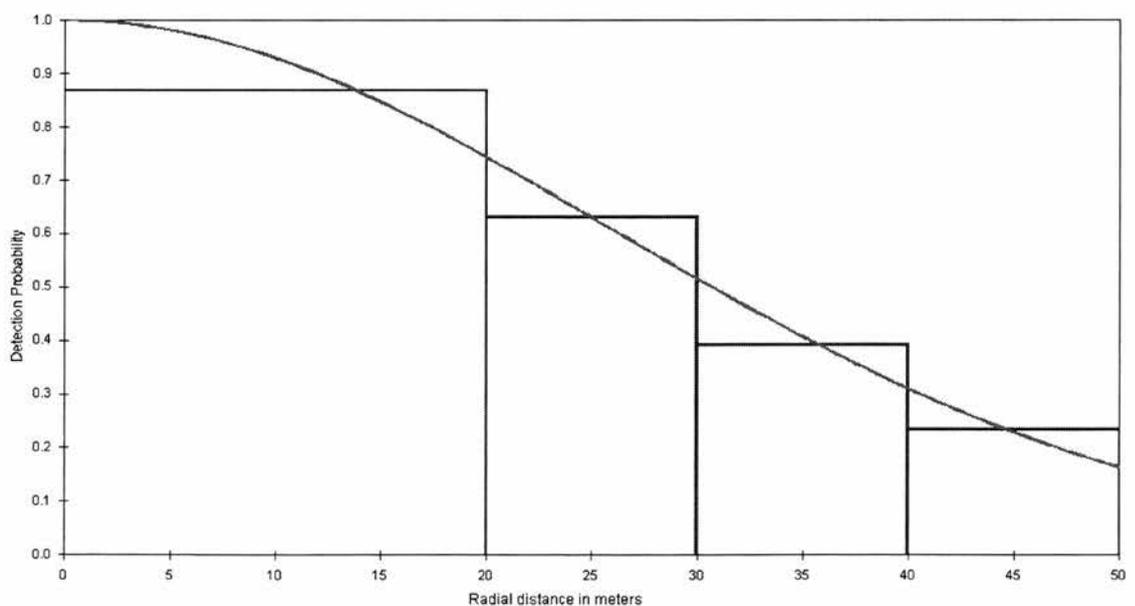
Distance sampling methodology used here follows Buckland *et al.* (2001). Right truncation was set at a maximum of 50m in order to maintain the independence of each point, which was every 110m along a transect. For all species of gleaners, a 50m cut-off resulted in 85% of all observations remaining within the analyses. As would be expected for species associated with more open habitats, the mean number of observations of chats, larks and shrikes included in the analyses fell to 56% of the original number when right truncated at 50m. No left truncation was used as it can have significant effects upon the data through the loss of observations close to the observer, a major determinant of the slope of  $f(x)$  at 0 (Buckland *et al.* 2001). Bin width selection overcame the potential problem of grouping of observations and resulted in good model fit (Len Thomas pers comm). The half normal key function with cosine expansion model was selected for the detection function as this provided the best data fit using AIC (see Table 2.11 for generic model design used).

For each focal species a histogram of distances was plotted to allow preliminary assessment of data for grouping, evasive behaviour, etc. Data 'bins' were initially set using information gained from the histogram, and were later adjusted using expected and observed frequency values produced in the models' chi-square goodness of fit test. This information was incorporated into subsequent test models alongside detectability plots, Akaike's Information Criterion (AIC), Chi-square GOF, and % CV to

develop the 'best' model possible. An example of a detection density plot for Olivaceous Warbler is presented in Figure 2.11.

**Table 2.11:** Multiple Covariate Distance Analysis (MCDS) General Model Parameters

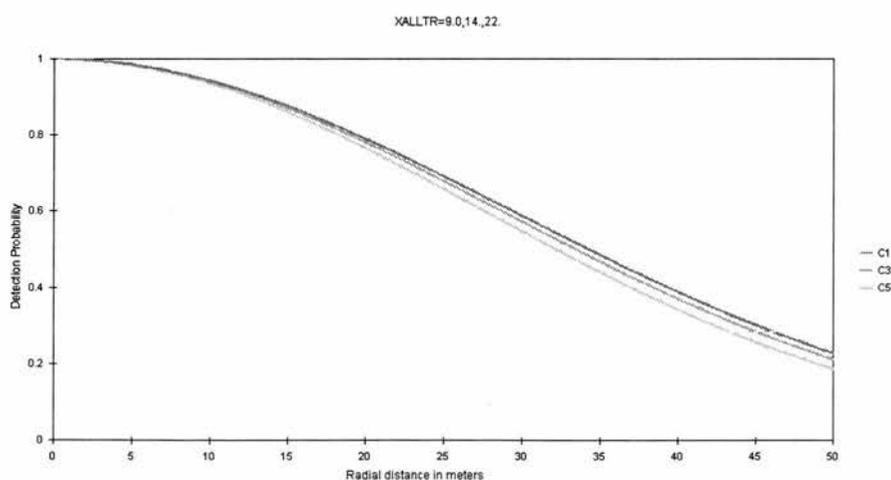
Parameter	Selection
<b>Data Filter</b>	
Data Selection	<i>by species</i>
Intervals	<i>see table</i>
Truncation	<i>see table</i>
<b>Model Definition</b>	
<b>Estimate</b>	
Stratum Definition	<i>by stratum (round * site)</i>
Density	<i>by stratum (round * site)</i>
Encounter Rate	<i>by stratum (round * site)</i>
Detection Function	<i>global</i>
<b>Detection Function</b>	
Models	<i>half-normal cosine</i>
Adjustment Terms	<i>manual selection</i>
Covariates	<i>see table</i>
Constraints	<i>none</i>
Diagnostics	<i>default</i>
<b>Cluster Size</b>	<i>N/A</i>
<b>Multipliers</b>	<i>N/A</i>
<b>Variance</b>	<i>estimated empirically</i>
<b>Miscellaneous</b>	<i>2-sided 95% confidence limits</i>



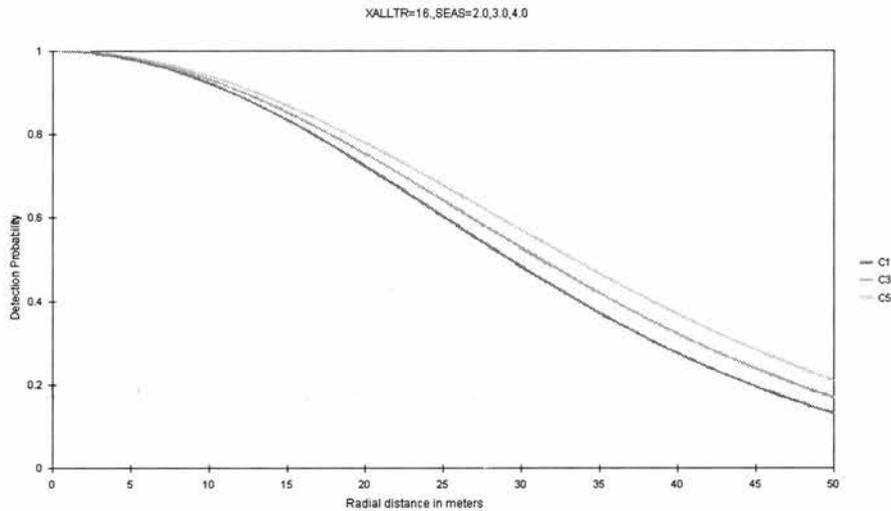
**Fig 2.11:** Example detectability density plot using Distance software for Olivaceous Warbler (n=785).

### 2.7.1 Covariates Within Distance Analysis

A number of covariates that are potentially significant (alongside distance from observer) to the detection probability plots were identified. For all bird species, the high degree of variation in tree density was likely to be an important factor in determining detection probability of an individual. Therefore tree density (taken from vegetation plots at each point) was included as a covariate within Multiple Covariate Distance Sampling (MCDS) models. For certain species season could play an important role in detectability, through seasonal changes in bird behaviour, vocalisation rate etc. As discussed previously, minutes after sunrise can effect detection probability due to diurnal changes in activity and was included as a potential covariate. However, it did not improve the model fit and was therefore excluded. Covariates were included only where prudent and were added in a stepwise fashion comparing model AIC in order to gain the model with the 'best fit'. Details of model components (bin size, bin intervals, right truncation distance, MCDS covariates, number of observed individuals, AIC, GOF and % CV,) for each species are given in Table 2.12. Examples of the effects of inclusion of two covariates upon detection probability plots are presented in Figures 2.12 and 2.13.



**Fig 2.12:** Distance detectability probability plots at C1 high (22), C2 moderate (14), and C3 low (9) tree densities (ha) for Gleaning Birds



**Fig 2.13:** Distance detectability probability lots during late autumn (C1), mid winter (C2), and early spring (C3) for Olivaceous Warbler

### 2.7.2 Effect of Observer

The level of skill in detecting and identifying a bird, as well as accurately measuring its distance from the observer, may all vary significantly between observers. The use of laser range-finders removes the problem of biases through variation in distance estimation between observers, as well as distance rounding, but not those of variation in detection (or identification) ability. If the ability to detect (or identify) individuals varies between observers, then the amplitude of the detection function curve will vary, though its shape will remain constant. Use of observers with highly developed field ornithology skills, as in this study; greatly reduce the biases associated with variation in detection and identification skills.

If the effort given to each distance from the observer varies i.e. observer *a* focuses upon a band at 40-50m, and observer *b* at 10-20m, the shape of the detection function will be affected, and resultant density estimates may differ. Significant inter-observer variation in either the rate of detection, or the distance at which birds were detected would require separate analysis. Effect of observer on detection probability in season one was assessed by comparing distance distributions from point counts carried out by JW and RM at the same study sites (but not points) on the same dates during the mid winter period. Comparisons were made using Kruskal-Wallis and showed no significant difference between observers ( $\chi^2=0.228$ ,  $p=0.633$ ,  $df=1$ ).

**Table 2.12:** Multiple Covariate Distance Sampling (MCDS) analysis model parameters for each study species. Candidate covariates included within each model were Tree Density (T), Season (S), and Flock Size (F).

Species	Left Bin (m)	Bin (m)	Right Truncation (m)	Covariates	Number of Observations	% CV	Goodness of Fit	Probability of Detection
Beautiful Sunbird	20	15	50	T	53	12.08		0.60
Bonellis Warbler	20	5	50	T	60	11.51	0.86	0.21
Brubru	20	10	50	T	28	22.05	0.67	0.63
Common Whitethroat	30	7	50	T	586	2.73	0.32	0.32
Cricket Warbler	15	10	45	T	22	4.89	0.35	0.50
Gleaners	20	10	50	T	2917	1.34	0.09	0.49
Gleaners (Palearctic)	20	10	50	T	1200	1.97	0.07	0.56
Grey-backed Camaroptera	10	10	50	T	36	22.14	0.11	0.34
Lesser Whitethroat	20	10, 5	50	T	245	4.78	0.48	0.47
Little Weaver	10	5	50	T	153	7.19	0.36	0.35
Northern Crombec	10	5	45	T	54	57.05	0.40	0.44
Olivaceous Warbler	20	10	50	TS	845	2.6		0.46
Orphean Warbler	20	5	50	T	16	25.19	0.58	0.41
Pygmy Sunbird	20	15	50	T	134	7.41		0.34
Sennar Penduline Tit	20	15	50	T	16	101.8		0.19
Subalpine Warbler	20	10	50	T	297	11.71	0.26	0.52
Warblers ( African)	20	10	50	T	1572	1.93	0.77	0.43
Warblers (African- not Olivaceous)	10	10	50	T	704	2.99	0.45	0.39
Warblers (Palearctic)	20	10	50	T	1200	1.97	0.07	0.56
Yellow-bellied Eromemola	15	10	45	T	36	12.81	0.25	0.54

Effect of observer on detection probability was assessed during season two using a series of 37 point counts carried out by each observer over a two day period. The mean number of sightings and distance to birds at each point were compared between observers using a paired t-test. There was no significant difference in mean distance to bird between PS and JW ( $t=0.895$ ,  $df= 36$ ,  $p=0.376$ ). Potential observer biases were tested using Kruskal-Wallis to compare distributions of distances recorded by each observer for all points. Results showed the null hypothesis, that there were no significant differences between observers, could not be rejected ( $\chi^2=0.19$ ,  $df= 1$ ,  $p=0.892$ ). Therefore observer was not found to be a significant factor and is ignored as a covariate in Distance (and SAS) analyses.

For all species with sufficient registrations within 50m, density estimates per hectare with upper and lower 95% confidence limits were calculated for each visit to each site.

## 2.10 Foraging Protocol

Due to relative ease of access, the Canal and Reserve study sites were selected for foraging observations; both sites were within the Alagarno area. Observations were made during mid autumn, late autumn and mid-winter of 2002.

The following Palearctic (P) and Afrotropical (A) *Sylviidae* were selected as focal study species:

- Olivaceous Warbler (A)
- Acacia Warbler (A)
- Cricket Warbler (A)
- Yellow-bellied Eromemola (A)
- Grey-backed Camaroptera (A)
- Northern Crombec (A)
- Little Weaver (A)
- Common Whitethroat (P)
- Lesser Whitethroat (P)
- Subalpine Warbler (P)
- Bonelli's Warbler (P)

Within each study site, focal bird species were searched for by two observers along a randomly placed transect. After each observation was completed, a minimum of 100m was walked before a subsequent observation of the same species was carried out, and transects were not used more than once during each study period. Thus the likelihood of the same individuals being observed during each study period was minimised. Each observation lasted a maximum of 180 seconds. A countdown digital watch with alarm allowed each of these observations to be broken down into 30 second blocks. All observations were dictated onto a Philips Dictaphone and later transcribed. Movement, feeding attempts, song/ call events, and each change in bird height or location within tree canopy were recorded continuously. Rates per second were then calculated for these variables. Variables recorded during each observation were:

### General

- Date
- Site
- Start time
- Length of observation

### Bird

- Species
- Flock or individual (and flock composition)
- Age & sex (where possible)

### Tree

- Species
- fruit/ flower/ seed
- Height
- % bare ground cover
- % leaf

**Activities**

- Location of bird in tree: top, middle, bottom / interior, exterior. **FS**
- Height of bird. **MS**
- Movement: hop, run, jump, fly. **TS**
- Horizontal distance moved. **TS**
- Vertical distance moved. **TS**
- Number feeding attempts ('pecks' at presumed prey). **FS**
- Feeding technique used: standing, jumping, jump-flight, flight (sally), hover. **FS**
- Prey size: small, medium, large. **FS**
- Prey substrate: air, branch, twig, trunk, leaf. **FS**
- Prey type: unknown, order. **FS**
- Song events. **FS**
- Call events. **FS**
- Chase events: who, what, where, duration. **FS**

**FS**= Frequencies per second were calculated for each observation.

**MS**= Mean values per observation calculated

**TS**= Total distance moved in each observation transformed into rate per second

A second methodology, where a focal tree was observed for a set period of time and foraging observations made of any focal species entering the tree, was quickly dropped. It was found to be a highly inefficient use of time, with the majority of observations yielding zero birds. Also it was not possible to observe prey items taken during foraging observations and therefore prey size and type was excluded from further analysis.

## 2.11 Habitat Modelling

Habitat data collected from the 25m radius vegetation plots were combined with raw counts of birds within a 50m radius of the point, the latter derived from point count data. The data set was randomly split into two sub-sets containing 85% (Initial data set) and 15% (Validation data set) of data respectively. The Initial data set was used to produce habitat preference General Linear Models (GLM's) using the protocol described below, the Validation data was then used for model validation.

Before any models were run, an assessment of variables likely to be significant for any of the focal bird species was made based of field observation. From previous studies (Vickery *et al.* 1999; Jones *et al.* 1996; Stoate *et al.* 2001) and observations during fieldwork, eight variables were identified as potential predictors of bird presence for use within habitat models. This resulted in a range of suspected and potential explanatory variables to be tested whilst avoiding data 'dredging' from taking place (Burnham and

Anderson 2002). Prior selection of variables removed the need for arbitrary or stepwise/automatic selection procedures, both of which have come under criticism (Altman and Anderson 1989; Guisan and Zimmermann 2000; Guisan *et al.* 2002; James and McCulloch 1990). No covariates were excluded solely on the basis of significant correlation with other covariates, as this may have resulted in the elimination of significant variables (James and McCulloch 1990). Three variables (Season, Year, and Minutes after Sunrise) were included in all models as they were assumed to have significant effects upon bird presence or detectability, and so were accounted for but were not of specific interest. This standard pool of covariates allowed predicted significant variables to be tested within a standardised framework for each species. The aim of this methodology was to maintain a degree of objectivity (and repeatability) and limit the likelihood of committing type I errors through use of excessive numbers of variables, so called ‘data-dredging’ (Burnham and Anderson 2002).

A linear relationship between each habitat variable and bird species occurrence was tested for, and any variables exhibiting a curved relationship were quadratic transformed before inclusion in GLM's. Residual deviance and residual degrees of freedom, alongside their ratio were used to assess the suitability of the data for use in GLM's (Crawley 1993). Habitat and environmental variables used in the analyses are presented in Table 2.13.

**Table 2.13:** Habitat variables recorded at each 25m radius vegetation plot centred at each point count, and names for inclusion within candidate general linear models. Densities presented are number of trees per plot.

Variable Name	Description
Mean Height	Mean height of all trees over 0.5m height
Tree Density	Density of all woody perennials (excluding <i>Calatropis procera</i> ) over 0.5m height
Acacia Density	Density of all <i>Acacia</i> species over 0.5m height
Balanites Density	Density <i>Balanites</i> over 0.5m height
Salvadora Density	Density <i>Salvadora persica</i> over 0.5m height
Calatropis Density	Density <i>Calatropis</i> over 0.5m height
Shrub Density	Density of shrubs ( <i>Guiera</i> , <i>Zizyphus</i> , <i>Annona</i> , <i>Maerua</i> , <i>Cassia</i> , <i>Prosopis</i> , <i>Stereospernum</i> ) over 0.5m
Tree Diversity	Tree Diversity (Shannon-Weiner Index)
Season	Season (in all models by default)
Minutes after Sunrise	Minutes after local sunrise (in all models by default)
Year	Year (in all models by default)

Assuming no more than  $m/10$  predictors can be used in a model, where  $m$  is the number of observations in the least well represented category (Harrell *et al.* 1996), data sets for all bird species were large enough to allow all 10 potential predictors to be included. The use of these 10 covariates in model selection for each species meant it was easy to compare species (Burnham and Anderson 2001).

Production and selection of GLM's was carried out using SAS™ 8.02 software. Bird count data showed Poisson distribution, with analysis in SAS accounting for this and for any over-dispersion. Model selection methodology closely follows that described by Burnham and Anderson (2002). GLM models were produced for all possible combinations of the seven selected variables (Season, Year, and Minutes after Sunrise included by default). A total of 255 ( $2^8$  minus null model) candidate models were produced. For each model Akaike's Information Criterion (AIC) was calculated. AIC is an estimate of the expected distance between the fitted model and the unknown true mechanism that created the observed data. The size of AIC value is not significant in itself, but differences between candidate model AIC values can be used for model selection. In order to assess these differences in AIC values, AIC Differences ( $\Delta_i$ ) were calculated:

$$\Delta AIC_i = AIC_i - AIC_{min}$$

Values of  $\Delta_i$  greater than 20 for a large data set would indicate a model is a poor approximating model for the data when compared to the model with the lowest AIC values (Burnham & Anderson 2002). The model with zero  $\Delta_i$  was selected as the 'best' model. The degree of similarity to neighbouring models was assessed using Akaike Weights ( $w_i$ ) and evidence ratios. Akaike Weights were calculated:

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum \exp(-\Delta_j/2)} \quad (\text{where } \sum w_i = 1).$$

Higher values indicate better model fit. Evidence ratios (E/R) were calculated for each model by dividing 'best' model  $w_1$  by  $w_j$  (see Table 2.14). The larger the Evidence Ratio, the larger the difference between models. The overall fit of the model to the data was determined through an equivalent of the  $R^2$  value. An initial 'Null Model' containing no covariates was run to produce the total variance available to be explained. The  $R^2$  equivalent was the calculated:

$$R^2 \text{ Equiv} = 1 - \frac{\text{Model variance}}{\text{Null model variance}}$$

Thus allowing an assessment of overall model fit (Flynn 1999; Guisan & Zimmermann 2000).

**Table 2.14:** The Number of models within each confidence set summing to various values and their Evidence Ratio values

$\sum w_i$	No of Models	E/R	E/R value
0.900	4	$w_1/ w_4$	1.6
0.950	6	$w_1/ w_6$	4.5
0.990	9	$w_1/ w_9$	36.9
0.999	11	$w_1/ w_{11}$	101.7

In order to further assess relative variable importance, all candidate models were ranked by  $w_i$  and the running total of  $w_i$  values calculated ( $\sum w_i$ ). The number of models included within  $\sum w_i$  totals of 0.95, or the 'Occam's Windows' (Madigan and Rafferty 1994) were calculated. This provided a cut-off point that allowed models achieving a predetermined performance to be identified and used in the calculation of relative variable importance. Each model  $w_i$  value in which a particular variable occurred were summed. The resultant  $w(+i)$  value is greater for variables occurring in more models, or in models with a greater Akaike weight. Higher values of  $w(+i)$  therefore indicate greater relative importance of the variable. The number of variables within each model (K) was also calculated (see Table 2.15).

For species exhibiting a strong preference for *Salvadora*, or a strong East-West split in distribution, separate models were developed using data sets from within and outwith the *Salvadora* belt. Within the study region, *Salvadora* is distributed in a well-defined broad belt in the NE only. Any apparent importance of *Salvadora* may therefore be a function of overlapping distributions, rather than selection of *Salvadora* by the bird species. Any strong preference for *Salvadora* may therefore mask habitat preferences outside of this belt.

**Table 2.15:** Example of a relative variable importance (excluding default variables: Season, Minutes after Sunrise and Year) for a hypothetical bird species. The high values for tree diversity, Balanites density and Salvadora density indicate these habitat variables are of greatest relative importance in explaining the occurrence of the bird species.

VARIABLE	w+(i)	RANKED MODEL NUMBER									
		102	122	123	100	67	103	64	120	121	101
Mean height	0.699	1	1	1	0	1	1	0	0	1	0
Tree Diversity	0.916	1	1	1	1	1	1	1	1	1	1
Acacia Density	0.429	0	1	0	1	0	1	0	1	1	0
Tree Density	0.234	0	0	1	0	0	0	0	1	1	1
Balanites Density	0.916	1	1	1	1	1	1	1	1	1	1
Salvadora Density	0.916	1	1	1	1	1	1	1	1	1	1
Shrub density (excluding Salvadora)	0.817	1	1	1	1	0	1	1	1	0	1
	K =	5	6	6	5	4	6	4	6	6	5

## 2.12 Validation of Predictive Models

Final predictive models were derived from best-fit habitat GLMs and average parameter estimates from habitat GLMs within the 0.950 Occam's window, i.e. those models explaining a high proportion of variation in bird abundance (see above). The parameter estimates from best-fit habitat models and the mean values from models falling within the 0.950 Occam's window (see above) were used to calculate a probability of occurrence for all points within Initial and Validation data sets. First the Logit (P) value was calculated:

$$\text{Logit (P)} = \text{constant variable} + x^i (\text{key variable } x) + y^i (\text{key variable } y) \dots$$

*i* = variable iteration

Then the probability of occurrence was obtained by transforming Logit (P) values:

$$\text{Probability of Occurrence} = \frac{e^{[\text{Logit (P)}]}}{1 + e^{[\text{Logit (P)}]}}$$

*e* = base of natural logarithm (2.718)

Initially the threshold probability was set at 0.5, with a probability of occurrence greater than 0.5 assumed to indicate species presence at a point and less than 0.5 absence

(Tabachnick and Fidell 1996). However, the selection of a threshold P values of 0.5 may not always be appropriate as the predictive ability of the model at this value may not be representative of the models overall predictive power. Therefore in order to identify the most suitable threshold probability the percentage of correctly predicted occupied and unoccupied points were derived for a range of threshold probabilities for each species. This was carried out for both Initial and Validation data (Table 2.16). Selection of threshold p value depended upon the purpose of the predictive model. In this example, accurate prediction of occupied points would be obtained if a threshold p of 0.1 were used, whilst a threshold p of 0.9 would be most suitable for accurate prediction of absence, and 0.4 may for overall predictive ability.

**Table 2.16:** Example percentages of correctly predicted presence and absences points for Initial and Validation data for range of threshold p values.

Threshold p	INITIAL		VALIDATION	
	Occupied	Unoccupied	Occupied	Unoccupied
0.1	88	43	80	45
0.2	86	56	79	57
0.3	84	68	75	60
0.4	81	76	73	65
0.5	70	89	50	69
0.6	68	90	47	70
0.7	57	92	43	75
0.8	54	94	40	80

The selection of threshold probability is therefore dependent upon the desired output of the model. Successful prediction of species presence may be best achieved using a different threshold probability to that best suited to successful prediction of absence. Greatest overall predictive power may be best achieved by a different probability altogether. It is therefore essential to identify the desired output prior to threshold probability selection. After selection of the most appropriate critical p value, probabilities of occurrences were used to assess the ability of the habitat models to discriminate between occupied and unoccupied points. This was done using a 2x2 classification table containing the number of correct and incorrect predictions of presence and absence, for both Initial and Validation data sets (Table 2.17) following the protocol of (Luck 2002a).

**Table 2.17:** The number of correct and incorrect predictions of presence and absence of key bird species at each point.

Predicted Occurrence	Observed Occurrence	
	Present	Absent
Present	a	b
Absent	c	d

These values were used to calculate a number of diagnostic values for use in assessing the predictive power of the model (Fielding and Bell 1997).

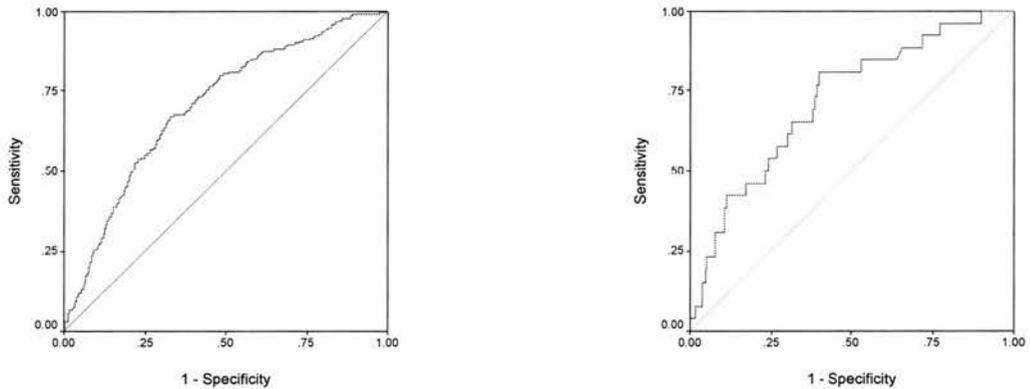
Prevalence	$(a+c)/n$
Sensitivity	$a/(a+c)$
Specificity	$d/(b+d)$
Correct classification rate	$(a+d)/n$
Positive predictive power	$a/(a+b)$
Negative predictive power	$d/(c+d)$
Kappa	$[(a+d)-((a+c)(a+b)+(b+d)(c+d))/n]/[n-((a+c)(a+b)+(b+d)(c+d))/n]$

where  $n$  = total number of points (see Table 2.15 for source of values  $a$ - $d$ )

Prevalence is the proportion of points where a specific bird species is present; Sensitivity, the ability of the model to predict presence; Specificity, the ability of the model to predict absence; Correct Classification Rate is the proportion of correct predictions, Positive Predictive Power is the proportion of correctly predicted presences, and Negative Predictive Power is the proportion of correctly predicted absences. Kappa is the improvement in predictive power above chance the model provides and is applicable only where prevalence is approximately 0.5.

An assessment of model predictive power across critical p values was undertaken by producing Receiver Operating Characteristic (ROC) Curves for each model. ROC removes potential biases associated with assessing model performance from a single selected threshold probability (Fielding and Bell 1997). For both data sets, ROC curves were produced by plotting proportions of true positive classifications (Sensitivity) against false positive classifications (1-Specificity), for all threshold probability values, see Figure 2.14 (Luck 2002b). The Area Under the Curve (AUC) indicates model performance, with an AUC value of 0.5 indicating a predictive ability no greater than

chance, whilst 0.9-1.0 show an excellent model predictive ability. The model providing the best predictive ability, i.e. that with greatest AUC and significant p value ( $<0.05$ ), was selected for further assessment.



**Fig. 2.14:** ROC curves of Common Whitethroat habitat model from the best-fit model only for Training (left) and Validation (right) data. Training data AUC= 0.705,  $P<0.0001$ , Validation data AUC = 0.719,  $P<0.0001$ . The area under the diagonal line of 0.5 represents values expected by chance alone.

It was found that the predictive ability of a model from data from outwith *Salvadora* band applied to non-*Salvadora* data provides poor prediction for occupied sites. For presence predictive ability, a GLM model derived from all sites performs most effectively. Any potential benefits of separating *Salvadora* from non-*Salvadora* sites for model generation may be outweighed by the resulting smaller sample size. However, the relatively poor positive predictive power shown by the overall model may be due to the inflated influence *Salvadora* presence has upon predictions of presence at sites out-with the *Salvadora* band.

## Chapter 3 : Seasonal Variation in Palearctic Migrant Warbler Densities in Sahelian West Africa

### 3.1 Introduction

Significant long-term declines in breeding populations of migrant passerine birds have been widely reported from temperate regions (Marchant 1992; Robbins *et. al.* 1989; Terborgh 1989). It has been suggested that in Europe these declines are linked to mortality at the African wintering grounds (Baillie and Peach 1992; Marchant 1992; Winstanley *et. al.* 1974). Over 25% of all European bird species winter in Africa (Jones 1998), with 5000 million individuals estimated to move into the continent each autumn (Moreau 1972). Whilst wintering in Africa, the majority (99%) of these migrant species are associated with seasonal savannah and open woodland, rather than high forest as is observed in the Neotropics (Grimmett 1979; Lovei 1989; Monkkonen 1992; Monkkonen *et. al.* 1992; Moreau 1972).

Within Western Africa, the greatest numbers of wintering Palearctic migrants occur just south of the Sahara in the Sahel and Sudan zones, with numbers of both species and individuals declining as one moves south (Jones 1998). The Sahel is a semi-arid region dominated by *Acacia* woodland and seasonal grassland. It receives 250-350mm annual rainfall during a short rainy season from June-Sept. Fluctuations in Sahelian rainfall show a significant positive correlation with subsequent breeding populations of migrant species in Western Europe (Baillie and Peach 1992; Bryant and Jones 1995). An 80% decline in Common Whitethroats breeding in Britain during the late 1960's was linked to a period of severe drought in the Sahel between 1965 and 1970 (Baillie and Peach 1992; Winstanley *et. al.* 1974). Similar declines in breeding populations of Sand Martin and Sedge Warbler in Western Europe were also associated with drought events in the Sahel (Bryant and Jones 1995; Foppen *et. al.* 1999; Peach *et. al.* 1991; Szep 1995). Since 1972 British populations of Common Whitethroat have shown a slight recovery, with recent breeding populations approximately 29% of those present prior to the crash (Baillie *et. al.* 2002). However, the slow rate of this recovery suggests that Sahelian winter habitats have not regenerated fully.

Habitat destruction has been rapid throughout the Sahel region due to a rapidly increasing human population. For example, in Senegal the extent of *Acacia nilotica* woodland declined by 90% between 1954-1986 (Mulle 1989) whilst Borno State in NE Nigeria experienced a 14% decline in woodland between 1976 and 1995 (Geomatics

International 1998). In both cases habitat loss was through human clearance for fuel wood, grazing, and conversion to intensive agriculture. The exact impact of this habitat loss and degradation upon wintering populations of Palearctic migrants is unknown, with few winter densities across habitats or sites published.

The arrival of Palearctic migrants in the Sahel as the area enters a period of prolonged drought (in stark contrast to the situation in much of East and Southern Africa) appears puzzling. 'Moreau's Paradox' questions why these individuals do not move the relatively short distance (300 km) south to seemingly more hospitable environments (Moreau 1972). Potential explanations put forward include competitive exclusion of Palearctic migrants from more southerly latitudes by Afrotropical species, unsuitability of rainforest habitats to many Palearctic species, and the unsuitability of Southern habitats during the rains (Elgood *et. al.* 1994; Fry 1992; Jones 1998; Moreau 1972).

Approximately 40% of Afrotropical species undergo intra-African migration, with many species apparently leaving the Sahel at the onset of the dry season (Elgood *et. al.* 1994; Jones 1998). It has been suggested that this provides a 'release' from competition and allows Palearctic migrants to occupy seasonally vacated niches. However, there is little published empirical data to support this, and the potential competition between Palearctic and Afrotropical species requires further study. Furthermore, estimates of productivity in the Sahel suggest invertebrate abundance may actually increase with the onset of the dry season, with late dry season fruiting of various shrubs and trees further maintaining favourable conditions (Morel 1973; Jones 1998; Stoate 1995; Stoate and Moreby 1995).

The need for baseline data on migrant species densities in the Afrotropics is well documented (Jones 1998; Kelsey 1992; Leisler 1990) although, only a handful of publications have presented any estimates (Browne 1982; Jones *et. al.* 1996; Stoate 1998; Vickery *et. al.* 1999). All of these studies were limited in geographical, seasonal, and species scope, and few compared relative densities of migrant and resident species, an essential first step in assessing the potential for competition between the two groups (Leisler 1992). The recent development of standardised methods of data analysis for the estimation of density now allows for more rigorous estimates of abundance to be carried out (Buckland *et. al.* 2000; Buckland *et. al.* 2001).

In this chapter I will focus on addressing the following hypotheses:

1. Palearctic warblers show no between-year differences in mid winter densities.
2. Mid winter densities of Palearctic warblers vary significantly between study sites due to variation in habitats or resource availability.
3. Mid winter densities of Palearctic warbler show significant inter-specific differences due to habitat preferences or variation in populations.
4. Palearctic warbler densities show significant variation between habitats due to differences in habitat preferences or resource availability.
5. Sites in the east of the study region show significant differences in mid-winter densities from those in the west due to the southerly extension of the Sahel in NE Nigeria.
6. Densities of Palearctic warblers differed between this study and those carried out previously, potentially due to habitat loss in the Sahel.
7. The presence of one species of Palearctic warbler will show a significant correlation with the presence of others due to competitive exclusion or habitat preferences.
8. Densities of Palearctic warblers vary seasonally due to arrival and departure dates from European breeding grounds.

## 3.2 Methods

Point counts were carried out in the Sahel of N Nigeria between October and April. Approximately 1800 point counts were carried out at c. 500 individual points, with habitat variables recorded at each point. Full details of study sites and methods of data collection are presented in Chapter 2.

Data on all bird species observed were recorded, though in this chapter five species of Palearctic Warbler are discussed in detail: Common Whitethroat *Sylvia communis*, Lesser Whitethroat *S. curruca*, Subalpine Warbler *S. cantillans*, Orphean Warbler *S. hortensis*, and Bonelli's Warbler *Phylloscopus bonelli*. All were relatively common winter visitors to the study areas. For comparisons of relative densities of Palearctic and Afrotropical Warbler densities, all species listed in Table 3.1 were grouped by residency to form single density estimates for Palearctic Warblers (Palearctic Warbler group), Afrotropical Warblers (Afrotropical Warbler group), and Afrotropical Warblers excluding Olivaceous Warbler *Hippolais pallida* (not Olivaceous Warbler group). The Afrotropical species selected for these analyses included insectivorous gleaning

species with body masses less than 20g, making them comparable with Palearctic Warblers.

**Table 3.1** Body mass and residency of Warbler study species included within analyses. Residency A= Afrotropical 'resident', P= Palearctic migrant.

Common Name	Scientific Name	Body Mass (g)	Residency
Cricket Warbler	<i>Spiloptila clamans</i>	7g	A
Northern Crombec	<i>Sylvietta brachyura</i>	7g	A
Yellow-bellied Eromemola	<i>Eremomela icteropygialis</i>	7g	A
Acacia Warbler	<i>Phyllolais pulchella</i>	6g	A
Little Weaver	<i>Ploceus luteolus</i>	13g	A
Grey-backed Camaroptera	<i>Camaroptera brachyura</i>	10g	A
Sennar Penduline Tit	<i>Anthoscopus punctifrons</i>	6g	A
Pygmy Sunbird	<i>Anthreptes platurus</i>	6g	A
Beautiful Sunbird	<i>Nectarinia pulchella</i>	7g	A
Scarlet-chested Sunbird	<i>Nectarinia senegalensis</i>	10g	A
Olivaceous Warbler	<i>Hippolais pallida</i>	11g	A
Lesser Whitethroat	<i>Sylvia curruca</i>	12g	P
Common Whitethroat	<i>Sylvia communis</i>	15g	P
Orphean Warbler	<i>Sylvia hortensis</i>	20g	P
Bonellis Warbler	<i>Phylloscopus bonelli</i>	9g	P
Willow Warbler	<i>Phylloscopus trochilus</i>	10g	P
Wood Warbler	<i>Phylloscopus sibilatrix</i>	10g	P
Subalpine Warbler	<i>Sylvia cantillans</i>	10g	P

### 3.3 Data Analysis

Point count data were analysed using Distance 4.0 software following Buckland *et. al* (2001). Model parameters used in Distance are presented in Table 3.2 and a full discussion of analyses using Distance is presented in section 2.7 of chapter 2.

**Table 3.2:** Multiple covariate distance sampling (MCDS) species-specific model parameters, all models contained tree density at each point as covariate, GOF tests were not possible for all models due to limited degrees of freedom.

Species	Left Bin (m)	Bin (m)	Right Truncation (m)	No. of Observation	% CV	Goodness of Fit	Probability of Detection
Bonellis Warbler	20	5	50	60	11.51	0.857	0.207
Common Whitethroat	30	7	50	586	2.73	0.317	0.317
Lesser Whitethroat	20	10, 5	50	245	4.78	0.478	0.468
Subalpine Warbler	20	10	50	297	11.71	0.262	0.519
Orphean Warbler	20	5	50	16	2.67	N/A	0.465
PalWar	20	10	50	1200	1.97	0.067	0.557
AfrWar	20	10	50	1572	1.93	0.773	0.426
NtOliv	10	10	50	704	2.99	0.451	0.389

Estimates of density per hectare, along with 95% confidence limits, were produced within Distance for each count period for each site. For mid winter comparisons of density all 16 sites were included, but only sites 1, 2, 3, 4, 6, 7, and 8 were used for analyses of seasonal changes in density, as these were visited during at least 3 seasons. Data were tested for normality and transformations carried out where required. Comparisons of densities between sites, species and seasons were made using one-way ANOVA's with Bonferroni *Post-hocs* (Zar 1999 but see Moran 2003). Where multiple tests were carried out, critical p values were set by dividing 0.05 by the number of tests carried out. Due to the strong easterly bias in Olivaceous Warbler distribution, not Olivaceous Warbler group comprising all African Warbler species excluding Olivaceous Warbler was also used for comparisons with the Palearctic Warbler group. The broad habitat classes given in Table 2.3 were used for comparisons of densities between these habitats (see Chapter 2 for full descriptions of habitat). Comparisons of Palearctic and Afrotropical Warbler species' occurrence across points were carried out using General Linear Models (GLM's) in SAS™ 8.02. The occurrence of Palearctic Warbler group was the dependent variable, with Afrotropical Warbler group or not Olivaceous Warbler group as independent variables. Year and Season were included as confounding factors. Critical p values were 0.05/ number of variables. Bird count data fitted a Poisson distribution, with analyses accounting for over dispersion. All other analyses were carried out using SPSS v11.5.

Comparisons of distances at which Afrotropical and Palearctic Warbler species were initially located indicated a highly significant correlation between the two groups ( $r_s = 0.904$ ,  $p < 0.0001$ ,  $n = 10$ ). This supports the assumption that detection distances were comparable between groups, and that the use of raw count data in analyses is appropriate (see Chapter 2 for a full discussion). A summary of hypotheses to be tested and their method of testing are presented in Table 3.3.

**Table 3.3:** Summary of hypotheses to be tested, their method of testing, and degrees of freedom.

Hypothesis		Sample Size
<b>1</b>	<b>Mid winter densities of Palearctic warblers did not differ significantly between study years</b> One way ANOVA of density estimates from 6 sites surveyed during both years	12
<b>2</b>	<b>Mid winter densities of Palearctic warblers varied significantly between sites</b> One way ANOVA of density estimates from each visit to each study site	22
<b>3</b>	<b>Inter-specific variation in densities of Palearctic warbler species occurs</b> One way ANOVA with Bonferonni Post-hoc of density estimates from each visit to each study site	22
<b>4</b>	<b>Mid winter densities of Palearctic warblers varied significantly between habitats</b> One way ANOVA of density estimates from each visit to each study site	22
<b>5</b>	<b>Mid winter densities of Palearctic warblers varied significantly between eastern and western study sites</b> Kruskall Wallis test	22
<b>6</b>	<b>Densities of Palearctic warblers have declined between previous studies and this one.</b> Independent t-test (assuming unequal variance) of warbler densities from 10 sites studied by Jones et al 1996 and the 7 western sites studied here.	17
<b>7</b>	<b>Palearctic warbler species occurrence shows a negative correlation with the presence of other Palearctic warblers</b> Pearsons' correlation of mid winter density estimates from each visit to each site	22
	Linear regression of raw counts from each mid winter point count	911
	Linear regression of raw counts from mid winter point counts where at least one of two test species present	265
<b>8</b>	<b>Seasonal variation in densities of Palearctic warblers occurs</b> One way ANOVA with Bonferonni Post-hoc of density estimates from each visit to each study site	36

## 3.4 Results

### 3.4.1 Mid-winter Densities

As only the relevant data subsets were included in each test, combined analyses were not appropriate (e.g. only sites duplicated across seasons were used in the analysis of seasonal change in abundance). The mean mid-winter density for Palearctic Warblers across all study sites was 1.41 ( $\pm 0.27$  SE). Considerable variation in mean midwinter densities for individual species was apparent across study sites (Fig 3.2). During mid-winter, Orphean Warbler were observed during point counts at Canal only and this species has not been included in comparisons of densities across sites, species or habitats.

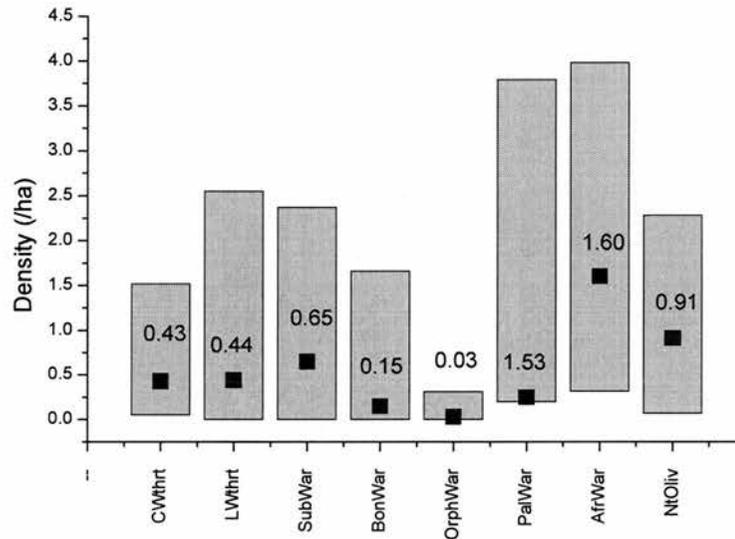
No significant between-year differences in mid winter densities were found for any species of Palearctic warbler when data from the six sites visited during both winters were tested ( $F_{1,10} < 2.7$ ,  $p > 0.05$ ).

Results from one-way ANOVA's of density estimates for each of the 16 sites visited (with 6 sites visited during both winters) indicated that densities did not differ significantly across sites for Common Whitethroat ( $F_{15,6}=1.0$ ,  $p=0.568$ ), Subalpine Warbler ( $F_{15,6}=1.6$ ,  $p=0.292$ ), or Bonelli's Warbler ( $F_{15,6}=1.0$ ,  $p=0.522$ ). However, significant differences were found in densities across sites in Lesser Whitethroat ( $F_{15,6}=8.1$ ,  $p=0.008$ ), and Palearctic Warbler group ( $F_{15,6}=12.1$ ,  $p=0.003$ ).

The 16 study sites visited during mid-winter (with 6 sites visited during both winters) were divided by broad habitat classes and variation in densities across the habitat classes tested. No significant differences were found in densities across habitats for Common Whitethroat ( $F_{2,19}=0.4$ ,  $p=0.693$ ), Subalpine Warbler ( $F_{2,19}=0.4$ ,  $p=0.705$ ), Bonelli's Warbler ( $F_{2,19}=3.3$ ,  $p=0.60$ ) or overall in the group Palearctic Warbler group ( $F_{2,19}=1.3$ ,  $p=0.307$ ). Although significant differences were present in the densities of Lesser Whitethroat across different habitats ( $F_{2,19}=3.7$ ,  $p=0.040$ ), Post-hoc tests did not show any significant differences between individual habitats ( $P > 0.05$ ).

Differences in densities between eastern ( $n=9$ ) and western ( $n=7$ ) sites were examined using a Kruskal Wallis test. Non significant differences in densities between east and west were found in Common Whitethroat ( $\chi^2=0.01$ ,  $p=0.970$ ,  $df=1$ ), Subalpine Warbler ( $\chi^2=1.53$ ,  $p=0.217$ ,  $df=1$ ), or Bonelli's Warbler ( $\chi^2=0.16$ ,  $p=0.691$ ,  $df=1$ ). However, a

significant difference was found in Lesser Whitethroat ( $\chi^2=5.85$ ,  $p=0.016$ ,  $df=1$ ), with mean densities of 0.70 and 0.07 per ha in eastern and western sites respectively. Possibly as a result of this, there were also significant differences between east and west sites in the group Palearctic Warbler group ( $\chi^2=4.71$ ,  $p=0.030$ ,  $df=1$ ), with average densities of 2.01 and 0.82 per ha respectively.



**Fig 3.2** Mean mid winter densities (black points) and density ranges (bars) of Palearctic Warbler species across all sites. Lesser Whitethroat and Palearctic Warbler group densities differed significantly across sites ( $p<0.01$ ).

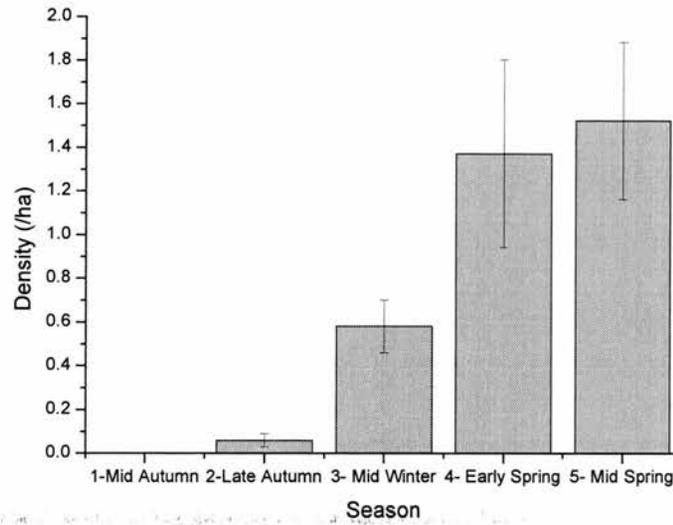
Mid-winter densities differed significantly between Palearctic warbler species across the 16 study sites ( $p=0.028$ ,  $F_{3,84}= 3.2$ ). Post-hoc tests showed that Bonelli's Warbler and Subalpine Warbler densities differed significantly from each other ( $p=0.017$ ), indicating the former species was less abundant across sites than the latter. However, no significant correlation was found between relative mid-winter densities at each site for any Palearctic warbler pair ( $P>0.05$ ,  $n =22$ ).

Comparison of Palearctic warbler densities found at western sites in this study with those found previously from the same area (Jones et al 1996) indicated a significant decline in density of Subalpine warbler ( $t=2.315$ ,  $p=0.045$ ,  $df=9.33$ ) from a mean of 1.59/ha ( $\pm 0.54$  SE) to 0.33/ha ( $\pm 0.07$  SE). No significant change in densities was found for Common Whitethroat, Lesser Whitethroat or Bonelli's Warbler ( $p>0.05$ ), with Common Whitethroat showing an increase in densities between studies (0.29- 0.32 individuals per ha), Lesser Whitethroat a decline (0.11- 0.05), and Bonelli's Warbler an increase (0.07-0.15).

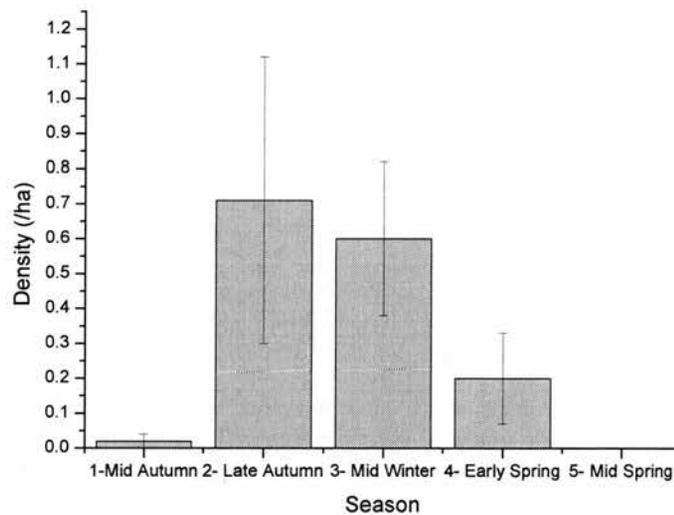
A significant correlation was found between the raw counts of Common Whitethroat and Subalpine Warbler at each point both during mid winter ( $F_{1,911}=19.4$ ,  $p<0.0001$ ). To test that the lack of a significant correlation between Lesser Whitethroat and either of the other two *Sylvia* Warbler species was not due to the easterly bias in distributions of Lesser Whitethroat, eastern sites only were used in a repeat of the analysis. Lesser Whitethroat still showed no significant relationship with either Common Whitethroat or Subalpine Warbler. It is also possible that any significant results obtained for Common Whitethroat and Subalpine Warbler were a function of the points without suitable habitat having zero probability of either species occurring. To check this, the analysis was repeated with only points at which at least one of the species in question was present. Results obtained indicate that a significant relationship still occurred, but that the direction of the relationship was reversed ( $F_{1,265}=47.5$ ,  $p<0.0001$ ). The significant positive relationship produced previously was presumably a function of the very large number of points at which neither species occurred, resulting in a skewing of the results.

### 3.4.2 Seasonal Variation in Densities

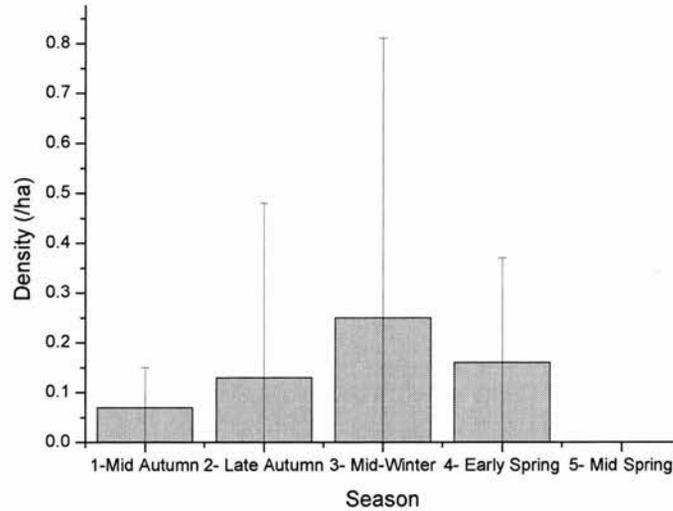
Densities of Palearctic Warblers varied considerably across seasons, with significant seasonal variation ( $P_{\text{crit}}=0.01$ ) found in Common Whitethroat ( $F_{4,31}=6.7$ ,  $p=0.001$ ). *Post hoc* analysis indicated that Common Whitethroat densities were significantly greater ( $p<0.05$ ) during early and late spring than late autumn (Fig 3.3). Lesser Whitethroat ( $F_{4,31}=1.7$ ,  $p=0.177$ ), Subalpine Warbler ( $F_{4,31}=2.5$ ,  $p=0.06$ ), Bonelli's Warbler ( $F_{4,31}=0.6$ ,  $p=0.630$ ), and Palearctic Warbler group ( $F_{4,31}=2.1$ ,  $p=0.110$ ) densities showed no significant differences between any seasons, although similar seasonal variation in densities was apparent (see Figs 3.4-3.6). Densities of Afrotropical Warbler group ( $F_{4,31}=1.9$ ,  $p=0.130$ ) and not Olivaceous Warbler group ( $F_{4,31}=3.3$ ,  $p=0.023$ ) also showed no significant differences in densities between seasons.



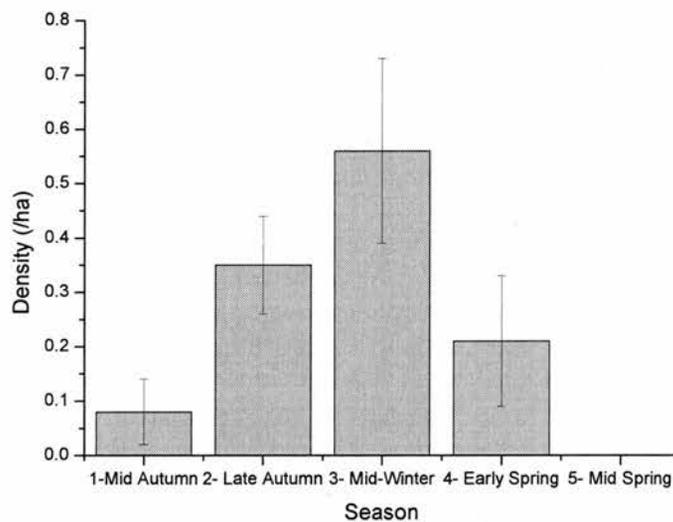
**Fig 3.3** Mean Common Whitethroat densities and SE across seasons. A significant difference in densities was found across seasons ( $F_{4,31}=6.7$ ,  $p=0.001$ ) with post-hoc analysis indicating mid and late autumn densities differed significantly from and early and mid spring (\*\*  $p<0.01$ ).



**Fig 3.4** Mean Lesser Whitethroat densities and SE across seasons. No significant difference in densities was found across seasons ( $F_{4,31}=1.7$ ,  $p=0.177$ ), although a trend of increasing density following autumn arrival followed by an early spring departure northwards is apparent.



**Fig 3.5** Mean Bonelli's Warbler densities and SE across seasons. No significant difference in densities was found across seasons ( $F_{4,31}=0.6$ ,  $p=0.630$ ), although a trend of increasing density following autumn arrival followed by a spring departure northwards is apparent.



**Fig 3.6** Mean Subalpine Warbler densities and SE across seasons. No significant difference in densities was found across seasons ( $F_{4,31}=2.5$ ,  $p=0.06$ ), although a trend of increasing density following autumn arrival followed by a spring departure northwards is apparent.

## 3.5 Discussion

### 3.5.1 Geographic Trends

The mean mid-winter density of 1.41 Palearctic warblers per hectare across all study sites was similar to the densities of 1.14 per ha found in northern Nigeria previously

(Jones, *et al.* 1996). However, the maximum density found in the previous study was twice the maximum of 3.40 individuals per ha found in this study. The maximum density from the 1996 paper was found at Watucal Forest Reserve, which during the current study was found to support 1.20 Palearctic warblers per ha.

Mean mid-winter densities of Common Whitethroat across all sites (0.44/ ha) were similar to the mean of 0.30/ ha found previously in Northern Nigeria (Jones *et. al.* 1996), with the density range overlapping with the maximum values of 1.3 and 1.02 per ha found previously in that paper and in the Gambia (Stoate *et. al.* 2001) respectively. However, the mean density for Lesser Whitethroat found in this study (0.43/ha) was approximately double that of 0.15/ha found previously in Northern Nigeria (Jones *et. al.* 1996). This may have been due to the more easterly location of many of the sites in this study, corresponding more strongly with the species' more easterly distribution in the region (Shirihai, Gargallo, *et. al.* 2001). If study sites in Central Northern Nigeria only are selected, average densities of 0.07/ ha are obtained, approximately half of those found previously in the same region.

Differences in Lesser Whitethroat densities between eastern and western sites may be due to habitat differences across the range (see Chapter 2 for full discussion), resulting in longitudinal variation in densities. This may be reflected in Lesser Whitethroats' more northerly winter distribution due to the southerly extension of the Sahel in the Lake Chad area, thus resulting in the restriction of this species to more NE areas within Nigeria. The lack of significant differences in Common Whitethroat and Subalpine Warbler densities between western and eastern sites may reflect these species more uniform distributions across Africa. This will be investigated in more detail in Chapter 4.

The mean Subalpine Warbler mid winter density of 1.59/ ha reported for N Nigeria previously (Jones *et. al.* 1996) was considerably greater than the mean of 0.65/ha in this study, though densities of 0.02 per ha from Mauritania (Browne 1982) were much lower than both. Average mid winter Bonelli's Warbler densities of 0.07 per ha from Northern Nigeria (Jones *et. al.* 1996) and 0.026 from Mauritania (Browne 1982) were lower than those found in this study (0.15/ ha). Perhaps surprisingly, densities of Common Whitethroat, Lesser Whitethroat, Subalpine Warbler and Bonelli's Warbler found in this study are all comparable with densities of males on the breeding grounds, as reported for Western Europe (Cramp 1992).

Orphean Warbler had until recently only rarely been observed in Nigeria (Elgood *et. al.* 1994). Observations during the late 1990's (Ottosson *et. al.* 2000) suggested an autumn passage through the extreme NE of the country, but data from this study suggest a small wintering population in the Lake Chad area. The long history of ornithological activity in the Lake Chad area (Dowsett 1969; Waldenstrom & Ottosson 2002) makes it unlikely that the species was previously overlooked. Habitat loss to the North of the area, or continued expansion of the Sahel southwards (Charney *et. al.* 1975; Eckholm and Brown 1977; Hellden 1991; Ibrahim 1978) may have resulted in the apparent range extension of the species into Nigeria.

### 3.5.2 Seasonal Trends

Seasonal changes in Palearctic Warbler densities generally reflect the timing of migration to and from temperate breeding grounds. The lack of significant differences across seasons in Lesser Whitethroat, Subalpine Warbler and Bonelli's Warbler may have been due to the general scarcity of the species throughout the study area, rather than no change occurring. In contrast, the most common species of Palearctic Warbler (Common Whitethroat) showed significant seasonal variation in abundance.

Densities of Common Whitethroat increased significantly from late autumn to spring. In West Africa the species occurs during winter across a broad belt between 10° N and 17° N. The low densities recorded in this study at 13° N during late autumn suggest that individuals were arriving at study sites throughout the autumn and winter. Presumably individuals moved south from further north in the Sahel as the vegetation died back with the onset of the dry season (Jones 1998; Moreau 1972). Individuals also moved into the study area (presumably from the south) prior to spring departure, as a staging area prior to trans-Saharan migration (Jones 1998; Stoate and Moreby 1995). Peak passage of Common Whitethroats in Jos (10° N) occurs during March and April, declining dramatically by May (Ross McGregor pers com). It seems likely that many individuals arriving in the Sahel during spring have come from these more southerly latitudes, though it has also been suggested migrants continue moving south from the northern Sahel until February at least (Lack 1986). The importance of the late dry season fruiting *Salvadora persica* to Common Whitethroats prior to trans Saharan migration has been discussed previously (Jones 1998; Stoate and Moresby 1995) and will be discussed further in Chapter 4. The assertion made in a previous study (Jones *et. al.* 1996), that Common Whitethroats arrive on Sahelian wintering grounds only after

the departure of Subalpine Warbler and Lesser Whitethroat, was not supported by this study, with all three species present from mid autumn until early spring.

The near-significant decline in densities of Subalpine Warbler between mid-winter and late spring, with no individuals present during this latter period, fits with the evidence that this species departs from the wintering grounds earlier than Common Whitethroat. A previous study from Nigeria during spring also found that Subalpine Warbler had largely departed their wintering sites by late March (Vickery *et. al.* 1999). The lack of springtime increase in numbers in the area, in contrast with Common Whitethroat, may be due to *Salvadora* fruit peaking in abundance during March-April, after the majority of Subalpine Warbler have departed. It may also be due to the more northerly distribution of Subalpine Warbler (along with Lesser Whitethroat) compared with Common Whitethroat, and hence a lack of individuals from further south utilising the area as a sub-Saharan fuelling site. The slight but non-significant increase in densities between late autumn and mid-winter suggests, as with Common Whitethroat, that birds continue to arrive from the north throughout the autumn.

The role of the Sahel in spring staging of Common Whitethroats, as indicated by the increase in densities at this time, stresses the importance of the area to this species for both wintering and passage populations. The loss of habitat in this area may have profound implications for species utilising the area as a spring departure point for trans-Saharan crossings. Individuals would be forced to either attempt crossings without adequate fat reserves, or use more southerly sites for departure points thus increasing the width of the Sahara barrier. It has been suggested that Common Whitethroats already use more southerly sites for departing than those used 30 years ago, presumably due to habitat loss to the north (Ottosson, Bairlein, *et al.* 2002). However, the paucity of spring records of other migrant species using the area in the same way suggests that the Nigerian Sahel is of limited value to many migratory species as a staging area during spring migration.

One of the sites in this study, Watucal FR, was used during two previously published studies. Mid winter Subalpine Warbler densities of 5.90 birds per hectare (Jones *et. al.* 1996; Vickery *et. al.* 1999), were over 20 times greater than those found in this study (0.25). The authors of that study believed that any error in density estimates would be in the direction of under- rather than over-estimation because they used absolute counts uncorrected for detectability. Also, the fact that no consistent pattern in the direction of changes in species' densities exist between the studies, suggests that

neither study is biased in its density estimates in one particular direction. This lends support to the suggestion that a major change in abundance of this species has occurred at Watucal FR. Habitat change at the site between the two study periods (1994 and 2001) has been marked, with average tree density declining by 80% to 80/ha. Woodland loss within Yobe State, where Watucal is located, has also been significant, with a 13% decline between 1976 and 1993 reported (Geomatics 1996). It seems most likely that habitat loss at this site is the cause for this decline, though why Subalpine Warbler appears to be the only species to have been affected is unclear. Data on European breeding populations of Subalpine Warbler are sparse but suggest that populations were stable and possibly increasing during the 1970's-80's at least (Cramp 1992; Shirihai *et. al.* 2001). However, the geographic isolation of the four described subspecies in Europe, and partial allopatry shown in winter grounds, may result in a failure to identify differential effects of winter habitat loss. The potential explanations behind the apparent decline of Subalpine Warbler at Watucal FR will be explored in more detail in Chapter 4. What is perhaps most concerning about the deforestation occurring at Watucal FR is that the site is a Forest Reserve, and as such legally protected.

The lack of significant differences in mid winter densities across all sites for Common Whitethroat, Subalpine Warbler and Bonelli's Warbler may reflect a generality in habitat selection by these species. However, the heterogeneous nature of vegetation within each site may be a more likely explanation, as this could mask any relationships with vegetation characteristics. The comparison of densities between broad habitat classifications may not therefore be appropriate in assessing species habitat requirements.

The correlation found between the occurrence of Subalpine Warbler and Common Whitethroat at individual points may be the result of two different and potentially opposing processes. The two species may have very similar habitat preferences and therefore select for the same sites, with the resultant potential for competition being very high. Alternatively, the two species may have very different methods of utilising habitats, resulting in little overlap in resource use and reduced conflict, thus allowing sympatry. The lack of a significant correlation between Lesser Whitethroat and either Subalpine Warbler or Common Whitethroat may equally be due to very different habitat requirements, or significant overlap in resource use and therefore competition. The first would result in geographic isolation due to habitat selection, the latter due to

competitive exclusion. Habitat preferences will be examined in more detail in Chapter 5, and habitat use in Chapter 6.

### **3.5.3 Densities of Resident and Migrant Species**

No significant correlation in occurrence was found across all seasons between Palearctic Warbler group and Afrotropical Warbler group. Presumably this was due to many species of Palearctic warbler not being present in their wintering ground during some of the seasons included in the analyses. When the data were tested using a GLM with season accounted for, the occurrence of Palearctic warblers was found to be significantly related to the presence of both Afrotropical warblers and the not Olivaceous warbler group. The apparently sedentary nature of Afrotropical Warblers observed in this study and others (Elgood, Heigham, et al. 1994; Morel 1973) contradicts the competition release hypothesis, suggesting that Palearctic Warblers are not released from competition by the 'abandonment' of the Sahel by Afrotropical counterparts. However, differences in foraging behaviour or prey selection may reduce potential competition between the groups even when in sympatry. This will be examined in more detail in Chapter 6.

## **3.6 Conclusion**

Densities of Palearctic Warblers described in this chapter are comparable with those previously published for both wintering and breeding areas, and follow patterns of abundance that match the timing of migration of each species. The distinct east- west differences in densities found for Lesser Whitethroat were presumably due to habitat differences found across the latitudinal gradient. Common Whitethroats appear to utilise the region during spring migration in particular, presumably for fattening prior to trans-Saharan crossing. The effects of drought and habitat loss may therefore have a dramatic effect upon this species. However, a large decline in densities of Subalpine Warbler at one study site in comparison to a previous study was associated with a concurrent loss of habitat. This indicates that migrant species may be affected by habitat loss. The significant positive correlation between densities of Palearctic and Afrotropical Warbler species suggests that this habitat degradation is also likely to impact upon resident species.

## Chapter 4 : Afrotropical Warbler Densities in Sahelian West Africa

### 4.1 Introduction

Recent declines in breeding populations of a number of Palearctic migrants in Western Europe have been attributed to habitat loss and drought on African wintering grounds (Baillie and Peach 1992; Jones 1998; Marchant 1992; Winstanley *et al.* 1974). Currently nothing is known of the effects of these events upon Afrotropical species however, and even baseline data on species densities and habitat requirements are unavailable.

Within Western Africa, the greatest numbers of individuals and species of wintering Palearctic migrants occur just south of the Sahara in the Sahel and Sudan zones (Jones 1998). The Sahel is a semi-arid region dominated by *Acacia* woodland and seasonal grassland. It receives 250-350 mm annual rainfall during a short rainy season from June-Sept. Fluctuations in annual rainfall have been found to show a significant positive correlation with subsequent breeding populations of migrant species in Western Europe (Baillie and Peach 1992). During the late 1960's, an 80% decline in Common Whitethroats breeding in Britain was linked to a period of severe drought in the Sahel between 1965 and 1970 (Baillie and Peach 1992; Berthold 1993; Winstanley *et al.* 1974;). Since 1972 British populations of Common Whitethroat have shown only a slight recovery (Baillie *et al.* 2002; Marchant 1992) suggesting that Sahelian winter habitats may not have regenerated fully from the drought episode. Concurrent habitat destruction has been rapid throughout the region due to a rapidly increasing human population. For example in Senegal the extent of *Acacia nilotica* woodland declined by 90% between 1954-1986 (Mullie 1989), whilst Borno State in NE Nigeria saw a 14% decline in woodland between 1976 and 1995 (Geomatics International 1998). In both cases habitat loss was through human clearance for fuel wood, grazing, and conversion to intensive agriculture. For Afrotropical resident species, this habitat loss may have a direct effect during both breeding and non-breeding periods. However, loss of breeding habitat may have a more rapid effect upon population size through reduced breeding success. In order to fully assess the likely effects of habitat degradation and loss, baseline data on relative densities of Afrotropical species across a range of habitats and over a wide geographic area are required.

The need for baseline information on Afrotropical species abundance is well documented (Jones 1998; Kelsey 1992; Leisler 1990; Leisler 1992). However, only a handful of publications have presented density estimates of Afrotropical species (Jones *et al.* 1996; Vickery *et al.* 1999). Both of these studies were extremely limited in geographical, seasonal, and species scope. The recent development of standardised methods of data analysis for the estimation of density allows estimates of abundance to be carried out with some degree of confidence (Buckland *et al.* 2001).

Comparison of relative densities of resident and migrant species is an essential first step in assessing the potential for competition between the two groups (Leisler 1992), which some authors have identified as potentially being great (Greenberg 1986; Lack 1971; Moreau 1972). Approximately 40% of Afrotropical species undergo intra-African migration, with many species apparently leaving the Sahel at the onset of the dry season (Elgood *et al.* 1994; Jones 1998). It has been suggested that this provides a 'release' from competition and allows Palearctic migrants to occupy seasonally vacated niches (Fry 1992; Moreau 1972). However, it has been widely stated that Afrotropical Sylviidae and their equivalents within the Sahel are sedentary and do not withdraw south (Elgood *et al.* 1994; Jones 1998; Morel 1973). This suggests that no such 'release' occurs for Palearctic Sylviidae, which represent a significant component of the Sahelian avifaunas during the winter. No data on seasonal changes in densities of these Afrotropical species have been published however.

In this chapter I address the following hypotheses:

1. Afrotropical warblers show no between-year differences in mid winter densities.
2. Mid winter densities of Afrotropical warblers varied significantly between study sites due to variation in habitats or resource availability.
3. Mid winter densities of Afrotropical warblers show significant inter-specific differences due to habitat preferences or variation in populations.
4. Afrotropical warblers densities show significant variation between habitats due to differences in habitat preferences or resource availability.
5. Sites in the east of the study region show significant differences in mid-winter densities from those in the west due to the southerly extension of the Sahel in NE Nigeria.

6. The presence of one species of Afrotropical warbler will show a significant negative correlation with the presence of others due to competitive exclusion or habitat preferences.
7. Densities of Afrotropical warblers do not vary seasonally due the groups' sedentary nature.
8. Presence of one species of Afrotropical warbler species will show a significant correlation with the presence of Palearctic warbler species due to habitat preferences or competitive exclusion.
9. The ratio of Afrotropical to Palearctic warbler species found in this study will be comparable to those found in previous studies from the region.
10. Significant correlations in the overall occurrence of Afrotropical and Palearctic warblers occur due to group-wide habitat preferences or competitive exclusion.
11. Significant correlations in the occurrence of individual Afrotropical and Palearctic warbler species occur due species-specific habitat preferences or competitive exclusion.

## 4.2 Methods

Variable distance point counts were carried out at 16 study sites between October and April during two winters between 2001 and 2002. Over 1800 counts were carried out at 500 points over the study period. At each point a 25m radius vegetation plot was established and a number of habitat descriptive taken. Full details of study sites and methods are presented in chapter 2.

Data on all bird species observed were recorded. Species selected for inclusion within this chapter were all species of African warbler, and all Afrotropical insectivorous gleaning species with body mass less than 15g (Table 3.2). Brubru was included within species comparisons due to its similar size to Orphean Warbler, but was excluded from comparisons of residency groups. For comparisons of relative densities of Palearctic and Afrotropical warbler species, all Afrotropical species (excluding Brubru) were grouped together to form single density estimates; Afrotropical warblers (Afrotropical Warbler group), with Afrotropical warblers excluding Olivaceous Warbler (Not Olivaceous Warbler group) also calculated (this species being the most abundant and was therefore removed to ensure no masking of patterns of other species). Densities of all Palearctic warblers (Palearctic Warbler group) included all migratory species contained in Table 3.2 (see Chapter 3 for full discussion).

### 4.3 Data Analysis

Point count data were analysed using Distance 4.0 software following Buckland *et al.* (2001). Final model parameters for each Afrotropical species are presented in Table 4.1 and Palearctic species model parameters in Table 3.2. For a full discussion of data analysis using Distance see section 2.7 in Chapter 2.

**Table 4.1:** Multiple covariate distance sampling (MCDS) species-specific model parameters. All models contained tree density at each point as covariate, with Olivaceous Warbler also containing Season. GOF tests were not possible for all models due to limited degrees of freedom.

Species	Left Bin (m)	Bin (m)	Right Truncation (m)	Number of Observation	% CV	Goodness of Fit	Probability of Detection
Acacia Warbler	20	15	50	55	12.27	N/A	0.355
Beautiful Sunbird	20	15	50	53	12.08	N/A	0.602
Brubru	20	10	50	28	22.05	0.675	0.629
Cricket Warbler	15	10	45	22	4.89	0.352	0.496
Grey-backed Camaroptera	10	10	50	36	22.14	0.114	0.337
Little Weaver	10	5	50	153	7.19	0.355	0.350
Northern Crombec	10	5	45	54	57.05	0.395	0.440
Olivaceous Warbler	20	10	50	845	2.60	N/A	0.458
Pygmy Sunbird	20	15	50	134	7.41	N/A	0.336
Sennar Penduline Tit	20	15	50	16	101.80	N/A	0.186
Yellow-bellied Eromemola	15	10	45	36	12.81	0.247	0.538

Estimates of species densities per hectare, with 95% confidence limits, were produced within Distance for each count period for each site. For mid winter comparisons of density, all 16 sites were included, but only sites 1, 2, 3, 4, 6, 7, and 8 were used for analyses of seasonal changes in density, as these were visited during at least 3 seasons. Comparisons of densities between sites, species and seasons were made using one-way ANOVA's with Bonferroni *post-hocs*. Where multiple tests were carried out, critical p values were set by dividing 0.05 by the no. tests carried out. All Palearctic warbler species were grouped into Palearctic Warbler group, Afrotropical warblers and equivalents into Afrotropical Warbler group. Due to the strong easterly bias in Olivaceous Warbler distribution, Not Olivaceous Warbler group comprising of all African Warbler species excluding Olivaceous Warbler was also used in the analyses.

The broad habitat classes given in Table 2.3 were used for comparisons of densities between these habitats. Principal component analysis indicated significant differences between habitat types ( $F_{2,738}=31.214$ ,  $p<0.05$ ). More detailed habitat analysis is included within Chapter 2. As in Chapter 3, the composition of data sets means that combined analysis was not appropriate for some analyses.

Comparisons of distances at which Afrotropical and Palearctic warbler species were initially located indicated a highly significant correlation between the two groups ( $p<0.0001$ ,  $r_s = 0.904$ ,  $n = 10$ ). This supports the assumption that detection distances were comparable between groups, and that the use of raw count data for some analyses are appropriate (see Chapter 2 for a full discussion). Comparisons of densities of Palearctic and Afrotropical warbler species occurrence across points were carried out using General Linear Models (GLM's) in SAS™ 8.02, allowing year and season to be controlled for. Bird count data fitted a Poisson distribution, with analyses accounting for over dispersion. All other analyses were carried out using SPSS v11.5.

A summary of hypotheses to be tested and their method of test are presented in Table 4.2.

## 4.4 Results

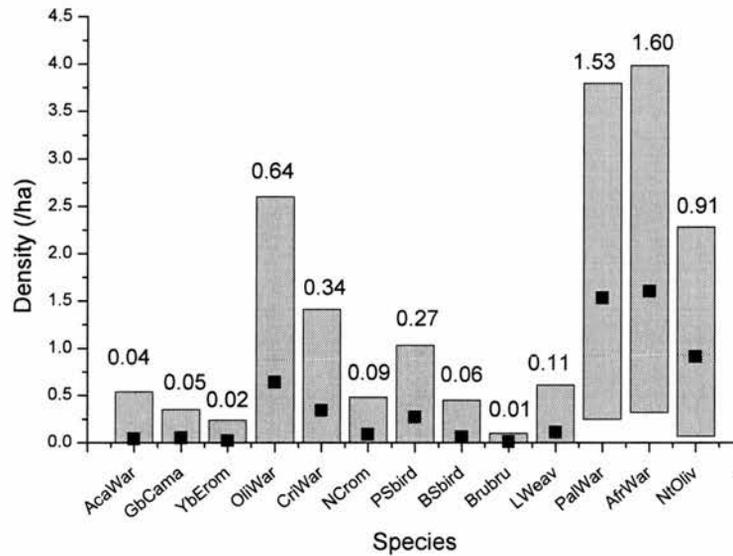
### 4.4.1 Mid-winter Densities

Considerable variation in mean midwinter densities was apparent across all study sites for each species (Fig 4.1). Insufficient data were available for Sennar Penduline Tit, and the species was excluded from analyses. No significant between-year differences in mid winter densities were found for any species of Afrotropical warbler when data from the six sites visited during both winters were tested ( $F_{1,10} < 2.0$ ,  $p > 0.05$ ).

Results from one-way ANOVA's of density estimates for each of the 16 sites visited (with 6 sites visited during both winters) indicated that densities did not differ significantly across sites for Acacia Warbler, Grey-backed Camaroptera, Northern Crombec, Pygmy Sunbird, Brubru, Cricket Warbler, or the Not Olivaceous Warbler group ( $p > 0.05$ ). However, significant differences were found in densities across sites in Beautiful Sunbird ( $F_{15,6}=17.4$ ,  $p=0.001$ ), Olivaceous Warbler ( $F_{15,6}=50.4$ ,  $p<0.001$ ), Little Weaver ( $F_{15,6}=6.204$ ,  $p=0.017$ ), Yellow-bellied Eromemola ( $F_{15,6}=9.2$ ,  $p=0.006$ ), the Afrotropical Warbler group ( $F_{15,6}=25.336$ ,  $p<0.001$ ), and the Palearctic Warbler group ( $F_{15,6}=12.1$ ,  $p=0.003$ ).

**Table 4.2:** Summary of hypotheses to be tested, their method of testing, and sample size.

	Hypothesis	Sample Size
1	<b>Mid winter densities of Afrotropical warblers did not differ significantly between study years</b> One way ANOVA of density estimates from 6 sites surveyed during both years	12
2	<b>Mid winter densities of Afrotropical warblers varied significantly between sites</b> One way ANOVA of density estimates from each visit to each study site	22
3	<b>Inter-specific variation in densities of Afrotropical warbler species occurs</b> One way ANOVA with Bonferonni Post-hoc of density estimates from each visit to each study site	22
4	<b>Mid winter densities of Afrotropical warblers varied significantly between habitats</b> One way ANOVA of density estimates from each visit to each study site	22
5	<b>Mid winter densities of Afrotropical warblers varied significantly between eastern and western study sites</b> Kruskall Wallis test	22
6	<b>Presence of one species of Afrotropical warbler species will show a significant negative correlation with the presence of others</b> Pearsons' Correlation of raw counts from each mid winter point count. Bonferonni corrected p value.	911
	Pearsons' Correlation of raw counts from eastern site mid winter point count. Bonferonni corrected p value.	548
	Pearsons' Correlation of raw counts from each mid winter point count where at least one of species pairs present. Bonferonni corrected p value.	497
7	<b>Seasonal variation in densities of Afrotropical warblers occurs</b> One way ANOVA with Bonferonni Post-hoc of density estimates from each visit to each study site	36
8	<b>Significant differences occur between mid winter densities of Afrotropical and Palearctic warbler species</b> One way ANOVA with Bonferonni Post-hoc of density estimates from each winter visit to each study site	31
	One way ANOVA with Bonferonni Post-hoc of density estimates from each winter visit to eastern study sites	17
	One way ANOVA with Bonferonni Post-hoc of density estimates from each winter visit to western study sites	13
9	<b>No significant differences occur between the ratio of Afrotropical to Palearctic species found in this study and those found previously</b> Independent t-test of ratios at individual sites from both studies	23
	Independent t-test of ratios from western sites in this study and all from previous study	16
10	<b>A significant correlation occurs between the presence of the Afrotropical warbler group and Palearctic warbler group</b> Pearsons' correlation of raw mid winter counts of Afrotropical and Palearctic warbler groups	911
	Pearsons' correlation of raw counts from all seasons of Afrotropical and Palearctic warbler groups	1863
	GLM with Palearctic warbler group winter abundance as dependent and Afrotropical warbler group and Year as independent variables	910
	GLM with Palearctic warbler group abundance in all seasons as dependent and Afrotropical warbler group, with Season and Year as independent variables	1578
11	<b>Afrotropical and Palearctic warbler species show a significant negative correlation in occurrence due to competitive exclusion</b> Correlation of raw mid winter counts of Afrotropical and Palearctic warbler species	911
	Correlation of raw mid winter counts from eastern study sites of Afrotropical and Palearctic warbler species	548
	Correlation of raw mid winter counts of Afrotropical and Palearctic warbler species from from points at which at least one of the warbler species was observed	497



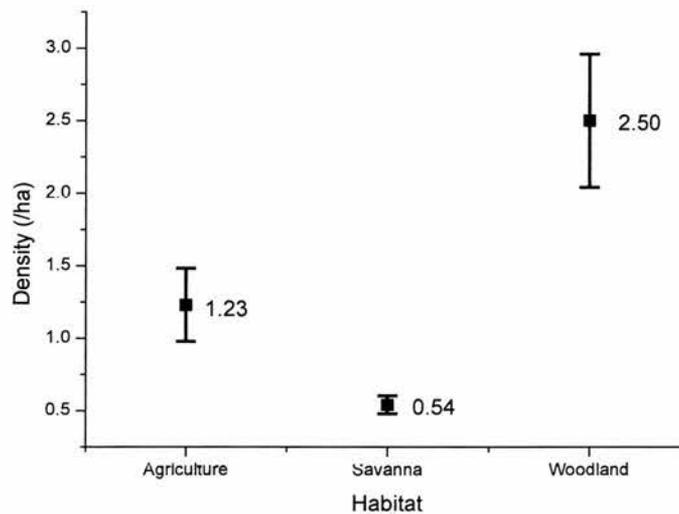
**Fig 4.1:** Mid winter densities and density ranges of Afrotropical warbler species across all sites. Beautiful Sunbird, Olivaceous Warbler, Yellow-bellied Eromemola, Palearctic Warbler group, and Afrotropical Warbler group densities differed significantly across sites ( $p < 0.01$ ). Densities did not differ between years for any species ( $F_{1,11} < 5.0$ ,  $p > 0.05$ ).

Mid winter densities of the four most common Afrotropical warbler species (Olivaceous Warbler, Cricket Warbler, Little Weaver, and Pygmy Sunbird) differed significantly from one another across the 16 study sites ( $F_{3,84} = 4.1$ ,  $p = 0.009$ ).

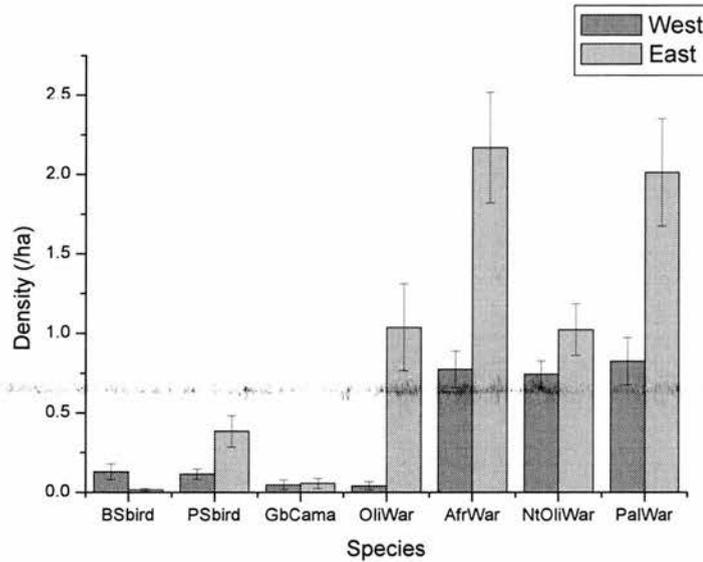
No significant differences in mid winter densities were found across the three main habitat types for the majority of species (see Table 4.3). However, significant differences were present in the densities of Olivaceous Warbler, not Olivaceous warbler group, and Afrotropical Warbler group across habitats. Post-hoc tests indicated Afrotropical Warbler group densities were significantly greater in woodland (Fig 4.2), though no significant post-hoc differences were found in Olivaceous Warbler or not Olivaceous warbler group.

**Table 4.3:** Mean mid-winter density estimates across three broad habitat types, with significant ANOVA results (error df=2, sample df=19).

Species	Density per ha			F	p
	Savanna	Agriculture	Woodland		
Acacia Warbler	0	0	0.11	1.9	0.178
Beautiful Sunbird	0.05	0.12	0.06	0.6	0.581
Brubru	0	0	0.02	1.9	0.180
Cricket Warbler	0.40	0.02	0.40	1.8	0.200
Grey-backed	0.01	0.09	0.10	2.4	0.121
<b>Camaroptera</b>					
Little Weaver	0.12	0.00	0.12	1.6	0.172
Northern Crombec	0.06	0	0.16	2.0	0.158
Olivaceous Warbler	<b>0.36</b>	<b>0</b>	<b>1.26</b>	<b>4.1</b>	<b>0.033</b>
Pygmy Sunbird	0.26	0.19	0.32	0.2	0.818
Yellow-bellied	0.02	0	0.04	0.5	0.643
<b>Eromemola</b>					
<b>Afrotropical warbler group</b>	<b>1.23</b>	<b>0.54</b>	<b>2.50</b>	<b>5.8</b>	<b>0.011</b>
<b>Not Olivaceous warbler group</b>	<b>0.86</b>	<b>0.59</b>	<b>1.09</b>	<b>3.7</b>	<b>0.044</b>
<b>Palaearctic warbler group</b>	1.38	0.86	1.97	1.3	0.307

**Fig. 4.2:** Mean ( $\pm$ SE) mid-winter densities of the Afrotropical warbler group (Afrotropical Warbler group) between three broad habitat types. Densities in woodland were significantly greater than those found in savanna and agriculture ( $F_{2,19}=5.8$ ,  $p=0.011$ ).

Significant differences in mid winter densities were found between eastern (n =9) and western (n =7) sites for Beautiful Sunbird, Olivaceous Warbler, Afrotropical Warbler group, and Palearctic Warbler group (see Fig. 4.3).

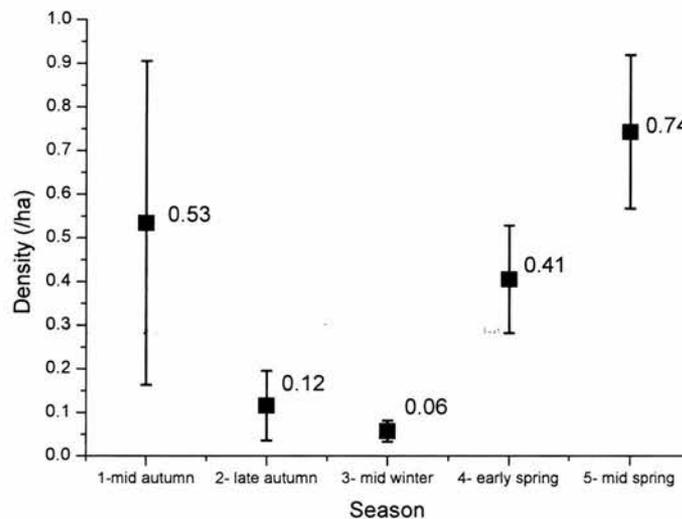


**Fig. 4.3:** Mean ( $\pm$ SE) mid-winter densities of Afrotropical warblers and Palearctic warblers in eastern and western study sites. Densities differed significantly between eastern and western sites in Beautiful Sunbird ( $\chi^2=5.93$ ,  $p=0.015$ ,  $df=1$ ), Olivaceous Warbler ( $\chi^2=11.46$ ,  $p=0.001$ ,  $df=1$ ), Afrotropical Warbler group ( $\chi^2=6.96$ ,  $p=0.008$ ,  $df=1$ ), and Palearctic Warbler group ( $\chi^2=4.710$ ,  $p=0.030$ ,  $df=1$ ). Non-significant differences were found in Pygmy Sunbird ( $\chi^2=2.30$ ,  $p=0.129$ ,  $df=1$ ), Grey-backed Camaroptera ( $\chi^2=0.89$ ,  $p=0.766$ ,  $df=1$ ), and not Olivaceous Warbler group ( $\chi^2=2.00$ ,  $p=0.193$ ,  $df=1$ )

Significant positive correlations ( $P_{crit}=0.005$ ) in the raw counts of individual species at each point were found between Little Weaver and Northern Crombec ( $r_s = 0.129$ ,  $n=911$ ,  $p<0.0001$ ). Olivaceous Warbler showed a strong easterly bias in distribution, but when eastern sites only were used in the analyses no significant correlation was present for this species ( $r_s<0.2$ ,  $n=548$ ,  $p>0.005$ ). It is possible that the correlations between species were a function of the points void of suitable habitat having a probability of either species occurring of zero. The analysis was repeated with only points in which at least one of the species in question was present. Results obtained showed no significant correlation between any Afrotropical warbler species ( $r_s<0.1$ ,  $n=497$ ,  $p>0.05$ ). This suggests that the initial correlation results are not biologically significant.

#### 4.4.2 Seasonal Variation in Densities

Significant seasonal variation was found in the not Olivaceous Warbler group ( $F_{4,31} = 3.3$ ,  $p = 0.023$ ), but not in the Olivaceous warbler group ( $F_{4,31} = 1.9$ ,  $p = 0.130$ ). Densities of individual Afrotropical warblers did not differ significantly ( $P_{crit} = 0.005$ ) across seasons for the majority of species. The exception to this was Little Weaver ( $F_{4,31} = 5.4$ ,  $p = 0.002$ ). Post-hoc results for Little Weaver are presented in Fig. 4.4.



**Fig. 4.4:** Mean Little Weaver densities ( $\pm$ SE) across season. Little Weaver differed significantly between late autumn and mid spring, and mid winter and mid spring ( $F_{4,31} = 5.4$ ,  $p = 0.002$ ).

#### 4.4.3 Afrotropical vs Palearctic Species Densities

Mean midwinter densities of Afrotropical warbler species of  $1.50 (\pm 0.28 \text{ SE})$  individuals per hectare did not differ significantly from the mean of  $1.41 (\pm 0.27 \text{ SE})$  found for Palearctic Warbler species across the same sites ( $F_{1,30} = 0.1$ ,  $p = 0.830$ ). If sites in the east only were used for the analysis, Palearctic Warblers still did not differ significantly in densities from Afrotropical counterparts, with densities of 1.96 and 2.08 respectively ( $F_{1,16} = 0.5$ ,  $p = 0.826$ ). Comparison of densities across western study sites only, with mean densities of 0.6 and 0.48 per ha for Palearctic and Afrotropical warblers respectively, showed no significant difference ( $F_{1,12} = 0.3$ ,  $p = 0.594$ ). Ratios of Palearctic to Afrotropical warbler densities found in this study are presented and compared to previously published data in Table 4.4. The mid winter density ratios at the 16 sites surveyed in this study ( $1.43 \pm 0.33 \text{ SE}$ ), were compared with those found at 10 sites

( $1.71 \pm 0.50$  SE) studies by Jones et al (1996), and no significant difference was found ( $t=0.5$ ,  $df=23$ ,  $p=0.631$ ). When the 8 sites from this study that were located within the same geographic area as those used by Jones et al. were used for the comparison, the mean ratio of  $1.52 (\pm 0.56$  SE) was also not found to differ significantly from the previous study ( $t=0.3$ ,  $df=16$ ,  $p=0.780$ ).

**Table 4.4:** Ratios of the mean densities of Palearctic and Afrotropical warbler species found during this and previously published studies. Values  $>1$  indicate Palearctic species were present at greater densities than Afrotropical.

Season	Density Ratio	Source	Country
Mid-winter	4.00	Morel 1968	Senegal
Mid-winter	1.69	Jones et al 1996	Nigeria
Mid-winter	1.03	Wilson, this study	Nigeria
Mid winter (east only)	0.99	Wilson, this study	Nigeria
Mid winter (west only)	1.25	Wilson, this study	Nigeria
Mid-winter	0.56	Lack 1987	Kenya
Mid-winter	0.35	Rabol 1987	Kenya
Mid-winter	0.02	Ulfstrand & Alerstam 1977	Zambia
Mid-winter	0.24	Ulfstrand & Alerstam 1978	Zambia
Spring	0.51	Vickery et al 1999	Nigeria
Spring	0.73	Vickery et al 1999	Nigeria
Spring	0.65	Wilson, this study	Nigeria
Spring (east only)	0.51	Wilson, this study	Nigeria
Spring (west only)	1.44	Wilson, this study	Nigeria

Analyses of count data from individual points indicated a significant positive correlation ( $P_{crit}=0.05$ ) between the occurrence of the Palearctic Warbler group and both the Afrotropical Warbler group ( $p=0.005$ ,  $r_s=0.1$ ,  $n=911$ ) and the Not Olivaceous Warbler group ( $p=0.019$ ,  $r_s=0.1$ ,  $n=911$ ). When data from all seasons were included in the analysis, a significant correlation was present between the Palearctic Warbler group and the not Olivaceous Warbler group densities ( $p=0.030$ ,  $r_s=0.50$ ,  $n=1863$ ) but not Afrotropical Warbler group ( $p=0.221$ ,  $r_s=0.028$ ,  $n=1863$ ). It is possible that changes in calling rate, and therefore detection probability, varied seasonally in Olivaceous Warbler, resulting in the lack of a significant correlation between the Afrotropical Warbler group and the Palearctic Warbler group. However, analysis of the proportion of detections made by call as opposed to sight were not found to differ significantly with season in any of the three groups (see Chapter 2 for full discussion).

In order to control for the effects of annual and seasonal variation in densities or detectability in these results, a General Linear Model was carried out with the Afrotropical Warbler group or the Not Olivaceous Warbler group as the dependent variable, and the Palearctic Warbler group as independent. The results confirmed the significant correlation between the Palearctic Warbler group and both the Afrotropical Warbler group and the Not Olivaceous Warbler group during mid winter, but only between the Palearctic Warbler group and the Not Olivaceous Warbler group across all seasons (see Tables 4.5 and 4.6). The very low  $R^2$  values are presumably due to the model not containing habitat variables that would explain much of the variation in bird abundance. This will be developed further in Chapter 5.

**Table 4.5:** GLM results testing relationship between mid-winter occurrence of Palearctic Warbler species and; a) Afrotropical Warbler (AfrWar) species; and b) Afrotropical Warblers excluding Olivaceous Warbler (NtOliWar).  $P_{crit}=0.03$ . Residual variance= 1357.9915, residual df= 910, residual variance/ residual df= 1.4923.  $R^2$  equivalent= 0.01 for both models.

	Source	DF	F	p	Parameter Estimate	Direction of Relationship
a)	Year	1, 908	1.6	0.2114		
	AfrWar	1, 908	8.5	0.0036	0.125	+
-----						
b)	Year	1, 908	1.2	0.2777		
	NtOliv	1, 908	5.6	0.0177	0.139	+

**Table 4.6:** GLM results testing the relationships between occurrence of Palearctic Warbler species and; a) Afrotropical Warbler (AfrWar) species; and b) Afrotropical Warblers excluding Olivaceous Warbler (NtOliWar)  $P_{crit}=0.02$ . Residual variance= 2269.4578, residual df= 1581, residual variance/ residual df= 1.4923.  $R^2$  equivalent= 0.01 and 0.05 respectively.

	Source	DF	F	p	Parameter Estimate	Direction of Relationship
a)	Season	4, 1575	18.0	<0.0001		
	Year	1, 1575	2.8	0.0937		
	AfrWar	1, 1575	4.2	0.0413	0.056	+
-----						
b)	Season	4, 1575	17.4	<0.0001		
	Year	1, 1575	2.3	0.1276		
	NtOliv	1, 1575	7.0	0.0084	0.100	+

When individual Afrotropical and Palearctic species were tested for correlation during mid winter, significant results ( $P_{crit}=0.005$ ) were found between Lesser Whitethroat and Olivaceous Warbler ( $p<0.001$ ,  $r_s=0.154$ ,  $n=911$ ) and Grey-backed Camaroptera ( $p<0.001$ ,  $r_s=0.134$ ,  $n=911$ ), Bonelli's Warbler and Northern Crombec ( $p<0.001$ ,  $r_s=0.230$ ,  $n=911$ ), and Common Whitethroat and Pygmy Sunbird ( $p=0.001$ ,  $r_s=0.106$ ,  $n=911$ ). As discussed in Chapter 3, Lesser Whitethroat shows a strong easterly bias in distributions. Correlations between this and Afrotropical species were therefore carried out for eastern sites only, with significant results found between Lesser Whitethroat and Grey-backed Camaroptera ( $p<0.001$ ,  $r_s=0.177$ ,  $n=548$ ).

When only points at which at least one of the species in question were present were used in the analysis, significant correlations ( $P_{crit}=0.005$ ) were found between the mid winter occurrence of Olivaceous Warbler and Common Whitethroat ( $p=0.001$ ,  $r_s=-0.147$ ,  $n=497$ ), Northern Crombec and Bonelli's Warbler ( $p<0.001$ ,  $r_s=0.244$ ,  $n=497$ ), and Olivaceous Warbler and Subalpine Warbler ( $p<0.001$ ,  $r_s=-0.225$ ,  $n=497$ ). In contrast to the first analyses however, there was no significant correlation across eastern sites between Lesser Whitethroat and Olivaceous Warbler, and Little Weaver and Bonelli's Warbler.

## 4.5 Discussion

### 4.5.1 Geographic Trends

Mean mid-winter densities of the Afrotropical warbler group across all sites in this study (1.50/ ha) were similar to the 1.20/ ha found in Nigeria by Jones *et. al* (1996). However, the strong easterly bias in distributions found in Olivaceous Warbler may result in artificially high results in this study, biasing any comparison. If western sites from this study only were included, then mean densities of 0.75 / ha were obtained, approximately half those found previously. A study in Senegal found densities of Afrotropical warblers at 0.1- 0.4/ ha, considerably lower than this study, however, only three species were included (Morel 1973). In east Africa, two studies from Kenya estimated Afrotropical insectivore densities of 2- 2.5 individuals per ha (Lack 1987), and 30.58 per ha (Rabol 1987). Previously published estimates of single Afrotropical warbler species densities from east Africa (Rabol 1987) were also generally greater than those found in this study, indicating that differences in Afrotropical warbler

densities between east and west Africa were not merely a function of lower species diversity.

Both the African Warbler group and Olivaceous Warbler occurred in greater densities in woodland, suggesting that Afrotropical warblers may be more specialised than Palearctic warblers, the latter not showing any significant differences between habitats (see Chapter 3). This would support the apparent association between resident species and more complex and dense habitats that has been previously described (Greenberg 1981; Lack 1986; Leisler 1990). However, broad habitat classes used in this analyses, combined with a high degree of habitat heterogeneity within each site, may not allow for more subtle habitat preferences to be identified. Habitat preferences will be explored in greater detail in the Chapter 5.

Olivaceous Warblers were recorded at only one site west of 12.25° E, and at this site (Watucal FR) the species was present at very low densities (0.07/ ha). The species' published distribution within Nigeria (Borrow and Demey 2001; Elgood *et al.* 1994) suggests a widespread distribution in the north, from Lake Chad (13.38° E) west to Sokoto (5.13° E) and south to Zaria (11.03° N) and the Jos Plateau (9.56° N). However, the similarities between resident birds of the race *leaneni* and the migratory race *opaca* may have confused the issue previously and it is possible that the resident individuals of the race *laeneni* are largely restricted to the NE of the country. This easterly bias in densities of Olivaceous Warblers may be an artefact of the species' Sahelian core habitat being more evident in the extreme NE of the country, where the Sahel has a southerly extension. A similar pattern was also found in one Palearctic warbler species, Lesser Whitethroat (see Chapter 3). The easterly bias shown in the African warbler group was presumably a function of the bias shown by Olivaceous Warblers (a significant component of the African warbler group), as was the significant difference in densities across all sites. The westerly bias in densities shown by Beautiful Sunbird may have been due to the Sahelian extension south in the NE of the country supporting lower numbers (the species apparently withdrawing south of the Sahel during the dry season, though see below).

Sennar Penduline Tit had previously only been recorded in the extreme NE of Nigeria (Elgood *et al.* 1994), presumably in association with the southerly extension of the Sahel zone in this region. A group of 3 observed at Dagona (12.45° N 10.35° E) was therefore a considerable extension south (or west) of their past range, as was a single Yellow-bellied Eromemola at Sambisa (11 40 N 14.20 E). As with the Orphean

Warbler (see Chapter 3), habitat loss to the North of the area, or continued expansion of the Sahel southwards (Hellden 1991, Eckholm & Brown 1977, Charney, Stone & Quirk 1975, Ibrahim 1978) may have resulted in the apparent extension of these species' ranges.

#### 4.5.2 Seasonal Trends

The majority of species of Afrotropical warbler and their equivalents showed no seasonal variation in this study. This supports the findings of previous authors (Elgood *et al.* 1994; Jones 1998). Only two species, Yellow-bellied Eromemola and Little Weaver, showed significant variation across the seasons, and in Yellow-bellied Eromemola this result may have been an artefact of the species' rarity throughout the region, rather than true changes in density. Post-hoc analyses further question the degree to which seasonal movement occurs in this species, as only one season-pair differs significantly. The density of Little Weaver appears to decline during mid-winter, a period when the majority of tree species have lost their leaves but before *Salvadora* fruiting has peaked. The species is assumed to be a resident across its range, with no reports of intra-African migration or itinerancy (Elgood *et al.* 1994) and the results are puzzling, but may indicate a withdrawal south of some Sahelian populations. It is also of interest that Beautiful Sunbird showed no significant change in densities across season despite the species being a known intra-African migrant (Elgood *et al.* 1994; Urban *et al.* 1997). It is possible that the census periods within this study fell outwith the period of Beautiful Sunbird influx into the area during the wet season.

The apparently sedentary nature of the majority of Afrotropical warblers and equivalents has profound implications for competition within the system. Contrary to the 'release' hypothesis, seasonal movement of Afrotropical warbler species away from the Sahel does not occur (Moreau 1972). Therefore potentially competing Palearctic species occupy the habitat concurrently with resident birds, suggesting that alternative mechanisms must be in operation to allow for this sympatry.

#### 4.5.3 Densities of Resident and Migrant Species

The ratio of Palearctic to Afrotropical warblers in west North Nigeria previously reported (Jones *et al.* 1996) did not differ significantly from that found in this study, suggesting that either no change in relative densities have occurred, or that changes have been

uniform between Palearctic and Afrotropical species. Results from Watucal Forest Reserve indicate that Palearctic Warblers have declined in abundance (Chapter 3), suggesting that the latter is most likely. This suggests that Afrotropical warblers have undergone a significant population decline. Unfortunately previously published data for individual Afrotropical warbler species from Watucal are not available. However, densities of Afrotropical warbler species of 1.92/ ha at Watucal during 1993/4 (Jones *et al.* 1996) were greater than the density of 1.20/ha found in this study. Without more data over a greater geographic and temporal scale it is not possible to evaluate this apparent difference.

Spring ratios from west North Nigeria of 1.44 were within the range of 0.95-1.44 reported previously (Vickery *et al.* 1999), with periods of migration and departure of Palearctic species presumably explaining the variation in values found. Comparison of ratios between east North Nigeria and west North Nigeria (Table 4.6) suggest that during both winter and spring passage the relative abundances differ. The densities of Palearctic species are proportionally greater than Afrotropical in west North Nigeria than east. This difference in relative abundance is assumed to be due to Olivaceous Warbler being largely absent from western sites but the dominant species of Afrotropical warbler in the east. However, this longitudinal gradient in relative abundance also appears to be present over a larger geographic area, with an apparent cline of decreasing dominance of Palearctic species with latitude and/or longitude. Ratios for Kenya and Zambia indicate that Palearctic species are in the minority in these regions. This may merely reflect the decline in Palearctic warbler abundance, and increase in Afrotropical warbler abundance with declining latitude previously described (Jones 1998).

Despite the ratios of Palearctic and Afrotropical warblers indicating the former were more abundant, no significant differences in densities of Palearctic and Afrotropical warbler species found in this study. This differs from previous work from West Africa that concluded that Palearctic species outnumbered Afrotropical by 2 and 20 times in the Sahel of Nigeria and Senegal respectively (Jones *et al.* 1996; Morel 1968). This may have been due to differences in the number of species included within the two respective residency groups, but may also reflect a decline in abundances of Palearctic species.

The low  $R^2$  values found in the General Linear Models (Tables 4.5 and 4.6) assessing the relationship between the presence of Afrotropical and Afrotropical excluding

Olivaceous warblers upon the presence of Palearctic species indicates that, despite the relationship being significant, it is weak and other factors such as habitat characteristics must explain the presence or absence of Palearctic species. This will be explored in Chapters 5 and 6.

The significant positive correlation in mid-winter raw counts of Palearctic and Afrotropical Warbler species (and the not Olivaceous Warbler group), and the significant relationship found between the occurrence of Afrotropical warbler species and Palearctic warblers in the GLM results, supports the findings of two previous studies (Jones, et al. 1996; Lack 1986). Results from data across all seasons also indicated a significant degree of association between the two residency groups. The mechanism for this apparent sympatry is unclear however. As with the correlation found between Subalpine Warbler and Common Whitethroat (Chapter 3), it is possible that similar habitat preferences result in species co-occurrence, or alternatively that difference in habitat use allow co-existence through reduced competition. This will be explored in more detail in chapters 5 and 6.

## 4.6 Conclusion

Densities of Afrotropical warbler species found in this study were comparable to those found previously, and lower than those found in East Africa. Olivaceous Warblers occurred in greater densities in eastern study sites, presumably due to habitats in this region being more suitable. The apparent preference of Afrotropical warbler species for woodland sites supports previous studies, and indicates the group prefer more complex habitats than Palearctic counterparts. It also suggests that the group may be more vulnerable to habitat loss or degradation than their Palearctic counterparts, with one species of the latter undergoing significant declines at one study site, presumably due to severe habitat loss. Only one species of Afrotropical warbler showed seasonal variation in abundance, suggesting competitive release of Palearctic warblers does not occur. This, combined with the significant correlation between abundances of Afrotropical and Palearctic species, would suggest that the potential for competition between the two groups is great. Whether the potential for competition between resident and migrants is greater in regions with a high or low ratio of Palearctic to Afrotropical warbler densities is unclear however.

## Chapter 5 : Habitat Selection by Palearctic and Afrotropical Warbler Species in Sahelian West Africa

### 5.1 Introduction

It has been estimated that approximately 5,000 million migratory birds winter within the African continent (Moreau 1972). The majority of these are present in the semi-arid Sahel region, with the number of species and individuals declining as one moves south (Jones 1998). The arrival of large numbers of migrants into the Sahel during the autumn coincides with the onset of a prolonged dry season, and this apparent paradox has been discussed by several authors (Fry 1992; Moreau 1972). Competitive exclusion of Palearctic migrants from more southerly latitudes by Afrotropical species, unsuitability of rainforest habitats to many Palearctic species, and the unsuitability of Southern savannas during the rains, have all been put forward as explanations to overcome the apparent disaccord between these two events (Elgood *et al.* 1994; Fry 1992; Jones 1998; Moreau 1972).

The Sahel also supports a distinct resident avifauna as well as a number of biome-restricted bird species (Fishpool & Evans 2001). A high potential for competition exists in habitats which experience a seasonal influx of migratory species (Greenberg 1986; Lack 1971; Leisler 1992; Moreau 1972). Within Africa it has been estimated that 10% of Palearctic migrant species potentially compete with each other, and 28% potentially compete with Afrotropical species (Lack 1971; Moreau 1972). Intra-African migration is carried out by c. 40% of Afrotropical species, generally in association with the rains (Elgood *et al.* 1994) and it has been suggested that this may 'release' Palearctic migrants from competition with Afrotropical species (Jones 1998; Moreau 1972). However, in West Africa at least, Afrotropical warbler species do not appear to withdraw south with the onset of the dry season and the concurrent arrival of Palearctic migrants (Jones 1998; Chapter 4). This suggests that the potential for competition between migrant and resident warbler species remains high throughout the dry season. In addition, the significant correlation in presence of Palearctic and Afrotropical species at individual points (see Chapter 3) indicates that geographic segregation does not occur. This raises the possibility of interspecific variation in habitat selection providing an alternative mechanism for reduction in competition, allowing sympatry between the groups. Past studies have concluded that Afrotropical species utilise more complex and dense habitats than their Palearctic counterparts (Bilcke 1984; Lack 1971; Rabol

1987), although the number of species pairs used for comparisons has been rather limited. Comparisons of relative densities of Palearctic migrant and Afrotropical species allow an initial assessment of the potential for competition. However, an understanding of habitat selection within species and groups would provide a better indication of the true potential for competition.

The current paucity of information on habitat selection of migrant species in their wintering grounds is of particular concern considering the conservation status of many species. Fluctuations in Sahelian rainfall show a significant positive correlation with subsequent breeding populations of migrant species in Western Europe (Baillie and Peach 1992; Bryant and Jones 1995). The limited data available however, suggests that dry season invertebrate resources may not be as limited as previously suspected (Fry 1992). An 80% decline in Common Whitethroats breeding in Britain during the late 1960's was linked to a period of severe drought in the Sahel between 1965 and 1970 (Baillie and Peach 1992; Winstanley et al. 1974). Similar declines in breeding populations of Sand Martin and Sedge Warbler in Western Europe were also associated with drought events in the Sahel (Bryant and Jones 1995; Foppen et al. 1999; Peach et al. 1991; Szep 1995). A decline in the abundance of Subalpine Warblers at one site in Northern Nigeria that was presumably the result of severe habitat loss was also described in Chapter 3. Since 1972 British populations of Common Whitethroat have shown slight recovery, with recent breeding populations approximately 29% of those present prior to the crash (Baillie et al. 2002). However, the slow rate of this recovery suggests that the Sahelian winter habitats have not regenerated fully. Despite conditions in the Sahel having been shown to affect winter survival of Palearctic species, the affects of these changing conditions upon Afrotropical species are completely unknown.

Habitat destruction has been rapid throughout the Sahel due to a rapidly increasing human population. In Senegal the extent of *Acacia nilotica* woodland declined by 90% between 1954-1986 (Morel & Morel 1992) whilst Borno State in NE Nigeria saw a 14% decline in woodland between 1976 and 1995 (Geomatics International 1998). In both cases habitat loss was through human clearance for fuel wood, grazing, and conversion to intensive agriculture. With a paucity of information on winter habitat requirements of Palearctic migrants, the exact impact of habitat loss and degradation upon wintering populations of Palearctic migrants is unknown. The apparent differential effects of habitat degradation upon Palearctic warbler species found at one site in Nigeria (see Chapter 3) have considerable implications in predicting the affects of

habitat change upon bird populations in the Sahel. More detailed analysis of habitat preferences are required in order to tease apart the processes responsible.

In this chapter I address the following hypotheses:

1. Palearctic and Afrotropical warblers exhibit interspecific variation in habitat selection.
2. The importance of *Salvadora* increases during spring for Palearctic but not Afrotropical species due to the formers' dependence on fruit prior to spring migration.
3. Afrotropical species exhibit greater interspecific variation in habitat selection than Palearctic due to the formers' greater degree of specialism.
4. Palearctic warblers select for more open habitats than Afrotropical counterparts.
5. Relative invertebrate abundance plays an important role in the dependence of warbler species on specific tree species.
6. Palearctic species exhibit weaker selection for key habitat variables than Afrotropical species due the formers' more generalist habitat preferences.
7. The effects of habitat loss or degradation will act differentially upon individual warbler species.
8. Habitat selection models provide good predictive models for identifying habitat suitable for individual species of warbler.

## 5.2 Methods

Point counts were carried out in Northern Nigeria between October and April. At each point, habitat variables were recorded within a 25m radius plot and invertebrate samples were taken at a subset of study sites. A full description of methods used is contained in Chapter 2.

Data on the abundance of all bird species were recorded, but gleaning passerines of mass less than 20g are discussed throughout this thesis (Table 2.7). From this group of 'warblers', a subset of three Palearctic *Sylvia* warblers (Subalpine Warbler, Common Whitethroat, and Lesser Whitethroat) and three Afrotropical warblers (Olivaceous Warbler, Cricket Warbler and Little Weaver) were selected as they were the most abundant (and therefore allowed analysis using GLM's), and provided a species

assemblage that was suitable for the assessment of habitat preferences in both resident and migratory species.

## 5.3 Data Analysis

### 5.3.1 Habitat Modelling

Habitat data from the 25m radius vegetation plots were combined with raw counts of birds within a 50m radius, the latter derived from point count data. The data set was split at random into two sub-sets containing 85% (Training) and 15% (Validation) of data respectively. The Training data set was used to produce habitat GLM's, the Validation data for model validation.

From previous studies (Jones *et al.* 1996; Stoate *et al.* 2001; Vickery *et al.* 1999) and observations during fieldwork, eight habitat variables were identified as potential predictors of bird presence and were used within habitat models alongside 3 confounding variables (see Table 2.12). No candidate variables were excluded solely on the basis of significant correlation with other covariates, as this may have resulted in the elimination of significant variables (James and McCulloch 1990).

The number of observations of Lesser Whitethroat were limited, preventing analysis across the complete data set. However, as Lesser Whitethroat was absent from all study sites during seasons 1 and 5 (the species arrives late and leaves early from Africa), data from these seasons were excluded from the GLM data set for this species. *Calatropis* density was also excluded as this variable was deemed to be the least interesting of explanatory variables because it is a low herbaceous plant with no foliage to speak of, and was therefore of little value to the warbler species. This is not believed to have significantly affected the outcome of the models. As discussed in Chapters 3 and 4, Lesser Whitethroat and Olivaceous Warbler exhibited a strong easterly bias in distribution, which was also found in one of the habitat variables (*Salvadora* Density). In order to test the effects of these easterly biases on model results, GLM selection procedures were repeated for data from eastern sites only.

Production and selection of General Linear Models was carried out using SAS™ 8.02 software and generally followed Burnham and Anderson (2002). Any variables

exhibiting a curved relationship with the dependent variable were quadratic transformed before inclusion within candidate GLM's. Bird count data fitted a Poisson distribution, with analysis in SAS accounting for this and any over-dispersion. GLM models were produced for all possible combinations of the eight selected variables ( $255, 2^8$  minus null model). The most parsimonious model was selected using  $\Delta AIC$ , with the best-fit model having a  $\Delta AIC$  value of 0. The critical p value for variables within models was 0.05 divided by the number of variables included within each model. The overall fit of the model to the data was assessed using the equivalent of the  $R^2$  value obtained from  $1 - \text{Model variance} / \text{Null model variance}$  (Flynn 1999; Guisan and Zimmermann 2000). To further assess relative variable importance to each warbler species models falling within the 0.95 'Occam's Window' (Madigan and Raftery 1994) were included within a table of relative importance. In order to ease comparisons of  $w(+i)$  values, proportions relative to the maximum  $w(+i)$  value were calculated (see Table 5.1). However, in Lesser Whitethroat the Akaike weights were too small for use in model selection. Examination of model  $\Delta AIC$ ,  $w_i$ , and E/R values indicated that models 1-4 would be more suitable for comparisons of relative variable significance across models (Table 5.2), and these models were therefore used. For a full discussion see section 2.11 in chapter 2.

### 5.3.2 Relative Strength Of Selection Across Warbler Species

In order to compare relative degrees of selection of significant variables between bird species, four data subsets were produced, one each for Common Whitethroat, Lesser Whitethroat, Subalpine Warbler and Olivaceous Warbler. Each subset contained 50 points at which only the relevant warbler species occurred, thus there was no replication of points between data sets. Selection of sites at which only one of the key species was present was in order to limit the potential effects of inter-specific interactions. The four data sets were merged into one and the raw count for each species transferred into a single variable KeyWarb. One additional class variable was included within the data set, SpPres, which identified which warbler species was responsible for the KeyWarb value for each respective point. Using this data subset, a GLM was produced using KeyWarb as the dependent variable with all other variables interacted with SpPres also included. Non-significant values (0.05/ no. of variables) were removed from the model in a backwards-stepwise manner until only significant variables were present. Comparisons of parameter estimates produced for each

warbler species from the final model provide a comparison of the relative degree of selection for each key habitat variable exhibited by each warbler species.

**Table 5.1:** Relative variable importance for each species across models falling within Occam's window of 0.95. Values of 1.0 indicate greatest relative importance of variables. To compare these results with significant values from the best-fit model, \* indicate variables with p values <0.005 within the best-fit model.

Species	Number of Models	Mean height	Tree Diversity	Acacia Density	Tree Density	Calatropis Density	Balanites Density	Salvadora Density	Shrub density (excluding Salvadora)
Common Whitethroat	14	1.0*	1.0*	0.4	0.3	0.6	1.0*	1.0*	0.8
Subalpine Warbler	12	0.3	0.7	1.0*	1.0*	0.8	0.3	1.0*	1.0*
Lesser Whitethroat (East)	4	0.9	1.0*	1.0*	1.0*		1.0*	1.0*	0.7
Olivaceous Warbler	14	1.0*	0.9	0.9	0.5	0.5	1.0	0.9*	0.6
Olivaceous Warbler (East)	11	1.0*	1.0	0.3	1.0*	0.9*	0.4*	1.0	1.0
Cricket Warbler	17	0.7	0.9	0.3	0.9*	0.3	0.2	1.0	0.4
Little Weaver	22	1.0*	1.0*	0.9*	0.3	0.9	0.1*	1.0	0.3

**Table 5.2:** Model Parameters for the top 8 Lesser Whitethroat models across all sites ranked by Akaike Differences ( $\Delta$ AIC). Values for  $\Delta$ AIC, Akaike Weights ( $w_i$ ) and Evidence Ratios (E/R) indicate that models ranked 1-4 would be most appropriate for use in assessing relative variable importance.

Model Rank	Model Number	AIC	$\Delta$ AIC	$w_i$	$\sum w_i$ (Occam's Window)	E/R
1	247	737.762	0.000	0.289	0.289	1.00
2	219	739.252	1.490	0.137	0.426	2.11
3	220	741.637	3.875	0.042	0.468	6.94
<b>4</b>	<b>163</b>	<b>742.173</b>	<b>4.411</b>	<b>0.032</b>	<b>0.500</b>	<b>9.07</b>
5	172	763.785	26.023	0.000	0.500	447421.35
6	95	764.112	26.349	0.000	0.500	526881.15
7	228	765.780	28.018	0.000	0.500	1213541.70
8	165	765.906	28.144	0.000	0.500	1292062.16

Interactions of Season were included in the best-fit GLM habitat selection models for each species in order to test whether the importance of *Salvadora* in particular increased with the onset of fruiting and prior to spring migration.

### 5.3.3 Validation of Predictive Models

Predictive models for each species were derived from the best-fit habitat model, and from average parameter estimates from models with  $\Delta AIC$  values  $< 2.0$ , the latter models assumed to have substantial support that they provide a good fit to the data (Burnham and Anderson 2002). Probability of occurrence values for each species was calculated for each point using model parameter estimates following the protocol of Luck (2002a). For a full discussion of methods used see section 2.12 in chapter 2. A summary of hypotheses to be tested and their method of test are presented in Table 5.3.

## 5.4 Results

A full discussion of habitats present within each study site, and across the region in general is presented in Chapter 2. Significant variations were found between east ( $n=9$ ) and western ( $n=7$ ) study sites in a number of habitat variables (see Fig 2.4).

### 5.4.1 Habitat Selection Models

Results from habitat selection GLM's are presented in sections 5.4.1.1- 5.4.1.6, with the directions of significant relationships existing for each species within the models presented in Table 5.12.

#### 5.4.1.1 Common Whitethroat habitat selection GLM results

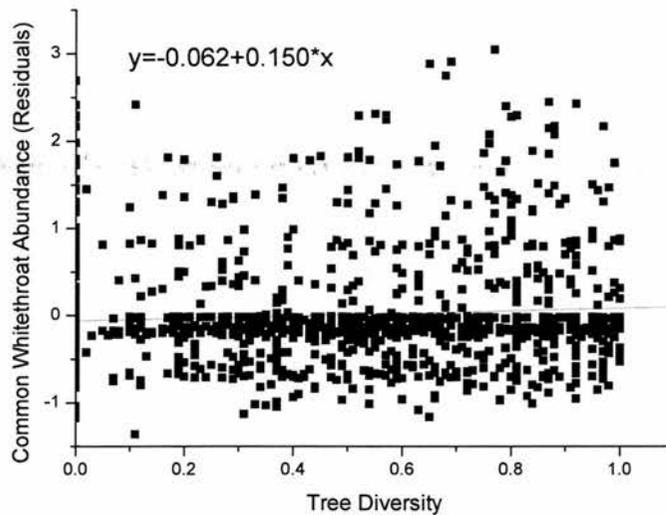
In the most parsimonious best-fit GLM for Common Whitethroat, two candidate variables were excluded (*Acacia* Density and Tree Density), whilst two further variables (Shrub Density and *Calatropis* Density) did not show a significant relationship with Common Whitethroat occurrence (Table 5.4). The seven remaining variables all had significant effects on Common Whitethroat abundance. The relationships exhibited by Common Whitethroat with Tree Diversity, Mean Tree Height, *Balanites* Density, and Season are illustrated in Figures 5.1- 5.4.

**Table 5.3:** Summary of hypotheses to be tested, their method of testing, and sample size.

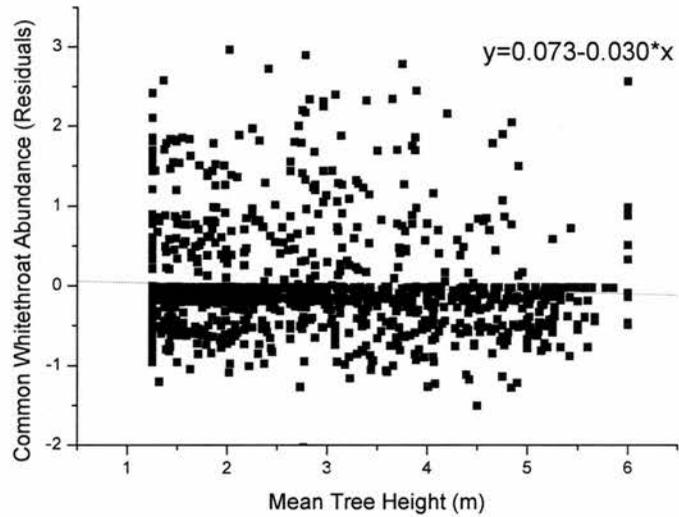
	Hypothesis	n
1	<b>Palearctic warblers exhibit interspecific variation in habitat selection.</b>	
	General Linear Models (GLM's) of raw count data (over-dispersion of Poisson distributed count data accounted for)	1581
	GLM's raw count data for Lesser Whitethroat during seasons 2, 3 & 4 only	1253
	GLM's of raw count data for Lesser Whitethroat from eastern sites during seasons 2, 3 & 4 only	826
2	<b>Afrotropical warblers exhibit interspecific variation in habitat selection.</b>	
	GLM's of raw count data	1581
	GLM's of raw count data for Olivaceous Warbler from eastern sites only	1047
3	<b>Palearctic warblers select for winter habitats similar to those in breeding grounds.</b>	
	Comparison of above GLM results with previously published breeding habitat preference data	
4	<b>The importance of <i>Salvadora</i> increases during spring for Palearctic species but not Afrotropical</b>	
	Addition of season* <i>Salvadora</i> interaction within best-fit habitat selection GLM for Palearctic and Afrotropical warbler species	1581
	Addition of season* <i>Salvadora</i> interaction within best-fit habitat selection GLM for Olivaceous Warbler and Lesser Whitethroat for eastern sites only	1047
5	<b>Palearctic warblers select for more open habitats than Afrotropical counterparts.</b>	
	Results from above GLMs	
6	<b>Afrotropical species exhibit greater interspecific variation in habitat selection than Palearctic.</b>	
	Results from above GLMs	
7	<b>Relative invertebrate abundance plays an important role in warbler occurrence</b>	
	One way ANOVA with Bonferonni post-hoc of relative invertebrate abundance across tree species and comparison of results with GLM's	179
	One way ANOVA with Bonferonni post-hoc of relative invertebrate abundance across seasons and comparison of results with GLM's	39
8	<b>Palearctic species exhibit weaker selection to key habitat variables than Afrotropical species</b>	
	GLM's of data from random subset of 50 points at which each of 4 most common warbler species occur. Occurrence of species A as dependent, occurrence of species B+C+D as covariate	200
9	<b>The effects of habitat loss or degradation act differentially upon warbler species</b>	
	Results from above GLMs	
10	<b>Habitat selection models provide good predictive models for identifying suitable habitat</b>	
	Percentage of correctly predicted presence and absence of warbler species at individual points.	
	Sensitivity, Specificity, and Correct Classification rates of predictivemodels	
	Receiver Operating Characteristic (ROC) Curves	

**Table 5.4:** Habitat GLM results for Common Whitethroat.  $P_{crit}=0.006$ . Residual variance= 1724.1858, residual df= 1581, residual variance/ residual df= 1.0906.  $R^2$  equivalent= 0.28.

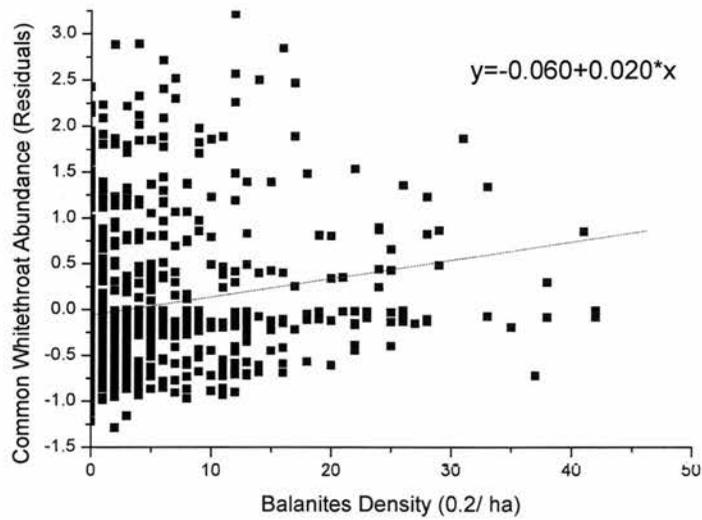
Source	DF	F	p	direction
Season	4, 1569	62.8	<0.0001	
Minutes Af Sunrise	1, 1569	12.3	0.0005	
Year	1, 1569	8.2	0.0042	
Mean Tree Height	1, 1569	19.1	<0.0001	-
Tree Diversity	1, 1569	18.2	<0.0001	+
Balanites Density	1, 1569	71.1	<0.0001	+
Salvadora Density	1, 1569	67.4	<0.0001	+
Shrub Density	1, 1569	4.9	0.0271	
Calatropis Density	1, 1569	3.4	0.0668	



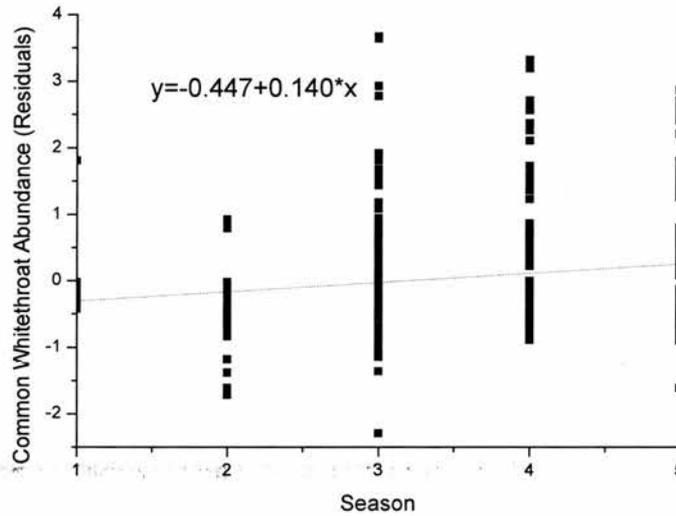
**Fig. 5.1:** Tree Diversity and Common Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1569}=18.2$ ,  $p<0.0001$ ).



**Fig. 5.2:** Mean Tree Height and Common Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1569} = 19.1$ ,  $p < 0.0001$ ).



**Fig. 5.3:** Balanites Density and Common Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1569} = 71.1$ ,  $p < 0.0001$ ).



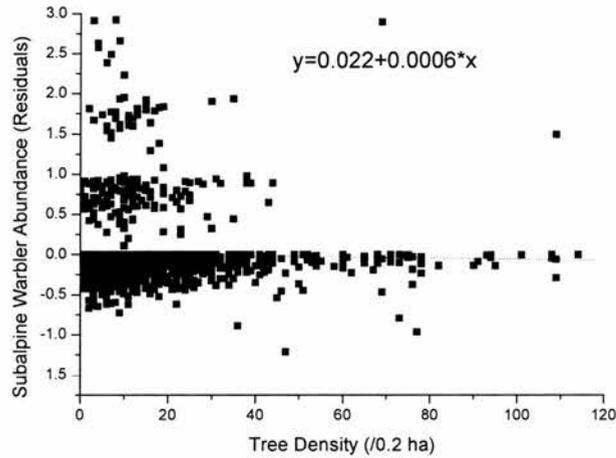
**Fig. 5.4:** Season and Common Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1569} = 62.8$ ,  $p < 0.0001$ ).

#### 5.4.1.2 Subalpine Warbler habitat selection GLM results

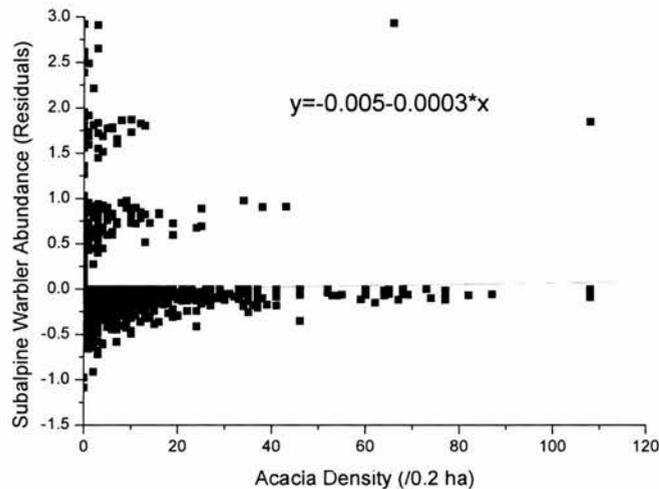
In the most parsimonious GLM for Subalpine Warbler, two variables were excluded (Tree Density and *Balanites* Density), whilst two further variables (Tree Diversity and *Calatropis* Density) did not show a significant relationship with Subalpine Warbler occurrence (Table 5.5). Thus seven variables exhibited significant effects on Subalpine Warbler abundance. Results for Tree Density and *Acacia* Density are shown in Figures 5.5 and 5.6 respectively.

**Table 5.5:** Habitat GLM results for Subalpine Warbler.  $P_{crit} = 0.006$ . Residual variance = 1128.1763, residual DF = 1581, residual variance / residual DF = 0.7136.  $R^2$  equivalent = 0.25.

Source	DF	F	p	direction
Season	4, 1569	44.9	<0.0001	
Minutes Af Sunrise	1, 1569	28.9	<0.0001	
Year	1, 1569	46.1	<0.0001	
Tree Diversity	1, 1569	5.0	0.0262	
Acacia Density	1, 1569	61.6	<0.0001	+
Tree Density	1, 1569	61.1	<0.0001	-
Salvadora Density	1, 1569	90.8	<0.0001	+
Shrub Density	1, 1569	41.4	<0.0001	+
Calatropis Density	1, 1569	8.4	0.0038	-



**Fig. 5.5:** Tree Density and Subalpine Warbler abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1569} = 61.6$ ,  $p < 0.0001$ ).



**Fig. 5.6:** *Acacia* Density and Subalpine Warbler abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1569} = 61.6$ ,  $p < 0.0001$ ).

#### 5.4.1.3 Lesser Whitethroat habitat selection GLM results

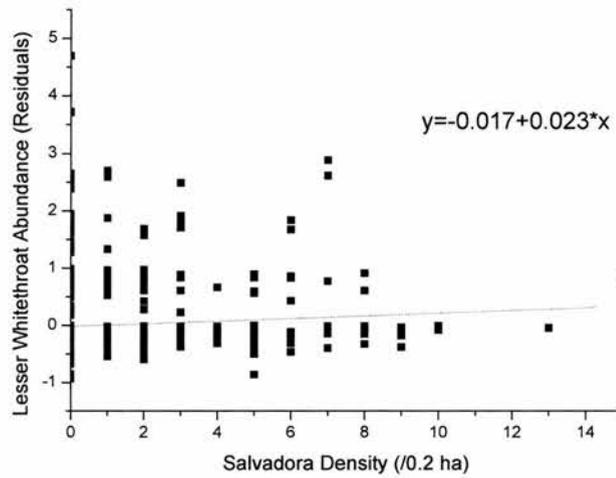
The most parsimonious model for Lesser Whitethroat contained all candidate variables, with one (Shrub Density) exhibiting a non-significant relationship (Table 5.6). Figures 5.7 - 5.10 illustrate the relationships exhibited by Lesser Whitethroat with *Salvadora*, *Balanites*, Tree Diversity, and Tree Height respectively. Comparable results were produced for Lesser Whitethroat when eastern sites only were included in the analysis (Table 5.7).

**Table 5.6:** Habitat GLM results for Lesser Whitethroat.  $P_{crit}=0.005$ . Residual variance=888.0343, residual df=1252, residual variance/ residual df= 0.7093.  $R^2$  equivalent= 0.23.

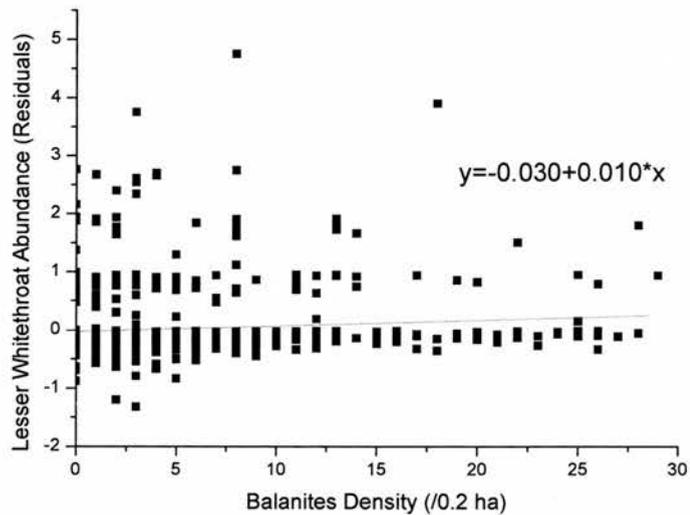
Source	DF	F	p	direction
Season	2, 1242	20.8	<0.0001	
Minutes Af Sunrise	1, 1242	35.2	<0.0001	
Year	1, 1242	0.3	0.5822	
Mean Tree Height	1, 1242	10.2	0.0014	+
Tree Diversity	1, 1242	69.1	<0.0001	+
Acacia Density	1, 1242	52.2	<0.0001	+
Tree Density	1, 1242	55.8	<0.0001	-
Balanites Density	1, 1242	68.1	<0.0001	+
Salvadora Density	1, 1242	78.5	<0.0001	+
Shrub Density	1, 1242	6.1	0.0139	

**Table 5.7:** Habitat GLM results for Lesser Whitethroat.  $P_{crit}=0.005$  in eastern sites only. Residual variance=708.7453, residual df=826, residual variance/ residual df= 0.8580.  $R^2$  equivalent= 0.21.

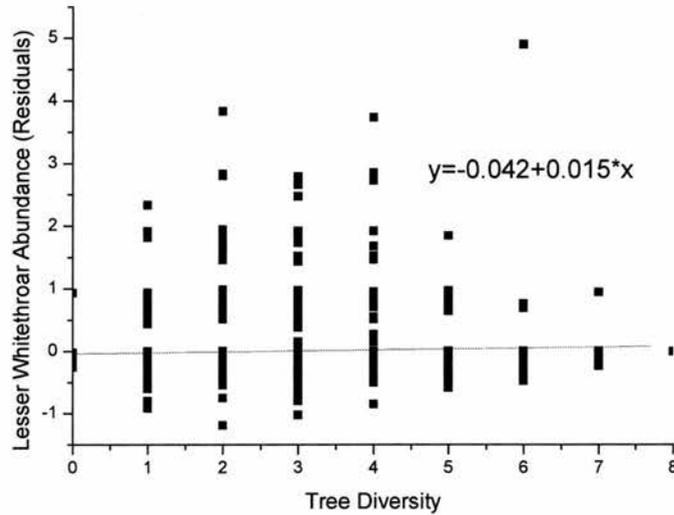
Source	DF	F	p	direction
Season	2, 816	6.9	0.0011	
Minutes Af Sunrise	1, 816	36.2	<0.0001	
Year	1, 816	0.9	0.3526	
Mean Tree Height	1, 816	4.0	0.0449	+
Tree Diversity	1, 816	65.8	<0.0001	+
Acacia Density	1, 816	23.7	<0.0001	+
Tree Density	1, 816	27.1	<0.0001	-
Balanites Density	1, 816	44.5	<0.0001	+
Salvadora Density	1, 816	29.8	<0.0001	+



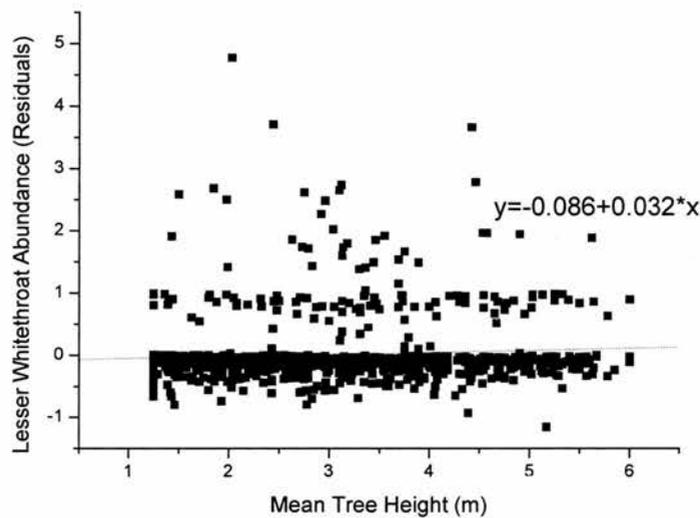
**Fig. 5.7:** *Salvadora* Density and Lesser Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1242} = 78.5$ ,  $p < 0.0001$ ).



**Fig. 5.8:** *Balanites* Density and Lesser Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1242} = 68.1$ ,  $p < 0.0001$ ).



**Fig. 5.9:** Tree Diversity and Lesser Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1242} = 69.1$ ,  $p < 0.0001$ ).



**Fig. 5.10:** Mean Tree Height and Lesser Whitethroat abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1242} = 10.2$ ,  $p = 0.0014$ ).

#### 5.4.1.4 Olivaceous Warbler habitat selection GLM results

The most parsimonious habitat model for Olivaceous Warbler (Table 5.8) contained all candidate variables except *Balanites* Density, though five of these variables (Tree Diversity, Tree Density, *Acacia* Density, *Calatropis* Density, and Shrub Density) were not significant in explaining Olivaceous Warbler occurrence. Olivaceous Warblers' relationship with mean tree height is presented in Figure 5.11. Results from the best-fit GLM for Olivaceous Warbler from eastern sites only (Table 5.9) contained all candidate

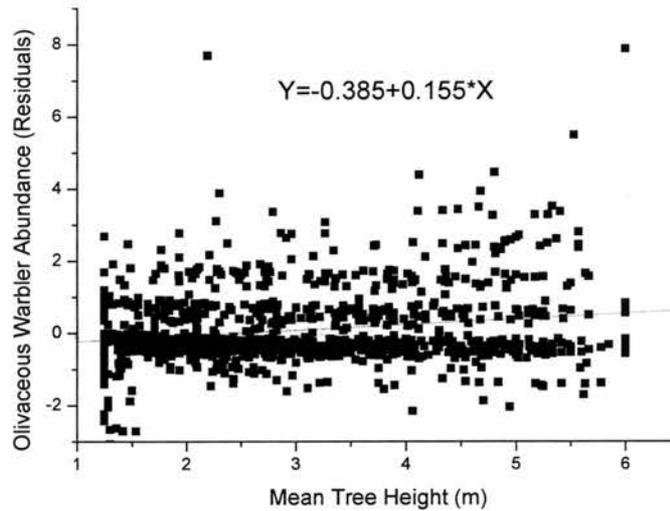
variables except *Salvadora* Density, with Tree Diversity the only non-significant candidate variable included. Olivaceous Warblers' relationship with mean tree height at eastern sites only is presented in Figure 5.12. Overall model fit was comparable between the two models, with  $R^2$  equivalent values of 0.29 and 0.28 for each model respectively.

**Table 5.8:** Habitat GLM results for Olivaceous Warbler.  $P_{crit}=0.006$ . Residual variance= 2119.4458, residual df= 1581, residual variance/ residual df= 1.3406.  $R^2$  equivalent= 0.29.

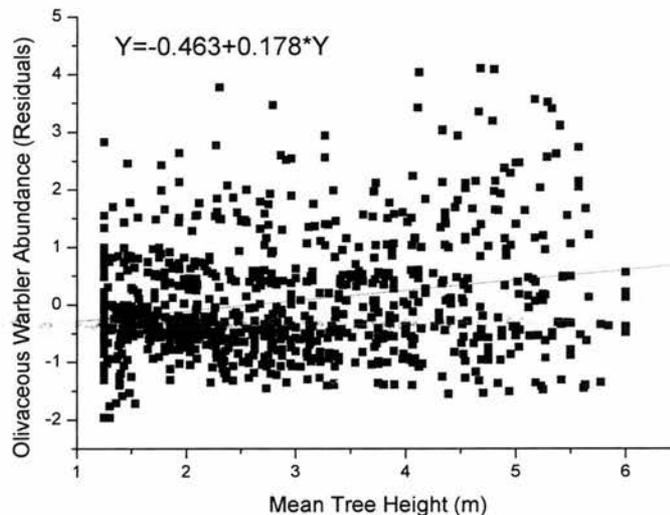
Source	DF	F	p	direction
Season	4, 1568	29.9	0.0011	
Minutes Af Sunrise	1, 1568	1.6	0.1999	
Year	1, 1568	1.7	0.1971	
Mean Tree Height	1, 1568	211.8	<0.0001	+
Tree Diversity	1, 1568	6.5	0.0111	
Tree Density	1, 1568	5.1	0.0238	
Acacia Density	1, 1568	4.7	0.0301	
Calatropis Density	1, 1568	2.4	0.1186	
Salvadora Density	1, 1568	17.4	<0.0001	+
Shrub Density	1, 1568	3.6	<0.0001	

**Table 5.9:** Habitat GLM results for Olivaceous Warbler from eastern sites only.  $P_{crit}=0.006$ . Residual variance= 1543.3022, residual df= 1048, residual variance/ residual df= 1.4726.  $R^2$  equivalent= 0.28.

Source	Num DF	F	p	direction
Season	4, 1036	10.6	0.0011	
Minutes Af Sunrise	1, 1036	0.0	0.9403	
Year	1, 1036	3.7	0.0536	
Mean Tree Height	1, 1036	120.8	<0.0001	+
Tree Diversity	1, 1036	4.5	0.0351	
Tree Density	1, 1036	30.4	0.0238	+
Calatropis Density	1, 1036	9.1	0.0026	-
Balanites Density	1, 1036	7.9	0.005	+



**Fig. 5.11:** Mean Tree Height and Olivaceous Warbler abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1568} = 211.8$ ,  $p < 0.0001$ ).



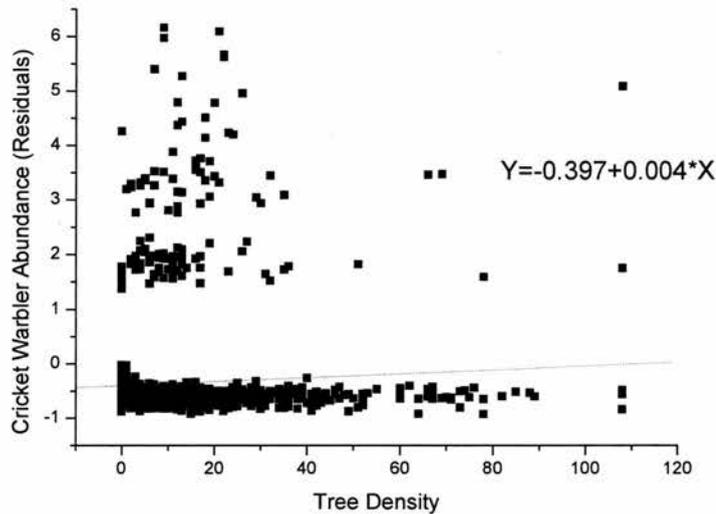
**Fig. 5.12:** Mean Tree Height and Olivaceous Warbler abundance in eastern sites only, residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1036} = 120.8$ ,  $p < 0.0001$ ).

#### 5.4.1.5 Cricket Warbler habitat selection GLM results

The best-fit model for Cricket Warbler contained four candidate variables, Mean Tree Height, Tree Diversity, Tree Density and *Calatropis* Density, though only one of these, Tree Density, showed a significant relationship, and overall model fit was poor (Table 5.10). Cricket Warblers' relationship with tree density is presented in Figure 5.13.

**Table 5.10:** Habitat GLM results for Cricket Warbler.  $P_{crit}=0.006$ . Residual variance=1107.6703, residual DF=1581, residual variance/ residual DF= 0.7006.  $R^2$  equivalent= 0.03.

Source	DF	F	p	direction
Season	4, 1571	2.2	0.069	
Minutes Af Sunrise	1, 1571	9.2	0.0024	
Year	1, 1571	2.7	0.1017	
Mean Tree Height	1, 1571	5.8	0.0164	
Tree Diversity	1, 1571	1.6	0.2105	
Tree Density	1, 1571	13.9	0.0002	+
Calatropis Density	1, 1571	4.6	0.0319	



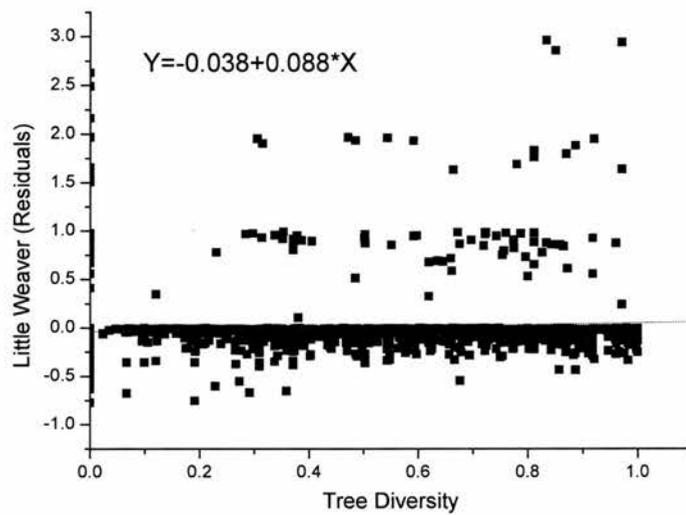
**Fig. 5.13:** Tree Density and Cricket Warbler abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1571} = 13.9$ ,  $p = 0.0002$ ).

#### 5.4.1.6 Little Weaver habitat selection GLM results

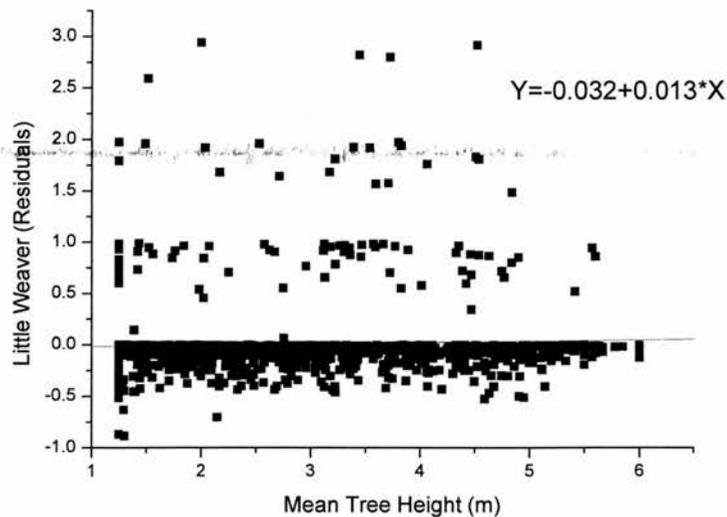
Of the candidate variables, five were included within the best-fit GLM for Little Weaver, though only Tree Density showed a significant relationship with the species occurrence (Table 5.11). Little Weavers' relationships with tree diversity and mean tree height are presented in Figures 5.14 and 5.15.

**Table 5.11:** Habitat GLM results for Little Weaver.  $P_{crit}=0.005$ . Residual variance=807.8368, residual df=1251, residual variance/ residual df= 0.5110.  $R^2$  equivalent= 0.21.

Source	DF	F	p	direction
Season	4, 1570	52.8	<0.0001	
Minutes Af Sunrise	1, 1570	38.5	<0.0001	
Year	1, 1570	8.1	0.0044	
Mean Tree Height	1, 1570	20.0	<0.0001	+
Tree Diversity	1, 1570	48.2	<0.0001	+
Tree Density	1, 1570	1.3	0.2589	
Acacia Density	1, 1570	21.2	<0.0001	+
Balanites Density	1, 1570	19.2	<0.0001	+



**Fig. 5.14:** Tree Diversity and Little Weaver abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1570} = 48.2$ ,  $p < 0.0001$ ).



**Fig. 5.15:** Mean Tree Height and Little Weaver abundance residuals derived from the habitat GLM. A significant relationship was found between the two ( $F_{1,1570} = 20.0$ ,  $p < 0.0001$ ).

**Table 5.12:** Summary of direction of significant relationships existing between each warbler species and habitat variables within best-fit GLM's.

	Mean Height (m)	Tree Diversity	Acacia Density	Tree Density	Balanites Density	Salvadora Density	Shrub Density	Calatropis Density
<b>Common Whitethroat</b>	-	+			+	+		
<b>Subalpine Warbler</b>			+	-		+	+	-
<b>Lesser Whitethroat</b>	+	+	+	-	+	+		
<b>Lesser Whitethroat (east)</b>	+	+	+	-	+	+		
<b>Olivaceous Warbler</b>	+					+		
<b>Olivaceous Warbler (east)</b>	+			+	+		-	-
<b>Cricket Warbler</b>				+				
<b>Little Weaver</b>	+	+	+		+			

For Palearctic species, comparisons of habitat preference results gained from best-fit habitat selection models and the relative importance of variables across all models falling within Occam's window of  $w_i < 0.95$  are consistent across the two methods (Table 5.1). Highly significant variables identified in the most parsimonious models for each species exhibited relative significance values of 1.0. We can therefore be confident of the habitat preferences identified. However, for Afrotropical species some disparity exists between results from the two methods, with variables identified as significant in best-fit models not always showing greatest relative importance, and vice-versa.

#### 5.4.2 Seasonal variation in importance of *Salvadora* and *Balanites*

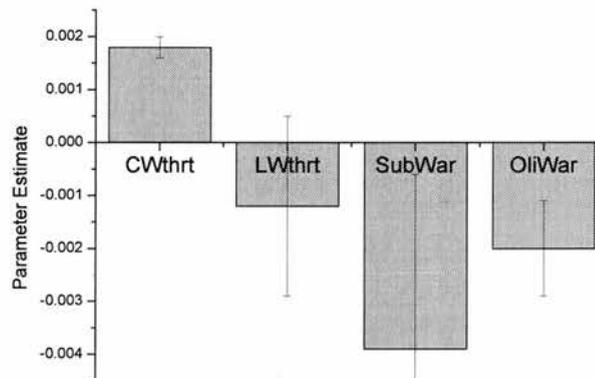
The addition of an interaction between season and *Salvadora* or *Balanites* was introduced into best-fit habitat GLM models in order to assess whether any seasonal change in dependence on particular tree species was occurring. In Common Whitethroat it was found that the importance of *Salvadora* increased significantly with season ( $F_{4,1561}=35.0$ ,  $p<0.0001$ ), but the importance of *Balanites* did not differ significantly across season. No significant change in importance of either *Salvadora* ( $F_{2,1238}=3.1$ ,  $p=0.0433$ ) or *Balanites* ( $F_{2,1238}=2.6$ ,  $p=0.0719$ ) was found across seasons for Lesser Whitethroat in eastern sites only, though it should be noted that this species was not present during mid spring. Unfortunately, insufficient data were available to test for seasonal changes in importance of habitat variables for Subalpine Warbler. In Afrotropical species, no significant seasonal change in importance of *Salvadora* was found in Olivaceous Warbler, with the tree species not present in best fit models for either Little Weaver or Cricket Warbler. *Balanites* was not present in best-fit models for either Olivaceous Warbler or Cricket Warbler, but showed a significant increase in importance during spring for Little Weaver ( $F_{4,1566}=3.04$ ,  $p=0.016$ ).

#### 5.4.3 Relative strength of selection across warbler species

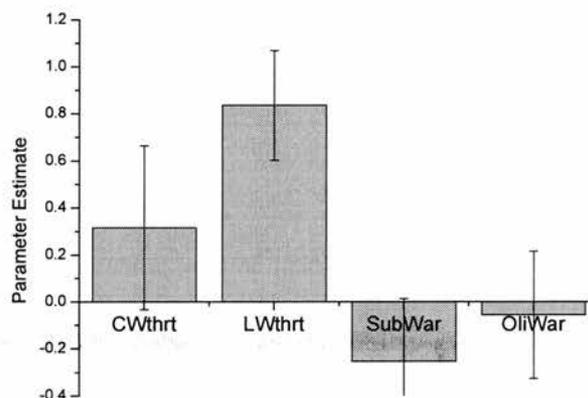
Comparisons of the relative degree of selection for individual habitat components across the four commonest warbler species suggest that only two variables (tree diversity and *Balanites* density) show significant differences in degree of selection between the three species of warbler (see Table 5.13). However, two further variables show differences in degree of variable selection that are approaching significance (mean tree height and tree density). Comparisons of the relative importance of each variable between warbler species expressed by parameter estimates obtained from relative importance GLMs are presented in Figures 5.16- 5.17. Some of these results differ from habitat selection GLM results presented in section 5.4.3, with key variables identified differing between the two methods of analysis. Results from the microhabitat selection GLM indicated that Subalpine Warbler, Olivaceous Warbler and Cricket Warbler did not show a significant relationship with tree diversity, whilst Subalpine Warbler and Cricket Warbler did not show a significant relationship with *Balanites* density. The direction of apparent selection also differs from habitat selection GLM results, with relative strength results indicating positive selection for both tree diversity and *Balanites* density, whilst those from relative importance GLM's indicating selection against these two variables by a number of warbler species.

**Table 5.13:** Results from a GLM comparing the relative importance of key habitat variables between the three key species of Palearctic warbler and Olivaceous Warbler. Significant p values indicate that significant differences in the degree of selection by each warbler species occur.  $P_{crit} = 0.004$ .

Source	DF	F	p
Mean Tree Height	1,132	1.6	0.211
Mean Tree Height* Species Presence	3,132	2.4	0.069
Species Presence	3,132	0.1	0.933
Tree Diversity* Species Presence	3,132	3.8	0.011
Tree Diversity	1,132	2.2	0.140
Acacia Density* Species Presence	3,132	0.9	0.467
Acacia Density	1,132	11.1	0.001
Tree Density* Species Presence	3,132	2.5	0.061
Tree Density	1,132	5.3	0.023
Balanites Density* Species Presence	3,132	6.6	<0.001
Balanites Density	1,132	1.9	0.166
Salvadora Density* Species Presence	3,132	1.4	0.260
Salvadora Density	1,132	2.1	0.150



**Fig. 5.16:** Parameter estimates ( $\pm$  SE) for *Balanites* Density across the four warbler species. A significant difference was found in the degree of selection across the warbler species ( $F_{3, 132} = 6.6$ ,  $p < 0.0001$ ).



**Fig. 5.17:** Parameter estimates ( $\pm$  SE) for Tree Diversity across the four warbler species. A significant difference was found in the degree of selection across the warbler species ( $F_{3, 132} = 3.8$ ,  $p = 0.011$ ).

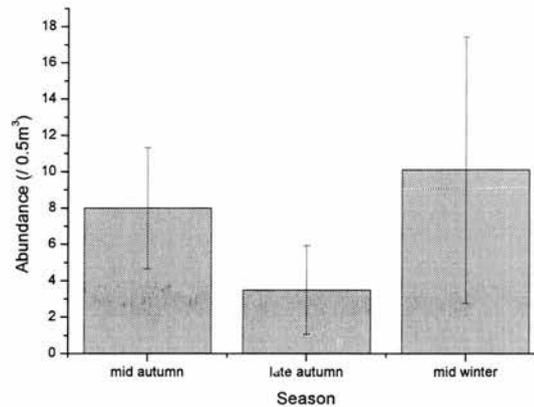
#### 5.4.4 Invertebrate Abundance

Invertebrate abundance varied considerably between tree species during late autumn (see Fig 5.18), with significant differences also occurring between a number of individual species (see Table 5.14 and 5.15). The mean length of invertebrates occurring on each tree species showed no significant difference between tree species ( $F_{7,172} = 1.0$ ,  $p = 0.459$ ). A significant difference was however, found in mean invertebrate length when ants were excluded ( $F_{7,172} = 6.8$ ,  $p < 0.0001$ ). This was due to the significantly greater mean length found on *Calatropis* and was presumably a function of the invertebrate load on *Calatropis* being dominated by ants. It is also possible that ants exclude smaller invertebrates but not larger. Seasonal variation in invertebrate abundance was found across the four common tree species, *Balanites*, *Salvadora*, *A. tortillis* and *Prosopis*, with *post-hoc* tests indicating that significant seasonal variation occurred only in *Salvadora* and *A. tortillis* (see Figs 5.19 and 5.20). Total invertebrate length and invertebrate length excluding ants did not differ significantly across season for *Salvadora*, *A. tortillis*, *Prosopis* or *Balanites*. However, *post-hoc* analysis indicated that mean length excluding ants was significantly greater for *Balanites* in mid winter than late autumn ( $p < 0.05$ ) despite results from the one-way ANOVA being non-significant ( $F_{2,93} = 2.8$ ,  $p = 0.064$ ).

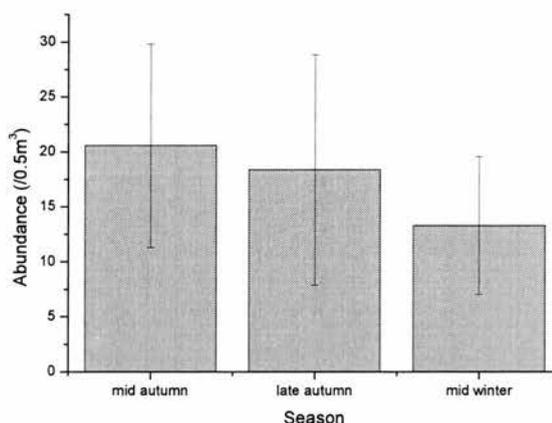


**Table 5.15:** Mean late autumn abundance of invertebrates excluding ants across tree species. Significant differences in abundance across species were found ( $F_{7,172}=17.5$ ,  $p<0.0001$ ), with significant post hoc differences ( $p<0.05$ ) indicated by \*.

	Abundance (0.5m <sup>3</sup> )	Balanites	Bauhinia	Calatropis	Prosopis	Salvadora	A. senegal	A. tortillis	Zizyphus
Balanites	5.2								
Bauhinia	3.4								
Calatropis	0.9	*							
Prosopis	7.1			*					
Salvadora	3.5								
A. senegal	4.9								
A. tortillis	13.4	*	*	*	*	*	*		
Zizyphus	9.0	*		*		*	*		



**Fig. 5.19:** Seasonal variation in mean ( $\pm$ SE) invertebrate abundance excluding ants for *Salvadora*. Significant seasonal variation was found in abundance excluding ants ( $F_{2,37}=8.8$ ,  $p=0.001$ ), with post-hoc analysis indicating significant differences in invertebrate abundance between mid autumn and late autumn ( $p<0.05$ ).

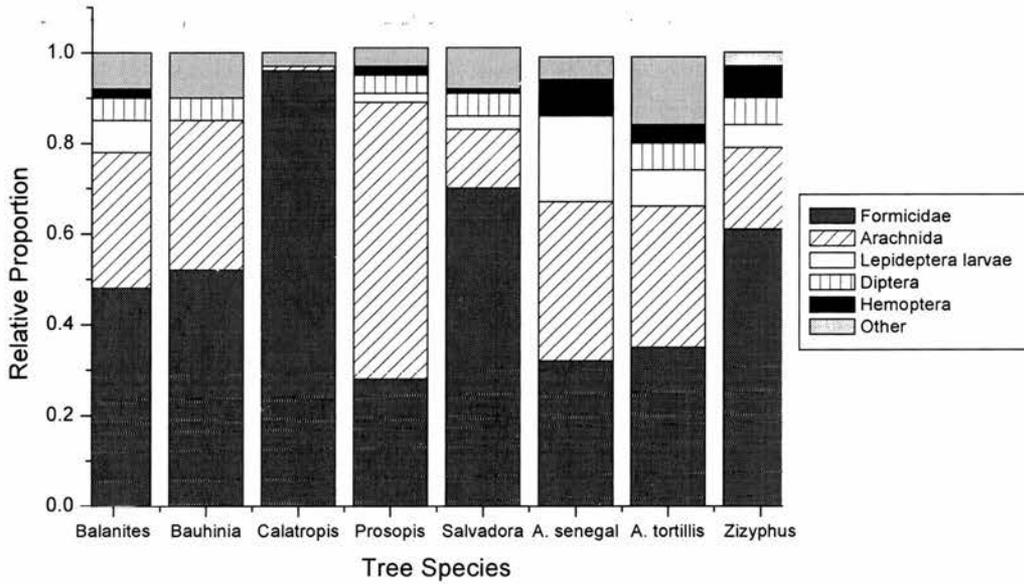


**Fig. 5.20:** Seasonal variation in mean ( $\pm$ SE) invertebrate abundance for *A. tortillis*. Significant seasonal difference was found ( $F_{2,104}=3.7$ ,  $p=0.027$ ) with post-hoc analysis indicating mid winter abundance was significantly lower than during mid autumn or late autumn ( $p<0.05$ ).

Analysis of the proportions of the five commonest invertebrate classes across seasons and tree species (Fig 5.21) indicated that only the proportion of Diptera differed significantly ( $F_{15,308}=6.1$ ,  $p<0.0001$ ). Post hoc analysis indicated that the proportion of Diptera in *Salvadora* increased to 0.42 during mid-winter, a significant increase on mid autumn and late autumn proportions of 0.06 and 0.05 respectively. A similar pattern was shown in *Balanites*, where the proportion of Diptera increased significantly from 0.09 to 0.22 during late autumn and mid winter. In contrast, the proportion of spiders in *Balanites* declining significantly from 0.19 to 0.16 between late autumn and mid winter ( $F_{15,308}=8.8$ ,  $p<0.0001$ ).

#### 5.4.6 Model Validation

The Receiver Operating Characteristic (ROC) Area Under Curve (AUC) values (see Chapter 2) indicated that predictive power was greatest for mean model parameters in Lesser Whitethroat, Subalpine Warbler, Cricket Warbler and Little Weaver. However, the best-fit habitat selection model parameters estimates performed best in Common Whitethroat and Olivaceous Warbler (Table 5.14). AUC values obtained for all species were greater than expected by chance alone, except where mean parameter estimates were used for Olivaceous Warbler across eastern study sites only, and the lowest AUC values occurred in Cricket Warbler. Values of AUC were consistent between Training and Validation data sets for each predictive model.



**Fig. 5.21:** Proportion of six invertebrate classes making up total invertebrate load for each tree species during mid autumn. Significant differences in proportions of Arachnida ( $F_{7,172}=13.2$ ,  $p<0.0001$ ) and Formicidae ( $F_{7,172}=10.7$ ,  $p<0.0001$ ) were found across tree species.

Using information similar to that in Table 2.15, critical p values were selected for use in predictive models that provided the best overall correct classification of occupied and unoccupied points. Prevalence (proportion of points where species found) was relatively low ( $<0.25$ ) for all species except Olivaceous Warbler (Table 5.16) and thus the Kappa value, which provides an indication of predictive improvement of the model above chance, is not appropriate for this data (Fielding and Bell 1997). Prevalence for Olivaceous Warbler of 0.27 and 0.39 for all sites and eastern sites only respectively, indicate that the species was relatively commonly encountered across sites. Values are comparable between Training and Validation data sets, indicating consistency in model predictive ability. Ability to correctly predict presence (Sensitivity) and absence (Specificity) were relatively consistent across species, though Specificity was notably lower for Subalpine Warbler and Olivaceous Warbler, and Sensitivity was low for Cricket Warbler. Classification rates showed the same overall pattern across species, with a high proportion of points correctly predicted not to hold a species (Negative Classification Rate). However, low Positive Classification Rates, resulting in relatively low Correct Classification Rates, offset this.

**Table 5.16:** Model parameters for best-fit and mean habitat selection models. Area under curve (AUC) indicates predictive model ability, with AUC=0.5 indicating that expected by chance alone, and 1.0 perfect predictive ability.  $P_{crit}=0.05$ . Sensitivity is the ability of the model to correctly predict presence; Specificity, the ability to correctly predict absence.

Species	Model	Critical p	Number of Models	Training Data Set				Test Data Set			
				AUC	P	Sensitivity	Specificity	AUC	P	Sensitivity	Specificity
<b>Common</b>		<b>0.3</b>									
<b>Whitethroat</b>	best		1	<b>0.705</b>	<b>&lt;0.0001</b>	<b>0.62</b>	<b>0.79</b>	<b>0.719</b>	<b>&lt;0.0001</b>	<b>0.79</b>	<b>0.76</b>
	mean		14	0.674	<0.0001	0.69	0.69	0.664	0.007	0.76	0.67
<b>Lesser</b>		<b>0.4</b>									
<b>Whitethroat</b>	best		1	0.644	<0.0001	0.71	0.67	0.572	0.313	0.63	0.66
	mean		4	<b>0.693</b>	<b>&lt;0.0001</b>	<b>0.71</b>	<b>0.63</b>	<b>0.682</b>	<b>0.010</b>	<b>0.63</b>	<b>0.67</b>
<b>Subalpine</b>		<b>0.5</b>									
<b>Warbler</b>	best		1	0.599	0.023	0.69	0.50	0.680	0.003	0.85	0.54
	mean		12	<b>0.600</b>	<b>&lt;0.0001</b>	<b>0.70</b>	<b>0.49</b>	<b>0.678</b>	<b>0.003</b>	<b>0.85</b>	<b>0.54</b>
<b>Olivaceous</b>		<b>0.2</b>									
<b>Warbler</b>	best		1	<b>0.686</b>	<b>&lt;0.0001</b>	<b>0.73</b>	<b>0.64</b>	<b>0.719</b>	<b>&lt;0.0001</b>	<b>0.79</b>	<b>0.67</b>
	mean		8	0.684	<0.000	0.71	0.68	0.712	<0.000	0.79	0.69
<b>Olivaceous</b>		<b>0.1</b>									
<b>Warbler</b>	best		1	<b>0.641</b>	<b>&lt;0.0001</b>	<b>0.96</b>	<b>0.26</b>	<b>0.668</b>	<b>0.001</b>	<b>0.96</b>	<b>0.20</b>
<b>(east)</b>	mean		3	0.523	0.269	0.27	0.77	0.519	0.689	0.32	0.77
<b>Cricket</b>		<b>0.1</b>									
<b>Warbler</b>	best		1	0.580	0.032	0.18	0.85	0.518	0.032	0.17	0.84
	mean		11	<b>0.592</b>	<b>0.040</b>	<b>0.22</b>	<b>0.88</b>	<b>0.593</b>	<b>0.067</b>	<b>0.22</b>	<b>0.88</b>
<b>Little</b>		<b>0.1</b>									
<b>Weaver</b>	best		1	0.736	<0.000	0.44	0.86	0.782	0.011	0.54	0.86
	mean		4	<b>0.737</b>	<b>&lt;0.000</b>	<b>0.44</b>	<b>0.87</b>	<b>0.783</b>	<b>0.011</b>	<b>0.54</b>	<b>0.86</b>

Overall negative classification rate was relatively high for both Olivaceous Warbler predictive models, indicating a high ability to predict species absence. However, the ability of the models to predict presence (Positive Classification Rate) was poorer, particularly in the model for eastern sites only. Prevalence was very low (<0.10) for Cricket Warbler and Little Weaver, indicating that the species were observed in relatively few point counts. The ability of the models to predict presence (Sensitivity) was relatively low, particularly when compared to their ability to predict absence (Murtaugh 1996). This was reflected in the very low Correct Classification Rates and high Negative Classification Rates. Prevalence (proportion of points where species found) was too low (<0.50) for the Kappa value (which provides an indication of

predictive improvement of the model above chance) to be applied to these data (Fielding and Bell 1997).

**Table 5.17:** Habitat model predictive performance criteria of key warbler species for Initial (I) and Validation (V) data sets. Prevalence is the proportion of points with the species present; Sensitivity the ability of the model to correctly predict presence; Specificity the ability to predict absence; Classification Rates indicate the proportion of points with correctly predicted occurrence (Positive), absence (Negative), and presence or absence (Correct).

Criteria	Olivaceous Warbler		Olivaceous Warbler (east)		Cricket Warbler		Little Weaver		Common Whitethroat		Subalpine Warbler		Lesser Whitethroat	
	I	V	I	V	I	V	I	V	I	V	I	V	I	V
Prevalence	0.27	0.27	0.39	0.39	0.07	0.09	0.06	0.05	0.21	0.19	0.12	0.12	0.11	0.15
Sensitivity	0.73	0.79	0.96	0.96	0.22	0.17	0.44	0.54	0.62	0.63	0.69	0.85	0.71	0.63
Specificity	0.64	0.67	0.26	0.20	0.88	0.87	0.87	0.86	0.79	0.76	0.50	0.54	0.67	0.66
Correct Classification Rate	0.67	0.70	0.53	0.49	0.83	0.81	0.84	0.84	0.75	0.74	0.52	0.58	0.67	0.66
Positive Classification Rate	0.43	0.47	0.46	0.43	0.13	0.11	0.17	0.16	0.43	0.38	0.16	0.20	0.20	0.24
Negative Classification Rate	0.87	0.89	0.90	0.89	0.93	0.92	0.96	0.97	0.89	0.90	0.92	0.96	0.95	0.91

## 5.5 Discussion

### 5.5.1 Effect Of Season, Minutes After Sunrise And Tree Diversity

As one would expect in migratory species, season was a significant variable for all three species of Palearctic warbler (see Chapter 3 for detailed discussion of seasonal change in densities of Palearctic warblers). As discussed in Chapter 4, Olivaceous Warbler showed no seasonal variation in densities across study sites, and it was therefore surprising that season was a highly significant variable within the species' best-fit habitat selection model. The seasonal variation in Little Weaver densities discussed in Chapter 4 was reflected in the significance of this variable within the best-fit model, despite the species' apparent sedentary nature (Elgood *et al.* 1994). Olivaceous Warbler showed no significant relationship with time of day (Minutes after

Sunrise) despite the Afrotropical Warbler group showing a significant change in detection rate with time of day (see Chapter 2). The highly vocal nature of Olivaceous Warbler, combined with a constant proportion of individuals located by call throughout the morning, may have resulted in the species maintaining a consistent detection rate through the morning. The species' preference for foraging within the canopy interior of large trees (pers obs) may also have resulted in changing foraging and climatic conditions through the day not impacting detection probability or distance.

The negative relationship shown by Common Whitethroat and Subalpine Warbler to minutes after sunrise was also expected considering the effect of time of day discussed in Chapter 2. The significant decline in occurrence of Cricket Warbler and Little Weaver with time of day may have resulted from changing foraging and climatic conditions 'forcing' the species into more dense cover, resulting in a reduced detection probability. Mean densities of Palearctic warblers and their detection distances did not differ significantly between the two study years (see Chapter 3), and the significant relationships shown by Common Whitethroat and Subalpine Warbler to year shown here were presumably due to differences in sites visited each year (see Chapter 3).

Tree diversity, by its definition, equates to the probability that one or more preferred tree species will be present, and the significant relationship found with this variable for all three Palearctic warbler species may be a function of this. Comparisons of relative variable importance across Occam's models suggests that Tree Diversity is present in the majority of models for all three Afrotropical species, though the significance of the variable within the GLM's is less universal. A high degree of heterogeneity in tree species may provide diverse foraging resources and greater structural complexity of vegetation, making the habitat more attractive. Analysis of foraging behaviour carried out in Chapter 6 will address this. It has been suggested that greater diversity of tree species, particularly those that produce fruit, will provide a more robust environment during periods of stress and therefore be more attractive to *Sylvia* species (Stoate 1995).

## 5.5.2 Habitat Selection By Palearctic Species

### 5.5.2.1 Common Whitethroat habitat selection

The preference for lower vegetation by Common Whitethroat indicated by the significant negative relationship with Mean Tree Height in the habitat selection GLM's is further supported by the significant relationship found with *Salvadora persica*, a low sprawling shrubby species which has previously been identified as an important resource for Common Whitethroats during pre-migration fattening (Jones 1998; Stoate and Moreby 1995). It is of interest to note that *Salvadora* was the most significant habitat parameter despite its occurring in the East of the study region, whereas Common Whitethroat were equally abundant in both eastern and western study sites (see Chapter 3).

The relationship between Common Whitethroat and non-*Salvadora* shrub species (Shrub Density) was not quite significant in the best-fit habitat selection model, and exhibited less than complete presence across models within Occam's window. This is perhaps surprising considering the importance of two species included within this group, *Gueira senegalensis* and *Zizyphus* species, found in previous studies (Jones *et al.* 1996; Stoate *et al.* 2001). Casual observations during this study also suggested that these species were of importance. However, the prevalence of other shrub species was low and highly localised across sites in this study, and this may have masked any relationship. It should also be noted that several tree species commonly occurring in NE Nigeria were not discussed in the study from Senegambia, namely *Acacia*, *Balanites*, and *Salvadora*, making direct comparisons of preferences difficult. The density of *Acacia* trees, the commonest group of non-shrubby tree species, was not a significant factor in Common Whitethroat occurrence in this study, further supporting the habitat preferences of Common Whitethroats described above. Likewise, mean tree density was not found to be a significant factor in Common Whitethroat occurrence, presumably due to the species' preference for more open habitats, over densely wooded areas (Cramp 1992; Moreau 1972; Stoate *et al.* 2001). The importance of *Balanites* to Common Whitethroat found in this study supports the findings of a previous study in Northern Nigeria (Vickery *et al.* 1999). However, the latter study also showed a significant positive relationship between density of *Piliostigma* and Common Whitethroat occurrence. This tree species was limited to a small number of sites in this study and was excluded from the GLM candidate variables. It is possible that Whitethroats are generalists in habitat use but have a clear rank order of shrub preference. The probability of an individual being faced with a direct choice between

several preferred shrub species is very low however, and the results obtained in identifying key shrub species will therefore be dependent upon the location of a study region and the dominant shrub species occurring there.

#### 5.5.2.2 Subalpine Warbler habitat selection

Subalpine Warblers showed a significant positive relationship with *Acacia* density and a negative relationship with overall tree density. This strongly indicates that *Acacia* species are an important habitat requirement of the species; as it proves a preference for *Acacia* distinct from the related effect of tree density. Alongside these two variables, Subalpine Warblers also selected for sites with *Salvadora* and other shrub species. The significant negative relationship with *Calatropis*, an indicator of disturbed or heavily degraded sites (von Maydell 1986) presumably reflects this species' preference for *Acacia* stands. The apparent lack of any relationship with *Balanites* density is perhaps surprising, as it has been identified as a significant habitat component in Common Whitethroats previously (Vickery *et al.* 1999), and in both Common Whitethroat and Lesser Whitethroat in this study. Exactly why the species does not select for *Balanites* is unclear, though the trees' dense and dark canopy may be unsuitable for the species. The only other study of Subalpine Warbler winter habitat requirements suggested that densities of *Cassia*, *Piliostigma*, *Zizyphus*, *Acacia seyal* and *A. senegal* all showed a significant positive relationships with Subalpine Warbler occurrence (Jones *et al.* 1996). The selection of *Acacia* spp was supported by this study, though the other 3 species were not included as single candidate variables in GLM models due to their very local distribution and scarcity in this study.

#### 5.5.2.3 Lesser Whitethroat habitat selection

Lesser Whitethroat showed habitat selection criteria similar to both Subalpine Warbler and Common Whitethroat, with analysis of data from easterly sites not differing from overall patterns. A significant positive relationship was shown with *Acacia* density, and mean tree height. Two tree species, *Balanites* and *Salvadora*, were highly important influences, as also shown with Common Whitethroat. Overall tree density showed a significant negative relationship, as in Subalpine Warbler. These results suggest that Lesser Whitethroat select for taller individuals of *Acacia*, *Balanites* and *Salvadora*. A previous assessment of Lesser Whitethroat habitat selection in N Nigeria found a significant positive relationship with *Zizyphus*, *Cassia* and *Piliostigma* densities (Jones *et al.* 1996). These species were uncommon and very local in distribution across study sites used here and were not included as candidate variables.

As discussed in Chapter 3, Lesser Whitethroat showed significant easterly bias in distribution in the study region. Four variables that Lesser Whitethroat exhibited a strong association with (Tree Density, Tree Height, Acacia Density, and *Salvadora* Density) also showed a significant bias to the East. Only one variable (*Balanites* Density) also exhibited a bias in distribution that did not agree with Lesser Whitethroat distributions, the tree being more abundant in the West than the East. It would therefore appear that the Easterly bias shown by Lesser Whitethroat is a function of habitat differences between the areas, presumably a function of the southerly extension of the Sahel in NE Nigeria. Why only Lesser Whitethroat is affected by these east-west differences is unclear, as both of the other two warbler species show habitat associations that would appear to predispose them to an easterly bias in distributions. However, parameter estimates from the comparison of relative degrees of selection between the three species appear to indicate that Lesser Whitethroat selects more strongly for habitat parameters it shares with Subalpine Warbler and Common Whitethroat. This suggests Lesser Whitethroat may be less general in its degree of selection of habitats, resulting in a more limited distribution.

### 5.5.3 Habitat Selection By Afrotropical Species

#### 5.5.3.1 Olivaceous Warbler habitat selection

Results from the best-fit habitat GLM for Olivaceous Warbler across all sites suggest the species selects for points with taller trees, and also for *Salvadora*. However, as discussed in Chapter 4, Olivaceous Warbler showed very strong easterly bias in distribution and it was possible that this may have affected the results of any habitat models. This potential problem was particularly relevant due to *Salvadora* also exhibiting a strong easterly bias in distribution. Results from GLM's fitted for eastern sites indicated that the significance of *Salvadora* in the initial model was indeed a function of overlapping distributions, rather than selection by Olivaceous Warbler *per se*. It would therefore appear that Olivaceous Warblers select for sites with taller trees, as indicated in the first model, but rather than *Salvadora* the species also strongly selects for areas with greater tree density. There is also weak selection against *Calatropis* and shrub species, and for *Balanites*. Selection against *Calatropis* may be related to the plants' close association with heavily grazed and open habitats (von Maydell 1986) and this may also explain the apparent avoidance of sites with greater shrub density. The preference exhibited for *Balanites* is perhaps not surprising considering it is the most widespread and common evergreen tree species in the

region, and therefore may be of importance in providing shelter from predators and the extremes of climate.

Comparison of Olivaceous Warbler GLM results with habitat differences between Eastern and Western sites (see Chapter 2) suggest that something other than the habitat preferences exhibited by Olivaceous Warbler may be responsible for the significant variation in densities between east and west. However, the two variables showing strongest selection by Olivaceous Warbler had greater values in the east than the west (Tree Density and Tree Height). The other three variables (*Balanites* Density, Shrub Density, and *Calatropis* Density) all showed differences in abundance that would suggest a western rather than eastern bias in distributions.

Relatively little information on habitat requirements of Olivaceous Warbler have been published previously, and the past conspecific status of Eastern and Western Olivaceous Warbler confuses the issue further. However, it appears that the African race of Eastern Olivaceous Warbler has previously be found to be associated with tall *Acacia* species (Cramp 1992). The habitat preferences identified in this study were broadly similar with those previously published, with selection for taller and denser stands of *Acacia*. The migratory form of Eastern Olivaceous Warbler (*Hippolais elaeica elaeica*) that occurs as a rare Palearctic migrant in NE Nigeria, has been found to occupy similar habitats to the resident race, with foraging generally occurring above 5m, and frequent use of *Balanites* also observed (Cramp 1992). In contrast, Western Olivaceous Warbler *Hippolais pallida opaca* that occurs as an uncommon Palearctic winter visitor in West Africa, has been found to avoid *A. tortillis* savanna and is more strongly associated with dense stands of tall *A. nilotica* stands, particularly as riparian woodland (Cramp 1992).

#### 5.5.3.2 Cricket Warbler habitat selection

Results from Cricket Warbler GLM's suggested that habitat variables considered here may not have been suitable for this species. Alternatively the species is thought to be a broad habitat generalist and therefore may exhibit no strong habitat preferences. Comparisons of relative variable importance indicate that Tree Diversity and Tree Density are the only ubiquitous variables across Occam's models (Table 6.12). Habitat preferences of Cricket Warbler have previously been described in very broad terms only, perhaps due in part to the species occurrence across all vegetation types within its' range. Analyses of finer scale habitat preferences will be carried out in Chapter 6, which will cast further light on the species' habitat preferences.

### 5.5.3.3 Little Weaver habitat selection

Little Weavers were found to exhibit preferences for sites with greater tree height, *Acacia* density and *Balanites* density. It is unclear why the species selects for these habitats, but the species does select similar habitats for breeding (pers obs). Previously published habitat preferences are rather general, but support these results (Urban *et al.* 1997).

### **5.5.4 Comparison Of Breeding And Winter Habitat Use By Palearctic Warblers**

The structural characteristics of vegetation selected by Palearctic warbler species in their Sahelian wintering grounds appear to be very similar to those in the breeding grounds (Cramp 1992, Shirihai *et al.* 2001). Common Whitethroats' selection for shorter trees, the low and shrubby *Salvadora*, and their near-significant association with shrub species are comparable with the species' preference for low and shrubby habitats in breeding grounds. The selection by Subalpine Warbler in breeding grounds for dense undergrowth with emergent trees is mirrored by results from winter grounds presented here, that indicate a preference for both *Acacia* species (the dominant tall tree genus) and shrub species. Lesser Whitethroats were found to select for taller trees, and *Acacia*, *Salvadora* and *Balanites*, though not overall tree density in winter grounds, with information from breeding grounds indicating a preference for sites with a strong vertical component somewhere between open country and closed forest. Unfortunately data for Bonelli's Warbler were somewhat limited and no GLM analyses could be undertaken. However, casual observation suggests that this species selects for taller *Acacia* trees, with information from breeding grounds also indicating a preference for open woodland. The similarities in habitat preferences between breeding and wintering sites are presumably due to species' morphology and foraging behaviour, that results in most efficient exploitation of resources when similar habitat structures are utilised.

### **5.5.5 Seasonal Change In Importance Of Key Tree Species**

The increase in importance of *Salvadora* through spring, combined with habitat selection results, indicate that *Salvadora* is extremely important to Common Whitethroats. Presumably this is due to the high fat content and energetic value of the berries, of particular importance to migratory species depositing fat reserves in

preparation for migration (Snow and Snow 1988; Stoate and Moresby 1995). The lack of significant seasonal changes in the importance of *Salvadora* to Subalpine Warbler and Lesser Whitethroat may be due to the spring departure of these species occurring prior to the peak in *Salvadora* fruit. This suggests that these two species must utilise different resources to Common Whitethroat during spring fattening.

No Afrotropical warbler exhibited a significant relationship with *Salvadora* occurrence, and the inclusion of the interaction between season and *Salvadora* in the Olivaceous Warbler best-fit model indicated no seasonal change in degree of selection. This should perhaps not be surprising considering the limited dependence of this species upon fruit. The significant seasonal change in selection of *Balanites* by Little Weaver may be due to changes in resource abundance that this particular species, but none of the others, was affected by, though what this change was is unknown.

#### **5.5.6 Selection Of More Open Habitats By Palearctic Warbler Species**

Previous authors have concluded that Palearctic species utilise more open and structurally simpler habitats than their Afrotropical counterparts (Bilcke 1984; Lack 1971; Rabol 1987). Two of the Afrotropical species discussed here did select for sites with greater tree density, whilst two Palearctic species selected against high densities and for more open habitats. Similarly, two Afrotropical species also selected for taller trees, with Palearctic species exhibiting one positive, one negative, and one non-significant relationship to tree height. It would therefore appear that Afrotropical species do generally select for structurally more complex habitats. However, it should be pointed out that two Palearctic species selected for habitats with greater tree diversity, whilst only one Afrotropical species did so. Without information on more Palearctic and Afrotropical species, perhaps 15-20 species-pairs, it is not possible to say for certain whether fundamental differences exist, or what these differences may be. Unfortunately insufficient data were obtained for the majority of species occurring in the region due to their relative scarcity, resulting in insufficient power to tease apart habitat preferences. Comparisons of foraging behaviour and habitat use to be carried out in Chapter 6 will, however, shed some light on the degree of separation occurring between Afrotropical and Palearctic species.

### 5.5.7 Role Of Invertebrate Abundance In Habitat Preferences

The tree species preferences exhibited by warbler species discussed here may be due to a number of factors. Autumn and mid-winter invertebrate abundances were comparable between *Balanites* and *Salvadora* but were significantly greater in *A. tortillis*. This would suggest that species select for the two former tree species due to reasons other than greater invertebrate loads. Previous studies have excluded ants from analyses of prey abundance due to their presumed unpalatability (Jones *et al.* 1996; Morel and Morel 1992; Vickery *et al.* 1999), despite evidence to the contrary from both breeding and passage sites (Cramp 1992; Stoate and Moreby 1995). If ants are excluded from the above analysis, the same pattern was found, despite the negative association between ants and other invertebrate's abundances found on *Acacia* and *Balanites*.

However, abundance of all invertebrates and invertebrates excluding ants, declined significantly between autumn and mid-winter in *A. tortillis* whilst remaining constant and increasing in *Balanites* and *Salvadora* respectively. This suggests that both these latter tree species provide more constant invertebrate resources than *A. tortillis*. Although the abundance of invertebrates remained constant in *Balanites* and *Salvadora*, the proportion of Diptera increased significantly. These changes may have been due to the onset of flowering and fruiting in the species. A significant increase in invertebrate abundance on *A. albida* during the dry season described previously (Stoate and Moreby 1995) was attributed to the tree species flowering and leafing during this period. The evergreen nature of *Salvadora* and *Balanites* may also have provided a more constant environment for invertebrates than the deciduous *Acacia* species. Previous work has highlighted the importance of *Salvadora* fruit to *Sylvia* warblers on passage (Jones 1998; Stoate and Moreby 1995) and the increasing importance of *Salvadora* for Common Whitethroats during spring (the period of peak fruit production) supports this. Alongside foraging resources, evergreen species may provide shelter from both the climate and predators during a period when the majority of other species of trees have lost their foliage.

It is perhaps not surprising that none of the three species of Afrotropical warbler discussed here showed a strong preference for *Salvadora*, as frugivory is not thought to feature highly in the diet. Although Olivaceous Warbler has been recorded eating *Salvadora* berries (Urban *et al.* 1997) it is possible that these observations referred to either Western Olivaceous Warbler or the migratory race of Eastern Olivaceous Warbler. Neither Little Weaver nor Cricket Warbler have previously been known to eat

fruit however, and it is possible that *Salvadora* berries are a less significant resource for the sedentary Afrotropical species than for their migratory Palearctic counterparts.

### 5.5.8 Strength of Key Habitat Parameter Selection

Although differences in the degree of habitat selection are apparent between species, these differences are greater within Palearctic species than between Palearctic species and Olivaceous warbler. However, this comparison is limited in value as only one species of Afrotropical warbler was used, the other two species showing little overlap in habitat preferences with Palearctic species. Ideally 15-20 species pairs would be used for a comparative study, something which would require a much larger scale study.

The differences in habitat selection results between habitat selection GLM's and relative degree of selection GLM's, with some species showing inconsistent relationships with key habitat variables, may be due to differences in the scale of the two analyses. Analyses of relative degree of selection between warbler species was carried out using 200 points at which one of the species was present. Patterns of selection identified in this analysis will therefore reflect smaller scale habitat preferences beyond that of the habitat selection GLM's which looked at all habitat present.

The relative strength of selection of habitat variables by Olivaceous Warbler and the Palearctic *Sylvia* warblers does not appear to suggest that the former species is more vulnerable to habitat degradation than its' Palearctic counterparts in terms of *Balanites* density or of tree diversity. These results may also be interpreted as Olivaceous Warbler not selecting for more complex habitats than the *Sylvia* warblers. However, it must be pointed out that only one species of Afrotropical warbler shared habitat associations with Palearctic and therefore allowed a comparison to be made, and that a number of significant habitat preferences were not shared by Palearctic and Afrotropical species.

### 5.5.9 Interspecific Variation In Habitat Selection By Warbler Species And The Potential For Competition Between Residency Groups

Marked interspecific variation in habitat selection was found to occur between the three commonest species of Palearctic warbler wintering in Northern Nigeria (Table 5.12). The greatest differences found were between Subalpine Warbler and Common Whitethroat, with only one habitat variable selected for by both species (*Salvadora*). These two species were found to have a highly significant positive correlation in occurrence across individual points (see Chapter 3), presumably due to a site containing habitat suitable for one species, having a high probability of suitable habitat for the other species also being present, with habitat selection differences limiting competitive exclusion.

The lack of a significant correlation between Lesser Whitethroat presence and the presence of either of the other two species of *Sylvia* warblers (section 3.4 in chapter 3), even when eastern sites only were selected, is of interest considering the degree of overlap in habitat preferences found here. Lesser Whitethroat shared four habitat parameters with Common Whitethroat (Mean Tree Height, Tree Diversity, *Balanites* Density and *Salvadora* Density), with the first of these selected against by Common Whitethroat and for in Lesser Whitethroat. Comparisons of parameter estimates indicate that two of these variables (Tree Diversity and *Balanites* density) were selected for more strongly by Lesser Whitethroat than Common Whitethroat. Three habitat parameters were shared between Subalpine Warbler and Lesser Whitethroat (*Acacia* Density, Tree Density, and *Salvadora* Density), with Tree Density selected for more strongly by Lesser Whitethroat. It might be expected that this greater degree of overlap in habitat preferences between Lesser Whitethroat and the other two species would result in a significant correlation in their occurrence. However, the apparent stronger selection by Lesser Whitethroat for variables shared with both Common Whitethroat and Subalpine Warbler suggest a greater degree of specialisation by this species and therefore an inability to coexist with either Common Whitethroat or Subalpine Warbler due to competitive exclusion.

All three species of Afrotropical warbler appear to differ considerably in habitat preferences (Table 5.12), with Cricket Warbler showing the least number of significant habitat associations, and Olivaceous Warbler and Little Weaver showing more complex habitat preferences. The only significant correlation in occurrence found between two Afrotropical species was for Little Weaver and Northern Crombec (see section 4.4 in chapter 4) and unfortunately insufficient data were available for habitat selection

analysis on the latter species, and therefore no comparison of habitat preferences between the species pair could be carried out.

One of the intentions of assessing habitat preferences of Afrotropical warblers was to investigate the potential for competitive overlap with Palearctic migrant counterparts. This in itself would suggest that competition in the Sahel between Afrotropical and Palearctic species is limited. Habitat preferences exhibited by Afrotropical and Palearctic species show little overlap, with Little Weaver and Lesser Whitethroat showing the greatest similarities. The significant correlation in occurrence of Lesser Whitethroat and Olivaceous Warblers at individual points was not explained by habitat selection GLM's as preferences differed considerably. The relationships may have been due to similarities in habitat preferences (resulting in a high potential for competition), or in contrast, the differences in habitat selection that reduced competition to a level at which sympatry could occur.

It would therefore appear that, relative to the Palearctic warbler species, Afrotropical warblers expressed a greater degree of separation in habitat preferences. This supports findings suggesting no significant correlation between Afrotropical species in their occurrence at individual points. Perhaps this should not be surprising considering that unlike the Palearctic species discussed, the species studied were not congeners. Unfortunately there was insufficient data to allow exploration of habitat associations within closer taxonomic groups. Analysis of foraging behaviour in Chapter 6 will indicate whether these species do indeed overlap in resource use.

### **5.5.10 The Effects Of Habitat Loss Upon Different Warbler Species**

#### 5.5.10.1 Implications of habitat preferences for Palearctic warbler populations

The shallow slope of the significant relationships found between Palearctic warbler species and habitat parameters suggests that the group may be robust to habitat degradation, with densities remaining relatively constant across a wide range of habitat types. Common Whitethroat in particular appears to be capable of surviving in extremely degraded habitats in the Sahel during the winter period. However, the apparent dependence of both over-wintering and migratory Common Whitethroat populations of this species upon the area for spring fattening, and in particular the importance of *Salvadora* fruit for this, suggests that the species may be vulnerable to loss of these resources. Failure of *Salvadora* fruiting, significant reductions in

*Salvadora* abundance, or loss of habitat resulting in Whitethroat departure locations being forced south, may all result in major negative impacts upon populations. Previous work on the impacts of reduced *Salvadora* fruiting upon fat loads in *Sylvia* warblers prior to spring migration in the Sahel indicates a significant negative effect (Stoate 1995). The results of reduced fruiting over a larger geographic scale may be severe considering the strong relationship found previously between condition during migration and subsequent arrival date on breeding grounds, productivity, and survival (Marra, Hobson & Holmes 1998; Nolet & Drent 1998). Periods of severe drought or increased grazing pressure in the Sahel are likely to result in reduced *Salvadora* fruiting. The effects of habitat degradation upon both over-winter and migratory survival date of arrival on breeding grounds, and subsequent breeding productivity remain unknown

Neither Lesser Whitethroat nor Subalpine Warbler exhibited increases in densities in the Sahel prior to spring migration. This may be a function of these species having a more northerly distribution than Common Whitethroat, thus no southerly populations utilise the Sahel as a spring staging area. Previous studies have however, concluded that Subalpine Warbler and Lesser Whitethroat are equally dependent upon *Salvadora* fruit as Common Whitethroat (Stoate and Moreby 1995). However, in this study their early spring departure from the Sahel is prior to the peak in *Salvadora* fruit abundance. This study suggests that populations of Lesser Whitethroat and Subalpine Warbler might be less susceptible to *Salvadora* loss in the Sahel. However, all species must undergo pre-migratory fattening, and also exhibit winter habitat preferences that may result in negative impacts of habitat loss in the region. The potential impacts of such habitat degradation are illustrated by one study site discussed here (Watucal Forest Reserve).

The apparent decline in densities of Subalpine Warbler but of no other Palearctic warbler species at Watucal FR between 1991 (Jones *et al.* 1996) and this study (see Chapter 3) may be explained by habitat preferences found here. As discussed in Chapter 3, habitat loss at Watucal FR was dramatic, with tree density declining by 82% between 1991 and 2001. This in itself should not have impacted solely upon Subalpine Warbler, as all species would presumably have been effected had tree loss been catastrophic. However, Common Whitethroat did not share the strong association of Subalpine Warbler to *Acacia* density, and Lesser Whitethroat occurred at only very low densities at Watucal FR. *Acacia* density declined by 57% from a mean of 79/ ha in 1991 to 53/ ha by 2001. As well as its association with *Acacia*, Subalpine Warbler was also the only species exhibiting a significant preference for Shrub species (*Maerua*,

*Cassia*, *Anona* and *Prosopis*) which declined by 95% at Watucal FR between studies. One of the conclusions of Jones *et al.* was that Subalpine Warbler was dependent upon *Zizyphus* trees to some degree. This tree genus is another that has undergone a huge reduction in abundance at the site, with densities declining by over 99%. It would appear that wintering Common Whitethroat were less susceptible to the habitat changes at Watucal FR, presumably due to the species' preference for shorter trees and *Balanites*, that were less affected by fuel wood collection (*Balanites* density declined by 'just' 23% between the two studies).

#### 5.5.10.2 Implications of habitat preferences for Afrotropical warbler populations

The apparent dependence of Olivaceous Warblers upon areas with greater tree density and height suggests that this species may be less vulnerable to short-term overgrazing than species depending upon habitats with shorter trees, or shrubby vegetation. However, use of woodland areas for timber extraction for fuel wood or construction, may have a more immediate effect upon populations. Prolonged overgrazing with an associated prevention of regeneration will also ultimately result in habitat loss.

The use of a broad range of habitats by Cricket Warbler suggest that this species may be fairly robust in terms of habitat degradation, and indeed casual observations suggest this species utilises the lower levels of trees of any size. Results here indicate the species occurrence is linked to tree density only, and this may be an artefact of the simple requirement that at least one tree be standing in order for Cricket Warbler to be present.

The selection of sites with greater mean tree height, *Acacia* density and *Balanites* density exhibited by Little Weaver suggests that this species may be susceptible to habitat change in the same way as Olivaceous Warbler. However, the species' omnivorous diet and diverse foraging behaviour (Urban *et al.* 1997) may result in a greater resilience to habitat loss than Olivaceous Warbler.

In comparison with the Palearctic species discussed above, two of the species discussed here (Olivaceous Warbler and Little Weaver) may be more susceptible to habitat degradation due to their selection for sites with greater tree density and tree height, the former not shown by any Palearctic species. It should be stressed that only species occurring in sufficient numbers to allow habitat preferences to be tested have been discussed here. This implies that only species 'robust' to habitat loss were included in analysis, resulting in significant biases when discussing potential effects of

habitat degradation. Interspecific variation in habitat selection shown by Palearctic and Afrotropical warblers discussed here provides an indication of the mechanism by which interspecific competition may be avoided. In Chapters 6 I will examine microhabitat selection and foraging behaviour in the Warbler species.

#### **5.5.12 Reliability Of Predictive Models In Identifying Suitable Habitat**

It seems most likely that the low positive classification rates obtained here using predictive models are due to a failure to detect a species at a particular point. If we assume that the predictive models are sound, the alternative explanation to low positive classification rates is that individuals were absent from suitable habitats. This would suggest that there is a super-abundance of habitat available, but limited birds to occupy it all. Evidence from European breeding grounds linking population declines of migrant species to Sahelian wintering habitats, rather than breeding grounds cast doubts on this for Common Whitethroat at least. However, data for other Palearctic warbler species are not available and it is possible that a superabundance of habitat occurs in the Sahel, resulting in suitable habitat remaining unoccupied. However, it is also possible that for all species, a superabundance of suitable habitat is present for the majority of time, but that severe drought events result in 'refuge' habitats becoming limited, resulting in the observed population crashes observed in a number of species. Alternatively, available habitat may be of poor quality, resulting in individuals ranging widely and being temporarily absent from a site with apparently suitable habitat. Unfortunately it is possible that the habitat models produced are not able to distinguish between marginal and poor habitats.

The relatively low Specificity value obtained for Subalpine Warbler compared to the other two species indicates that a greater proportion of points where the species was predicted to be absent actually held the species. This suggests that the model performs less well. Alternatively Subalpine Warbler may exhibit a greater generality in habitat preferences than the other two species, resulting in the model being less able to identify unsuitable habitats. The decline in Specificity for Olivaceous Warbler in eastern sites may have been a function of the species' easterly bias in distribution producing artificially high Specificity values across all sites, which were then reduced to a more realistic value when eastern sites only were included within the analysis. The AUC values produced for Common Whitethroat and Little Weaver of  $>0.7$  indicated that the model may be a useful tool for predicting the species abundance, but was still short of

the value of 0.9 cited as indicating a models' highly accurate predictive performance (Fielding & Bell 1997). The AUC values for Lesser Whitethroat, Subalpine Warbler, Olivaceous Warbler and Little Weaver of 0.6-0.7 indicate relatively poor overall model performance. It is perhaps unsurprising that the lowest AUC values were produced for Cricket Warbler considering the species' apparent high degree of generality in habitat association, making prediction of occurrence more difficult. However, when assessing model performance, it must be borne in mind that the models aim to identify potential habitat for individual species rather than predict presence or absence. The predictive models may be best employed in identifying unsuitable habitats, with higher critical p values selected to maximise this ability with remaining habitats assumed to be suitable, though not necessarily occupied.

## 5.6 Conclusion

The Palearctic warbler species discussed in detail in this Chapter all selected for habitats similar to those utilised in their respective breeding grounds. All species of Palearctic warbler appeared robust to habitat degradation, with individuals even occurring in apparently poor habitat. However, the importance of *Salvadora* to Common Whitethroat, particularly prior to spring departure across the Sahara barrier, suggests that this species may be vulnerable to loss of, or drought events causing failure of fruiting, of this tree species. In contrast, loss of dense stands of taller *Acacia* tree species may affect Subalpine Warblers, Olivaceous Warblers and Little Weaver more greatly. However, sufficient data were only obtained to carry out analyses on the most common species. It is therefore possible that less abundant species may be impacted more significantly by habitat loss, or that species studied have already undergone population decline due to historic habitat loss.

Afrotropical warbler species, in contrast to their Palearctic counterparts, do not select for fruiting tree species. Afrotropical warbler species appear to show a greater degree of habitat separation than their Palearctic counterparts, although the sample size was small. The observed interspecific differences between *Sylvia* warblers in habitat preferences suggest that small-scale sympatry within this group is possible only when habitat preferences differ. This suggests that there may be less potential for direct competition between Afrotropical and Palearctic species than previously thought. Predictive models produced here provide a useful tool in identifying habitat unsuitable for the four warbler species discussed.

## Chapter 6 : Microhabitat Use and Foraging Behaviour of Sylviidae in Sahelian West Africa

### 6.1 Introduction

The arrival of Palearctic migrants in the Sahel of West Africa coincides with the onset of an extended dry season, and this apparent paradox has been well discussed (Fry 1992; Moreau 1972). Despite the difficulties associated with directly measuring competition (Huston 1994), the sudden arrival of large numbers of migrants on wintering areas already occupied by resident species has been identified as having significant potential for competition (Greenberg 1986; Lack 1971; Leisler 1992; Moreau 1972). This competition is likely to be limited to food or shelter resources, due to migrant species not being involved in breeding activities. Potential conflict could be avoided in a number of ways. Geographic avoidance would manifest itself through differences in relative abundances across space, and has been shown to occur in Nearctic migrant birds in their winter grounds (Greenberg 1986; Keast 1980; Rappole and McDonald 1994). Temporal avoidance could result in changes in distribution or resource use depending upon the presence/absence of competitors (Rabøl 1987). However, whether the arrivals of migrants into an area 'forces' changes in the behaviour/distribution of resident species through past or present competition, or whether migrants merely occupy newly or seasonally vacated niches is difficult to tease apart (Leisler 1992; Salewski *et al.* 2003). Differences in resource use and capture methods between species have been well documented (Bilcke 1984; Chiple 1977; Lack 1986; Herrera 1998; Rabøl 1987), however whether these differences are in response to competition, past or present, is unclear. Overt interspecific aggression appears rare (Curry-Lindahl 1981; Edington 1983; Rabøl 1987; Salewski 2000; pers obs), perhaps due to 'ghosts' of past competition (Connell 1980) becoming less evident as time passes (Mayr 1963), though several studies have found high levels of interspecific aggression in response to playback experiments (Robinson and Terborgh 1995; Rolando and Palestini 1991). Where aggression does occur, resident species appear dominant over migrant counterparts, irrespective of body mass (Leisler 1992; pers obs).

Several authors have concluded that migrant species utilise habitat peripheries, undertaking more rapid and frequent foraging movements, and capitalise on more unpredictable resources than their resident counterparts (Greenberg 1981; Greenberg

1986; Herrera 1998; Lack 1986a; Leisler 1990; Leisler 1993; Rabol 1987; Salewski 2000; Tramer and Kemp 1980; Winkler and Leisler 1992). Greater foraging technique diversity has been found in migrant than resident species, with foraging diversity positively correlated with prey diversity (Lovette and Holmes 1995). A more generalist approach to foraging behaviour would allow migrants to utilise seasonally abundant resources, as well as reducing costs of antagonistic interactions with specialist species which can dominate a single resource. The reduced level of neophobia exhibited by migrant species, and their apparent willingness to utilise 'novel' habitats, supports the suggestion that migrants are able to access fluctuating resources more readily than resident species (Greenberg 1983; Leisler 1992), perhaps due to behavioural flexibility in learning that in turn may result in a greater potential for the evolution of migration (Lefebvre *et al.* 1998). The inference often made from migrants' foraging behaviour is that it permits avoidance of competition with resident species (Bilcke 1984; Lack 1971; Rabol 1987). Whether migrant diets differ from those of residents is unclear however, with some studies reporting no differences (Leisler 1990; Sherry and Holmes 1996) and others finding that residents take a wider diversity of prey than migrant species (Lack 1986a).

The differences in foraging behaviour between migrant and resident species have been attributed to differential morphological adaptations for migration (Gaston 1974; Winkler and Leisler 1992; but see Niemi 2004; Keast 1980). For example migrant species have lower muscle mass and longer femoral length than residents, matching the formers' reduced use of legs for clinging, and preference of bipedal hopping for locomotion (Leisler *et al.* 1989). It appears that birds select vegetation types they are morphologically suited to, although smaller species and individuals may also be forced to peripheral vegetation through competitive exclusion, rather than through selection (Forstmeier and Kessler 2001). The relationship between morphology and habitat may explain the strong (but not exclusive) similarity found between breeding and wintering habitat requirements in both Nearctic and Palearctic species (Monkkonen *et al.* 1992: Chapter 5). Although habitat preferences are comparable between winter and summer grounds, variation in resource availability between breeding and wintering sites can result in variation in the foraging behaviour of migrant species (Lovette and Holmes 1995). Alongside foraging rates, foraging method has also been found to vary between seasons (Lovette and Holmes 1995). In American Redstarts *Setophaga ruticilla*, summer prey were dominated by large energy-rich caterpillars and tipulid flies (Omland and Sherry 1994); winter prey by small Diptera, Hymenoptera, Homonoptera, and adult Lepidoptera (Lovette and Holmes 1995). Differences in foraging activity, with a

reduction in aerial attack, glean, sally-hover and flutter chase manoeuvres during winter, were presumably due to these differences in diet (Greenberg 1995; Lovette and Holmes 1995). The majority of the studies discussed above are from the Nearctic-Neotropical system, and unfortunately there are virtually no equivalent studies from the Palearctic-Afrotropical system.

The amount of time spent foraging in the tropics has been found to be greater than in temperate regions (Lovette and Holmes 1995; Marcotullio and Gill 1985; Ricklefs 1971; Weathers and Sullivan 1989). Presumably low prey abundance and/or shorter day length in the tropics results in extended foraging periods, even in migratory species where demands from breeding activity are not present. Greater foraging speeds found in migrants at winter grounds compared to summer were assumed to be in order to compensate for reduced prey availability, allowing foraging rates to be maintained (Lovette and Holmes 1995). This in turn implies that resource availability in tropical wintering grounds may be lower than that in the temperate zone.

In chapters 3 and 4 I presented data on relative abundance of Afrotropical and Palearctic warblers species that indicated sympatry in distribution, whilst in chapter 5 I showed that habitat preferences between Palearctic and Afrotropical species showed some overlap. These results both suggest that the potential for competition between the two residency group exists. For this to be the case, one may expect overlap in microhabitat selection and foraging behaviour to occur. Data presented in this chapter will assess the degree of such overlap and examine the apparent effects of the abundance of potential competitors on a species' habitat preferences. However, as discussed above, the lack of overlap in habitat selection or foraging behaviour may be due to 'ghosts' of past competition, whilst seasonal shifts in these attributes may be due to changes in resource availability rather than competition. The use of exclusion experiments would be required in order to tease apart these factors. The hypotheses I will focus upon in this chapter are therefore:

1. Across both Afrotropical and Palearctic warblers, some species occupy the same sites, habitats, microhabitats and forage in the same manner and thus the potential for interspecific competition is great.
2. Afrotropical and Palearctic warbler residency groups occupy the same sites, habitats, microhabitats and forage in the same manner and thus the potential for inter-residency group competition is great.

3. Seasonal divergence in microhabitat use and foraging behaviour, as well as change in the strength of selection for individual tree species, occurs between residents and migrants due to increasing competition with increased densities of Palearctic species.
4. The presence of potentially competing warbler species will significantly effect the degree of selection of key habitat attributes due to competitive exclusion.

## 6.2 Methods

### 6.2.1 Study Period and Sites

Fieldwork was carried out at two study sites in Northern Nigeria located near Alagarno (N 13.1° E 13.3°) from Oct 2001 to Dec 2001. At each study site, habitat variables were collected in 25m radius vegetation plots centred at individual point counts (see Chapter 2). Locations, vegetation attributes and broad habitat classes for each study site derived from the vegetation plots are given in Chapter 2, and full descriptions of the methods used for data collection are presented in section 2.10 of Chapter 2. Variables recorded for each observation are presented in Tables 6.2-6.3, and the number of observations obtained for each species in Table 6.4. The following Palearctic (P) and Afrotropical (A) *Sylviidae* were selected as focal study species for observations of microhabitat use and foraging behaviour:

• <b>Bonelli's Warbler</b>	<i>Phylloscopus bonelli</i>	P
• <b>Common Whitethroat</b>	<i>Sylvia communis</i>	P
• <b>Lesser Whitethroat</b>	<i>Sylvia curruca</i>	P
• <b>Subalpine Warbler</b>	<i>Sylvia cantillans</i>	P
• <b>Grey-backed Camaroptera</b>	<i>Camaroptera brachyura</i>	A
• <b>Olivaceous Warbler</b>	<i>Hippolais pallida</i>	A
• <b>Acacia Warbler</b>	<i>Phyllolais pulchella</i>	A
• <b>Cricket Warbler</b>	<i>Spiloptila clamans</i>	A
• <b>Yellow-bellied Eromemola</b>	<i>Eromemola icteropygialis</i>	A
• <b>Little Weaver</b>	<i>Ploceus luteolus</i>	A
• <b>Northern Crombec</b>	<i>Sylvietta brachyura</i>	A

**Table 6.1:** General Variables Recorded During Focal Species Observations

	<b>Variable</b>	<b>Class/ Value</b>	<b>Sampling Frequency</b>	
General	Date	Latt/ Long	per observation	
	Start Time			
	Location			
	Length of Observation			
Bird	Species		per observation	
	Age/ Sex			
	Flock Size			
Tree	Species	m	per movement event	
	Height			
	Leaf			%
	Fruit			%
	Flower			%

**Table 6.2:** Positional and Foraging Variables Recorded During Focal Species Observations

<b>Variable</b>	<b>Class/ Value</b>	<b>Sampling Frequency</b>
Location within tree	top, middle, bottom	per movement event
Location within tree canopy	interior, exterior	
Height of bird	metres	per movement event
Movement	hop, run, jump, fly	
Horizontal distance moved	m	per movement event
Vertical distance moved	cm	
Number of feeding attempts	cm	per event
Feeding technique	standing, jumping, jump-flight, flight (sally), hover	
prey size	small, medium, large	
Prey substrate	air, leaf, twig, branch, trunk	
Prey type	Order	
Song events		
Call events		
Chase events	aggressor species	

**Table 6.3:** Number of individual foraging observations obtained for each species, Status A indicates Afrotropical species, P Palearctic species.

	No. Observations at Reserve	No. Observations at Canal	Total No. Observations
Acacia Warbler	0	10	10
Bonelli's Warbler	0	10	10
Common Whitethroat	2	2	4
Cricket Warbler	8	14	22
Grey-backed Camaroptera	3	1	4
Lesser Whitethroat	9	13	22
Little Weaver	2	7	9
Northern Crombec	5	6	11
Olivaceous Warbler	36	54	90
Subalpine Warbler	9	15	24
<b>Palearctic Total</b>	<b>20</b>	<b>40</b>	<b>60</b>
<b>Afrotropical Total</b>	<b>54</b>	<b>92</b>	<b>146</b>
<b>Total</b>	<b>74</b>	<b>132</b>	<b>206</b>

### 6.3 Data Analyses

Only observations of over 20 seconds in duration were used in data analysis as any observations shorter than this were not believed to provide an adequate sample. For observations greater than 20 seconds, foraging and movement data were converted into a single rate per second for each variable recorded in order to allow comparison across observations. Microhabitat data was also converted into mean values for each observation. Variable residuals were tested for normality and data transformed where appropriate. The small sample sizes of observations for the majority of species, and the resultant low statistical power, limit the analyses it is possible to carry out and may result in an increased likelihood of Type II errors occurring. One-Way ANOVAs with Tukey post-hocs were used to test for differences across observer, study periods, site and residency. No significant difference was found in any foraging parameters between observers ( $F_{1,204} < 3.8$ ,  $p > 0.05$ ), and data collected by both PS and JW were combined for all analyses.

### 6.3.1 Microhabitat Selection

Assessment of differences in microhabitat selection between species and residency group was carried out using Principal Component Analysis (PCA). Three principal components were derived from the following five microhabitat variables:

1. Bird Height
2. Tree Height
3. Tree foliage density
4. Position within canopy
5. Height of bird in tree/ Tree height ratio

The three principal components showed normal distribution and were tested for inter-specific, residency group, and seasonal differences using One-way ANOVA with Bonferonni *post hoc*.

### 6.3.2 Foraging Behaviour

Variation in foraging behaviour across species and residency were tested in the same way as microhabitat selection (see above), with the following variables used in production of three principal components:

1. No. Gleans per second (intake rate)
2. Vertical distance moved
3. Horizontal distance moved
4. Total distance moved per second
5. Distance flown per second
6. No. of movements per second

Variation in foraging method diversity was assessed independently using independent t-tests (Zar 1999).

### 6.3.3 Seasonal variation in strength of tree selection

If seasonal variation in the use of habitat resources exists due to competitive exclusion, one may expect to find divergence in direction or degree of selection for key habitat variables. In order to test this, best-fit habitat GLM's developed in Chapter 5 were used with an additional independent variable of an interaction between season and key tree species being included. The increased selection of a particular tree resource by one warbler species that is mirrored by a reduced selection of the same resource by another species could be interpreted as competitive exclusion. Any uniform change in selection of a tree species could be interpreted as being driven by changes in resource availability rather than due to competition.

### 6.3.4 Influence of abundance of potential competitors

If interspecific competition is taking place, one may predict that the strength or direction of selection for a key habitat component may vary according to the presence or absence of a competing species. This may occur through direct displacement of subordinate species or individuals, or through interference competition leading to interspecific avoidance. This may be expressed in a species showing significant relationship with key habitat variables in the presence or absence of a competitive species. This was tested by introducing the presence or absence of a potentially competing species alongside its interaction with a key habitat variable into the habitat selection GLM's produced in Chapter 5. Species pairs were identified using results from the microhabitat and foraging PCA analyses described above. The selection of which of the species within each pair was the dependent variable was dictated by which species had a habitat selection GLM available. Where models were available for both species, the migratory species was selected as the dependent variable, as the model then accounted for seasonal variation in abundance. For the Subalpine Warbler-Lesser Whitethroat pair, both species were selected as dependent variables in two separate models in order to allow the easterly distribution of Lesser Whitethroat to be accounted for. The key habitat attribute for inclusion within the model was the variable with the greatest F value in the initial GLM results. The use of models developed in Chapter 5 was felt justified as a specific hypothesis was being tested. Summaries of the methods used to test each hypothesis are presented in Table 6. 4.

**Table 6.4:** Methods used for hypothesis testing

	<b>Hypothesis</b>	<b>Sample Size</b>
<b>1</b>	<b>Afrotropical and Palearctic species occupy the same sites, habitats, microhabitats and forage in the same manner.</b>	
	Principal Component Analysis of microhabitat variables followed by One Way ANOVA of microhabitat selection PCA results, with species as grouping variable	204
	Principal Component Analysis of foraging behaviour variables followed by One Way ANOVA of foraging behaviour PCA results with species as grouping variable	204
<b>2</b>	<b>Afrotropical and Palearctic warbler residency groups occupy the same sites, habitats, microhabitats and forage in the same manner.</b>	
	One Way ANOVA of microhabitat selection PCA results, with residency as grouping variable	204
	One Way ANOVA of foraging behaviour PCA results with residency as grouping variable	204
	Independent t-test of foraging diversity between residency groups in observations in which foraging occurred	173
<b>3</b>	<b>Seasonal divergence in microhabitat use and foraging behaviour occurs between residents and migrants.</b>	
	One Way ANOVA of microhabitat selection PCA results for all Afrotropical warbler group, with season as grouping variable	145
	One Way ANOVA of microhabitat selection PCA results for all Palearctic warbler group, with season as grouping variable	58
	One Way ANOVA of foraging behaviour PCA results for all Afrotropical warbler group, with season as grouping variable	145
	One Way ANOVA of foraging behaviour PCA results for all Palearctic warbler group, with season as grouping variable	58
	Best-fit habitat selection GLM's from Chapter 5 with interaction of season with key tree species included as covariates	
	Independent t-test of foraging diversity of Palearctic species in observations in which foraging occurred with season as grouping variable	47
	Independent t-test of foraging diversity of Afrotropical species in observations in which foraging occurred with season as grouping variable	124
<b>4</b>	<b>The presence of a competing species will significantly effect the degree of selection of key habitat variables of a warbler species.</b>	
	Best-fit habitat selection GLM's from Chapter 5 with presence of potential competitor species and its' interaction with a key habitat variables included as covariates	

## 6.4 Results

### 6.4.1 Initial vs subsequent observation periods

Analyses of data from the initial 30 seconds of individual observations and subsequent 30 second periods from the same observation indicated that no significant difference in any foraging parameters between the two for Olivaceous Warbler ( $F_{1,323} < 0.1$ ,  $P > 0.05$ ), Subalpine Warbler ( $F_{1,122} < 1.3$ ,  $P > 0.05$ ), Lesser Whitethroat ( $F_{1,107} < 2.1$ ,  $P > 0.05$ ), Cricket Warbler ( $F_{1,91} < 2.2$ ,  $P > 0.05$ ), Palearctic Warblers excluding Bonelli's Warbler ( $F_{1,256} < 5.8$ ,  $P > 0.05$ ) or Afrotropical Warbler ( $F_{1,146} < 3.6$ ,  $P > 0.05$ ) and therefore all periods were used in these analyses. However, significant differences for Bonelli's Warbler were found in no. gleans per second ( $F_{1,57} = 11.9$ ,  $P = 0.001$ ), no. moves per second ( $F_{1,57} = 14.9$ ,  $P < 0.001$ ), distance flown per second ( $F_{1,57} = 11.9$ ,  $P = 0.001$ ), and total distance moved per second ( $F_{1,57} = 7.9$ ,  $P = 0.007$ ). The initial 30 second period for Palearctic Warbler and Bonelli's Warbler were therefore excluded from analyses.

### 6.4.2 Focal Species Observations

Of all warbler individuals located for possible focal observations ( $n=885$ ), 72% were in *A. tortillis*, 21% in *Balanites*, 5% in *Salvadora*, and 1% in *Zizyphus*. The low proportion of observations occurring within *Salvadora*, despite the tree species preferential selection by the majority of warblers during point counts (see chapter 4), suggests that individuals may be difficult to locate or follow when in this tree species. The results of the focal observations will therefore be biased against *Salvadora* utilisation, as this species was strongly selected for by several warbler species but is relatively poorly represented in the foraging observation data. This bias in observations away from *Salvadora* towards more open tree species, such as *A. tortillis* resulted in tree species being excluded from PCA's.

### 6.4.3 Microhabitat selection

The relative importance of each microhabitat variable within each of the three Principal Components (PCs) produced is presented in Table 6.5. No significant differences were found between residency groups for any of the three microhabitat PCs ( $F_{1, 203} < 2.7$ ,  $p > 0.05$ ).

**Table 6.5:** Microhabitat variables incorporated within Principal Component Analysis

		Component		
		1	2	3
<b>Variables</b>	<b>Bird Height</b>	0.979	-0.092	-0.014
	<b>Tree Height</b>	0.489	-0.697	0.512
	<b>Foliage density</b>	0.170	0.489	0.535
	<b>Position within canopy</b>	-0.042	0.446	0.633
	<b>Bird/ Tree height ratio</b>	0.764	0.479	-0.394
<b>Initial Eigenvalues</b>	<b>Total</b>	1.81	1.16	1.10
	<b>% of Variance</b>	36.24	23.24	22.10
	<b>Cumulative %</b>	36.24	59.49	81.58

Significant differences in microhabitat selection were apparent across all warbler species for PC1 and PC2 (Table 6.6). The greatest differences were apparent when comparing species occurring at relatively large heights in trees and high bird: tree height ratios, with those occurring in short trees. Visual assessment of species values is presented in Figure 6.1. Species to the right of the plot indicate those utilising taller trees and occurring towards the tree crown (high bird: tree height ratio), whilst those in the upper section were most often observed in shorter trees. The species on the figure are widely scattered, though several groups are evident. The first group (Lesser Whitethroat and Subalpine Warbler) are found at lower heights, greater tree height, and thus have a lower bird height: tree height ratio. The second group (Olivaceous Warbler and Northern Crombec) appear to be found at greater heights and have a greater tree height: bird ratio. The third group (Common Whitethroat and Acacia Warbler) occur at greater heights, have a greater tree height : bird height ratio, and select for shorter trees. Three further species (Bonelli's Warbler, Cricket Warbler, Little Weaver and Grey-backed Camaroptera) did not show any obvious grouping. The low sample size obtained for Common Whitethroat and Grey-backed Camaroptera indicate caution

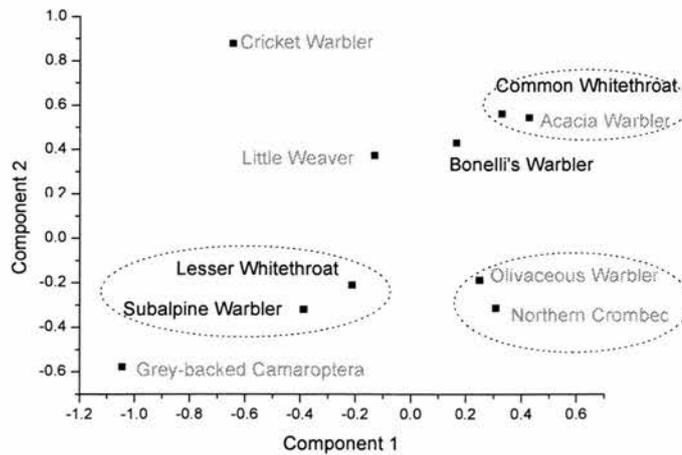
should be used when interpreting results. These results suggest that inter-specific competition within these pairs (see Fig. 6.1) will be greatest, and this will be tested in section 6.5.6.

Results from *post-hoc* analyses of between-species differences in principal components indicated that principal component 1 differed significantly between Cricket Warbler and Olivaceous Warbler, and principal component 2 between Cricket Warbler and Common Whitethroat, Subalpine Warbler, Olivaceous Warbler and Northern Crombec ( $p < 0.05$ ).

It should be noted that PC3, which showed non significant interspecific differences in values, was dominated by location within the canopy, suggesting this variable was not important.

**Table 6.6:** Comparison of microhabitat Principal Components across warbler species. A significant difference was found for PC1 and PC2,  $df=9, 195$ .

	Sum of Squares	Mean Square	F	p
Factor 1	27.27	3.03	3.3	0.0008
Factor 2	33.17	3.69	4.2	0.0001
Factor 3	15.85	1.76	1.8	0.0658

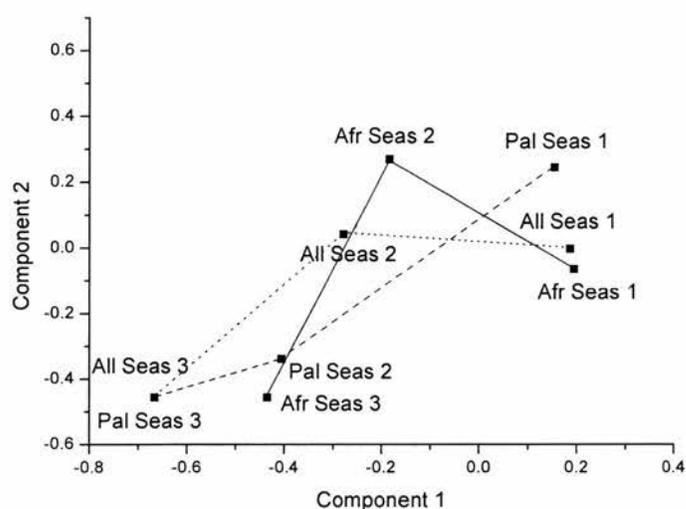


**Fig 6.1:** Mean values of PC1 and PC2 for all warbler species microhabitat selection. A significant difference across all species was found for both Factor 1 ( $F_{9,195} = 3.3, p = 0.0008$ ) and 2 ( $F_{9,195} = 4.2, p = 0.0001$ ). From inspection of the plot, four broad groups were identified. Species to the right were observed at greater height and bird height: tree height ratio. Species towards the top of the plot utilise shorter trees.

#### 6.4.4 Seasonal variation in microhabitat selection

Comparison of seasonal variation in microhabitat selection was carried out using PCs 1 and 2 described above. Results from One-way ANOVA indicated that significant declines in values between mid autumn and mid winter occurred in PC1 across all species grouped together ( $F_{2,202} = 7.2$ ,  $p=0.001$ ), Afrotropical Warblers ( $F_{2,143} = 3.1$ ,  $p=0.047$ ), and Palearctic Warblers ( $F_{2,56} = 3.7$ ,  $p=0.030$ ). Palearctic warblers as a group also showed significant decline in PC2 values ( $F_{2,56} = 3.7$ ,  $p=0.030$ ) across the same seasons. Examination of the plots of the seasonal change in PC values (Fig 6.2) indicates that for all warbler groups the height of birds within trees and the height of the trees utilised were lower later in the season, with the tree height: bird height ratio also declining between mid autumn and mid winter.

When microhabitat PCs 1 and 2 were compared across seasons for individual species, significant differences were found in PC 2 for Bonelli's Warbler ( $F_{1,8} = 19.7$ ,  $p=0.002$ ) and PC 1 in Olivaceous Warbler ( $F_{1,88} = 4.8$ ,  $p=0.031$ ) only.



**Fig 6.2:** Mean values of microhabitat PCs 1 and 2 for all warblers grouped (All), Afrotropical species (Afr) and Palearctic warbler species (Pal) across the three study seasons (1-mid autumn, 2- late autumn, 3-mid winter). A significant difference across all seasons was found for PC1 in All, ( $F_{2,202} = 7.2$ ,  $p=0.001$ ) Afr ( $F_{2,143} = 3.1$ ,  $p=0.047$ ) and Pal ( $F_{2,56} = 3.7$ ,  $p=0.030$ ), and in PC 2 for Pal ( $F_{2,56} = 3.7$ ,  $p=0.030$ ). Groups to the right were observed at greater height and higher bird height: tree height ratio. Groups towards the top of the plot utilised shorter trees.

### 6.4.5 Foraging Behaviour

The independent t-test of foraging diversity when sites at which foraging was observed were selected, indicated that no significant difference between the two residency groups occurred ( $t=1.6$ ,  $p=0.119$ ,  $df=45$ ), with Afrotropical species exhibiting a diversity of 2.5 ( $\pm 0.96$  SE) and their Palearctic counterparts 1.95 ( $\pm 0.28$  SE).

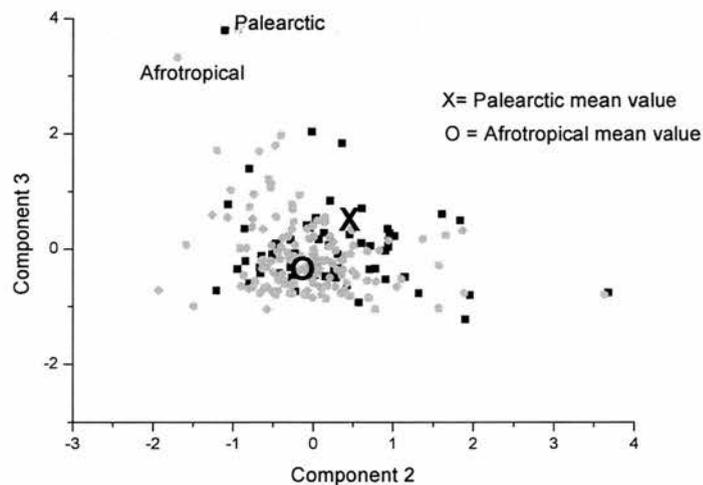
As with microhabitat preferences, three PCs were produced for the foraging behaviour variables (Table 6.7), with greatest inter-group differences found when PCs 2 and 3 were analysed (Table 6.8). The relative importance of each foraging behaviour variable within the three principal components used in this analysis are presented in Table 6.8. Analysis of the principal components used to test inter-specific differences in foraging behaviour indicated a significant difference in components 2 and 3 between the two residency groups (Table 6.9). However, a plot of the values indicated a high degree of overlap between the two groups (Fig 6.3), and the lack of significant between-group difference in PC1 suggest that no reliable difference between the two residency groups.

**Table 6.7:** Foraging behaviour variables incorporated within Principal Component Analysis

		Component		
		1	2	3
	Intake rate (/ Sec)	0.481	0.423	-0.410
	Horizontal movement (cm/ Sec)	0.828	-0.409	0.194
	Vertical Movement (cm/ Sec)	0.557	0.596	0.264
	All movement (cm/ Sec)	-0.184	0.114	0.899
	No Moves (/ Sec)	0.704	0.338	0.043
	Distance Flown (/ Sec)	0.676	-0.612	0.035
Initial Eigen values	Total	2.21	1.20	1.09
	% of Variance	36.91	20.06	18.11
	Cumulative %	36.91	56.97	75.08

**Table 6.8:** Comparison of Principal Components across warbler residency groups. A significant difference was found for all three PC,  $df=1, 203$ .

	Sum of Squares	Mean Square	F	p
<b>Factor 1</b>	1.12	1.12	1.1	0.2900
<b>Factor 2</b>	4.78	4.78	4.9	0.0280
<b>Factor 3</b>	4.72	4.72	4.8	0.0290



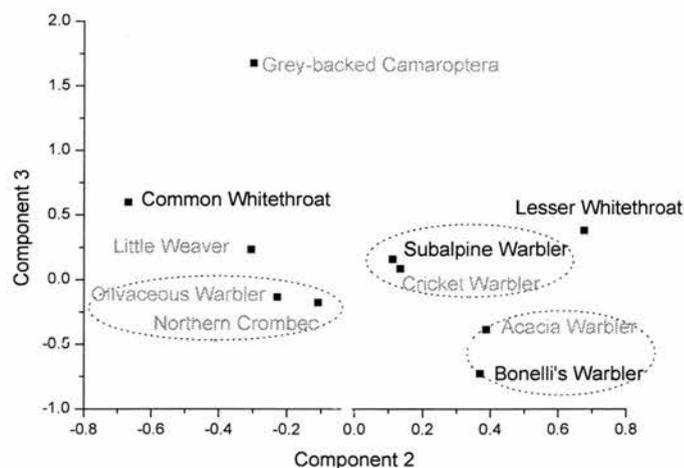
**Fig 6.3:** Values of foraging behaviour PC2 and PC3 for Afrotropical and Palearctic warbler species. A significant difference between the two residency groups was found for both Factor 2 and 3 ( $F_{1,203} = 4.9$ ,  $p=0.028$  and  $F_{1,203} = 4.8$ ,  $p=0.029$  respectively), though considerable overlap was apparent. Points to the right of the graph indicate greater distance flown and vertical movement. Points in the upper region indicate a greater number of movements and lower intake rate.

#### 6.4.6 Interspecific variation in foraging behaviour

Greatest interspecific differences in foraging behaviour were found when PC 2 and PC 3 were analysed ( $F_{9,195}=2.5$ ,  $p=0.090$  and  $F_{9,195}=3.1$ ,  $p=0.0015$  respectively). Examination of results of *post-hoc* analyses indicated that PC 2 differed significantly between Lesser Whitethroat and Olivaceous Warbler, whilst PC 3 between Grey-backed Camaroptera and Bonelli's Warbler, Acacia Warbler, and Olivaceous Warbler ( $p<0.05$ ). A plot of mean values of PC 2 and 3 for each species (Fig 6.4) indicates that three groups are evident.

Examination of the plots of mean PC 2 and 3 values for each species suggests that three sub-groups exist. One sub-group (Olivaceous Warbler and Northern Crombec) have relatively greater distance flown, lower vertical distance moved, greater intake rate, and lower overall distance moved. A second sub-group (Subalpine Warbler and Cricket Warbler) has greater vertical movement rates, and lower distance flown. The third sub-group (Acacia Warbler and Bonelli's Warbler) have lower distance flown, greater vertical distance, lower overall distance moved, and greater intake rate. Three further species did not appear to be members of any sub-group (Little Weaver, Grey-backed Camaroptera, Common Whitethroat, and Lesser Whitethroat). One of these latter three species, Grey-backed Camaroptera, appears to be quite isolated from the other species, exhibiting greater movement rates and lower intake rates than the other species. However, low sample sizes for Common Whitethroat and Grey-backed Camaroptera mean that for these two species, results should be interpreted with care. These results suggest that inter-specific competition within these pairs (see Fig 6.4) will be greatest, and this will be tested in section 6.5.6.

It should also be noted that PC1, which showed non-significant interspecific differences in values, was dominated by horizontal distance moved and number of moves per second, suggesting these variables were not important in explaining inter-specific variation in foraging behaviour.

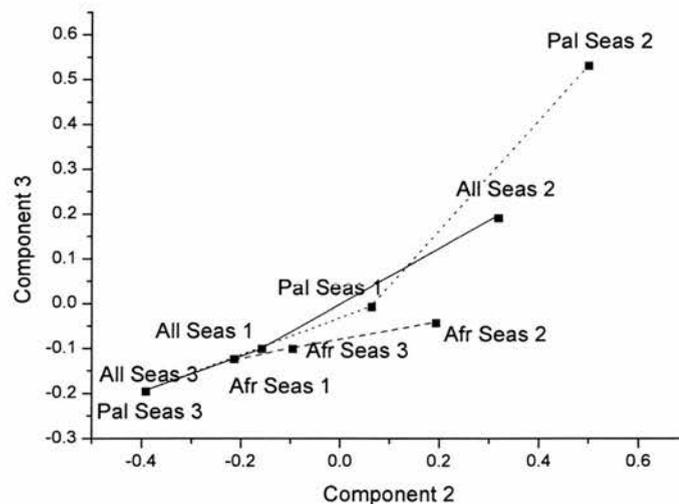


**Fig 6.4:** Mean values of PC2 and PC3 for all warbler species foraging behaviour. A significant difference across all species was found for both Factor 2 ( $F_{9,195} = 2.5$ ,  $p = 0.0009$ ) and 3 ( $F_{9,195} = 3.1$ ,  $p = 0.002$ ). From inspection, three broad groupings were identified. Species to the right of the graph have greater distance flown and vertical movement. Species in the upper region have a greater number of movements and lower intake rate.

### 6.4.7 Seasonal variation in foraging behaviour

Comparison of seasonal variation in foraging behaviour was carried out using the principal components 2 and 3 described above. Results from One-way ANOVA indicated that significant between-season differences occurred only in PC2 across all species grouped together ( $F_{2,202}=8.3$ ,  $p<0.001$ ). When foraging PCs 2 and 3 were compared across seasons for individual species, significant differences were found in PC 2 for Acacia Warbler ( $F_{1,8}=5.8$ ,  $p=0.042$ ) and PC 2 in Subalpine Warbler ( $F_{1,22}=5.6$ ,  $p=0.027$ ). Examination of the plots of seasonal changes in values of PC2 and PC3 (Fig 6.5) indicate that all species as a group showed an increase in the distance flown and a reduction in vertical movement.

When observations were selected at which foraging took place, no significant difference in foraging diversity between seasons 1 and 2 were found for either Palearctic ( $t=0.339$ ,  $df=7$ ,  $p=0.744$ ) or Afrotropical species ( $t=-1.016$ ,  $df=36$ ,  $p=0.316$ ).



**Fig 6.5:** Mean values of foraging behaviour PCs 2 and 3 for all warblers grouped (All), Afrotropical species (Afr) and Palearctic warbler species (Pal) across the three study seasons (1- mid autumn, 2- late autumn, 3- mid winter). A significant difference across all seasons was found for PC2 in All ( $F_{2,202}=8.3$ ,  $p<0.001$ ). Groups to the right of the graph have greater distance flown and vertical movement. Groups in the upper region have a greater number of movements and lower intake rate.

#### 6.4.8 Seasonal change in degree of selection for key tree species

In the best-fit habitat GLM's presented in Chapter 5, three tree species showed a significant relationship with three or more species of warbler. *Balanites* showed a non-significant seasonal change in importance for Common Whitethroat, Little Weaver, and Olivaceous Warbler, with insufficient data to allow the model to be run for Lesser Whitethroat. For *Salvadora*, sufficient data was only available to test for seasonal change in degree of selection by Common Whitethroat, which exhibited an increased degree of selection for *Salvadora* ( $F_{4,970} = 5.4$ ,  $p = 0.0003$ ). Changes in the degree of selection of *Salvadora* by Subalpine Warbler and Lesser Whitethroat could not be tested. Similarly, insufficient data were available to test for the degree of selection of *Acacia* species by Lesser Whitethroat and Subalpine Warbler, though Little Weaver showed a significant decline in selection for *Acacia* between mid autumn and early spring, before increasing again during late spring ( $F_{4,971} = 4.5$ ,  $p = 0.0014$ ).

#### 6.4.9 Influence of abundance of potential competitors

Results from the microhabitat selection and foraging behaviour PCA indicate that several species pairs have a high potential for inter-specific competition (Common Whitethroat-Acacia Warbler, Subalpine Warbler-Cricket Warbler, Subalpine Warbler-Lesser Whitethroat, Olivaceous Warbler-Northern Crombec). No significant relationship was found between the interaction of a key habitat variable and the presence of potentially competing species across any of the four species pairs tested (Tables 6.9-6.13).

**Table 6.9:** Habitat GLM results for Common Whitethroat with presence of Acacia Warbler and Acacia Warblers interaction with *Balanites* inserted as covariates.  $P_{crit}=0.006$ . Residual variance= 1724.1858, residual df= 1581, residual variance/ residual df= 0.7136.  $R^2$  equivalent= 0.28.

		DF	F	p
Acacia	Warbler	1, 1567	0.3	0.6189
Presence				
Acacia	Warbler	1,567	0.1	0.7335
Presence * <i>Balanites</i>				
Season		4, 1567	62.8	<0.0001
Minutes after sunrise		1, 1567	12.3	0.0005
Year		1, 1567	7.8	0.0052
Mean tree height		1, 1567	17.7	<0.0001
<i>Balanites</i> density		1, 1567	70.8	<0.0001
<i>Salvadora</i> density		1, 1567	66.9	<0.0001
Tree diversity		1, 1567	17.5	<0.0001
Shrub density		1, 1567	4.9	0.0268
<i>Calatropis</i> density		1, 1567	3.4	0.0659

**Table 6.10:** Habitat GLM results for Subalpine Warbler with presence of Cricket Warbler and Cricket Warblers interaction with *Salvadora* inserted as covariates.  $P_{crit}=0.006$ . Residual variance= 1724.1858, residual df= 1581, residual variance/ residual df= 0.7136.  $R^2$  equivalent= 0.51.

		DF	F	p
Cricket	Warbler	1, 1567	0.0	0.964
Presence				
Cricket	Warbler	1,567	0.3	0.5668
Presence * <i>Salvadora</i>				
Season		4, 1567	44.8	<0.0001
Minutes after sunrise		1, 1567	29.2	<0.0001
Year		1, 1567	45.7	<0.0001
Tree diversity		1, 1567	4.8	0.0294
<i>Acacia</i> density		1, 1567	60.9	<0.0001
Tree density		1, 1567	60.5	<0.0001
<i>Salvadora</i> density		1, 1567	74.8	<0.0001
Shrub density		1, 1567	41.3	<0.0001
<i>Calatropis</i> density		1, 1567	8.4	0.0039

**Table 6.11:** Habitat GLM results for Subalpine Warbler with presence of Lesser Whitethroat and Lesser Whitethroats interaction with *Salvadora* inserted as covariates.  $P_{crit}=0.006$ . Residual variance= 1724.1858, residual df= 1581, residual variance/ residual df= 0.7136.  $R^2$  equivalent= 0.51.

		DF	F	p
Lesser Whitethroat Presence		1, 1567	1.7	0.1997
Lesser Whitethroat Presence * <i>Salvadora</i>		1, 1567	0.6	0.4564
Season		4, 1567	44.5	<0.0001
Minutes after sunrise		1, 1567	28.5	<0.0001
Year		1, 1567	45.9	<0.0001
Tree diversity		1, 1567	4.9	0.027
Acacia density		1, 1567	62.8	<0.0001
Tree density		1, 1567	62.0	<0.0001
<i>Salvadora</i> density		1, 1567	86.1	<0.0001
Shrub density		1, 1567	42.8	<0.0001
Calatropis density		1, 1567	8.4	0.0039

**Table 6.12:** Habitat GLM results for Olivaceous Warbler from eastern sites with occurrence of Northern Crombec and Northern Crombecs interaction with meant tree height included as covariates.  $P_{crit}=0.006$ . Residual variance= 1543.3022, residual df= 1048, residual variance/ residual df= 1.4726.  $R^2$  equivalent= 0.28.

		DF	F	p
Northern Crombec presence		1, 1034	0.1	0.7606
Northern Crombec presence * mean tree height		1, 1034	0.2	0.6385
Season		4, 1034	10.5	<0.0001
Minutes after sunrise		1, 1034	0.0	0.9252
Year		1, 1034	3.6	0.0569
Mean tree height		1, 1034	115.0	<0.0001
Tree diversity		1, 1034	4.6	0.0327
Calatropis density		1, 1034	29.9	<0.0001
Acacia density		1, 1034	9.1	0.0026
Balanites density		1, 1034	8.0	0.0049
Shrub density		1, 1034	7.7	0.0057

**Table 6.13:** Habitat GLM results for Lesser Whitethroat from eastern sites with presence of Subalpine Warbler and Subalpine Warblers interaction with *Salvadora* included as covariates.  $P_{crit}=0.006$ . Residual variance= 708.7453, residual df= 826, residual variance/ residual df= 0.8580.  $R^2$  equivalent= 0.22.

		DF	F	p
Subalpine	warbler	1, 813	3.2	0.0735
presence				
Subalpine	warbler	1, 813	2.2	0.1384
presence * <i>Salvadora</i>				
Season		2, 813	8.0	0.0004
Minutes after sunrise		1, 813	40.6	<0.0001
Year		1, 813	2.8	0.0939
Mean tree height		1, 813	5.2	0.0223
Tree diversity		1, 813	58.8	<0.0001
Acacia density		1, 813	19.3	<0.0001
Tree density		1, 813	21.3	<0.0001
Balanites density		1, 313	38.1	<0.0001
<i>Salvadora</i> density		1, 813	31.0	<0.0001
Shrub density		1, 813	0.9	0.3314

## 6.5 Discussion

### 6.5.1 Microhabitat Selection

Results from analyses of microhabitat principal components showed no significant differences between the two residency groups. This high degree of overlap in microhabitat use could be interpreted as indicating a high potential for competition to be present. This follows results found by Salewski *et al.* (2003), which concluded that niche partitioning did not occur through microhabitat selection. The high diversity of species within each residency group, particularly the Afrotropical group that contained six species in six different genera, may result in diversity of microhabitat selection, and therefore a low potential for between-group competition. Examination of inter-specific variation in microhabitat selection would tend to support this, with Afrotropical and Palearctic species' characteristics dispersed amongst one another, and no clear separation of the residency groups apparent. This would suggest that the greatest potential for competition exists between species of the same residency group.

The apparent irrelevance of location within canopy in explaining inter-specific or inter-group variation in microhabitat selection differs from the findings of previous authors

who found resident species foraged in the centre of the canopy (Jablonski and Lee 1998). This study was carried out in the temperate region however, where mass was consistently greater in residents than migrants and presumably reflected in microhabitat preferences. The difference in mass between residency groups found in temperate latitudes may have been responsible for the displacement of migrants from tree crown interiors by residents (Alatalo and Suhonen 1990). In the Sahel, considerable overlap in body mass occurs between resident and migrant species, potentially reducing the degree of separation between the two groups. However, a study from Africa found that resident species of Wheatear (*Oenanthe* spp) were dominant over migrant counterparts irrespective of body mass (Leisler 1992).

### 6.5.2 Foraging Behaviour

In contrast to microhabitat, there were significant between-residency group differences in foraging behaviour. This may suggest reduced direct competition, though differences in foraging behaviour do not necessarily equate to differences in diet or resources used. The greater distances flown and vertical movement rate of Palearctic species would support previous authors' work, though the suggestion that these differences are in order for migrants to avoid resident competitors through increased movement remains unproven, and the use of removal experiments would presumably help clarify this issue. However, a high degree of overlap was observed between the two residency groups. Analysis of interspecific variation in foraging behaviour indicated significant differences, with several sub-groups exhibiting similar foraging behaviour identified. In comparison with microhabitat use however, there appears to be greater overlap in attributes between residency groups, suggesting greater potential for competition between residents and migrants at the species level. Previous authors have found that Palearctic species have a greater diversity of foraging method than resident species and have suggested this was due to a generalist foraging strategy (Salewski *et al.* 2003). No significant difference in foraging diversity was found in this study, although the Shannon Wiener index can be sensitive to sample size (Magurran 1988) and this may have affected results.

These results suggest that at the group level the potential for competition through foraging behaviour may be low between residents and migrant groups, but that at the species level, competition may be more pronounced. This differs from previous authors who concluded that niche partitioning via foraging behaviour occurred (Salewski 2003).

However, this latter study compared single Palearctic species with Afrotropical counterparts.

### 6.5.3 Seasonal variation in microhabitat selection and foraging behaviour

One may predict that a divergence in microhabitat selection and foraging behaviour would occur between the two residency groups over the autumn to winter period as the numbers of migrant individuals, and therefore potential competitors, increases. The plot of mean microhabitat and foraging behaviour principal components for resident groups (Fig 6.2 and 6.5) indicate that Afrotropical and Palearctic species have similar characteristics during mid autumn, and that the groups remain similar through late autumn and mid winter by undergoing comparable seasonal changes. This suggests that increasing competition does not drive divergence of behaviour at the group level. This may be due to competition not occurring, its' occurring at a level that does not drive divergence, or that it is avoided through some other mechanism. Alternatively, resources may be extremely limited, removing the potential for species to diverge in microhabitat use and resulting in high levels of competition.

Only two species of warbler showed significant inter-seasonal variation in microhabitat selection, whilst two different species showing significant variation in foraging behaviour. This suggests that seasonal change in microhabitat selection and foraging behaviour is not widespread at the species level. However, the low sample sizes used for these tests suggest that more work may be required in order to tease apart seasonal change in individual species. Interspecific differences in microhabitat selection, foraging behaviour, and also habitat preferences (see Chapter 5) may have reduced competition to a level low enough to allow sympatry, without seasonal change in behaviour being required.

The observed seasonal change in microhabitat selection in both residency groups, with birds utilising lower sections of the trees in mid winter than autumn, may be due to the loss of leaves by the majority of tree species by mid winter, the upper regions of the trees being exposed, with reduced levels of invertebrates, and provide poor shelter from potential predators. It is possible that the increase in the distance flown shown by foraging behaviour results was due to reduced invertebrate abundances, resulting in an increase in movement between trees. Alternatively, the increased abundance of Palearctic species in the area resulted in increased interference competition and

therefore avoidance movement. The increase in vertical distance moved may also have been due to increased foraging effort, though why horizontal distance moved did not increase is unclear. It is possible that resources were superabundant during the study, and that during times in which they are limited competition may be more pronounced, resulting in divergence of microhabitat characteristics.

Results from habitat selection GLM's in which interactions between season and key tree species were included suggest that for *Balanites* at least, no significant change in selection of the tree species occurs. This suggests that the method by which *Balanites* is utilised as a resource, rather than the degree to which the species itself is utilised, changes between seasons. Unfortunately insufficient data were available to test for changes in the degree of selection for *Salvadora* other than for Common Whitethroat, with results for this species suggesting that the degree of utilisation of *Salvadora* as a resource does change seasonally. The rapid increase in densities of Common Whitethroats during spring (Chapter 3) and their dependence on *Salvadora* fruit (Chapter 5) may result in a high potential for competition. However, there appear to be relatively few potential inter-specific competitors present during spring. The species' two congeners have departed the area at this time, and no small Afrotropical passerines are dependent upon fruit to the same degree as their migrant counterparts.

### **6.5.5 Influence of abundance of potential competitors upon warbler presence**

No species pairs tested using habitat selection GLM's showed a significant relationship between the occurrence of dependent species and the presence of potential competitors, whether within or between residency group pairs were tested. This is perhaps most surprising in the Lesser Whitethroat- Subalpine Warbler species pair. The potential for competition between these two species, as identified by microhabitat selection results, supports findings presented in Chapter 5 that indicated substantial overlap in habitat preferences. The non-significant results obtained suggest that, even if interspecific competition is occurring, it does not reveal itself in bird distributions, with species apparently occurring independently of one another. Alternatively, habitat variables tested in the model are not the variables that are competed for, or competition is avoided through a mechanism that was not examined here. It is also possible that a superabundance of resources existed during the study, resulting in limited competitive exclusion occurring. This raises the possibility that periods when resources do become limiting may result in increased levels of competition.

Experiments in which food availability is manipulated would allow any such relationship to be identified, though the practicalities of this in the Sahel may be problematic.

## 6.6 Conclusions

The potential for competition between residency groups appears to be limited according to microhabitat and foraging observations made during this study. A greater potential for inter-specific competition appears to exist. Palearctic species appear to forage lower down in tree canopies than Afrotropical species, though whether this indicates a preference for peripheral habitats is open to interpretation. If any competition is taking place it does not appear to effect species distributions, with no evidence of competitive exclusion found. The use of experiments where potential competitors are excluded or food availability is manipulated would be the next logical step in following up results obtained in this study.

## Chapter 7 : Discussion

### 7.1 Warbler Densities

Despite the importance of the Sahel to wintering Palearctic migrants being well known, little work has been carried out in the region. Palearctic warbler densities found in this study were comparable to those from the small numbers of previous studies (Browne 1982; Jones 1996; Stoate 2001; Vickery 1999). As one would expect, seasonal variation in Palearctic warbler densities closely matched the timing of migration of each species. However, the late autumn arrival of birds in the study sites, with many densities peaking during mid-winter or early spring, suggests that many birds are spending the autumn period further north in the Sahel, gradually moving south with deteriorating conditions associated with the onset of the dry season.

Perhaps surprisingly, even less work has been carried out on the Afrotropical species in the Sahel. Baseline data on abundance is lacking, and no previous work on densities of individual Afrotropical warbler species has been published from West Africa. Densities of Afrotropical warblers as a group were comparable between this study and one previous study (Jones *et al.* 1996), and greater than another study in which only three species were included in analyses (Morel 1973). There is little consistency in studies in East Africa which found densities of Afrotropical species that were similar to those found here (Lack 1987) but also 30 times greater (Rabol 1987). Densities of individual warbler species in the latter study were also found to be greater than individual Afrotropical warbler species here, indicating that differences in densities of the group as a whole were not merely a function of lower species diversity in West Africa when compared to the East.

The ratio of Palearctic to Afrotropical warbler species varied from 1.1 during mid-winter, to 1.7 during spring, indicating that Palearctic species were more numerous than their Afrotropical counterparts. These results are similar to the ratio of 0.95 found previously in Nigeria during mid-winter (Jones 1996) and 1.44 during spring (Vickery *et al.* 1999), though were considerably lower than a study in Senegal that found ratios of 5 during mid-winter (Morel 1968). In East and South Africa, the ratio appears to be much lower (0.24-0.55), with Afrotropical species generally outnumbering Palearctic (Lack 1987; Rabol 1987; Jones 1998). This trend matches the previously described pattern of declining densities and diversities of Palearctic species with declining latitude and

increasing longitude (Jones 1998). The similarly relatively high densities of Palearctic and Afrotropical warblers across study sites, combined with the latter's sedentary behaviour, suggest that inter-group competition is not avoided through geographical or seasonal separation, and that niche separation must be taking place through habitat selection or foraging behaviour.

### 7.3 Habitat Selection

Very strong similarities were found in the structure of habitats selected by Palearctic species during winter with those described previously for breeding grounds. Common Whitethroat selected for areas with low and open shrubby vegetation in this study, with breeding site habitats exhibiting comparable habitat structure (Cramp 1992). Subalpine Warbler showed preference for *Acacia* species, and the combination of this with the preference it also showed for *Salvadora* and other low shrubby species is comparable with the breeding season preferences for dense scrub with emergent trees (Cramp 1992). In breeding grounds, Lesser Whitethroat selects for habitats intermediate between open country and closed forest with a strong vertical component (Cramp 1992). Results presented here indicate that on winter grounds Lesser Whitethroat select for taller trees alongside greater densities of *Acacia*, *Balanites* and *Salvadora*. Whether these similarities are due to morphological adaptations resulting in similar habitats being utilised in winter and breeding grounds, or due to competitive exclusion by resident species is unclear, though the use of exclusion experiments could tease apart the two possible explanations. It is of interest to note that densities were similar to those of males found in temperate breeding grounds suggesting that intraspecific interactions may determine density on non-breeding as well as on breeding grounds (Cramp 1992).

No previous work on habitat preferences of Afrotropical warblers in the Sahel has been published. However, results from this study do support the general descriptions of habitat preferences previously described for Africa (Urban *et al.* 1997).

The relative abundances of invertebrates between the three dominant tree species suggest that, whilst *A. tortillis* provide a greater resource during the autumn than *Salvadora* and *Balanites*, this difference is reduced during the winter due to declining abundance on *A. tortillis*. Unfortunately data were not available for the spring but it is possible that during this period invertebrate numbers continue to increase on

*Salvadora* and *Balanites*, increasing their importance to both Palearctic and Afrotropical species. The peak in *Salvadora* fruit during spring may stimulate a flush of invertebrates. During spring the majority of tree species have lost their leaves, and therefore the key resource may be the shade and shelter provided by the evergreen *Salvadora* and *Balanites* rather than invertebrate abundance. Invertebrate abundance data from throughout the year would help clarify any relationships. However, it is interesting to note that none of the three species of Afrotropical warbler showed a significant association with *Salvadora*. This suggests it is the trees' fruit that is of importance, as one would expect Afrotropical species to select for *Salvadora* if invertebrates were the key resource.

#### 7.4 Competition

In order for competition to take place, species or individuals must occur in the same geographic area and utilise the same resources. Direct competition would also be most pronounced where the same method of resource use are employed, though this is not required for interference competition to take place. Results presented in this thesis indicate that Palearctic and Afrotropical warbler species (Chapters 3 and 4) exhibit a high degree of sympatry between the two groups. The sedentary nature of the Afrotropical warbler species found here and by previous authors (Morel 1968; Elgood 1994) contradicts the competition release theory as an explanation for Palearctic species occupying the Sahel, suggesting a high potential for competition exists between the two groups. It is possible that populations showed parallel shifts southward, with birds from further north occupying territories vacated by individuals moving south. Alternatively, movement south with the onset of the dry season may have occurred prior to this study period, and this could not be detected. Habitat selection analyses suggested that overlap in preferences is not complete, and that the greatest potential for competition may exist within the migrant Palearctic group. The strong similarities between Lesser Whitethroat and both Subalpine Warbler and Common Whitethroat habitat preferences suggest this group in particular may experience the greatest competition.

Results from microhabitat selection observations indicate that the potential for competition between resident groups is present, with considerable overlap found. However, this result may be due to the high diversity of species and genera within the Afrotropical warblers, and their corresponding widely distributed microhabitat

preferences. This, combined with the apparent separation of residency groups in foraging behaviour and the variation in habitat selection discussed above, suggests that competition may be more limited than microhabitat selection results initially suggest. Results from models testing the effects of the presence of potential competitors upon species occurrence would tend to support this. The lack of a significant positive relationship would suggest that differences in habitat selection do occur, whilst the lack of a negative relationship suggest that competitive exclusion does not occur. In contrast to microhabitat selection, foraging behaviour did show a significant separation between residency groups. However, overlap was considerable and examination of individual species' characteristics indicated a wide scatter of both resident and migrant species. Whereas microhabitat selection appeared to show similarities within-residency group, foraging behaviour attributes had greater between-residency groupings. This would suggest that segregation of residency groups might be occurring at the foraging behaviour but not habitat or microhabitat levels.

In contrast to previous studies, no significant differences were found in the diversity of foraging methods used between resident and migrant species, and the assertion that migrant species avoid competition with residents by being more generalist cannot be supported. However, the overall trend for Palearctic species is to fly greater distances and to have a greater movement rate than Afrotropical counterparts, suggesting that some aspects of foraging behaviour may also play a role in avoidance of competition.

Previous authors (Greenberg 1986; Lack 1986a; Winkler and Leisler 1992; Rabol 1987) have suggested that migrant species utilise more open and secondary habitats than their resident counterparts, with this increased generalist approach in order to avoid competition from resident species. Results from this study found that two species of Palearctic warbler selected for sites with lower tree densities, with the third (Common Whitethroat) showing no strong selection relationship with tree density. This contrasts with Afrotropical species in which two species showed significant selection for sites with greater tree density, with again the third showing no significant relationship with tree density. This would suggest that Palearctic warbler species are indeed selecting for more open habitats and thus may be using more marginal habitats than resident species. This raises the possibility that Afrotropical warblers are better able to dominate primary habitats and exclude migrant competitors. However, as habitat preferences of Palearctic warblers in this study matched breeding ground preferences, difference in tree density preferences may simply reflect different habitat requirements. A greater degree of diversity in habitat selection by Afrotropical species may also be

inferred by results from habitat selection models presented in chapter 5, with Palearctic species exhibiting greater overlap in habitat preferences. However, two of the three Afrotropical species (Little Weaver and Cricket Warbler) appeared to be somewhat general in habitat preferences in comparison with Palearctic. It is possible that whilst habitat selection is quite general, Afrotropical species are more specialised in resource use within these habitats than their Palearctic counterparts. This possibility is supported by casual observations of several Afrotropical warblers apparently showing quite specialised foraging behaviour. Northern Crombec predominantly foraged on tree trunks and major branches in the manner of a Nuthatch (*Sitta* sp.), Sennar Penduline Tit were most frequently observed foraging on the tips of outermost branches, and Yellow-bellied Eromemola in the uppermost foliage of the canopy. In contrast, the *Sylvia* warblers were generally observed in the canopy interior. Observations of microhabitat selection partly supported this greater diversity in habitat selection or method, with Afrotropical species exhibiting a greater spread in characteristics (Chapter 6). However, no such pattern was found in foraging behaviour characteristics. This suggests that habitat and microhabitat selection rather than use of resources is the method by which niche separation occurs.

Seasonal divergence in microhabitat selection or foraging behaviour between resident and migrant groups was not observed. This may have been due to limited resources preventing such divergence, and not allowing the associated avoidance of competition, or alternatively the lack of any competition to drive such divergence following the arrival of Palearctic species. The shift to foraging in lower areas within trees by both groups was presumably associated with a reduction in invertebrate loads with the onset of the dry season, and concurrent loss of leaves in the majority of tree species. Alternatively, a greater proportion of individuals may have been observed in the lower parts of trees following the loss of leaf cover, removing the bias in observations possibly present during the earlier part of the season.

### **7.5 Conservation implications of results**

Findings of habitat selection patterns (Chapter 5) suggest that Palearctic warblers are relatively robust to habitat degradation or loss, with large declines in tree densities resulting in a relatively small decline in warbler abundance. However, dramatic declines in tree density have already been observed in one study site (Watuca Forest Reserve) and appear to be occurring across the region (Geomatics International 1998). It would

therefore be dangerous to conclude that populations are secure from such habitat loss as historic changes and effects could not be detected in this study. There is also already bias in the species studied in this thesis, with only species occurring in sufficient numbers to allow analyses examined. Therefore species sensitive to habitat loss or degradation may already have been excluded from analyses due to lack of data. If we assume that current conditions in the Sahel of Nigeria have already been significantly degraded, applying results from this study to other relatively 'pristine' areas, one may conclude that severe degradation could occur before any detrimental effects upon bird populations were found. This may not be the case however, and such habitat loss may result in populations declining from greater levels than found in this study following relatively little habitat degradation. An expansion of the range of habitats and geographic area studied would allow any such relationships to be accounted for.

Unfortunately an assessment of changes in bird abundances and associated changes in habitat characteristics was only possible for one study site, Watucal Forest Reserve that was surveyed during 1994 (Vickery *et al.* 1996). Results from this site showed that habitat loss has been rapid, with tree density declining by 80% in the 8 years between the two studies. Concurrently, the densities of Subalpine Warbler declined by 95%, with populations of Afrotropical warbler species also showing a significant decline at this site. Subalpine Warbler shows preference for sites with dense stands of *Acacia*, which declined by 57% between these two studies. This suggests that habitat loss in the region is occurring at an alarming rate (doubly so considering this site is a 'protected' forest reserve) and is capable of impacting severely upon bird populations. Unfortunately without long-term monitoring it is impossible to properly assess that rate of habitat loss and its' impact upon bird populations. Furthermore, though data from the European breeding grounds suggest a stable Subalpine Warbler population during the 1970's and 80's (Cramp 1992; Shirihi *et al.* 2001), information on recent populations are not available, and the geographic isolation of the four described subspecies breeding in Europe, alongside partial allopatry in winter grounds, makes an assessment of population status difficult. Long-term monitoring of migrant populations across Europe is therefore essential in order to assess the potential impact of processes in Africa upon breeding populations.

Habitat loss appears to be widespread, and the apparent spread South and West of a number of Sahelian species (Orphean Warbler, Sennar Penduline Tit, Yellow-bellied Eromemola) is presumably due to habitat loss, through either climatic or anthropogenic

effects, 'forcing' species into new areas. This is supported by the apparent southerly shift in spring departure latitudes of Common Whitethroat in the Lake Chad area (Ottoosson *et al.* 2001). If true, this would result in migrant species crossing a wider barrier during migration, or alternatively maintaining existing departure points that are less suitable for pre-migration fattening. Increased barrier width has the potential to increase mortality or reduce the condition of individuals following the crossing. The effects of this on different species are likely to vary considerably. For example the Spotted Flycatcher is widely believed to currently be at its barrier width limit due to the relatively small amounts of fat it appears able to deposit. An increase in Sahara width may therefore have catastrophic effects upon the species. Although this species and others (Wood Warbler, Willow Warbler, Icterine Warbler, Melodious Warbler, Nightingale, etc.) do not use the Sahel during spring migration (pers obs), a shift south of the apparently unsuitable Sahel will increase the stresses placed upon these populations. If more southerly habitats such as the Guinea or Derived Savannas do not shift south, the limited use of the Sahel zone during northward spring migration by many Palearctic species may limit the negative effects of habitat degradation. In contrast, autumn migration coincides with the end of the Sahelian rainy season, and conditions appear to be more hospitable for migrants during this time, with the region used by a greater diversity of migrant species. Loss of Sahelian habitat through expansion south of the Sahara without an associated shift south of the Sahel would result in a reduction in the available habitat, directly affecting species associated with Sahelian habitat.

This study demonstrated differential habitat selection by warbler species and indicated that habitat degradation is likely to impact upon species to varying degrees. The apparent association with more open habitats exhibited by Palearctic species (Chapter 5; Lack 1971; Bilcke 1984; Rabol 1987) indicates that Afrotropical species may be more susceptible to habitat loss, with a reduction in tree densities resulting in a greater loss in bird abundance. The apparent greater degree of specialisation of Afrotropical species would also make the group less able to adjust behaviour and habitat use during times of stress. However, it may not be possible to apply general rules about the effects of habitat loss across all species or residency groups. The selection of areas of taller trees by Olivaceous Warbler and Lesser Whitethroat indicate that periods of intensive fuel wood gathering may affect these species to a greater extent than others. Species such as Subalpine Warbler, Little Weaver, and Lesser Whitethroat that select for *Acacia* trees, a key fuel wood resource, would also be impacted most severely by this activity. The dependence of the three *Sylvia* warblers upon *Salvadora*, (and

Subalpine Warbler also upon other shrubby species) suggests that these warblers may be most vulnerable to intensive grazing that would directly impact these resources. A drought event similar to that of the 1960's would increase grazing pressure upon these resources, and potentially result in a failure to fruit. The broad habitat preferences found for Cricket Warbler suggest this species is relatively robust to habitat degradation. However, it is also possible that this study failed to quantify a key habitat feature that Cricket Warbler is dependent upon.

The significant increase in densities of Common Whitethroat observed during spring was presumably associated with pre-migratory fattening of the species prior to trans-Saharan crossing (Stoate & Moreby 1995). Although *Salvadora* fruit have been previously identified as a key resource for Common Whitethroats during this period (Stoate & Moreby 1995), the significant increase in spring densities was not limited solely to sites supporting *Salvadora*. This suggests that individuals arrive in the Sahel from other latitudes during the spring, presumably from wintering grounds to the south, although it has also been suggested that migrants continue to arrive in the Sahel from the north until February (Lack 1990). Spring migration of Common Whitethroat in Jos, 3° to the south also peaked during this period, before dropping off significantly in May (Ross McGregor pers com). Two factors may explain the fact that no other species of *Sylvia* showed a pronounced peak in densities during spring. First, spring migration of Lesser Whitethroat and Subalpine Warbler occurs prior to the peak in *Salvadora* fruit production and ripening, thus this resource is not available to the species to the same extent as to Common Whitethroat. Secondly, Common Whitethroat winter over a larger latitudinal range than either of the two other *Sylvia* warbler species, with large populations wintering well to the south of the study region. Spring migration therefore results in the Sahel being utilised as a staging area (rather than initial departure point) for migrant Common Whitethroats from the south prior to crossing the Sahel. Populations of Common Whitethroat may therefore be more susceptible to habitat loss and degradation in the Sahel as the species appears strongly dependent upon a single resource that is relatively limited in distribution on the southern edge of the Sahara. Unfortunately, without a better understanding of the importance of *Salvadora* over a larger geographic area it is difficult to assess the likely impact of loss of this species, or its' failure to produce fruit.

An indication of the importance of fruit to Common Whitethroat populations was provided by a study in Senegal. The failure in fruiting of *Nitraria retusa* (an important food for some migrant species during spring passage) due to Locust *Schistocerca*

*gregaria* swarms, resulted in significantly lower body fat levels in Common Whitethroat (Stoate 1995). This is likely to have resulted in a reduced maximum flight range, delayed departure date, increased mortality during the Saharan crossing, and reduced individual fitness prior to the breeding season (Marra Hobson & Holmes 1998; Nolet & Drent 1998). Although this event occurred over a relatively small geographic area, and is unlikely to have noticeably effected European populations, it gives an indication of the potential effects of the failure or removal of resources from the Sahel. It is interesting to note that the population crash in Common Whitethroats during the Sahelian drought of the late 1960's was associated with a failure in *Salvadora* fruiting. The poor subsequent recovery of Common Whitethroat may have been due to a reduction in the abundance of *Salvadora* in the Sahel due to over-exploitation during the drought.

A severe drought event similar to that experienced during the 1960s may result in an increased dependence of bird populations upon key resources. This is likely to result in increased inter- and intra- specific competition, which in turn may further impact populations. The negative affects associated with such a drought event in the Sahel are likely to be further compounded by increased utilisation of resources for grazing and fuel wood extraction, further impacting bird populations. The prediction of the effects of future events upon bird populations may therefore be difficult.

## 7.6 Future Work

To monitor the effects of habitat change on bird species, ideally, a system of sites would be established across the Sahel, with regular assessment of bird densities and habitat being carried out. This would allow identification of any changes in bird populations, and allow changes to be linked with conditions in wintering grounds. An extension of the study area to the north, would allow the importance of higher latitudes to Palearctic migrants during autumn migration to be assessed. A greater latitudinal range in study sites would also allow any seasonal shifts in distribution to be identified such as that suggested in Common whitethroat, as well as identify longer-term shifts in distribution due to habitat change. The development of GPS technology now makes it possible for individual points to be relocated, thus allowing direct comparisons to be made. This baseline data would be extremely important in identifying the effects of any drought events upon populations, and assessing habitat requirements during these

periods of increased stress. At the very least, sites censused during this study should be censused again at regular intervals using the same sampling methods.

The identification of individuals through colour ringing would allow an assessment of within and between- winter site fidelity. This may have profound implications upon the impact of habitat loss upon populations, permitting work linking wintering behaviour with breeding fitness, survival, etc.. It would also allow an assessment of territory size, habitat use, and interactions with both conspecifics and other potential competitors to be carried out.

A more comprehensive sampling of invertebrate and fruit abundance than that possible in this study, combined with an assessment of relative calorific values, would allow key resources to be identified more precisely. An understanding of the effects of environmental change upon these resources would permit a better prediction of bird population responses to environmental change. This would also have to involve faecal sample analysis to assess dietary preferences. Individual body condition within and between years would provide an indication of the effects of fluctuating resources upon individual fitness.

This study developed predictive models from habitat preferences for a range of species, and these indicated a possible use in the construction of large scale predictive models. The incorporation of satellite images in these models to map habitat distributions over a large scale, would allow bird distributions and densities to be mapped over a large geographic area. Not only would this allow present-day distributions and populations to be estimated, but in addition habitats or areas identified as holding significant or important populations of warblers could then receive highest priority in any conservation activities. The maintenance and conservation of key habitat attributes identified in this study should be incorporated into farming and grazing management practices within the region. The maintenance of woodland plots for sustainable fuel wood production would benefit both local people and bird populations. Research into the levels of fuel wood extraction and grazing that would be possible without resulting in woodland loss would be a key component in conservation activities. Research into potential benefits to farmers of maintaining warbler habitat within their farms would therefore be a priority. More detailed work into defining the exact causes of habitat loss by treating the various human activities/ processes individually would be essential prior to the application of any conservation measures. The effects of past habitat change on populations and distributions could be estimated and compared with

observed changes. Finally these results could be used in predicting the effects of current and future habitat loss upon populations. The mapping of the distribution of *Salvadora* across the entire region using satellite images would be an important component of this work. In combination with ground-truthing of bird densities and habitat attributes, it would allow an assessment of the tree species' importance to Palearctic warbler species in the Sahel, particularly Common Whitethroat. An assessment of long-term change in distribution of *Salvadora* would establish whether population changes observed in Common Whitethroat could be attributed solely to the loss of *Salvadora*. These predictions could then be tested through ground truthing and if correct, could be used to assess the likely effect of past and future habitat change upon populations.

Data on foraging behaviour and microhabitat selection of warbler species was somewhat limited and did not allow a thorough assessment of differences between species from different residency groups to be carried out. The results that were gained suggest that increased effort in acquiring foraging observations may yield interesting and valuable insights. The use of removal or playback experiments may help clarify the degree of competition, if any, occurring within the system

## **7.7 Conclusion**

This study has provided new data on the abundances and seasonal patterns of occurrence for both Palearctic and Afrotropical species. It has demonstrated the efficacy of model selection GLM's in developing an understanding of habitat selection, and potentially very useful predictive models. It has highlighted areas of conservation concern for several Palearctic warblers and raised many questions on the vulnerability of Afrotropical species to habitat loss. Finally it has emphasised our lack of knowledge of behaviour in the Sahel and the need for further detailed work and urgent investigation.

## Chapter 8 : References

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Appendix 1: Warbler Density Estimates

Round	Season	Site	Common Whitethroat			Olivaceous Warbler			Subalpine Warbler			Lesser Whitethroat		
			Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL
1	Late autumn	Reserve	0.04	0.01	0.23	4.18	3.10	5.64	0.50	0.20	1.26	0.60	0.31	1.17
1	Late autumn	Canal	0.04	0.01	0.23	4.68	3.35	6.52	0.32	0.12	0.84	0.60	0.30	1.21
2	Mid winter	Reserve	1.09	0.67	1.78	2.44	1.85	3.22	0.24	0.10	0.55	2.01	1.34	3.03
2	Mid winter	Canal	0.09	0.02	0.31	2.76	1.97	3.86	0.23	0.07	0.69	1.10	0.66	1.83
2	Mid winter	Watucal FR	0.42	0.20	0.88	0.06	0.01	0.32	0.27	0.10	0.74	0.36	0.11	1.13
2	Mid winter	Nguru Agric	0.27	0.12	0.60	0.00			0.29	0.14	0.63	0.00		
2	Mid winter	Watucal Agric	0.13	0.04	0.48	0.00			0.00			0.00		
2	Mid winter	Watucal Rd	0.34	0.13	0.91	0.00			0.23	0.09	0.60	0.00		
2	Mid winter	School	1.30	0.77	2.19	0.10	0.03	0.40	0.44	0.22	0.91	3.82	0.88	16.66
2	Mid winter	Bore Hole	0.56	0.32	0.97	0.03	0.01	0.19	0.04	0.01	0.20	0.00		
2	Mid winter	Pratincloe	0.14	0.05	0.40	0.05	0.01	0.27	0.33	0.13	0.88	0.00		
2	Mid winter	Commiphora	0.26	0.11	0.61	0.75	0.42	1.32	0.68	0.41	1.13	2.33	0.56	9.73
2	Mid winter	Quail	0.22	0.08	0.64	1.15	0.61	2.15	0.61	0.31	1.17	0.50	0.17	1.46
3	Early spring	Reserve	4.26	3.20	5.67	2.21	1.60	3.07	0.00			1.05	0.60	1.83
3	Early spring	Canal	0.53	0.31	0.90	4.13	3.23	5.29	0.00			0.15	0.05	0.44
3	Early spring	Watucal FR	1.37	0.85	2.20	0.06	0.01	0.32	0.49	0.20	1.23	0.06	0.01	0.32
3	Early spring	Nguru Agric	0.38	0.19	0.77	0.00			0.16	0.06	0.44	0.00		
3	Early spring	Watucal Rd	0.48	0.21	1.05	0.00			0.52	0.22	1.24	0.50	0.07	3.37
3	Early spring	School	1.44	0.93	2.23	0.21	0.06	0.66	0.00			0.00		
3	Early spring	Bore Hole	1.43	0.81	2.50	0.11	0.03	0.40	0.00			0.00		
3	Early spring	Commiphora	1.70	1.11	2.59	1.12	0.48	2.61	0.00			1.00	0.20	5.11
4	Mid spring	Reserve	3.03	2.19	4.19	2.46	1.84	3.29	0.00			0.00		
4	Mid spring	Canal	0.48	0.23	1.02	3.64	2.83	4.69	0.00			0.00		
4	Mid spring	Watucal FR	2.32	1.48	3.64	0.06	0.01	0.32	0.00			0.00		
4	Mid spring	Nguru Agric	0.76	0.46	1.26	0.00			0.00			0.00		
4	Mid spring	Watucal Rd	1.97	1.23	3.16	0.00			0.00			0.00		
4	Mid spring	School	0.85	0.47	1.55	0.31	0.11	0.85	0.00			0.00		
5	Mid autumn	Reserve	0.16	0.03	0.90	2.58	1.82	3.68	0.09	0.02	0.47	0.00		

Appendix 1: Warbler Density Estimates

Round	Season	Site	Common Whitethroat			Olivaceous Warbler			Subalpine Warbler			Lesser Whitethroat		
			Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL
5	Mid autumn	Canal	0.00			2.29	1.58	3.31	0.26	0.09	0.78	0.00		
5	Mid autumn	School	0.00			0.36	0.16	0.83	0.00			0.00		
5	Mid autumn	Bore Hole	0.00			0.00			0.00			0.00		
6	Late autumn	Reserve	0.25	0.08	0.72	4.43	3.19	6.15	0.51	0.24	1.10	2.81	1.82	4.34
6	Late autumn	Canal	0.00			3.62	2.50	5.23	0.62	0.28	1.38	0.29	0.10	0.85
6	Late autumn	School	0.07	0.01	0.36	0.31	0.14	0.69	0.17	0.06	0.50	0.00		
6	Late autumn	Bore Hole	0.00			0.16	0.05	0.48	0.00			0.50	0.07	3.37
7	Mid winter	Reserve	0.74	0.41	1.34	2.03	1.31	3.14	1.02	0.51	2.05	2.81	1.70	4.64
7	Mid winter	Canal	0.09	0.02	0.47	2.76	1.79	4.26	0.70	0.31	1.59	0.48	0.21	1.11
7	Mid winter	Watacal FR	1.20	0.63	2.29	0.09	0.02	0.49	0.50	0.20	1.20	0.18	0.05	0.66
7	Mid winter	Nguru Agric	0.66	0.32	1.37	0.00			0.44	0.20	0.98	0.00		
7	Mid winter	School	0.46	0.21	1.02	0.05	0.01	0.29	1.35	0.81	2.23	1.93	0.41	9.04
7	Mid winter	Bore Hole	0.14	0.04	0.50	0.21	0.07	0.68	0.06	0.01	0.32	0.00		
7	Mid winter	Gashua	0.08	0.02	0.28	0.00			0.17	0.07	0.39	0.00		
7	Mid winter	Geidam	0.26	0.12	0.59	0.00			0.16	0.07	0.38	0.00		
7	Mid winter	Damasak	0.04	0.01	0.21	0.12	0.05	0.33	0.37	0.20	0.70	0.58	0.11	2.97
7	Mid winter	WofMalam	0.04	0.01	0.20	0.24	0.10	0.60	1.24	0.84	1.83	0.00		
7	Mid winter	Malafatori	0.86	0.42	1.76	0.60	0.34	1.06	2.34	1.64	3.32	0.80	0.41	1.54

Appendix 1: Warbler Density Estimates

Round	Season	Site	Bonelli's Warbler			Afrotropical Warbler group			Palearctic Warbler group			Acacia Warbler		
			Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL
1	Late autumn	Reserve	0.00			5.48	4.21	7.15	1.22	0.75	1.97	0.00		
1	Late autumn	Canal	0.33	0.14	0.80	6.98	5.29	9.21	0.95	0.53	1.70	1.38	0.55	3.43
2	Mid winter	Reserve	0.00			3.90	2.95	5.14	3.59	2.58	5.00	0.00		
2	Mid winter	Canal	0.73	0.32	1.66	3.99	2.90	5.48	1.62	1.13	2.32	0.00		
2	Mid winter	Watucaal FR	1.60	0.82	3.10	1.20	0.68	2.10	1.14	0.68	1.90	0.00		
2	Mid winter	Nguru Agric	0.00			0.27	0.10	0.70	0.63	0.38	1.04	0.00		
2	Mid winter	Watucaal Agric	0.00			0.33	0.12	0.88	0.23	0.09	0.57	0.00		
2	Mid winter	Watucaal Rd	0.00			0.20	0.07	0.60	0.53	0.27	1.02	0.00		
2	Mid winter	School	0.00			0.35	0.12	1.02	2.28	1.53	3.41	0.00		
2	Mid winter	Bore Hole	0.00			0.65	0.30	1.39	0.60	0.34	1.04	0.00		
2	Mid winter	Pratncloe	0.00			0.58	0.24	1.44	0.57	0.27	1.22	0.00		
2	Mid winter	Commiphora	0.00			1.27	0.81	1.99	1.51	1.13	2.02	0.00		
2	Mid winter	Quail	0.00			3.60	2.12	6.12	1.58	0.95	2.62	0.00		
3	Early spring	Reserve	0.07	0.01	0.36	4.27	3.29	5.53	5.54	4.34	7.08	0.00		
3	Early spring	Canal	0.13	0.02	0.71	7.64	6.29	9.29	0.72	0.44	1.19	0.72	0.30	1.71
3	Early spring	Watucaal FR	0.64	0.29	1.39	1.60	0.92	2.75	2.22	1.57	3.13	0.08	0.01	0.43
3	Early spring	Nguru Agric	0.08	0.02	0.45	0.08	0.01	0.41	0.59	0.35	1.01	0.00		
3	Early spring	Watucaal Rd	0.15	0.03	0.83	0.54	0.24	1.21	1.00	0.55	1.80	0.00		
3	Early spring	School	0.00			1.12	0.58	2.17	1.25	0.82	1.89	0.00		
3	Early spring	Bore Hole	0.00			2.45	1.50	4.00	1.29	0.73	2.28	0.00		
3	Early spring	Commiphora	0.00			2.31	1.14	4.71	1.59	1.09	2.32	0.00		
4	Mid spring	Reserve	0.00			4.82	3.68	6.31	3.16	2.34	4.26	0.00		
4	Mid spring	Canal	0.00			6.48	5.31	7.91	0.54	0.27	1.08	0.39	0.14	1.09
4	Mid spring	Watucaal FR	0.00			2.26	1.49	3.44	2.43	1.59	3.73	0.00		
4	Mid spring	Nguru Agric	0.00			0.42	0.23	0.77	0.69	0.43	1.11	0.00		
4	Mid spring	Watucaal Rd	0.00			1.09	0.61	1.94	1.71	1.08	2.69	0.00		
4	Mid spring	School	0.00			0.79	0.37	1.67	0.74	0.41	1.33	0.00		
5	Mid autumn	Reserve	0.00			3.95	2.95	5.27	0.25	0.07	0.97	0.00		

Appendix 1: Warbler Density Estimates

Round	Season	Site	Bonelli's Warbler			Afrotropical Warbler group			Palearctic Warbler group			Acacia Warbler		
			Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL
5	Mid autumn	Canal	0.26	0.07	0.95	4.29	2.88	6.39	0.44	0.19	0.99	0.25	0.05	1.41
5	Mid autumn	School	0.00			0.79	0.44	1.42	0.06	0.01	0.31	0.00		
5	Mid autumn	Bore Hole	0.00			0.75	0.40	1.40	0.06	0.01	0.33	0.00		
6	Late autumn	Reserve	0.00			6.54	4.87	8.79	3.30	2.23	4.87	0.00		
6	Late autumn	Canal	0.39	0.10	1.51	6.11	4.44	8.41	0.87	0.47	1.60	0.38	0.13	1.14
6	Late autumn	School	0.00			0.66	0.33	1.29	0.28	0.11	0.76	0.00		
6	Late autumn	Bore Hole	0.00			0.54	0.24	1.21	0.06	0.01	0.33	0.00		
7	Mid winter	Reserve	0.00			3.64	2.61	5.07	4.31	2.95	6.31	0.00		
7	Mid winter	Canal	0.39	0.13	1.15	4.07	2.81	5.91	1.40	0.86	2.26	0.25	0.07	0.94
7	Mid winter	Watural FR	0.36	0.12	1.08	1.21	0.62	2.35	1.88	1.16	3.07	0.36	0.12	1.07
7	Mid winter	Nguru Agric	0.00			0.37	0.16	0.84	1.01	0.52	1.98	0.00		
7	Mid winter	School	0.00			0.53	0.26	1.08	2.27	1.46	3.52	0.00		
7	Mid winter	Bore Hole	0.00			0.82	0.35	1.90	0.18	0.05	0.68	0.00		
7	Mid winter	Gashua	0.00			0.23	0.10	0.56	0.24	0.11	0.52	0.00		
7	Mid winter	Geidam	0.00			0.49	0.25	0.94	0.39	0.21	0.72	0.00		
7	Mid winter	Damasak	0.00			0.60	0.33	1.08	0.48	0.27	0.86	0.00		
7	Mid winter	WoffMalam	0.00			0.65	0.37	1.14	1.28	0.92	1.79	0.00		
7	Mid winter	Malafatori	0.00			2.04	1.34	3.09	3.92	2.39	5.32	0.00		

Appendix 1: Warbler Density Estimates

Round	Season	Site	Beautiful Sunbird			Brubru			Pygmy Sunbird		
			Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL
1	Late autumn	Reserve	0.15	0.03	0.83	0.04	0.01	0.20	0.66	0.24	1.80
1	Late autumn	Canal	0.00			0.07	0.02	0.28	0.11	0.02	0.59
2	Mid winter	Reserve	0.08	0.01	0.43	0.00			0.68	0.23	2.03
2	Mid winter	Canal	0.00			0.11	0.03	0.44	0.00		
2	Mid winter	Watucaal FR	0.27	0.07	1.08	0.00			0.13	0.02	0.71
2	Mid winter	Nguru Agric	0.00			0.00			0.08	0.01	0.43
2	Mid winter	Watucaal Agric	0.15	0.03	0.62	0.00			0.14	0.02	0.77
2	Mid winter	Watucaal Rd	0.00			0.00			0.00		
2	Mid winter	School	0.00			0.00			0.00		
2	Mid winter	Bore Hole	0.00			0.00			0.82	0.28	2.36
2	Mid winter	Pratincloe	0.00			0.00			0.00		
2	Mid winter	Commiphora	0.04	0.01	0.23	0.00			0.11	0.02	0.61
2	Mid winter	Quail	0.00			0.00			0.55	0.18	1.64
3	Early spring	Reserve	0.38	0.09	1.66	0.04	0.01	0.20	0.66	0.26	1.64
3	Early spring	Canal	0.00			0.26	0.09	0.70	0.33	0.11	0.98
3	Early spring	Watucaal FR	0.55	0.24	1.28	0.00			0.00		
3	Early spring	Nguru Agric	0.00			0.00			0.00		
3	Early spring	Watucaal Rd	0.00			0.00			0.00		
3	Early spring	School	0.00			0.00			0.00		
3	Early spring	Bore Hole	0.05	0.01	0.30	0.00			2.57	1.16	5.68
3	Early spring	Commiphora	0.05	0.01	0.30	0.00			0.71	0.26	1.97
4	Mid spring	Reserve	0.31	0.09	0.98	0.00			0.11	0.02	0.59
4	Mid spring	Canal	0.00			0.11	0.03	0.35	0.66	0.22	1.96
4	Mid spring	Watucaal FR	0.55	0.20	1.55	0.09	0.02	0.34	0.00		
4	Mid spring	Nguru Agric	0.09	0.03	0.29	0.00			0.00		
4	Mid spring	Watucaal Rd	0.00			0.00			0.00		
4	Mid spring	School	0.00			0.00			0.00		
5	Mid autumn	Reserve	0.14	0.03	0.80	0.00			0.21	0.04	1.14

Appendix 1: Warbler Density Estimates

Round	Season	Site	Beautiful Sunbird			Brubru			Pygmy Sunbird		
			Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL	Density	L 95% CL	U 95% CL
5	Mid autumn	Canal	0.00			0.07	0.01	0.40	0.43	0.12	1.57
5	Mid autumn	School	0.00			0.00			0.14	0.02	0.77
5	Mid autumn	Bore Hole	0.20	0.07	0.61	0.00			0.29	0.08	1.06
6	Late autumn	Reserve	0.00			0.27	0.10	0.78	0.41	0.11	1.52
6	Late autumn	Canal	0.00			0.14	0.04	0.55	0.21	0.04	1.18
6	Late autumn	School	0.00			0.00			0.00		
6	Late autumn	Bore Hole	0.00			0.00			0.57	0.18	1.82
7	Mid winter	Reserve	0.14	0.03	0.80	0.07	0.01	0.39	0.62	0.16	2.41
7	Mid winter	Canal	0.00			0.00			0.43	0.12	1.57
7	Mid winter	Watucaal FR	0.28	0.07	1.04	0.00			0.40	0.11	1.47
7	Mid winter	Nguru Agric	0.11	0.03	0.44	0.00			0.31	0.08	1.14
7	Mid winter	School	0.00			0.00			0.41	0.14	1.24
7	Mid winter	Bore Hole	0.00			0.00			0.57	0.22	1.50
7	Mid winter	Gashua	0.00			0.00			0.00		
7	Mid winter	Geidam	0.06	0.01	0.22	0.00			0.08	0.01	0.42
7	Mid winter	Damasak	0.18	0.07	0.48	0.00			0.08	0.02	0.45
7	Mid winter	WofMalam	0.00			0.00			0.00		
7	Mid winter	Malafacuri	0.00			0.00			1.08	0.46	2.50