

**Comparative ecology of the endemic Cyprus Warbler
and the congeneric Sardinian Warbler:
implications of recent coexistence**



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This thesis is submitted to the University of Cambridge
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For my parents

Author's declaration

This thesis is the result of my own research and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. The text does not exceed 80 000 words and no part has been submitted to any other university in application for a higher degree or diploma.

Victoria Ruth Jones

Abstract

In 1992 the Sardinian Warbler was first recorded breeding in Cyprus. Since then, survey results from Paphos District suggest that the endemic Cyprus Warbler population has declined, while the Sardinian Warbler breeding population has increased and expanded in Paphos District.

Colour-ringed Cyprus and Sardinian Warblers were observed during 2003 to 2005 breeding seasons on seven scrub study plots located across Paphos District. Both species appeared to establish home-ranges without reference to the other species, resulting in considerable interspecific home-range overlap. A playback experiment indicated that Cyprus Warblers reacted equally strongly to conspecific and congeneric song in areas where the two species coexist, but less strongly to congeneric than conspecific song in areas where Sardinian Warblers did not yet breed.

The vegetation composition of Cyprus and Sardinian Warbler home-ranges was very similar. There was no indication that the species competed for nest sites.

Cyprus and Sardinian Warbler have similar breeding biology; they laid similar sized first clutches and had similar chick output per pair for first nesting attempts. However Sardinian Warblers had a higher frequency of second nesting attempts and this resulted in a higher chick output per pair per year than was achieved by Cyprus Warblers. In both species total chick output per year was higher for pairs that nested early. Nest survival was similar for the two species.

Cyprus and Sardinian Warbler diets were very similar. Body condition of both species' chicks was higher earlier in the breeding season. Cyprus Warblers had higher productivity but lower chick body condition in the zone where their population has declined than in the zone with fewest breeding Sardinian Warblers. Productivity was positively related to arthropod biomass available on different plots for Sardinian Warbler, but not for Cyprus Warbler. There was no evidence of a negative impact of either species on the number or condition of nestlings produced by the congener.

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Chapter 1

General introduction

Islands and conservation

Of the 127 species of bird to have become extinct since 1500, more than 100 have been island endemics (Brooks 2000). Islands typically have high levels of endemism in comparison to equivalent areas of mainland, and the restricted range of island endemics means that threats like habitat destruction or arrival of new predators, competitors or pathogens often act rapidly and synergistically to bring about population declines. Climate change is causing relatively rapid alterations in patterns of temperature and precipitation, and prompting both geographic changes in the distribution of flora and fauna and temporal changes in the phenology of life-cycle events. This is likely to exacerbate an already serious situation for some island endemics. Survival of species depends on their ability to adapt to changing conditions in their original range or to track their favoured environment by altering their geographic range. Islands are often small in size and limited in altitudinal range, so island endemics may be limited in their capacity to respond to future changes.

Range changes are occurring naturally in many widespread species, while in other cases human activity is resulting in the introduction of non-native species. As a consequence of these processes many species, including island endemics, must cope not only with changes in food supply and habitat, but also with new community structure. Whatever the cause, these changes bring species into coexistence in novel assemblages, applying new selective pressures, generating new evolutionary responses and raising new conservation issues.

Introduction to the study species

Cyprus Warbler (*Sylvia melanothorax*) is one of only three endemic bird species among the Mediterranean countries¹ of southern Europe. It has the most restricted range of all *Sylvia* species, breeding only on Cyprus, and is therefore listed on Annex I of the EU Birds Directive. The Cyprus Warbler is a partial migrant. Some of the population winter on Cyprus, the remainder winter in Israel, Jordan and the Red Sea coasts of Egypt and Sudan, but the wintering range is not fully documented (Fig. 1.1). As an island endemic, yet a partial migrant, the Cyprus Warbler is very unusual. Cyprus Warblers are relatively widespread and common on Cyprus, but the total population size is unknown and published estimates vary from 4000-8000 (Heath *et al.* 2000) to 70 000-140 000 (BirdLife International 2004). Cyprus Warblers occur in a variety of habitats including forest edge, agricultural habitat and scrub. According to Flint and Stewart (1992) the species' distribution on Cyprus closely follows the 340-350 mm isohyets and it is absent from the Mesaoria plain in central Cyprus because the area is too dry (see Appendix 4 for precipitation map of Cyprus).

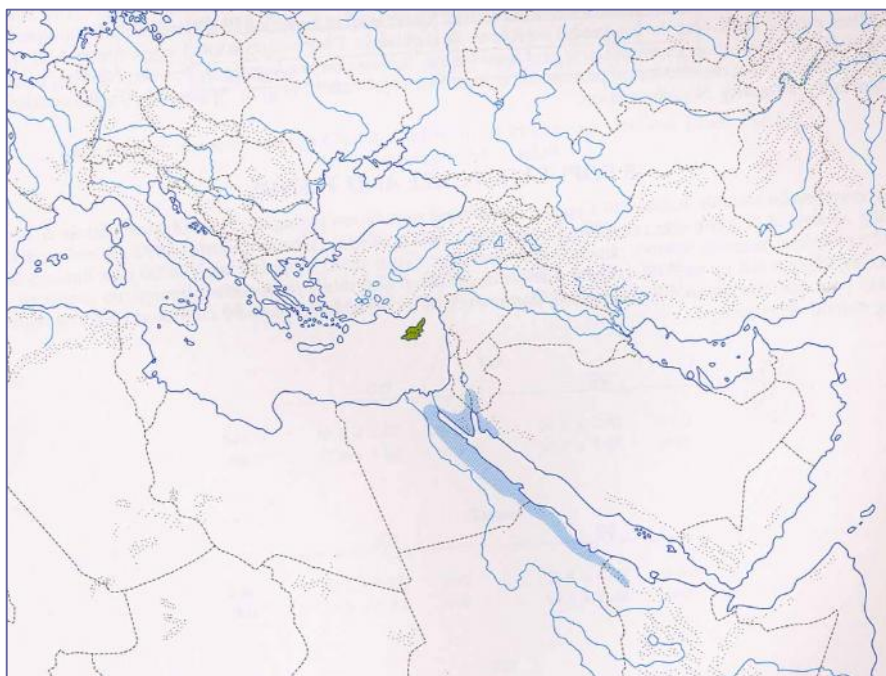


Figure 1.1 Distribution of the Cyprus Warbler (reproduced from Shirihai *et al.* 2001). Breeding/wintering areas are green and wintering areas are shown in blue.

¹ Bordering the Mediterranean Sea.

In contrast to the Cyprus Warbler, the Sardinian Warbler (*Sylvia melanocephala*) is the most widespread of all *Sylvia* species. Its breeding range covers much of the Mediterranean, the coast of North Africa and Turkey, while its winter range covers much of the breeding range and extends into northern Africa (Fig. 1.2). There are two extant races of the Sardinian Warbler, *S. m. melanocephala* and *S. m. momus*.

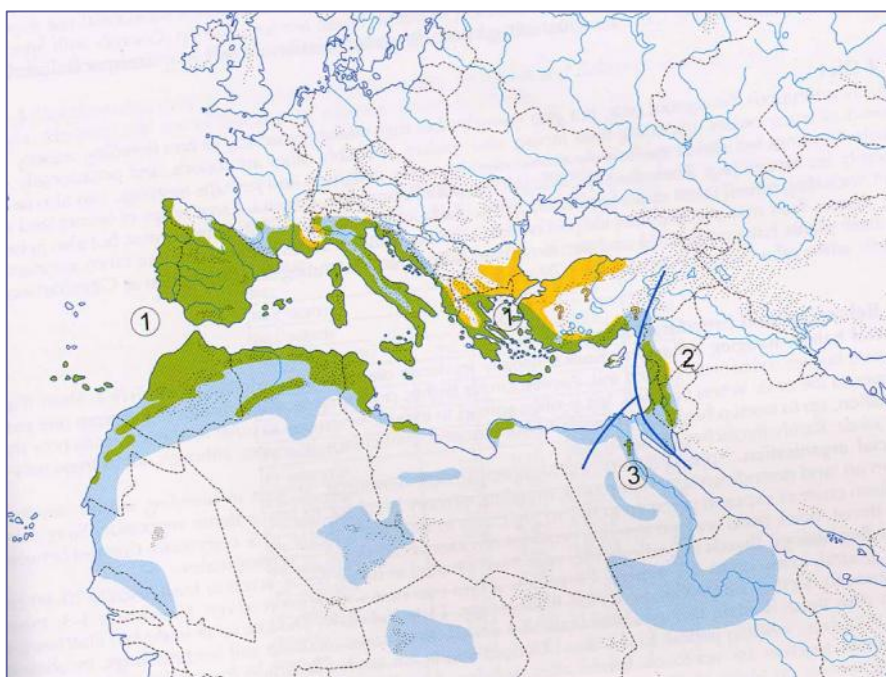


Figure 1.2 Distribution of the Sardinian Warbler (reproduced from Shirihai *et al.* 2001). Breeding areas are shown in yellow, breeding/wintering areas are green and wintering areas are shown in blue. Number 1 indicates the range of the race *Sylvia melanocephala melanocephala*, number 2 indicates the range of the race *Sylvia melanocephala momus*, number 3 indicates the range of the extinct race *Sylvia melanocephala norissae*.

According to Heath *et al.* (2000), between 1970 and 1990 population and range size of the Sardinian Warbler increased in Spain, Slovenia, Malta and Bulgaria and its range also increased in Italy. This range extension has been chiefly northwards, which suggests that climate change could be responsible (Cozens *et al.* 2000). The Sardinian Warbler was a winter visitor to Cyprus until 1992 when breeding was first recorded near the western tip of southern Cyprus in the Akamas area of Paphos District (Frost 1994). Since then the population of breeding Sardinian Warblers has increased and expanded eastwards in range (Pomeroy & Walsh 2000, 2002).

Sardinian Warblers can now be found breeding in variable densities across most of Paphos District. A second breeding population has become established since 2001 in the eastern Kyrenia mountain range in Northern Cyprus (P. Flint, pers. comm.). The provenance of these breeding populations of Sardinian Warblers is unknown, but the nearest breeding population is in Turkey. At the start of this project, wintering Sardinian Warblers were known to belong to the race *Sylvia melanocephala melanocephala*, but it was not known whether breeding and wintering populations were of the same provenance.



Plate 1.1 Cyprus Warbler male (D. Nye)



Plate 1.3 Sardinian Warbler male (BirdLife Cyprus)



Plate 1.2 Cyprus Warbler female (reproduced from Shirihai *et al.* 2001)



Plate 1.4 Sardinian Warbler female (BirdLife Cyprus)

Cyprus Warbler and Sardinian Warbler are small *Sylvia* species weighing approximately 11 g and 12 g respectively (Appendix 1). Males of both species have a grey back and black head. Cyprus Warbler males have distinctive black spotting or scalloping on a white background on their throat and breast (Plate 1.1), while Sardinian Warbler males have a white throat and breast (Plate 1.3). Females of both

species have a brown back and wings; Cyprus Warbler females have variable numbers of dark flecks or spots on a pale background on the throat and breast (Plate 1.2), while in Sardinian Warbler females the throat and breast are white (Plate 1.4). Both species feed chiefly by gleaning arthropods as they move through the vegetation, but fruit is also an important component of the diet, particularly in winter (Shirihai *et al.* 2001).

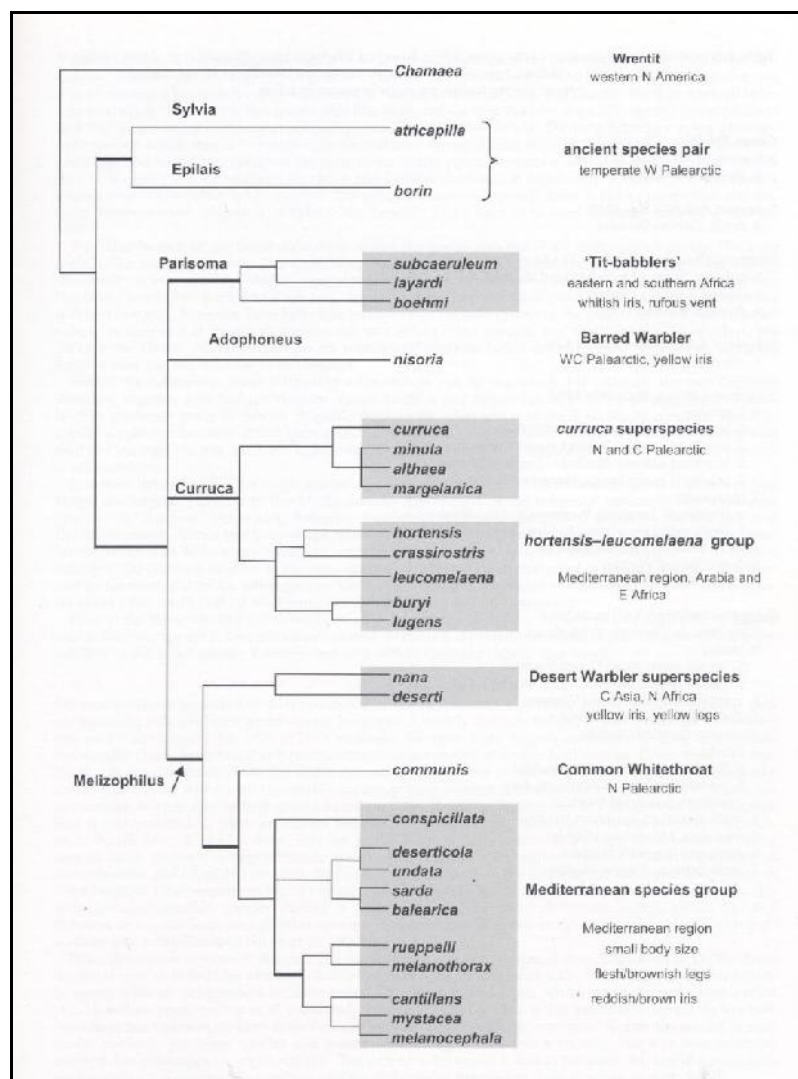


Figure 1.3 Phylogenetic relationships of the genus *Sylvia* (reproduced from Shirihai 2001). The dendrogram represents a consensus phylogeny based on mitochondrial DNA sequences, DNA-hybridisation and phenotypic characters.

Cyprus and Sardinian Warblers were once thought to be part of a superspecies (Cramp & Perrins 1994) along with Menetries Warbler (*Sylvia mystacea*). However, genetic (Shirihai *et al.* 2001) and biogeographical (Flint 2001) work has since

established that, while they are relatively closely related, the Sardinian Warbler is more closely related to Menetries Warbler, while the Cyprus Warbler is more closely related to Ruppell's Warbler (*Sylvia rueppelli*) (Fig. 1.3).

Counts conducted since 1997 (Pomeroy & Walsh 2000, 2002) have indicated that as the Sardinian Warbler population increased and expanded in range throughout Paphos District, the Cyprus Warbler population has declined in western Paphos District (the area first colonised by breeding Sardinian Warblers). Unfortunately, since monitoring only began in 1997 it is not known whether the Cyprus Warbler population decline began before or after Sardinian Warblers began to breed on Cyprus. However, their opposing population trends have prompted concern that the arrival of breeding Sardinian Warblers may have had a negative impact on Cyprus Warblers in Paphos District (Pomeroy & Walsh 2000, 2002). Evidence for the two species' opposing population trends will be reviewed in Chapter 2.

Diagnosing causes of decline

Correct diagnosis of the cause(s) of decline is usually essential for effective conservation in the long term (Jones 2004). Unfortunately conservation measures are often only put in place when a species has already declined to a small population size, by which stage negative demographic and genetic processes may already be at work (Lande 1988, Woodroffe & Ginsberg 1998). Early diagnosis of the causes of decline may allow appropriate measures to be put in place at an early stage. Early intervention is likely to be more cost-effective in maximising the likelihood of species' survival than the 'fire-fighting' approach which becomes necessary where decline is detected late, causes are incorrectly diagnosed or cannot be reversed, or lack of funding prevents intervention.

Population monitoring is key to recognising a decline in its early stages. Knowledge of the timing and location of population declines facilitates the process of diagnosing the cause (Sutherland 2000). Systematic consideration of all possible causes of decline is then important in narrowing down the list to those factors which coincide

temporally or geographically with the population decline and are therefore most likely to be important. Often what emerges is not a single cause but a suite of factors acting together to effect a population decline. Disentangling these factors and identifying those which can be addressed is a complex task, but targeted conservation measures based on the evidence available are likely to be more effective in the long term than addressing the most obvious factor without considering the alternative explanations for decline (Caughley & Gunn 1995).

Early diagnosis of decline also facilitates the process of understanding a species' ecological requirements. While a species is still relatively numerous there is time to carry out research to gain vital insights into its ecology. Basing research on the ecology of a remnant population (while important) may be misleading; often current conditions for such populations represent the end-point of a process of population decline and range contraction driven by external pressures. Thus species may become confined to refuges because these areas have a reduced density of predators (Miller & Mullette 1985, Bunin & Jamieson 1995), competitors (Kenward & Holm 1989) or vectors of disease (Warner 1968) rather than because such areas fulfil the species' ecological requirements. Early diagnosis of decline allows the ecology of a species to be studied before it becomes obscured.

Where early intervention has not occurred for whatever reason and a species is on the brink of extinction, research into its ecology may not be considered the highest priority and scarce resources may be directed into 'fire-fighting' measures (including captive breeding) in preference. In efforts to save the Hawaiian Goose (*Branta sandvicensis*), captive breeding and release did little to assist in recovery of the wild population, because the causes of decline had not been diagnosed or addressed (Caughley & Gunn 1995). This approach can be counter-productive, potentially leading to the unhappy situation where there is a secure captive population, but the more valuable wild population has meanwhile become extinct.

Conservation action is likely to be most effective when decisions made are evidence-based (Pullin & Knight 2001). The case of the Large Blue Butterfly (*Maculina arion*) illustrates the importance of ecological research. The decline of this species in the UK

was known and documented for decades and the various conservation measures employed failed because the cause was incorrectly diagnosed (Caughley & Gunn 1995). Collection of butterflies was thought to be a problem, but a reserve established to exclude collectors became overgrown and the butterflies disappeared. Weather, inbreeding depression, pesticides and habitat change were all suspected causes of decline, but none were investigated. Eventually, thorough ecological research revealed the importance of the fact that the larvae of the Large Blue Butterfly are obligate parasites of *Myrmica* ant species' nests, a fact which had been known for fifty years, but not investigated in relation to the butterfly's conservation. It transpired that the critical factor in conserving the butterfly was to manage the habitat in a very specific way to encourage the survival of *M. sabuleti* ant colonies (Elmes & Thomas 1992). By conducting research the host species and age of colony with which caterpillars had highest survival could be identified, and the conditions necessary for that ant species to thrive were documented. Unfortunately the British population had by this time become extinct. However ecological research has been fundamental to developing a good understanding of how best to manage habitat for the species and has helped to ensure that the subsequent introduction of Large Blue Butterflies from Northern Europe has been successful (Butterfly Conservation News 2006).

The case of the Lord Howe Woodhen (*Gallirallus sylvestris*) demonstrates how carrying out early research into putative causes of decline can ultimately speed up population recovery. In this case, by the early 1970's only 6-10 breeding pairs of Woodhen remained and these were confined to remote areas of the Pacific island's mountains (Miller & Mullette 1985). A captive breeding programme was instigated, but simultaneously ecological research was conducted to try to identify the cause of decline. There were large numbers of introduced rats in the area where the remaining birds were breeding; introduced cats, pigs, owls and the endemic Lord Howe Island subspecies of Pied Currawong (*Strepera graculina crissalis*) also inhabited the island and were under suspicion. With their reputation as devastating predators of island birds, it would have been easy to assume that control of rats and cats would address the main causes of decline. Instead, biologists carried out a comprehensive study of the ecology of the Lord Howe Island Woodhen, testing food shortage and nest-site shortage, as well as predation, as explanations for the Woodhen's decline. By a

process of elimination they concluded that neither food shortage, nest-site shortage nor predation by rats, cats, owls or the Currawong was the problem; the range of the breeding Woodhens was the only area of the island not habitable by pigs, which were known predators of petrels and were considered likely predators of Woodhens. Control of pigs and release of captive-bred Woodhens has resulted in expansion of the species' range on the island and the population size had increased to at least 127 individuals by 2002 (NSW National Parks & Wildlife Service 2002).

In the Woodhen example, the cause of decline was relatively simple. In more complex cases where decline has been caused by multiple interrelated factors, recovering the species may be more difficult, but research is even more important to elucidate which factors can be addressed and how.

Potential causes of Cyprus Warbler decline

It is rarely possible to correctly diagnose causes of a decline without knowledge of a species' natural history. The Cyprus Warbler had been little studied prior to this project and our knowledge of its ecology was based largely on anecdotal sources (McNeile 1948-1955, Ashton-Johnson 1961). This project constitutes the second step in the process of diagnosing the cause(s) of decline of Paphos District Cyprus Warblers, which has been documented by Pomeroy and Walsh (2000, 2002). It will continue to be important to monitor populations of Cyprus and Sardinian Warblers across Paphos District to see whether the population trends of the two species continue or stabilise. Below I discuss the four most obvious potential causes of the Cyprus Warbler population decline, but more candidate factors may be added to the list in future:

- Habitat loss or degradation
- Climate change
- Hunting
- Impact of Sardinian Warbler

In this study, I will focus on the potential impact of Sardinian Warbler. Clearly further study will be required to assess the importance of each of the potential causes, but I will comment briefly on the first three possibilities, before investigating the fourth in detail.

Habitat loss or degradation

There has certainly been a loss of habitat in Paphos District during the period of known Cyprus Warbler decline. The continued rise in tourism has resulted in many areas of scrub and low intensity farmland being built on, particularly in coastal areas. However Pomeroy and Walsh's (2002) counts were conducted at set count sites, which were mostly inland and did not alter during the course of the study. Therefore, while worth investigating, it does not immediately seem the most likely cause of decline.

Climate change

According to Flint and Stewart (1992), Cyprus Warbler does not occur where average rainfall is less than c.340mm; hence it is absent from the dry, central Mesaoria plain (Appendix 4). Pomeroy and Walsh's (2002) finding that Cyprus Warbler abundance increased with increasing altitude is consistent with this and might suggest climate change as a possible explanation for Cyprus Warbler decline. As in many parts of the Mediterranean, temperature has been gradually increasing, while rainfall has been decreasing in Cyprus over time; during the 20th century, precipitation decreased by approximately 1 mm per year, with years of drought becoming more frequent (Cyprus Meteorological Service 2006). Within Paphos District, the lower-lying coastal areas receive the least rainfall. It could therefore be that the range of Cyprus Warblers is contracting inland away from these drier areas. This could have caused the observed decline in Cyprus Warblers in the Akamas area, which is relatively low-lying.

Hunting

In Paphos District, as elsewhere on the island, local hunters shoot game-birds legally and other birds illegally. However the skulking nature of warblers probably makes them unlikely targets for these hunters. Small birds continue to be trapped (using lime-sticks, mist nets and tape lures) and traded for human consumption in Cyprus

and this is a more serious problem for warblers. The activity is illegal, but the law has been poorly enforced until recently. In 1992 the Cyprus Ornithological Society (1957)

estimated that up to 12 million birds were caught and killed annually. Cyprus Warbler is one of the many species affected by trapping, but it is difficult to gauge the scale of the losses. In the past few years, the situation has improved somewhat and trapping activity has been reduced. However a resurgence in trapping activity this year suggests that the problem is not yet resolved (BirdLife International 2006). Paphos District does not suffer the high levels of trapping recorded further east (Cromarty & Ayre 2006), and any impact of trapping would be expected to affect Sardinian Warblers as well. Therefore, while certainly a cause for concern, I do not consider that trapping is likely to be the main cause of the observed decline in Cyprus Warblers in Paphos District.

Negative impact of Sardinian Warbler

In this thesis I concentrate on the potential impact of the Sardinian Warbler, since its arrival as a breeding species has been highlighted previously as a potential cause of the Cyprus Warbler decline (Pomeroy & Walsh 2000). Below, I explore the possible mechanisms via which Sardinian Warblers might have a negative impact on Cyprus Warblers.

The potential impact of Sardinian Warbler on Cyprus Warbler

There are two clear ways in which a newly established breeding population of a congener could impact negatively on a native species; through interspecific competition for resources, or through 'apparent competition' where a predator or pathogen impacts on one or both prey species more in the presence of the other prey species (Holt 1977, Holt 1984, Hoi & Winkler 1994, Holt & Lawton 1994).

Apparent competition

Disease has been implicated in the decline of numerous species worldwide (Dobson & May 1986), including Red Squirrels (*Sciurus vulgaris*) in the UK (Tompkins *et al.*

2002), Pink Pigeons (*Columba mayeri*) in Mauritius (Swinerton *et al.* 2005) and numerous bird species endemic to Hawaii (Warner 1968). A decline may be prompted by the introduction of a new pathogen to which a species has no resistance, a new host to act as a reservoir for the pathogen or a new vector allowing transmission.

Climate change may alter the geographic range of vectors for various pathogens and it could be that Cyprus Warblers are being exposed to new diseases as a result. Cyprus and Sardinian Warbler populations have always come into contact during winter and at least eight other *Sylvia* species occur in Cyprus on passage (Flint & Stewart 1992). It therefore seems unlikely that breeding Sardinian Warblers could have introduced new pathogens to which Cyprus Warblers have not previously been exposed. However, it is possible that either the breeding population of Sardinian Warbler is of different provenance to the population that over-winters on Cyprus and therefore carries different pathogens, or that the presence of Sardinian Warblers during the breeding season has simply increased the density of potential hosts during the period of the year when transmission is most likely. Disease as a potential cause of decline is investigated in a pilot study. The results of this study, which are shown in Appendix 3, suggest it cannot be ruled out as a potential cause of decline.

The impact of apparent competition through predation can be severe, as is illustrated by the example of the Numbat (*Myrmecobius fasciatus*). This Australian marsupial appears to have declined partly because introduced rabbits have provided a source of prey to support large populations of introduced foxes and cats, which also predate Numbats (Caughley & Gunn 1995). The potential impact of mutual predators of Cyprus and Sardinian Warblers will be assessed and discussed in Chapters 4 and 5.

Interspecific competition for resources

Competition occurs ‘when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply competition occurs when the animals seeking that resource nevertheless harm one another in the process’ (Birch 1957). Interspecific competition occurs when two different species compete for the same resource and one or both species suffer a

reduction in fecundity, growth or survivorship as a result. There are two main ways for one species to affect negatively the availability of a resource to the other. 'Exploitation competition' occurs when use of a resource by individuals of one species reduces the amount of that resource available to individuals of the other species. 'Interference competition' occurs when behavioural interactions between two species interfere with resource use. For example, exclusion of one species from the territories of another species is a form of interference competition, as is two species literally bumping into one another and wasting search time (Hassell 1971).

Interspecific competition has been a major topic of ecological research and is considered to be a strong ecological force shaping the evolution of relationships between species within communities (Ricklefs 1975, Diamond 1978, Schoener 1982). The concept of the niche is central in much of the literature on interspecific competition. Elton (1927) defined niche as 'the functional role and position of the organism in its community'. The 'fundamental niche', the array of resources and conditions which allow the species to persist, is rarely exhibited in nature because the portion of the fundamental niche that can be occupied is usually restricted by competition from other species. The narrower range of conditions actually occupied by a species in nature is known as the 'realised niche'.

Closely related species usually have similar ecology and are likely to be similar in size and morphology; a newly arrived close congener could therefore pose a considerable threat as a competitor. Darwin recognised this point in 'The Origin of Species' (1859):

'As the species of the same genus usually have, though by no means invariably, much similarity in habitats and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera'.

The principle of competitive exclusion (Gause 1934, Hardin 1960) states that, if two species coexist in a stable environment, then they do so as a result of niche differentiation. If there is no such differentiation or if it is precluded by some feature of the environment then one competing species will eliminate or exclude the other. This

principle forms the basis of studies of interspecific competition, but is very difficult if not impossible to test, leading Cody (1979) to describe the competitive exclusion principle as an 'unusable tautology'. Either outcome, coexistence or exclusion can be attributed to the principle and to disprove it one would have to demonstrate that the niches of two species are identical. Since the niche is a multi-dimensional ecological space and it is difficult to be certain that all relevant axes have been measured, the principle cannot be disproved (Caughley & Sinclair 1994).

Much previous work on interspecific competition between congeners has centred on explaining niche differences, divergence in feeding behaviour or morphological traits in terms of current (ecological) or past (evolutionary) competition. Such work has furthered understanding of potential mechanisms for coexistence, but has been criticised for treating the competitive exclusion principle as a self-evident truth and failing to consider alternative explanations for patterns found (Dunham 1980, Wiens 1989).

Although often postulated, the existence of interspecific competition is difficult to prove. There are a number of theoretical prerequisites for its existence (Caughley & Sinclair 1994):

- The two species must overlap in resource use.
- The resource must be limited.
- Use of the resource by one species must have a negative effect on the availability of that resource to the other species.
- This reduced resource availability must have a negative effect on the fitness of individuals of one or both species (defined as the ability of individuals to achieve genetic representation in the next generation).

Possible approaches to the study of interspecific competition

The theory behind interspecific competition has been widely investigated through models (Volterra 1931, Lotka 1932, MacArthur & Levins 1964, Bowers & Turner 1997, Morris 1999). However it is undoubtedly difficult to quantify the relationships between species in a natural setting. Communities can be simplified and relationships

examined by using experiments on animals or plants in captivity (Park 1948, Taniguchi & Nakano 2000, Eckstein 2005, Dame & Petren 2006), but the way in which organisms behave in an artificial setting does not necessarily reflect what actually happens in natural communities. Experiments on organisms in captivity, while informative, have also tended to be limited taxonomically and therefore the findings cannot automatically be applied to higher organisms with more complex behavioural responses in natural environments.

In wild populations, two main approaches have been used. The experimental approach involves manipulating the density of the two species concerned or the availability of resources, to see whether this alters parameters of fitness or success. In a wide range of taxa this has variously been achieved by manipulating neighbour density using nest boxes in hole-nesting bird species (Gustafsson 1987, Torok & Toth 1999), lethal removal of adults (Connell 1961, Martin & Martin 2001b), non-lethal removal of adults (Cory & Barrett 2006), release of a population of one species into sympatry with another (Bonesi & Macdonald 2004), manipulation of offspring density by brood enlargement/reduction (Minot 1981) or reducing food availability (Hart *et al.* 2006).

The comparative approach asks whether the distribution, resource use and abundance of natural populations in different ecological situations are consistent with competition theory (Dunham 1980). The approach usually focuses on whether or not there are differences in niche, morphology, behaviour or some measure of success between areas where two species occur syntopically and areas where they do not (Bourski & Forstmeier 2000, Bryce *et al.* 2002, Kawakami & Higuchi 2003). The comparative approach has been applied in previous studies to try to determine whether interspecific competition has an important impact upon species. Dunham (1980) suggested that the strongest class of evidence for interspecific competition was the direct observation of one species invading with resulting replacement or niche adjustment as coexistence is established (Diamond 1978).

Previous work on invasion and interspecific competition

Published studies on recent sympatry tend to focus on the impacts of human-introduced species on native species (Petren & Case 1996, Bryce *et al.* 2002, Morita

et al. 2004, Thompson 2006) and in this respect there may be a bias in the literature towards studies where a negative impact is proven. The case of Cyprus and Sardinian Warblers is certainly unusual, as it involves closely related congeners which have some history of sympatry (but only in winter) and a natural alteration in breeding range, rather than a human-induced introduction.

Previous studies of invasions by congeners have had mixed results. Some have demonstrated a negative impact on the native congener; for example Huckins *et al.* (2000) compared lakes in the U.S.A. with and without an introduced species, the Redear Sunfish (*Lepomis micropholus*), and concluded that this species were having a negative impact on a native congener, the Pumpkinseed Sunfish (*L. gibbosus*) through exploitation competition for food. Gurnell *et al.* (2004) studying native Red Squirrels (*Sciurus vulgaris*) and introduced Grey Squirrels (*S. carolinensis*) in Italy and the UK found that the presence of Grey Squirrels led to reduced fecundity and lower recruitment in Red Squirrels; exploitation competition for food was the suggested mechanism involved. However, not all introduced species appear to have a negative impact on native species. Rabalais (2006) found no evidence from experiments to suggest that interspecific competition between native Coldwater Crayfish (*Orconectes eupunctus*) and its invasive congener Gapped Ringed Crayfish (*O. neglectus chaenodactylus*) was responsible for the decline of Coldwater Crayfish in the U.S.A. Similarly Kawakami and Higuchi (2003) found no evidence that the increase in the Japanese White-eye (*Zosterops japonicus*) had had a negative impact on the endemic Bonin Island White-eye (*Apalopteron familiare*); indeed they suggested that the endemic species might benefit from forming mixed species flocks with Japanese White-eyes in winter.

Previous work on competition and coexistence in Sylvia

In terms of interspecific interactions among *Sylvia*, anecdotal information from Menorca suggests that the arrival of the Dartford Warbler (*Sylvia undata*) may have contributed to the decline there of the Balearic Warbler (*S. sarda balearica*). The Dartford Warbler was first recorded breeding on Menorca in 1975, and since then has increased in numbers while the Balearic Warbler went from being scarce and local to disappearing from the island in the 1970's and 1980's (Muntaner 1980). Insufficient

information is available to be sure in this case, but the example highlights the possibility that arrival of a new *Sylvia* species might impact negatively on a resident congener.

Cody and Walter (1976) and Cody (Cody 1978, 1979) found that among the *Sylvia* warbler communities of Morocco, Sardinia, England and Sweden there was a wide range of intensity of interspecific competition, but that the different *Sylvia* species tended to have different foraging height distributions. In Morocco where interspecific territory overlap was common between Sardinian Warbler and four other *Sylvia* species, Sardinian Warblers did not respond to playback of congeneric song. In contrast, in Sardinia Cody and Walter found Sardinian Warblers to be dominant over the two other *Sylvia* species with which it interacted and even observed chasing and fighting between congeners; they suggested that song was a major mechanism through which congeners interacted. More recently, Martin and Thibault (1996), studying *Sylvia* warblers in Corsica and Sardinia, found no evidence of interspecific territoriality or aggression, and suggested that interspecific competition is reduced by species segregating ecologically and behaviourally while foraging.

In experimental work on *Sylvia* warblers, Garcia (1983) noted that in English woodlands Garden Warblers (*Sylvia borin*) and Blackcaps (*S. atricapilla*) appeared to be interspecifically territorial during the breeding season. To investigate whether this was genuine interspecific territoriality or selection of different habitat patches by the two species, Garcia removed Blackcaps (which arrive earlier than Garden Warblers in the spring) and found that Garden Warblers readily occupied vacant Blackcap territories. This suggested that interspecific competition between the two species might have been responsible for the observed pattern of territory distribution.

Approach taken in the present study

One approach to investigating whether Sardinian Warblers are having a negative effect on Cyprus Warblers through interspecific competition would be to carry out reciprocal removal experiments (Martin & Martin 2001b). However, both species are difficult to catch, making non-lethal removal of a large number of individuals very difficult to achieve. Lethal removal would raise ethical questions for an endemic

species and, even if licences could be obtained, it would be a controversial approach. Therefore in this study I use the comparative approach to investigate whether interspecific competition occurs between Cyprus and Sardinian Warblers and to attempt to gauge its potential importance as an agent of Cyprus Warbler decline.

On a broad scale, the gradual spread of Sardinian Warblers in Paphos District has resulted in potential for a natural experiment, since there are now effectively three zones, furthest west a zone in which Sardinian Warblers predominate (zone 1), in central Paphos District a zone where both species occur (zone 2) and in eastern Paphos District a zone where Sardinian Warblers do not yet breed in numbers and Cyprus Warblers predominate (zone 3). Ecological parameters for both species can therefore theoretically be compared between the zone where each species predominates and the mixed-species zone in order to see whether either species is more successful in the absence of the other.

However the distribution of Cyprus and Sardinian Warblers in Paphos is patchy at a fine scale, so that it is possible to find small areas with mostly Cyprus Warblers or mostly Sardinian Warblers throughout zones 1 and 2. On a fine scale, population densities change in response to local conditions experienced by each individual (Tilman & Kareiva 1997) and competition is resolved at the level of individual interactions (Morris 1999). Therefore I decided also to address coexistence and examine interactions between Cyprus and Sardinian Warbler pairs at the level of their individual home-ranges, for each species comparing various parameters of fitness and success in pairs with a conspecific nearest neighbour with the same parameters in pairs with a congeneric nearest neighbour. In order to reduce the complexity of the situation, I have chosen to focus my study on scrub habitat. I follow colour-ringed Cyprus and Sardinian Warblers on seven study plots in three consecutive field seasons (Chapter 2).

Aims and structure of the thesis

This thesis has a number of aims:

- To gather more detailed information on the ecology of the Cyprus Warbler in order to better understand the species' requirements.
- To compare the ecology of the Cyprus and Sardinian Warbler and evaluate whether any differences in ecology could explain the two species differing population trends in Paphos District.
- To examine whether or not there is evidence for interspecific competition or other negative impacts of coexistence for either species.
- To evaluate the likelihood that the arrival of breeding Sardinian Warblers has contributed to the observed decline in Cyprus Warblers.
- To contribute to understanding of the evolutionary processes underpinning species' coexistence.

In Chapter 2, I present the evidence showing that Cyprus Warblers have declined, while Sardinian Warblers have increased across Paphos District, and I discuss the methodological approach taken in this study. In Chapter 3, I use home-range mapping of ringed birds to examine the spatial distribution of the two species and a playback experiment to assess what interspecific behaviour can reveal about the relationship between the two species. In Chapter 4, I compare vegetation composition of the two species' home-ranges to see whether there are fine-scale differences in habitat selection. I also compare nest-sites used by the two species to assess the likelihood that interspecific competition for nest-sites occurs and to evaluate the potential effects of coexistence on nest predation. In Chapter 5, I compare the breeding biology of the two species and examine whether measures of productivity supply any explanation for the trends observed at the population level, or any evidence for negative effects of coexistence. In Chapter 6, I use arthropod trapping to assess patterns of food availability and faecal analysis to compare the diet of Cyprus and Sardinian Warblers. I then investigate what nestling body condition reveals about any impacts of coexistence. Finally, in Chapter 7 I synthesise my findings to assess the likely importance of the arrival of breeding Sardinian Warblers

as a potential cause of the decline in Cyprus Warblers. I discuss the implications of coexistence for the conservation of the Cyprus Warbler and make suggestions for the direction of future research.

Chapter 2

Recent population trends, general methods and study sites

An introduction to Cyprus

At 9250 km², Cyprus is the third largest island in the Mediterranean. It lies less than 100 km from Turkey, and less than 200 km from Syria and Lebanon in the east Mediterranean basin at 34°33' to 35°42'N and 32°16' to 34°36'E (Fig. 2.1).

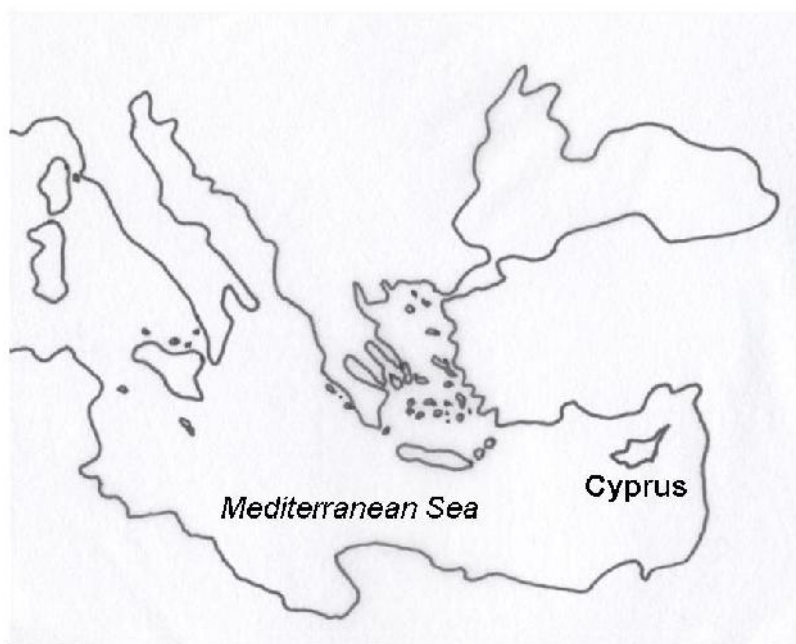


Figure 2.1 Location of Cyprus within the Mediterranean basin.

The island is dominated by two mountain ranges, the Troodos mountains rising to 1961 m and further north, the Kyrenia range rising to 1024 m. These two mountain ranges run approximately east-west and between them lies the Mesaoria plain, much of which lies below 100 m. Cyprus has an extreme Mediterranean climate with long, very hot, dry summers and cool, wet, changeable winters (Flint & Stewart 1992). The island has a variety of natural vegetation; 18 % of the island is woodland, and about

half of the land area is cultivated. Elsewhere there is some high maquis, mostly in the east of the island and on coastal promontories but over much of the island, uncultivated and undeveloped land is covered by xerophytic shrubs forming low maquis, or in drier areas, the lower, more open garrigue. In the most heavily grazed or driest areas, open phrygana habitat predominates. Since 1974, Cyprus has been divided by the 'green line', a UN buffer zone running east-west through the island and passing through the island's capital Nicosia. The north of the island is occupied by Turkey, while the south of the island entered the EU in 2004. My research and previous bird counts by Pomeroy and Walsh (2000, 2002) were based in Paphos District, the western-most district in southern Cyprus (Fig. 2.2). Topographically, the district rises from the lower-lying coastal towards the foothills of the Troodos Mountains further inland.

Cyprus has two endemic bird species, the Cyprus Warbler (*Sylvia melanothorax*) and the Cyprus Wheatear (*Oeanthe cypriaca*) as well as four endemic sub-species. Forty-six resident and 27 migratory species breed regularly on Cyprus. The island lies on a major migration route and more than 200 bird species occur as passage migrants, including a number of *Sylvia* species. However, only Cyprus Warbler, Sardinian Warbler (*Sylvia melanocephala*) and Spectacled Warbler (*Sylvia conspicillata*) breed on Cyprus. The latter species breeds mainly around the central plain of Cyprus (Flint & Stewart 1992) and is relatively scarce in Paphos District.

Evidence for differing population trends in Cyprus and Sardinian Warblers

Since 1997, Pomeroy and Walsh (2000, 2002) have conducted annual bird counts during the main bird breeding season in Paphos District. They have used 'Timed Species Counts' or TSCs (Pomeroy 1997, Pomeroy & Dranzoa 1997), which involve counting all species observed during a one hour period at a particular site. Species seen or heard in the first 10 min are scored 6, those recorded between 11 and 20 minutes are scored 5 and so on, so that those species recorded in the last 10 minutes are scored 1. The counts were designed to contribute to the Cyprus

Breeding Bird Atlas (Whaley & Dawes 2003), which is based upon 5 km grid squares. Ninety-two TSC sites were distributed across Paphos District, with at least one TSC site located in each grid square. The set of sites covers all the main terrestrial habitats and a range of altitudes up to 1000 m. The methodology was designed for all bird species and is not ideal for warblers, which are cryptic (Pomeroy & Walsh 2002). The TSC method also has limitations as a measure of abundance because the highest point on the scale is 6; once a species has been recorded in the first 10 minutes and been scored 6, any further increase in abundance cannot be detected by this method. Thus an asymptote in TSC scores over time does not necessarily represent an asymptote in abundance of birds. Despite this limitation, the TSC scores provide a general indication of the relative abundance of Cyprus and Sardinian Warblers between years in different zones.

Since Pomeroy and Walsh (2002) found that the Sardinian Warbler population size increased and its range expanded eastwards in Paphos District during the period between 1997 and 2001, for the purposes of my study, I have split Paphos District into three zones which reflect the spread of Sardinian Warblers (Fig. 2.2):

- **Zone 1** furthest west where Sardinian Warbler predominates
- **Zone 2** in central Paphos District where both Cyprus and Sardinian Warbler occur
- **Zone 3** furthest east where Cyprus Warbler predominates and Sardinian Warbler had not yet been recorded breeding when the project began

Meanwhile, during the period 1997 to 2001, Pomeroy and Walsh (2002) recorded a decline in Cyprus Warblers, particularly in western Paphos District.

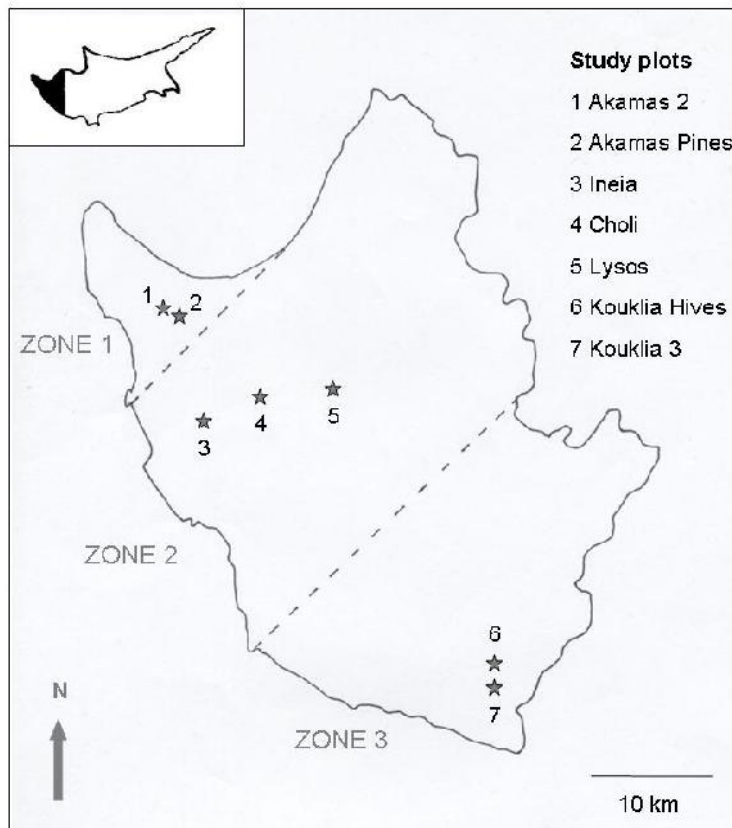


Figure 2.2 Paphos District, Cyprus showing locations of zones and study plots.

To assess temporal changes in the species' abundances over the past decade in more detail, I present Pomeroy and Walsh's TSC data in the context of the zones I have used in my own study. The data set includes Pomeroy and Walsh's published data from 1997 to 2001 (Pomeroy & Walsh 2002), but also their more recent unpublished TSC data from 2002-2005 (Fig. 2.3). Between 1997 and 2005 Cyprus Warbler TSC scores show a (non-significant) decrease over time in zone 1 (Spearman rank correlation: $r_s = -0.400$, d.f.=7, $p = 0.286$), a gradual (non-significant) decrease in zone 2 ($r_s = -0.567$, d.f.=7, $p = 0.112$) and a gradual (non-significant) increase in zone 3 ($r_s = 0.667$, d.f.=6, $p = 0.071$). In contrast TSC scores for Sardinian Warbler showed a relatively steep (significant) increase over time in zone 1 ($r_s = 0.745$, d.f.=7, $p = 0.021$), a steep (significant) increase in zone 2 ($r_s = 0.820$, d.f.=7, $p = 0.007$) and a gradual (non-significant) increase in zone 3 ($r_s = 0.667$, d.f.=6, $p = 0.071$). It is

notable that since the initial decrease of Cyprus Warbler TSCs between 1997 and 1999 its TSC scores may have stabilised.

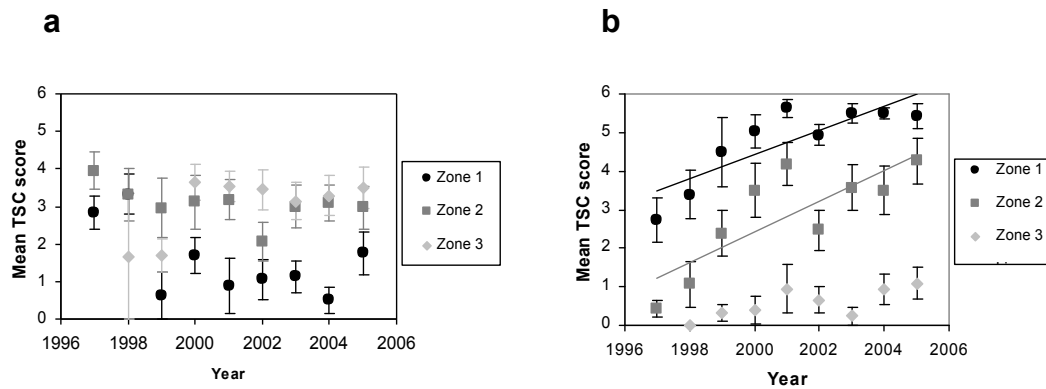


Figure 2.3 a) Cyprus and b) Sardinian Warbler mean $\pm$ SE TSC scores for sites in all habitats. TSC scores averaged over multiple visits per year for each site and then averaged across sites in zone 1, zone 2 and zone 3. Data reproduced with kind permission of Pomeroy and Walsh. Trend-lines shown where Spearman rank correlations were significant.

I chose to focus my research in scrub habitat. Therefore, I have extracted TSC counts for sites in scrub habitat from Pomeroy and Walsh's data and graphed these separately (Fig. 2.4).

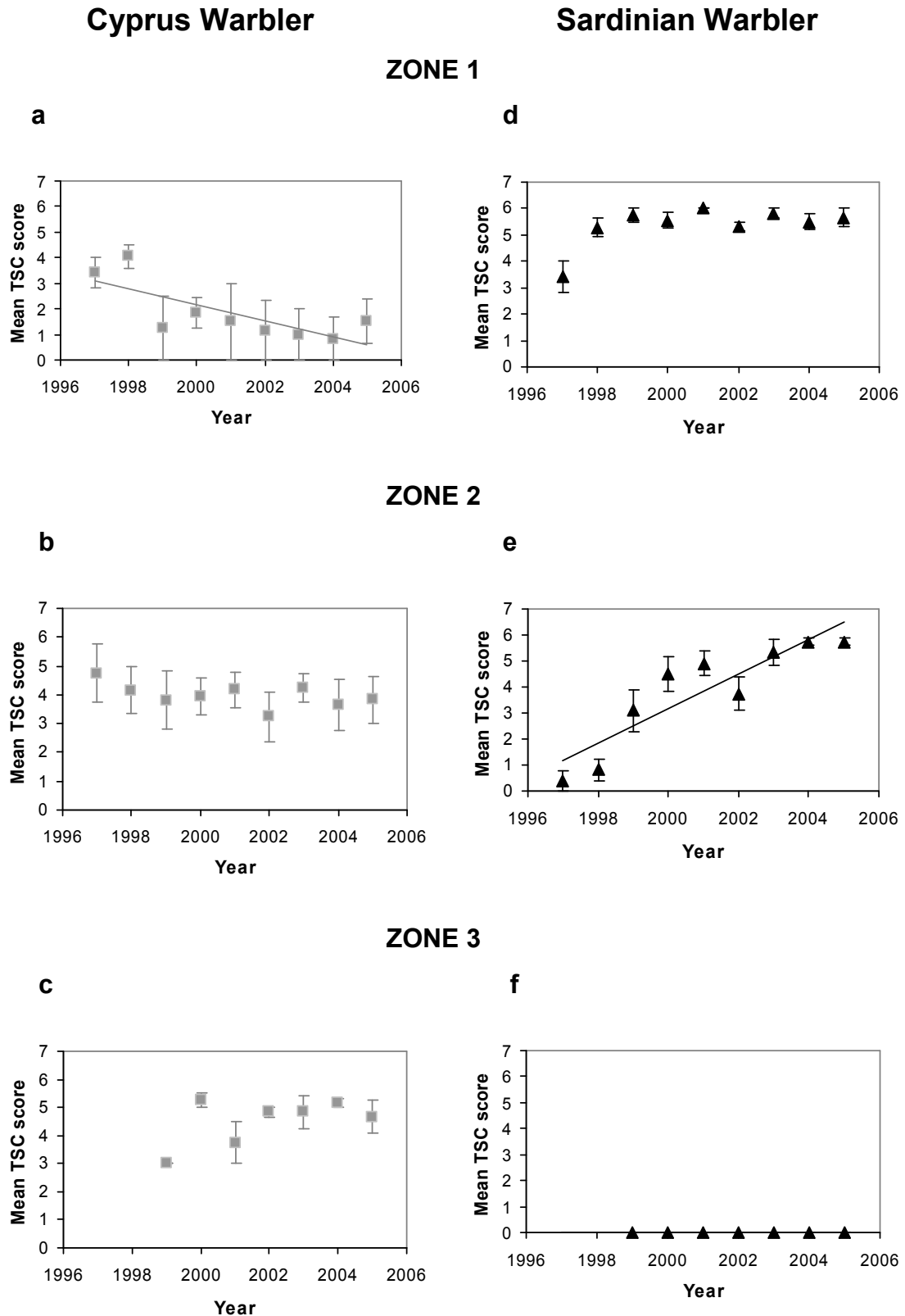


Figure 2.4 Cyprus and Sardinian Warbler mean $\pm$ SE TSC scores for scrub sites. TSC scores averaged over multiple visits per year for each site and then averaged across sites in zone 1, zone 2 and zone 3. Trend-lines shown where Spearman rank correlations were significant. Data reproduced with kind permission of Pomeroy and Walsh.

The TSC data for scrub sites show a moderate (significant) decrease ($r_s = -0.703$, d.f.=7, $p = 0.035$) in Cyprus Warbler TSCs over time in zone 1, a slight (non-significant) decrease in zone 2 ($r_s = -0.433$, d.f.=7, $p = 0.244$) and a slight (non-significant) increase in zone 3 ($r_s = 0.234$, d.f.=5, $p = 0.613$). For Sardinian Warblers, TSC scores show a slight (non-significant) increase over time in zone 1 ($r_s = 0.433$, d.f.=7, $p = 0.244$), a steep (significant) increase in zone 2 ($r_s = 0.946$, d.f.=7, $p < 0.001$), while no Sardinian Warblers were recorded in scrub habitat in zone 3 between 1997 and 2005. One interesting point from these graphs is that, while the TSC scores for Cyprus Warblers and Sardinian Warblers from zone 1 show opposing trends with similar slopes, the steep increase in Sardinian Warbler TSCs in zone 2 is accompanied by only a very slight decrease in Cyprus Warbler TSC scores. In zone 3 Cyprus Warbler TSC scores show a steady increase with no change in Sardinian Warbler TSC scores. This could suggest that, even if Sardinian Warblers are affecting Cyprus Warbler populations, they are not the only factor to do so.

Study sites

Seven study plots were selected for this study (Fig. 2.2); two in zone 1 (Akamas 2 and Akamas Pines), three in zone 2 (Ineia, Choli and Lysos) and two in zone 3 (Kouklia Hives and Kouklia 3). The closest plots were 620 m apart; this is approximately 10 times the length of the average warbler territory (Chapter 3). There were no cases of either species moving between plots within a breeding season and only one case of a bird fledging on one plot and breeding on another plot the following year. Thus the plots were far enough apart to be considered independent. The most distant plots were 41 km apart. GPS coordinates for plot locations are given in Table 2.1.

Site	GPS coordinates for study plots (UTM)	
	East	North
Akamas 2	36 439702	38 74542
Akamas Pines	36 439929	38 73964
Ineia	36 442486	38 66634
Choli	36 449152	38 71539
Lysos	36 457084	38 72506
Kouklia Hives	36 464172	38 42311
Kouklia 3	36 464257	38 41302

Table 2.1 Global Positioning System (GPS) coordinates (Universal Transverse Mercator Grid) for the location of the seven study plots in Cyprus. Coordinates given are the centre-points of plots.

I chose to locate all plots in the same habitat, because otherwise effects of different habitats might have obscured any effects of zone. Scrub habitat was chosen because it is a common habitat, which appears to support relatively high densities of breeding *Sylvia*, but few other breeding species. In addition it is one of the most common habitats in the Akamas area of western Paphos District where the decline in Cyprus Warbler was first noted. Lastly, the relatively low, open nature of the vegetation facilitates observation of these cryptic species and allows the observer to move easily through the study area.

Patches of any one habitat in Cyprus tend to be relatively small and the size of study plots was generally constrained by patch size. Plot sizes varied from 3.0 ha to 5.8 ha in size. Scrub habitat is frequently developed for building related to tourism in Paphos District, so study plots in less accessible areas were chosen to reduce the chance of plots being altered during the course of the three year study. In general, study plots consisted of a goat/sheep grazed mosaic of low maquis and garrigue habitat (Plate 2.1) with xerophytic vegetation 0.4 to 2 m high dominated by spiny shrubs such as *Genista sphacelata*, *Calycotome villosa* and *Rhamnus oleiodes* along with non-spiny *Teucrium creticum*, *Lithodora hispidula*, *Pistacia* and *Cistus* species. More open areas were generally dominated by low growing cushions of *Thymus capitatus* and *Sarcopoterium spinosum*. Trees, where present, tended to be *Quercus coccifera*,

Ceratonia siliqua, *Olea europea* or *Pinus brutia*. Topography varied from relatively flat (Kouklia 3, Ineia) through gently sloping (Lysos, Kouklia Hives) to steeply sloping (Akamas 2, Akamas Pines, Choli). Plots varied in altitude from 160 to 540 m. Other passerine species breeding commonly on study plots were Linnet (*Carduelis cannabina*) and Black-headed Bunting (*Emberiza melanocephala*).



Plate 2.1 Typical low maquis/garrigue habitat of study plots.

All study plots were mapped using a 30–50 m grid of numbered grid points, marked with tags; locations for all observations were recorded in relation to these grid points. To obtain an accurate geographic location for each grid point, multiple GPS readings were recorded for the point at intervals of more than a week and then averaged. As far as possible all pairs of Cyprus and Sardinian Warblers present within each plot were monitored during 2003, 2004 and 2005 breeding seasons. In 2003, useful data were collected from only six of the original seven study plots. The seventh plot was abandoned because vegetation proved too dense and high to allow proper observation; this plot was replaced in the study by Akamas 2 in 2004 and 2005. In 2003 and 2004, winter visits were also made to the plots to search for ringed birds.

As many Cyprus and Sardinian Warblers as possible were ringed with a unique combination of three colour rings to allow individual identification within and between years (Chapter 3).

Permits for the project were kindly supplied by the Ministry for the Interior, Government of Cyprus. Over the course of three field seasons the author and seven other observers carried out fieldwork. Approximately 1000 observer days were spent on the study plots during breeding seasons 2003-2005. Study plots were visited in rotation, so that usually half a day was spent on each plot twice a week. Methodology for specific aspects of research is described in the relevant chapter.

Statistical analysis

Specific information on statistical methods is presented in each chapter, but here I describe the general approach taken.

Statistical analysis was carried out using SPSS 12.0.1 and GenStat 8.1. Where the data did not fit assumptions of parametric tests, variables were either transformed, or tested using non-parametric techniques. Variables expressed as proportions were arcsine square root transformed prior to analysis. All tests were two-tailed and means are quoted $\pm$ one standard error throughout the thesis. Statistical significance was established at $p < 0.05$. Sequential Bonferroni adjustment (Rice 1989) was used to reduce the risk of a Type I error when conducting multiple statistical tests. Significant p values are shown in bold in tables.

Wherever linear models were used, model residuals were tested for normality, and the final minimal model was obtained by sequentially dropping non-significant terms, using a backwards elimination approach. I checked for interactions between all fixed terms, but p values for interactions are only mentioned where significant. P values of non-significant terms were obtained by individually adding each non-significant term to the minimal model. Where no terms were found to have a significant effect, p values were obtained by adding each non-significant term into the model individually.

Where mixed models were employed, the random term was retained in the model even when it was found to have a non-significant influence on the explanatory power of the model. Where generalized linear mixed models (GLMMs) were fitted with binomial error structure, a logit link function was employed. Effect sizes are only shown for significant terms in the minimal model. For fixed factors with multiple levels, effect sizes for each level are given in relation to the first, which is allocated an effect size of zero.

Chapter 3

Spatial distribution and interspecific behaviour of Cyprus and Sardinian Warblers

Introduction

In birds of temperate regions, the start of the breeding season in early spring is marked by increasing levels of male territorial behaviour. Perhaps the most obvious of these is song, which is known to have several intraspecific functions; chief among these are the attraction (Eriksson & Wallin 1986, Mountjoy & Lemon 1991) and stimulation (Brockway 1965, Hinde & Steel 1976, Kroodsma 1976a) of mates and the repulsion of rival males (Peek 1972, Krebs *et al.* 1978).

Few species occupy habitats in isolation; often several bird species occur syntopically and while some locate their territories irrespective of other species, others defend exclusive territories not only intraspecifically, but also against members of other species. In such cases, behaviours usually associated with intraspecific territoriality are directed towards the other species (Simmons 1951). How such 'interspecific territoriality' arises and why it occurs has long been debated. Singing (Ward & Slater 2005) and territory defence are energetically costly activities, raising the possibility that interspecific territoriality might be maladaptive. Indeed, Murray (1971, 1981) suggested that interspecific territoriality resulted from recognition errors or misdirected intraspecific aggression. Cody (1969) also considered that interspecific territoriality arose through misdirected intraspecific aggression, but that this could be adaptive. In his theory of 'character convergence' Cody suggested that, in competing coexisting species, natural selection favours convergence of traits which play a role in species recognition because this encourages interspecific territory defence and thus the exclusion of competitors. Murray (1976), however, demonstrated that there was little evidence to support the theory of 'character convergence'. In any case, while

interspecific territoriality may occur between closely related species, there are many examples of interspecific territoriality between species which are not closely related and bear no strong physical resemblance to one another (Miller 1968, Reed 1982, Garcia 1983).

Historically, different authors have used the term 'interspecific territoriality' to mean different things. To avoid confusion, I define my own use of terms below:

- *Interspecific aggression* - where one species responds to the other species with behaviour normally associated with intraspecific aggression.
- *Interspecific territoriality* - where one species responds to the other species in an aggressive manner, resulting in little or no overlap between the two species' territories, as usually occurs in intraspecific territoriality.

Orians & Willson (1964) suggested that, under conditions of competition, natural selection should favour ecological divergence rather than costly interspecific aggression, but that interspecific territoriality might arise in situations where limitations of the environment or the presence of other species prevented such divergence. Since this early work, several authors have inferred or found evidence for a link between behavioural interactions and underlying ecological relationships (Catchpole 1978, Catchpole & Leisler 1986, Prescott 1987, Martin & Martin 2001a). Reed (1982) found that Chaffinch (*Fringilla coelebs*) and Great Tit (*Parus major*) territories overlap on mainland Scotland (where both species respond only to conspecific song), but are mutually exclusive on offshore islands (where both species respond to both conspecific and heterospecific song). He postulated that, because the two species have similar foraging habits, the structurally simpler woodland habitat present on the islands limits the extent to which the two species' territories can overlap, encouraging interspecific territoriality.

In previous work on syntopic coexistence of *Sylvia* species, Zbinden & Blondel (1981) and Martin & Thibault (1983) suggested that differences in microhabitat selection explained the coexistence of several *Sylvia* species within a single habitat, while

Cody & Walter (1976) and Cody (1978, 1985) suggested that interspecific interaction leading to interspecific aggression was the main mechanism responsible.

Cody & Walter (1976) observed a 'good deal' of aggressive behaviour between Sardinian Warblers (*Sylvia melanocephala*) and Marmora's Warblers (*S. sarda*) in Sardinia. Gibb (1947) noted similar aggression between Sardinian Warblers and Spectacled Warblers (*S. conspicillata*) in Malta, and found Sardinian Warblers to be dominant in interspecific conflicts. In neither case was the aggression observed associated with segregation of territories. Martin & Thibault (1996), studying a number of coexisting *Sylvia* species (including Sardinian Warbler) in Mediterranean matorral, found no evidence of interspecific territoriality nor any direct interspecific interactions between the species.

Playback of male song has been used by many researchers to simulate intrusion into a focal male's territory. In a well-designed experiment, the strength of the focal male's response can be used to gauge the degree of aggression shown and inferences can be made about the relationship between the species tested. Male birds generally react more strongly to playback of conspecific song than heterospecific song (Catchpole & Slater 1995), since defending their mate and territory against conspecific males is of key importance. Some previous work on species pairs has found asymmetric responses to playback, with one species appearing to be dominant and reacting aggressively to playback of the other species' song while the other is behaviourally subordinate and retreats from playback of the dominant species' song (Catchpole 1978, Martin & Martin 2001a). In interspecific interactions, it is common for the larger species to dominate (Daily & Ehrlich 1994, Basset 1995, Shelley *et al.* 2004). Cyprus Warblers (*S. melanothorax*) are marginally smaller than Sardinian Warblers (Cozens *et al.* 2000) and could therefore potentially be behaviourally subordinate in interspecific interactions between the two species.

Breeding Cyprus and Sardinian Warblers now occur syntopically throughout Paphos District. The spatial distribution and behavioural relationship between Cyprus and Sardinian Warbler may provide important information regarding the ecological relationship between these two species, and thus inform the overall question of

whether Sardinian Warbler may be displacing Cyprus Warbler. It is particularly important to establish whether or not these two species exhibit interspecific spatial segregation; if they do, then competition for space could explain the Cyprus Warbler decline. In this chapter I take three different approaches to the topic:

- *Mapping* to determine whether or not Cyprus and Sardinian Warbler exhibit spatial segregation of home-ranges. The key question addressed is 'Are Cyprus and Sardinian Warblers interspecifically territorial?'
- *Playback* to investigate whether the two species respond aggressively towards one another. The key question addressed is 'Do Cyprus and Sardinian Warblers respond aggressively to playback of each other's song?'
- *Behavioural observations* of interactions between the two species collected over three field seasons to help in interpreting the results of the mapping and the playback experiment. The key question addressed is 'Do Cyprus and Sardinian Warblers exhibit aggressive behaviour towards congenetics as frequently as towards conspecifics?'

Methods 1: Spatial distribution

Bird marking

Mist nets were erected at different locations in each site and birds were lured with minidisk tracks of either Sardinian or Cyprus Warbler song. Use of a long lead between the minidisk player and the speaker allowed the observer to play intermittent bursts of song, which was more realistic and less likely to result in habituation than constant playback. Many adults were caught and colour-ringed before breeding began. Later, unringed adults were often caught at the nest while feeding chicks. This usually took place when the chicks were seven days old and could be ringed during the same visit. Birds were fitted with two plastic/celluloid colour rings on one leg and one colour ring above the metal ring on the other leg.

Home-range mapping

Territory mapping was carried out at all study plots in 2003, 2004 and 2005 field seasons. As many birds as possible were colour-ringed and the study plots were visited in rotation, so that usually half a day was spent on each plot twice a week. Over the course of three field seasons the author and seven other observers carried out fieldwork. Observers covered the plot in a methodical manner searching for signs of breeding activity and noting the location, identity and activity of all Cyprus and Sardinian Warblers seen, while attempting to identify visually individuals heard. Locations were established by taking a compass bearing and estimating the distance from observer to bird and then taking a compass bearing and estimating the distance to the nearest marked grid-point. The approximate location of the bird could then be calculated as a UTM XY coordinate. This means of noting down bird locations resulted in sequential observations always being separated by more than 20 seconds, which is ample time for either species potentially to travel from one side of its home-range to the other. In this way observations could be considered to be biologically independent.

GPS locations of all birds seen and nesting attempts found for each pair could then be entered into GIS Arcview 3.2 with the 'Animal movement' extension (Hooge & Eichenlaub 1997) to produce home-range maps. Only observations made between 01 March and 30 June were included for home-range mapping since this was the main breeding period; nest building/ egg-laying had begun by 01 March and birds were therefore relatively settled. During the post-breeding period, prior to autumn migration, home-range boundaries appear to relax (pers. obs.) and therefore only observations up to 30 June were included; this was generally two weeks after eggs from the very last nests hatched.

Observations of birds engaged in mobbing predators were removed, because birds sometimes engaged in this activity outside their own home-range, often with several pairs joining forces. Both Cyprus and Sardinian Warblers rarely forage outside their home-range and pair home-range was considered more informative than male defended territory for addressing questions of interspecific resource competition. It was also important to include all observations of breeding pairs in the mapping,

because there were many cases where only the male or the female were ringed and the unringed partner could only be positively identified elsewhere in their territory when, during a continuous period of observation, they visited their nest or spent time with the ringed female or ringed fledged young. For pairs where both male and female were ringed, I tested whether the home-range of the two sexes differed. Having found that they did not (below) I included locations of both males and females in the home-range analysis. In order to avoid bias from having repeated observations of both members of the pair at the nest location, each nest location for a pair was included only once as an observation.

Spatial distribution analysis

The number of birds ringed on the plots increased through successive breeding seasons. Observations of colour ringed birds from 2003 (the first year of the study) were considered too sparse to produce useful home-range maps. Therefore home-range analysis was confined to years 2004 and 2005. Ninety-five percent Minimum Convex Polygons (MCPs) were used to estimate pair home-range. The removal of 5% outlying observations guarded against inaccuracies in home-range estimation through inclusion of one-off events such as males straying into another home-range to seek extra-pair copulations. MCP was chosen over kernel analysis because it is simple, easily comparable with other studies and relatively robust to serial autocorrelation (Swihart & Slade 1985a,b, Harris 1990).

Independence of observations

Concerns about the statistical effect of serial autocorrelation have mainly been explored in mammalian data sets (Swihart & Slade 1985, Harris *et al.* 1990, McNay & Bunnell 1994) where, in many cases, an animal can take hours or days to traverse its home-range. In highly mobile birds with small territories, the biological relevance of statistical serial autocorrelation is questionable (Barg *et al.* 2005). Although simple polygon techniques have been shown to be affected relatively little by autocorrelation (Anderson & Rangstad 1989), as an exploratory exercise, I checked for autocorrelation in the data set by plotting the distance between sequential observations of an individual against the time interval separating those observations.

These data were log-transformed to achieve normality and then Pearson correlations were used to test for an association between the two variables.

Home-range size calculated from pairs with the most observations

In order to determine how many observations were needed to achieve an asymptote, I used ringed individuals for which 20 or more observations had been collected in a single field season and used bootstrapping to plot the number of samples against the cumulative home-range area. For pairs which were present in both years, only data for the year with the larger number of observations were included. On average, both species required more than 30 observations to represent adequately their entire home-range area. Home-range sizes of all Cyprus and Sardinian Warbler pairs for which more than 20 or more observations had been collected were compared using independent samples t-tests on log-transformed MCP area data.

Home-range size calculated by inter-centre distance

Minimum home-range size was also estimated for those pairs which had a conspecific nearest neighbour, using the distance from each home-range centre to the nearest conspecific pair's home-range centre as the minimum home-range diameter and then calculating the area of the resulting circle. To investigate whether there was any difference in average home-range size between Cyprus Warblers and Sardinian Warblers, once the effect of different plots was removed, I examined the distance separating home-range centres, comparing only individuals of each species which had a conspecific as their closest neighbour. I used a linear mixed model (LMM) with distance between home-range centres as the dependent variable, species and year as fixed factors and site as a random factor.

Use of home-range centres

Since I had 30 or more observations for relatively few individuals, I was unable accurately to measure home-range overlap; instead I used the 95% MCP (which can be generated for three or more observations) to obtain the home-range centre of each pair (the arithmetic mean of all X and all Y coordinates). I then based my analyses of the relative spatial arrangement of the two species on the distribution of pair home-range centres. As with all analyses of nearest-neighbour distances, some

inaccuracies may have occurred in relation to home-ranges at the edge of the plot where nothing was known about the location of pairs beyond the boundary.

Use of nest location as a surrogate for home-range centre

Occasionally neither member of a pair could be caught and ringed and fewer than three observations were obtained for the pair, often including one or more nest locations. Omitting data-poor pairs from the map would have biased nearest-neighbour analyses for all adjacent pairs on the study plot to an unacceptable degree. Therefore, for those pairs with only a nest location, this was used as a surrogate for home-range centre. For those pairs with two observations, the arithmetic mean of the two observations was used as a surrogate for home-range centre. The potential error introduced by this approach was assessed using data from all 2005 pairs for which an MCP was obtained and comparing the location of the pair's first nest, or the mean of locations for a pair's two nests to the mean home-range centre, calculated from using all observations for that pair. For each pair I then compared this distance with the distance from the pair's home-range centre to the nearest conspecific home-range centre to give a relative measure of error.

Similarity of male and female home-range

To determine whether male and female home-range centres coincided, I mapped separate 95% MCPs for male and female members of all those pairs for which there was a minimum of six observations for each sex. I then compared the distance between the two home-range centres with the distance from the pair's home-range centre (from 95% MCP) to the nearest conspecific home-range centre.

Categorizing by species of nearest neighbour

Different study plots had different proportions of the two species. Where one species was relatively scarce on a site, distances between conspecific home-range centres were necessarily very large. In this context, comparing mean distances from home-range centres to nearest conspecific with distances to nearest congeneric does not address the question of interspecific territoriality, but rather reflects the relative proportions of the two species on the study plot. To avoid this confounding effect, each pair was first categorised by whether its closest neighbour was conspecific or

congeneric. The question of whether or not the two species exhibit interspecific territoriality was then phrased, 'Does the identity of a pair's nearest neighbour (conspecific or congeneric) have an effect on how far apart the two home-range centres are?' If Cyprus and Sardinian Warblers show interspecific territoriality, we would predict that the identity of a pair's nearest neighbour should have no effect on how far away their home-range centre is. If the two species do not show interspecific territoriality, we would predict that distance to heterospecific nearest-neighbour centres would be shorter than distances to conspecific nearest-neighbour centres. To test these predictions LMMs were run for each species separately, with distance to nearest neighbour as the dependent variable, species of nearest neighbour and year as fixed factors and site as a random factor.

Methods 2: Playback experiment

Sound recordings

A Sony MZ-N1 minidisk recorder was used in conjunction with a Sennheiser ME66 shotgun microphone (mounted in a Sennheiser MZW 426 windjammer with MZH 60 windshield), to record song from 20 Cyprus Warbler and 20 Sardinian Warbler males in 2005. Recordings were obtained from birds located inside and outside study plots. Linnet (*Carduelis cannabina*) was selected as a control species because it breeds syntopically with Cyprus and Sardinian Warblers in Cyprus, but has quite different song and is not thought to be a competitor for food; studies elsewhere in Europe have found that both adults and nestlings are almost exclusively granivorous (Eybert & Constant 1992, Cramp & Perrins 1994, Bradbury *et al.* 2003). Control song was obtained from five different Linnets.

Recordings were transferred into Audacity, a sound analysis programme and the average inter-phrase interval was then measured for the 20 individuals of each warbler species and for the five Linnet recordings. The 12 highest quality recordings were selected for each warbler species, comprising recordings from four individuals from each of zones 1, 2 and 3. Sequential phrases of song were then cut from the recording of each individual, separated by the average inter-phrase interval for the

species and linked together into a 2 min section of song from that individual bird. Where less than 2 min of quality recording was available for an individual, as many phrases as possible were placed in sequence and the sequence was then repeated for 2 min.

The volume of different recordings was standardised using Audacity and 12 playback tracks were assembled. For each track, the three stimuli were randomly selected from the pool of 12 Cyprus Warbler, 12 Sardinian Warbler and five Linnet recordings, such that recordings from individual warblers were used only once, while recordings from individual Linnets were used two or three times on different playback tracks. Each group of three stimuli was then randomly allocated to one of six possible orders (which were repeated twice). In each case, inter-phrase periods comprised ambient noise taken from a quiet period during recording, as did pre-stimulus, post-stimulus and rest periods. The format for each track is shown in Table 3.1.

Minute from start	Playback period
1	PRE-STIMULUS
2	
3	STIMULUS 1
4	
5	POST-STIMULUS 1
6	
7	REST
8	
9	STIMULUS 2
10	
11	POST-STIMULUS 2
12	
13	REST
14	
15	STIMULUS 3
16	
17	POST-STIMULUS 3
18	

Table 3.1 Format of playback tracks. Pre-stimulus, post-stimulus and rest periods comprise ambient noise.

Field playback experiments

Playback experiments were carried out between the end of March and the end of May 2005, to coincide with the main breeding season. While birds did breed from early March to late June, the very beginning of the breeding period was excluded as many birds had not yet fully established their territories, while towards the end of the breeding season there was a notable reduction in singing and territorial behaviour. All playback experiments were initiated between 07:00 and 11:00, since this is the period of peak territorial activity, and birds tended to reduce their effort during the hottest period of the day.

The main playback experiment was carried out on 12 Cyprus males and 12 Sardinian males from zone 2. These comprised some males from zone 2 study plots (Ineia, Lysos and Choli) and some males from other areas of scrub habitat within zone 2. A further six playback experiments were carried out on Cyprus Warbler males in zone 3 (from study plots Kouklia Hives and Kouklia 3 and other scrub habitat within this zone).

To avoid problems with possible aversive responses or habituation to playback study plot males which had been captured for ringing using playback at mist nets in 2005 were not used as subjects for these experiments. Since the locations of study plot males' territories were known, the speaker was placed facing upwards in a bush at the centre of the territory. When males from off-plot were used, they were observed for a period and when the same male had been observed singing from three different locations, the speaker was placed at the centre of this triangle. Areas of vegetation less than 2 m in height were used for these experiments since large bushes and trees might obscure the view of the subject male's activity. Potential perches were freely available and therefore perch location was considered unlikely to influence the behaviour of focal males. Experience indicated that warblers behave normally in the presence of a stationary observer at a 20 m distance. The experimenter selected a good vantage point, 20 m from the speaker and set up small coloured tags in a cross shape at 5 m and 10 m distances from the speaker, to aid with distance estimation. An extension cable allowed control over the minidisk player. The experimenter then

waited for 5 min so that, if the subject male was in the immediate area, he could settle after the disturbance.

The playback track which had been randomly selected for use on this male was then played (at a minidisk and speaker volume kept constant between experiments) and the experimenter kept note of the number of flights made, number of song phrases, number of song flights, number of chitters (annoyance calls) and the closest distance from the speaker for each 1 min period. In addition, following the start of each stimulus, the number of seconds elapsing before the subject flew towards the speaker was recorded. All playback experiments were carried out by myself or J. Koorevaar and we standardised our activity by conducting four test experiments together and comparing results. We then settled on a standard definition of any ambiguous behaviour (for example, a flight was defined as covering a distance greater than 2 m). Results of these test experiments were not included in the analysis, as the presence of two observers may have affected the birds' behaviour. These birds were not subsequently used in the 'real' experiments.

If the experiment was disturbed for any reason (for example, arrival of a predator, rain, interference by a neighbour) the experiment was abandoned and that individual was not used again. In addition, if more than one playback experiment was conducted at a site in a day, birds with territories separated by at least 50 m were used to prevent habituation. Experiments were not carried out during rain or high wind, both of which affected the behaviour of the birds and the audibility of the playback tracks.

Playback experiment analysis

Since song-flights and chittering were uncommon behaviours in response to playback, analysis was confined to 'flight', 'song', 'closest approach' and 'latency to approach' measures. Data were first examined with the birds' responses separated into 'stimulus' and 'post-stimulus' periods. Responses to the stimulus were not confined to the period while the stimulus was playing; sometimes the post-stimulus response was greater than the stimulus response (Table 3.5). This was probably because birds often had to approach the area of the speaker from some distance

away if they were near the edge of their territory when playback began and they frequently continued to respond for a short time after playback finished. However, there was no consistent pattern when during-stimulus and post-stimulus periods were analysed separately and I decided to analyse the two periods as a single block to best represent the total response.

Flights and songs were presented as number of flights per minute and number of songs per minute so that the pre-stimulus period (2 min) could be compared with during and post stimulus periods (4 min when combined). For closest approach to the speaker and latency to approach, dummy variables were inserted in cases where no approach to the speaker was made. For latency to approach 240 s was the dummy variable, since this represented the end of the post-stimulus period of observation and was the maximum possible time. For closest approach to the speaker, the dummy variable was 30 m, since the structure of the habitat meant that birds could not usually be observed at a distance greater than 20-25 m.

As a result of these dummy variables and a relatively high number of cases where the bird did not respond, the distribution for these two variables was non-normal and could not be transformed to fit parametric test assumptions. Principal Component Analysis (PCA) or Exploratory Factor Analysis (EFA) can be used to collapse a number of measures of response into a smaller number of factors. However, these techniques are often used inappropriately and are most effective with large sample sizes and high subject-to-item ratios. In this case the sample size is 12 and the subject-to-item ratio is 3:1, since I took four different behavioural measures of response to playback. The ratio falls short of the 5:1 ratio recommended as a minimum by some authors for EFA (Gorusch 1983, Hatcher 1994) and the 5:1 to 10:1 subject to variable ratio recommended for PCA (Nunnally 1978). Therefore, non-parametric tests were carried out, with the randomized-block design of the experiment minimising any effect of stimulus order.

Friedman tests were conducted, since the design was essentially repeated measures with each subject tested under four different conditions. It should be borne in mind that the different measures of behavioural response are not independent of one

another in the sense that a bird that reacts strongly in one respect may react strongly in other measures too. Sequential Bonferroni adjustment was used to reduce the risk of making a Type I error by measuring four different types of behavioural response. Post-hoc Wilcoxon tests for paired samples were used to investigate further significant results from Friedman tests.

Catchpole (1978) suggested that proximity to the speaker gives the clearest indication of an individual's level of aggression. Therefore the proportion of birds approaching to within 5 m of the speaker in response to conspecific or congeneric stimuli was examined as a potential measure of aggression. I chose 5 m because in natural encounters approach to within 5 m often results in a chase. In addition the markers placed at 5 m around the speaker facilitated estimation of this distance. A generalized linear mixed model (GLMM), fitted with binomial error structure, was used to analyse the data on Cyprus and Sardinian Warbler approach to within 5 m of the speaker in zone 2. For each species separately, stimulus, order and their interaction were fitted as fixed factors, while individual was fitted as a random factor.

A GLMM with binomial error structure was used to analyse the data on whether or not Cyprus Warblers approached to within 5 m of the speaker with different stimuli in the two zones. Zone, stimulus, order and their interactions were entered as fixed factors and individual as a random factor.

Following binomial GLMMs, pairwise comparisons were made between levels of a factor by subtracting the predicted mean of level one from the predicted mean of level two and dividing the result by the standard error of the difference between the pair. The resulting value was then compared to a table of critical values of the t distribution to determine the p value.

Methods 3: Behavioural observations

Approximately 1000 observer days were spent on the study plots during breeding seasons 2003-2005. During this time, detailed observations of conspecific and

heterospecific behavioural interactions were recorded. Where possible we recorded the species and sex of any individual involved in an encounter and details of which individual initiated any aggression and how the other party responded.

Results 1: Spatial distribution

Ninety-five percent MCPs for Cyprus and Sardinian Warbler pairs at seven study plots in the 2004 and 2005 breeding seasons (Fig. 3.1) clearly show that, at sites where both species were present, Cyprus and Sardinian Warbler home-ranges overlap. While conspecific home-ranges are generally spatially segregated with small areas of overlap at the edges, there is no evidence for similar segregation of heterospecific home-ranges. Therefore, Cyprus and Sardinian Warblers do not appear to show any evidence of interspecific territoriality; indeed each species appears to locate home-ranges irrespective of the other.

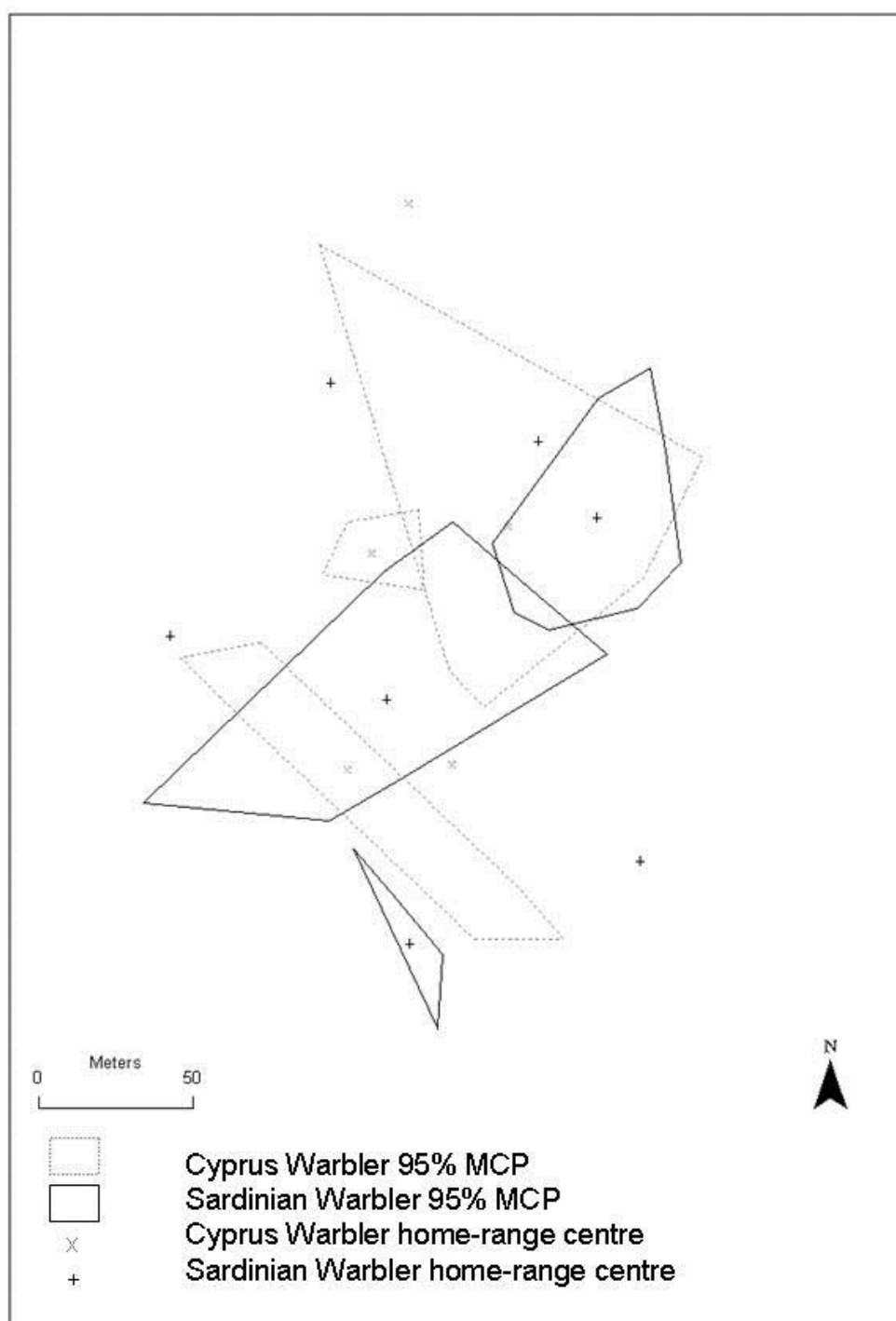


Figure 3.1a 95% Minimum Convex Polygons of five Cyprus and seven Sardinian Warbler home-ranges at Akamas 2 during the 2004 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

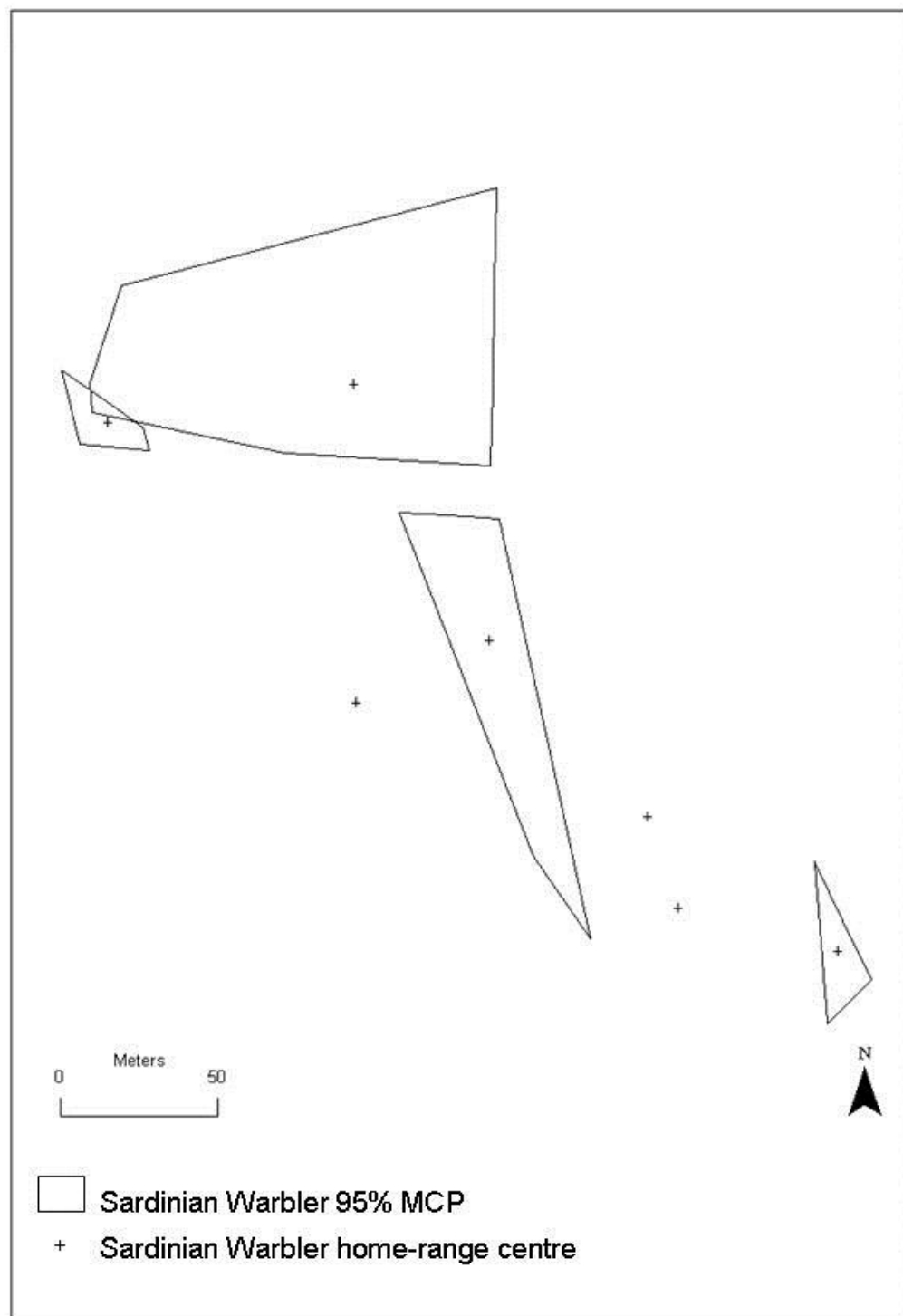


Figure 3.1b 95% Minimum Convex Polygons for seven Sardinian Warbler home-ranges at Akamas Pines during the 2004 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

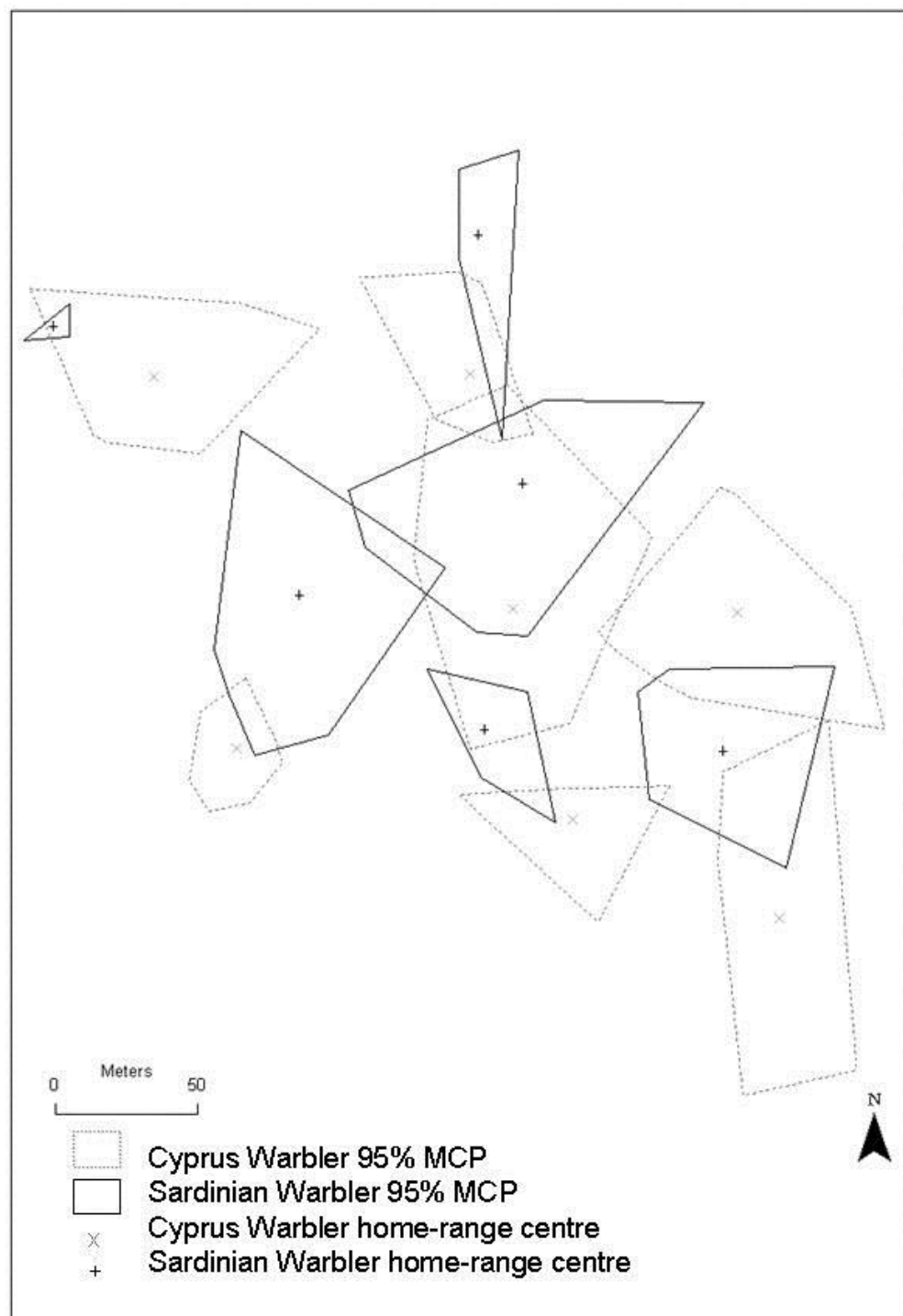


Figure 3.1c 95% Minimum Convex Polygons for seven Cyprus and six Sardinian Warbler home-ranges at Ineia during the 2004 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

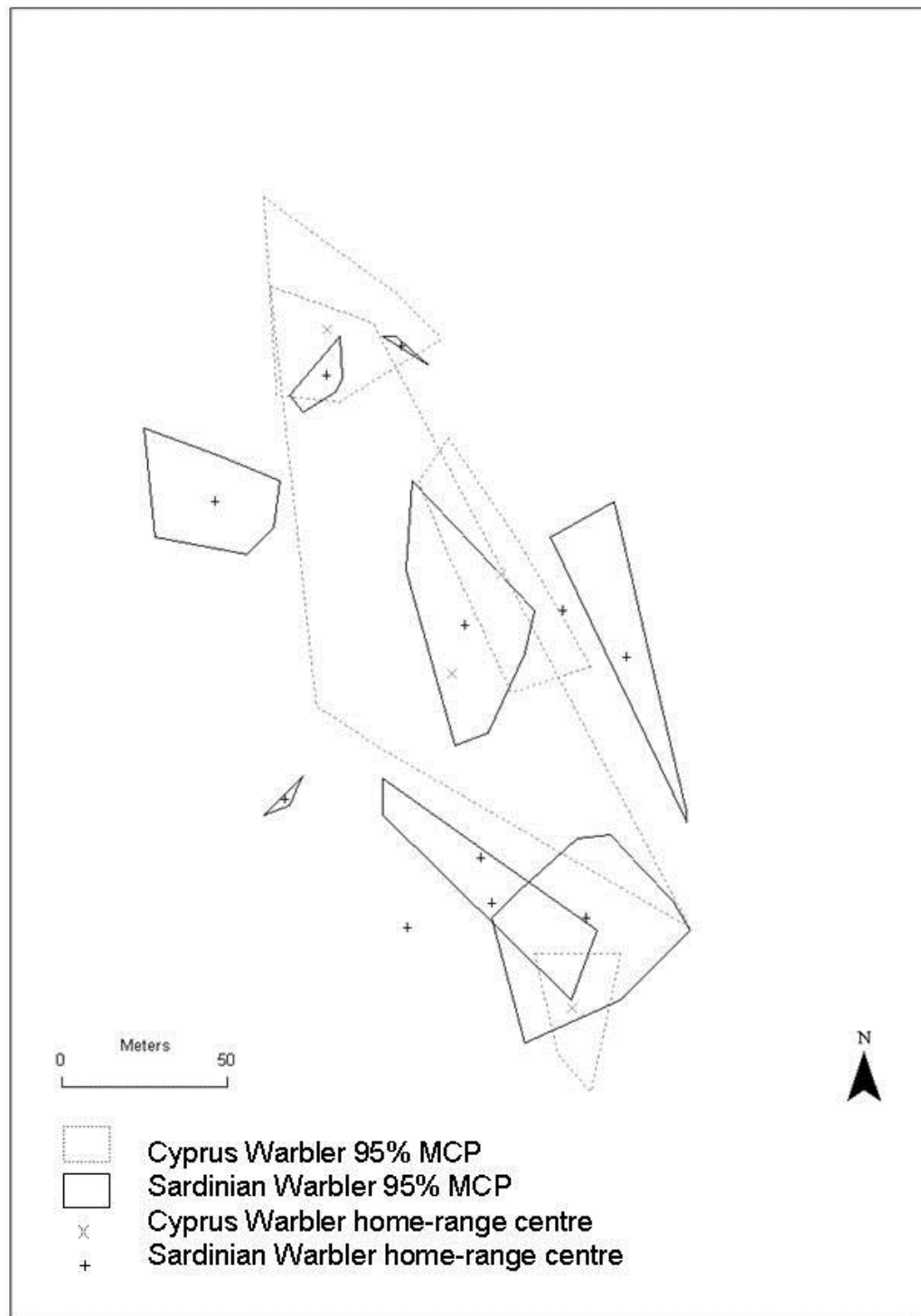


Figure 3.1d 95% Minimum Convex Polygons for four Cyprus and eleven Sardinian Warbler home-ranges at Choli during the 2004 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

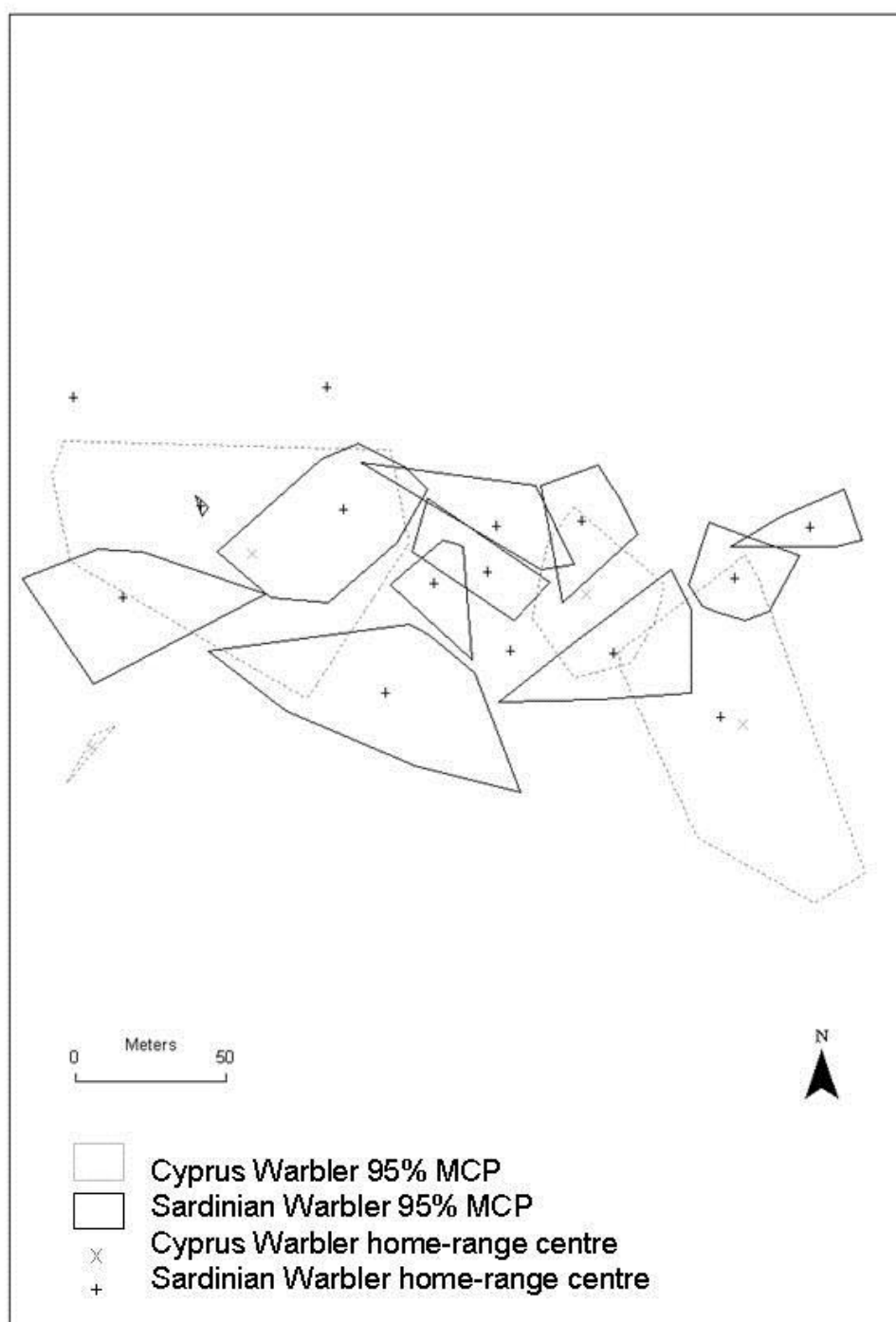


Figure 3.1e 95% Minimum Convex Polygons for four Cyprus and fifteen Sardinian Warbler home-ranges at Lysos during the 2004 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

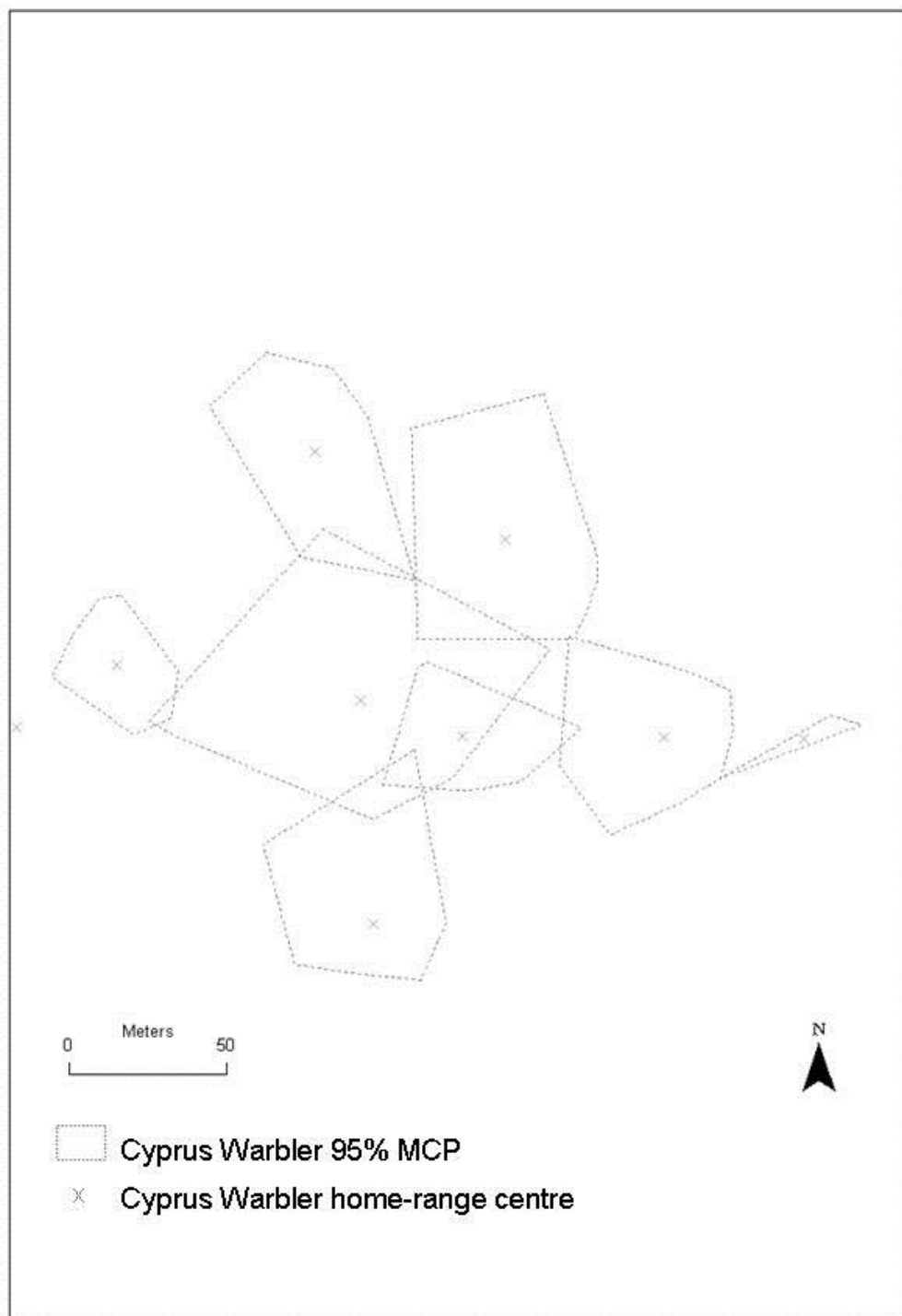


Figure 3.1f 95% Minimum Convex Polygons for nine Cyprus Warbler home-ranges at Kouklia Hives during the 2004 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

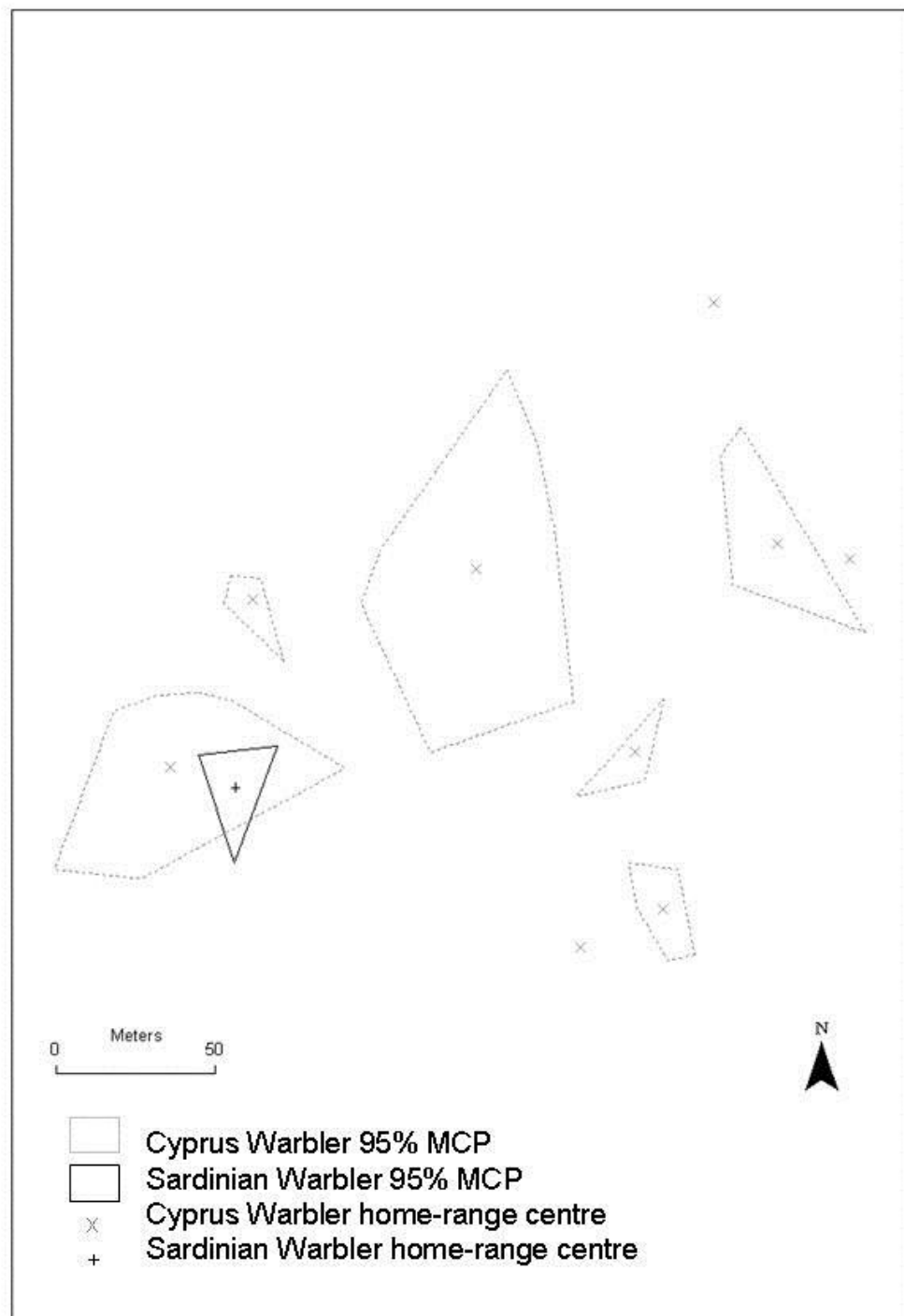


Figure 3.1g 95% Minimum Convex Polygons for nine Cyprus and one Sardinian Warbler home-ranges at Kouklia 3 during the 2004 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

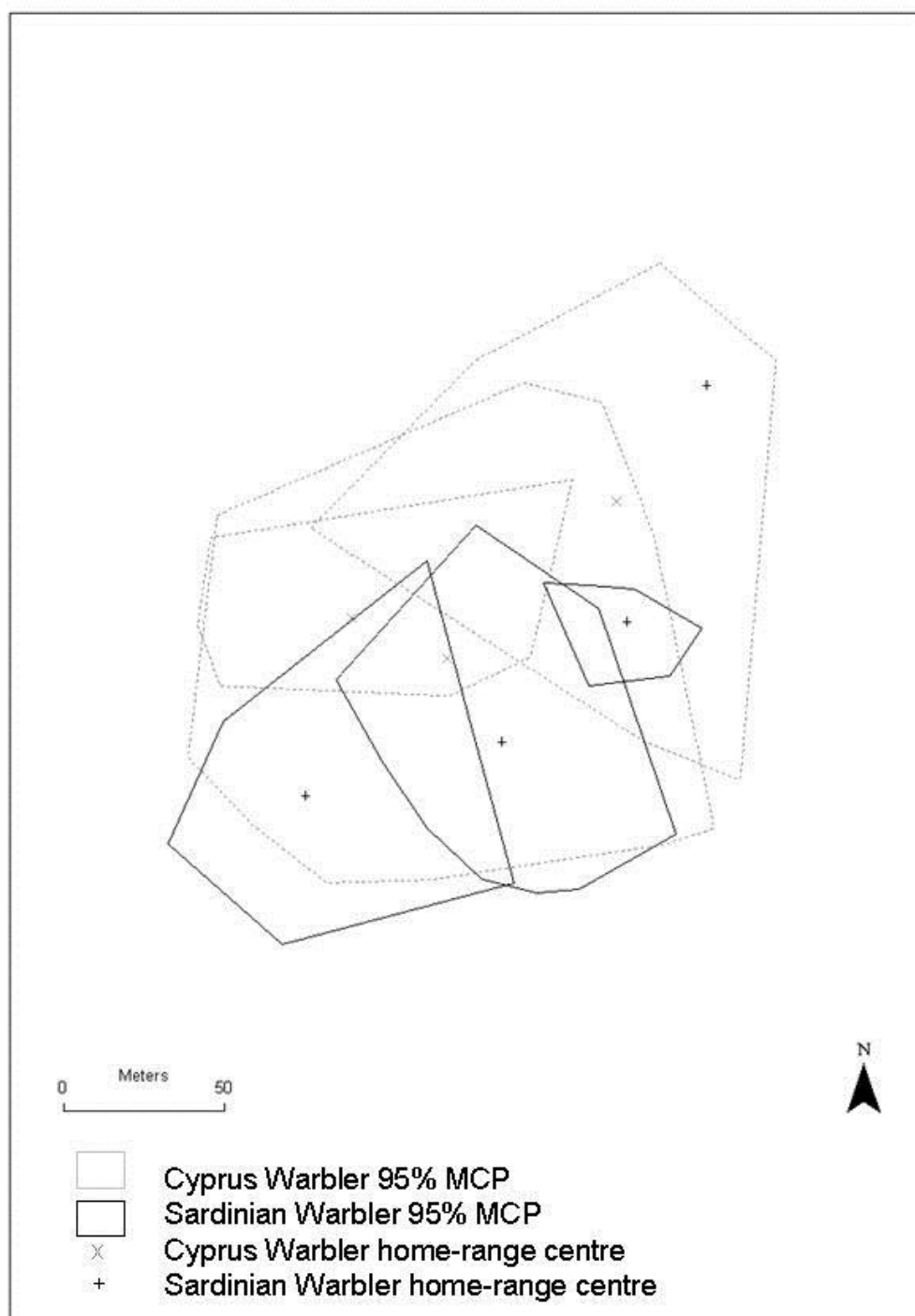


Figure 3.1h 95% Minimum Convex Polygons for three Cyprus and three Sardinian Warbler home-ranges at Akamas 2 during the 2005 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

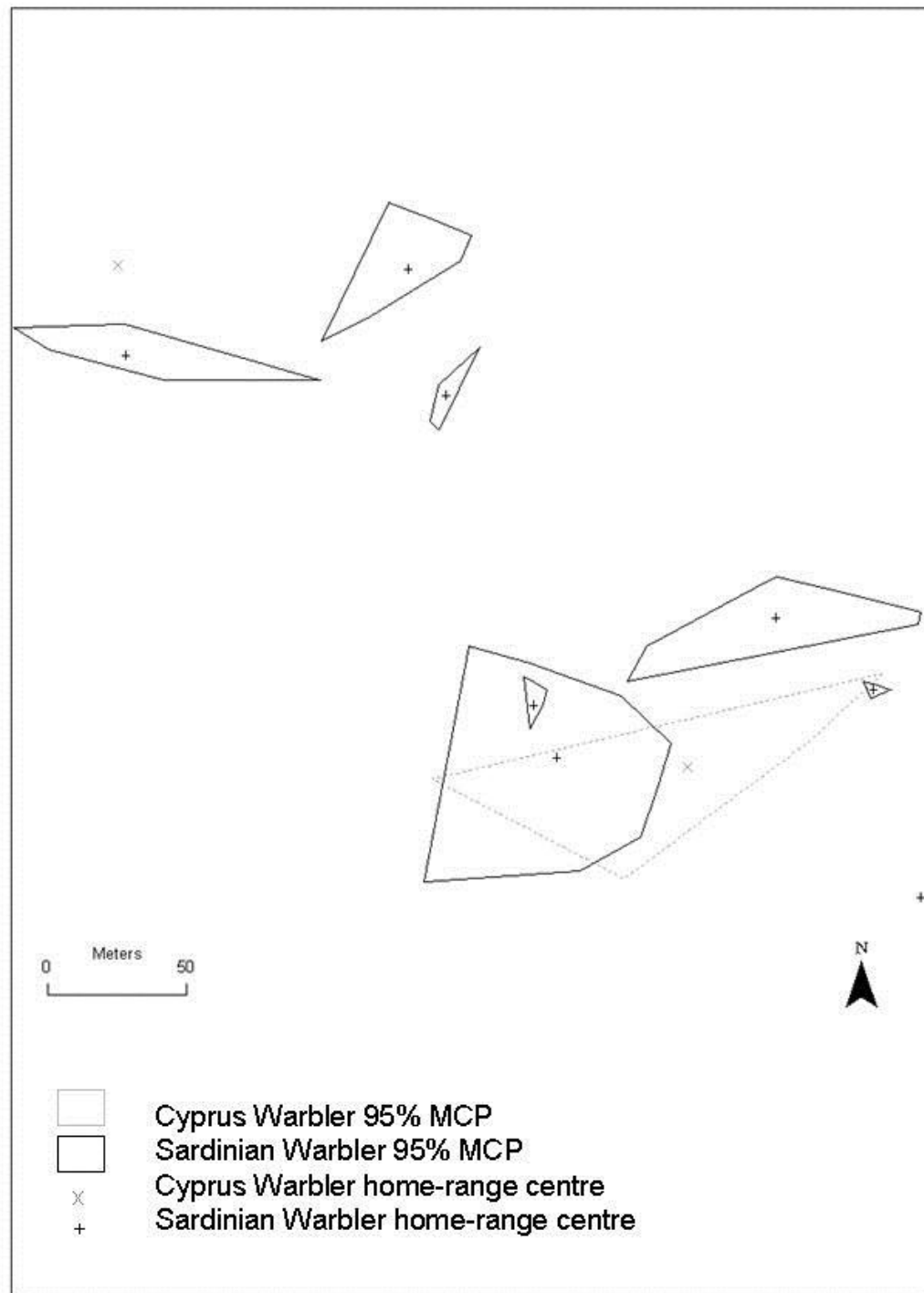


Figure 3.1i 95% Minimum Convex Polygons for two Cyprus and eight Sardinian Warbler home-ranges at Akamas Pines during the 2005 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

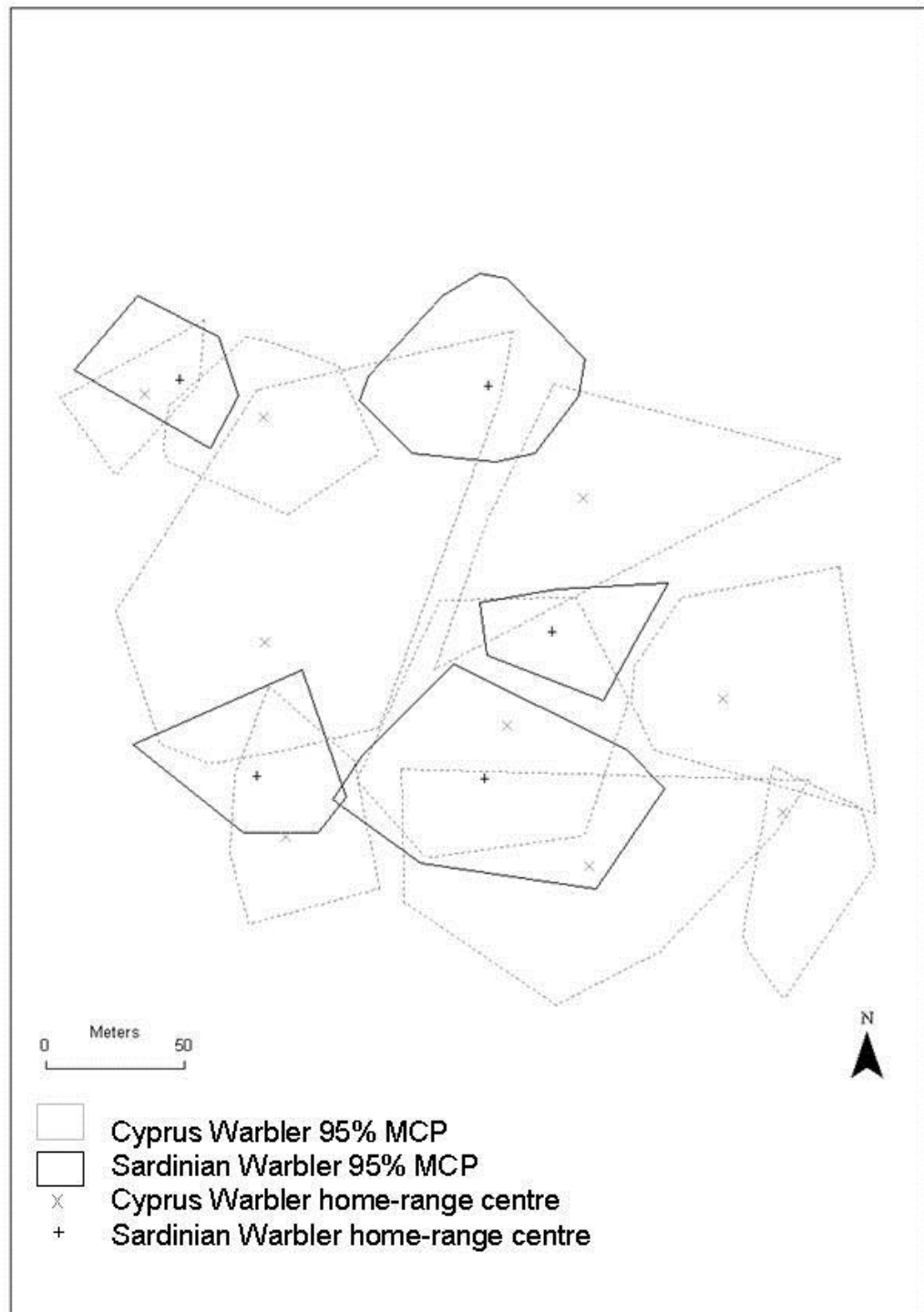


Figure 3.1j 95% Minimum Convex Polygons for nine Cyprus and five Sardinian Warbler home-ranges at Ineia during the 2005 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.



Figure 3.1k 95% Minimum Convex Polygons for four Cyprus and thirteen Sardinian Warbler home-ranges at Choli during the 2005 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

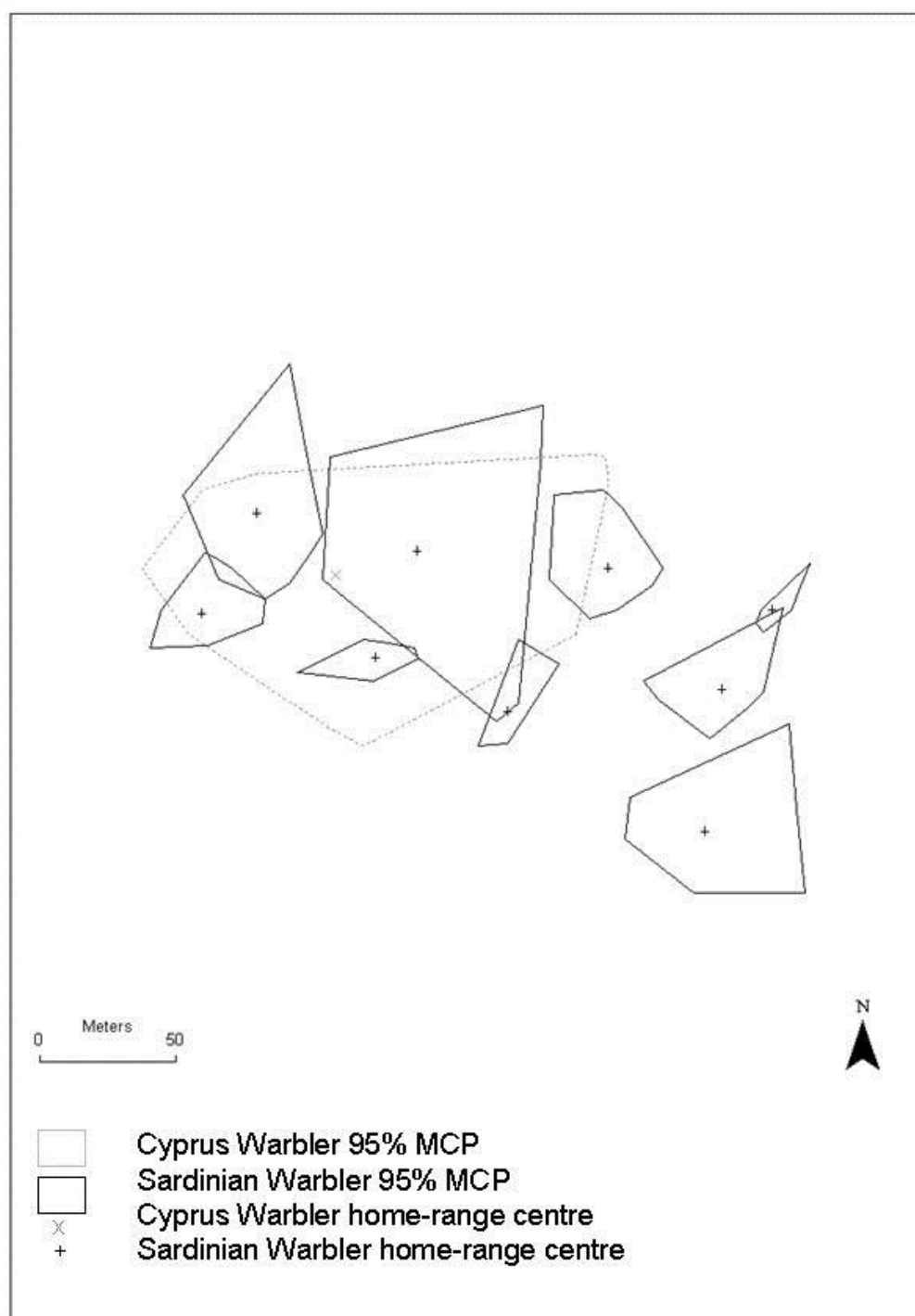


Figure 3.11 95% Minimum Convex Polygons for one Cyprus and nine Sardinian Warbler home-ranges at Lysos during the 2005 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

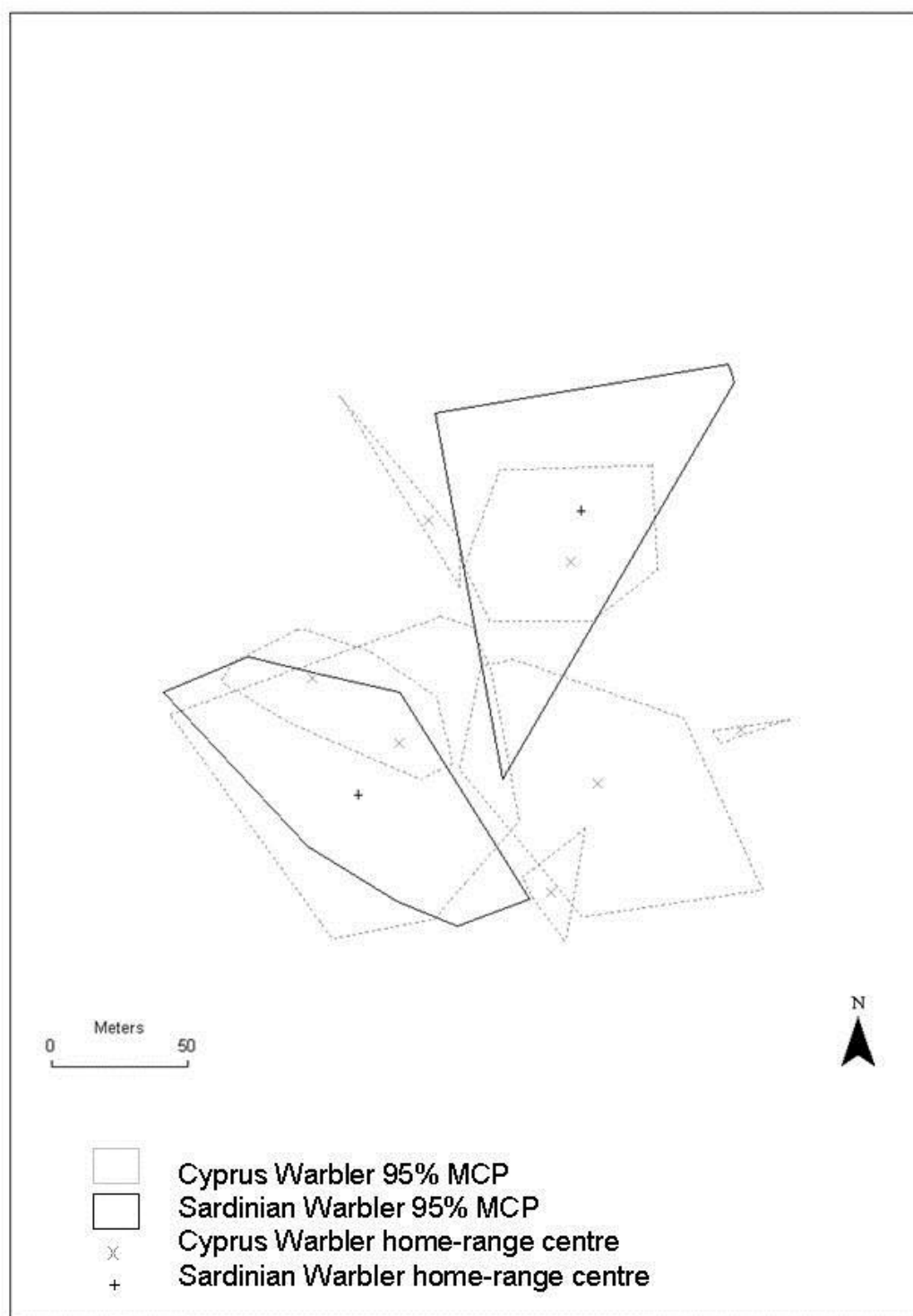


Figure 3.1m 95% Minimum Convex Polygons for seven Cyprus and two Sardinian Warbler home-ranges at Kouklia Hives during the 2005 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

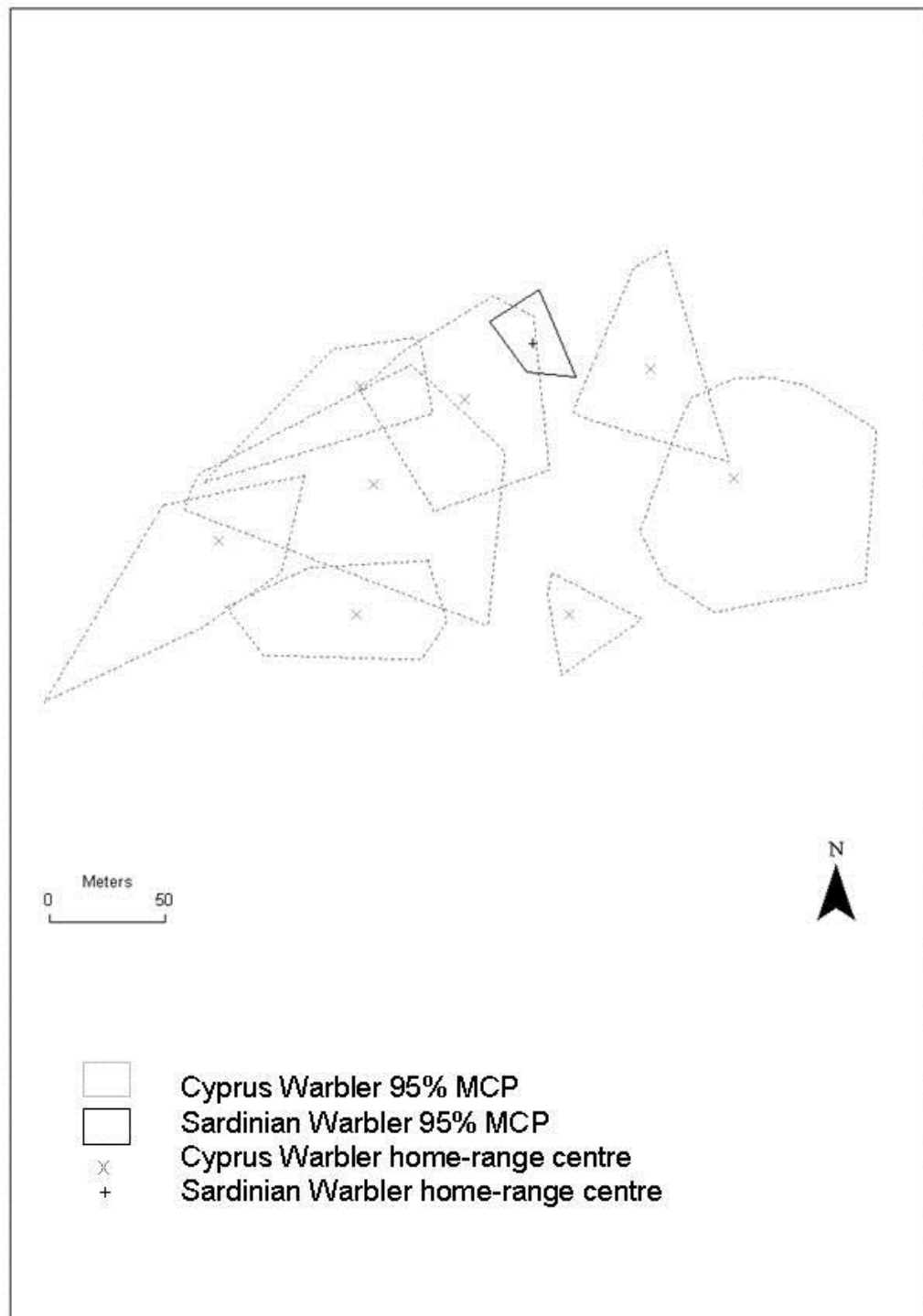


Figure 3.1n 95% Minimum Convex Polygons for eight Cyprus and one Sardinian Warbler home-range at Kouklia 3 during the 2005 breeding season. Home-range centres shown are the arithmetic mean of MCP coordinates or nest-site surrogates.

Independence of observations

To demonstrate that sub-sampling the location data is unnecessary, I used data for male locations in 2004 and plotted how far birds moved between sequential observations against how many minutes separated the observations. There was no significant association between time and distance (Fig. 3.2).

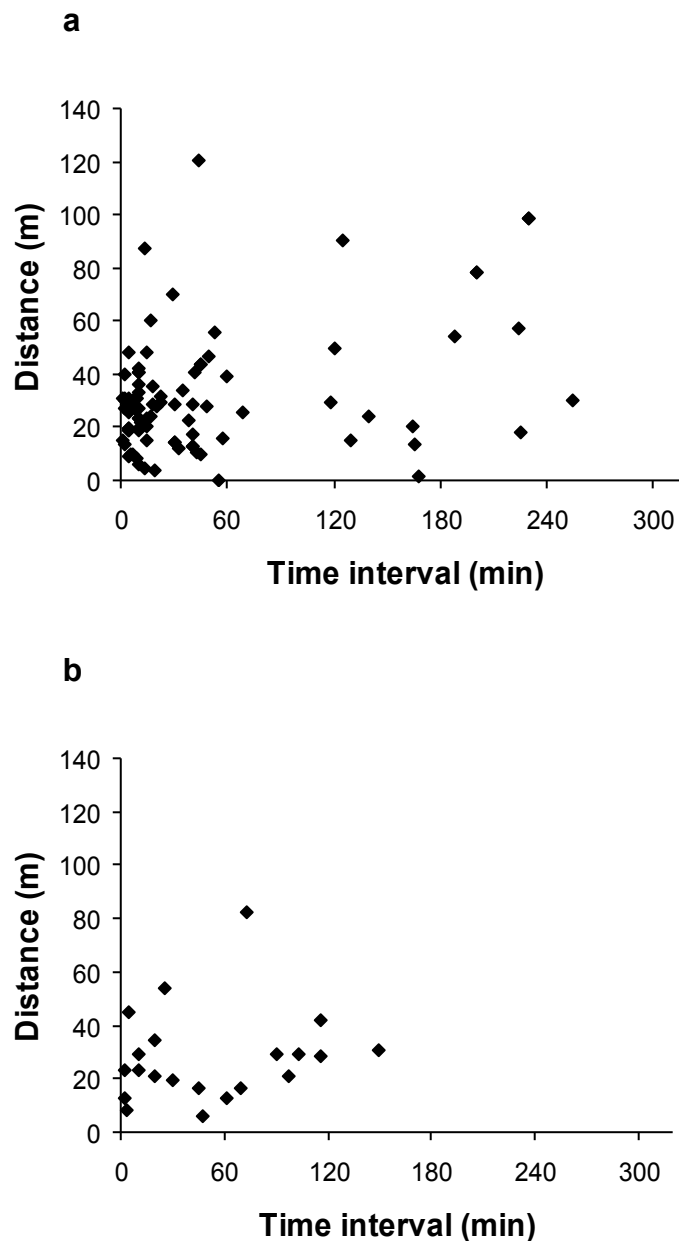


Figure 3.2 (a) Cyprus Warbler (Pearson correlation: $r=0.188$, d.f.=86, $p=0.079$) and (b) Sardinian Warbler ($r=0.233$, d.f.=19, $p=0.310$) male locations from 2004; distance between pairs of consecutive observations plotted against time interval separating them.

Observations made 0-5 min apart were separated on average by a distance of 25 m in Cyprus Warblers and 22 m in Sardinian Warblers (approximately a third to a half of the length of the average home-range – see below). Given the small size of these species' home-ranges and their potential to travel the length of their home-range in seconds, I consider sequential observations to be biologically independent.

Home-range size calculated from pairs with the most observations

For Cyprus Warbler, some home-range areas had reached an asymptote by 30 observations, while others were only reaching an asymptote at 50 or more observations (Fig. 3.3a). For Sardinian Warblers, many home-range areas had reached an asymptote by 30 observations. Interestingly, for this sub-sample of pairs for which more than 20 observations were collected, Cyprus Warbler mean home-range size was somewhat larger ($5358 \pm 917 \text{ m}^2$, $n=19$) than for the sub-sample of Sardinian Warbler home-ranges ($3244 \pm 448 \text{ m}^2$, $n=16$). However there was no significant difference between the two species in home-range size measured by this method (independent samples t-test: $t=1.74$, $d.f.=33$, $p=0.092$).

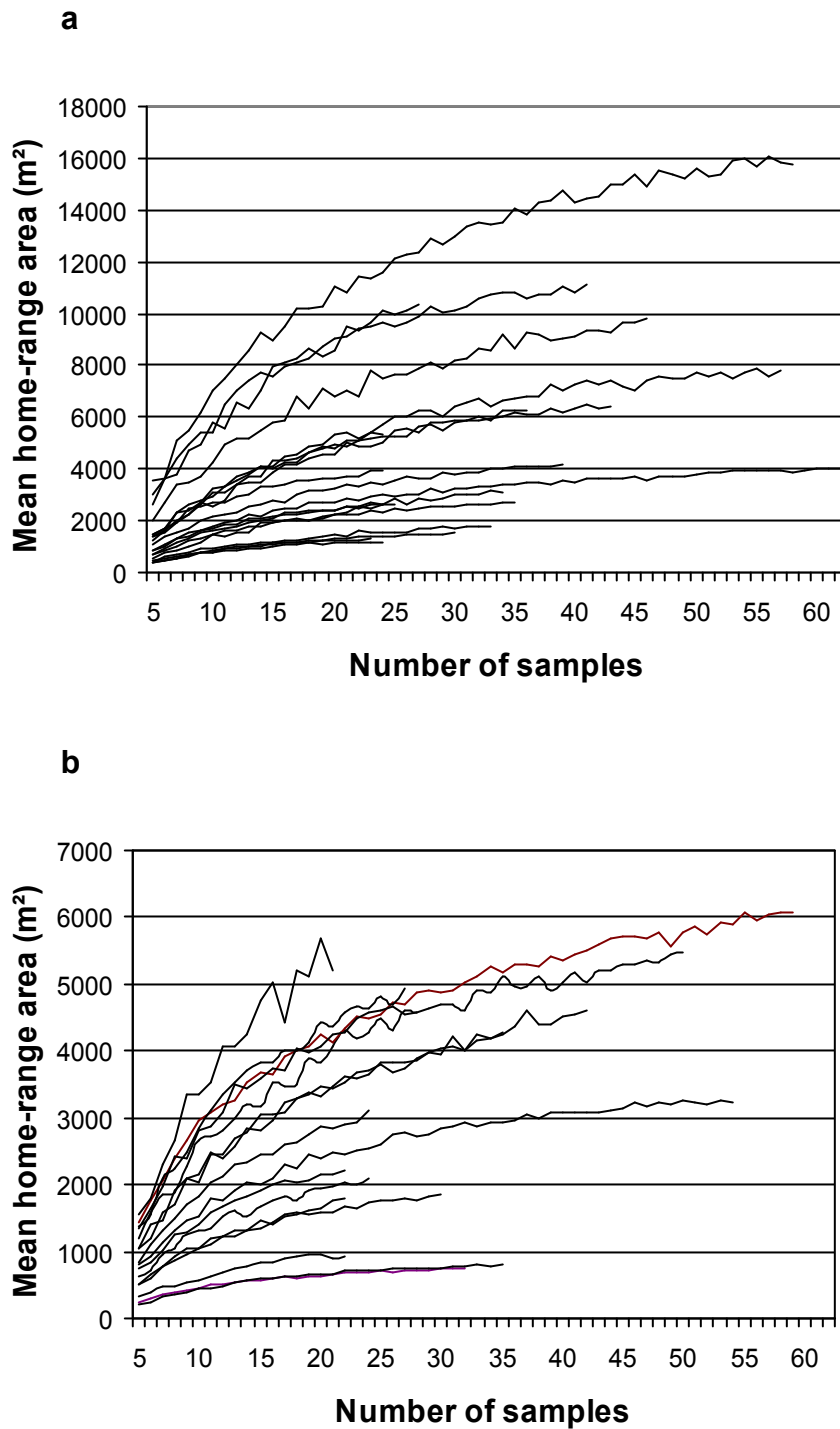


Figure 3.3 Mean home-range area of all (a) Cyprus Warbler ($n=19$) and (b) Sardinian Warbler ($n=16$) pairs for which more than 20 observations were collected in either 2004 or 2005. Mean home-range area was generated by bootstrapping observations in random order with replacement 100 times for each sample size from 5 to the total number of samples for that pair.

Home-range size calculated by inter-centre distance

Home-range areas estimated using inter-centre distance (Fig. 3.5) tended to be smaller than those measured from individuals with 20 or more observations (Fig. 3.4) despite the fact that home-ranges of the latter had not all reached an asymptote.

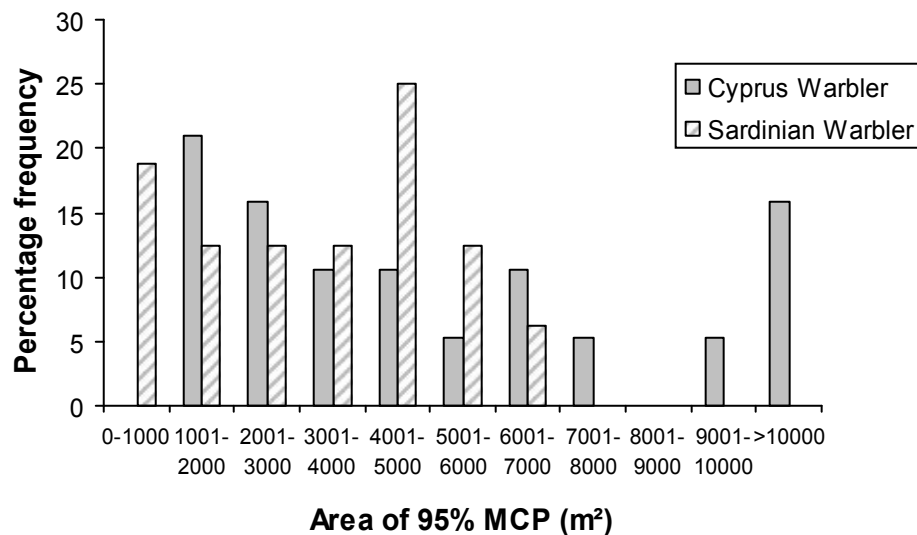


Figure 3.4 Frequency of different Cyprus (n=19) and Sardinian Warbler (n=16) home-range areas, taken from 95% MCPs pairs for which 20 or more observations were collected in 2004 or 2005 (on any study plot).

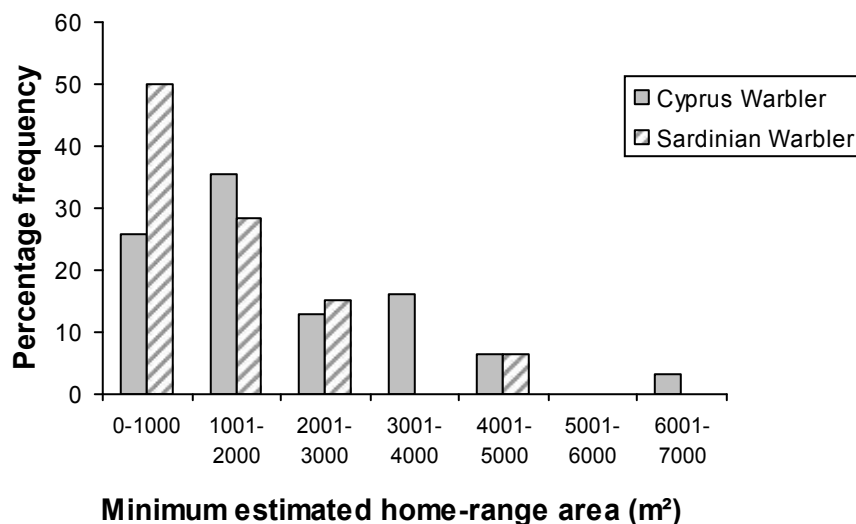


Figure 3.5 2004 and 2005 home-range areas as estimated from Cyprus Warbler (n=30) and Sardinian Warbler (n=46) pairs which had a conspecific nearest neighbour (on any study plot). Home-range estimated using distance to conspecific neighbour as the diameter of a circle representing home-range.

Using the circle method, mean home-range area was $2115 \pm 266 \text{ m}^2$ ($n=30$) for Cyprus Warblers and $1315 \pm 178 \text{ m}^2$ ($n=46$) for Sardinian Warblers. These values are considerably smaller than those obtained from 95% MCPs using pairs with 20 or more observations. This may have been because real home-ranges are irregular in shape and tend to overlap slightly (the circle method is based on nearest neighbour circles being non-overlapping) and also because in reality the distance to closest conspecific on one side is by definition smaller than the distance to other neighbouring conspecifics; therefore, the home-range area estimated using the shortest distance to a conspecific will inevitably underestimate true home-range area. Despite its shortcomings the circle method for estimating minimum home-range area could be useful where insufficient observations were obtained to measure accurately average home-range size.

I compared the distance separating conspecific nearest-neighbour home-range centres for Cyprus and Sardinian Warblers. There was no significant effect of species (LMM: $X^2=2.47$, d.f.=1, $p=0.116$) or year ($X^2=0.05$, d.f.=1, $p=0.831$) on distance between conspecific home-range centres. This suggests that there was no significant difference between the two species in home-range size.

Use of nest location as a surrogate for home-range centre

On average, the distance to the nearest conspecific home-range centre was three (Cyprus Warbler) or four (Sardinian Warbler) times greater than the distance between a pair's nest and their home-range centre (Table 3.2). These values increased slightly when the mean position of two nests was used. The results suggest that the nest position or the mean of two nest positions provide a satisfactory substitute for the home-range centre.

Species	Single nest location versus home-range centre			Mean of two nest locations versus home-range centre		
	Distance from home-range centre to 1 nest (A)	Distance from home-range centre to nearest conspecific (B)	B / A	Distance from home-range centre to mean of 2 nests (C)	Distance from home-range centre to nearest conspecific (D)	D / C
Cyprus Warbler	25.4 ± 2.74 (22)	63.3 ± 10.5 (22)	3.02 ± 0.435 (22)	22.2 ± 4.90 (6)	52.7 ± 8.35 (6)	3.26 ± 1.01 (6)
Sardinian Warbler	15.5 ± 1.60 (34)	54.2 ± 5.64 (34)	4.16 ± 0.475 (34)	13.5 ± 1.64 (20)	56.6 ± 6.77 (20)	4.90 ± 0.671 (20)

Table 3.2 Mean ± SE distance (m) from each pair's home-range centre to either its one nest or to the mean position of its two nests, compared to the distance from the home-range centre to the nearest conspecific home-range centre. Sample sizes shown in brackets.

Similarity of male and female home-ranges

To determine whether male and female home-ranges coincided, I mapped male and female observations separately. On average (Table 3.3), the distance to nearest conspecific home-range centre was ten (Cyprus Warbler) and eight (Sardinian Warbler) times the distance between male and female home-range centres. The finding that male and female home-range centre locations were very close together suggests that which member of the pair was ringed was unlikely to bias the home-range analyses.

Species	Distance between male & female home-range centres (A)	Distance from pair home-range centre to nearest conspecific (B)	B / A
Cyprus Warbler	10.2 ± 4.13 (3)	49.9 ± 11.6 (3)	9.70 ± 6.54 (3)
Sardinian Warbler	9.26 ± 2.72 (4)	67.5 ± 11.8 (4)	8.44 ± 1.72 (4)

Table 3.3 Mean ± SE distance between male and female home-range centres and distance separating each pair's mean centre from nearest conspecific home-range centre. Sample sizes shown in brackets.

Breeding density of warblers

To enable comparison with other worker's estimates, the breeding density of Cyprus and Sardinian Warbler pairs was calculated for 2004 and 2005 (Table 3.4). Highest

breeding densities recorded were 2.23 Cyprus Warbler pairs/ha at Kouklia Hives in 2004 and 5.59 Sardinian Warbler pairs/ha at Choli in 2005.

Study plot	Breeding density of Cyprus Warblers (pairs/ha)		Breeding density of Sardinian Warblers (pairs/ha)	
	2004	2005	2004	2005
Akamas 2	1.67	1.00	2.34	1.33
Akamas Pines	-	0.42	1.47	1.68
Ineia	1.21	1.55	1.03	0.86
Choli	1.72	1.72	4.73	5.59
Lysos	0.90	0.30	4.78	2.69
Kouklia Hives	2.23	1.49	-	0.50
Kouklia 3	1.88	1.67	0.21	0.42

Table 3.4 Density of Cyprus and Sardinian Warbler breeding pairs on different study plots in 2004 and 2005, calculated by dividing for each species number of home-ranges on the plot by study plot area.

Interspecific home-range distribution

To quantify how the two species were distributed in relation to one other, I examined the distance between the home-range centres of pairs on each plot using a separate LMM for each species. For Cyprus Warbler, species of nearest neighbour was found to have a significant effect on distance to nearest neighbour home-range centre ($X^2=9.11$, d.f.=1, $p=0.003$; Fig. 3.6a), with the distance from Cyprus Warbler pairs to Cyprus Warbler nearest-neighbours being greater than the distance to Sardinian Warbler nearest-neighbours. Year was not found to have a significant effect ($X^2=0.19$, d.f.=1, $p=0.662$). For Sardinian Warblers, species of nearest neighbour was found to have a significant effect on distance to nearest neighbour home-range centre ($X^2=4.14$, d.f.=1, $p=0.042$; Fig. 3.6b), with the distance from Sardinian Warbler pairs to Sardinian Warbler nearest-neighbours being greater than the distance to Cyprus Warbler nearest-neighbours. Year was not found to have a significant effect ($X^2=0.92$, d.f.=1, $p=0.339$).

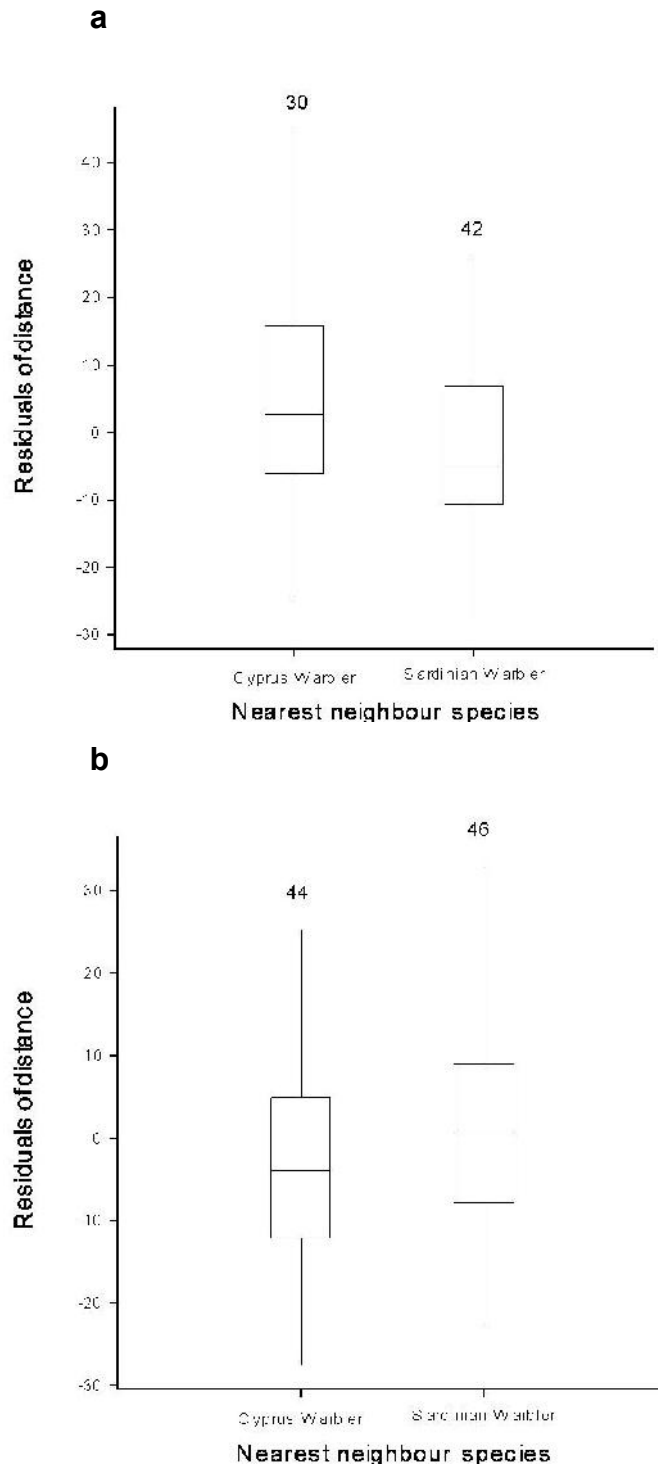


Figure 3.6 Box plots (horizontal line - median value, box - interquartile range, whisker - largest and smallest value within 1.5 interquartile ranges of top and bottom). 2004 and 2005 breeding season, all study plots; mean distance from (a) Cyprus Warbler and (b) Sardinian Warbler pair home-range centre to nearest neighbour home-range centre, where nearest neighbour is either Cyprus Warbler or Sardinian Warbler. For graphical illustration, residuals were generated by running LMM for Cyprus and Sardinian Warbler separately on distance to closest neighbour with year as fixed factor and site as random factor, but without including nearest neighbour species as a fixed factor. Sample sizes shown above whiskers.

Results 2: Playback experiment

Zone 2 Cyprus Warbler response to playback

Wilcoxon matched pair tests were used to determine whether there was a consistent pattern for response during the stimulus versus post-stimulus. The results are summarised in Table 3.5. No consistent pattern emerged, but the post-stimulus response was substantial and could not be ignored; therefore the two periods were grouped for all subsequent analysis.

Species tested	Response measure	Stimulus		
		Cyprus Warbler	Sardinian Warbler	Linnet
Cyprus Warbler	Flights	(+)	(+)	(+)
	Songs	-	(-)	(-)
Sardinian Warbler	Flights	(+)	(-)	+
	Songs	(+)	(-)	(-)

KEY: + during>post - during<post () non-significant difference

Table 3.5 Summary of differences between during-stimulus and post-stimulus responses for response measures: number of flights and number of songs.

After sequential Bonferroni adjustment, a significant difference was found between Cyprus Warbler responses to the different stimuli for all four measures: number of flights per minute (Friedman: $X^2=18.68$, d.f.=3, $p<0.001$; Fig. 3.7a), number of songs per minute ($X^2=9.53$, d.f.=3, $p=0.011$; Fig. 3.7b), closest approach to the speaker ($X^2=13.79$, d.f.=2, $p<0.001$; Fig. 3.7c) and latency to approach the speaker ($X^2=10.67$, d.f.=2, $p=0.004$; Fig. 3.7d).

Cyprus Warblers made no flights pre-stimulus, a relatively low mean number of flights per minute in response to Linnet song and a very similar, higher mean number of flights per minute in response to both Cyprus and Sardinian Warbler stimuli (Fig. 3.7a). The same pattern was observed for song response, with Cyprus Warblers singing a low mean number of songs per minute pre-stimulus, more mean songs per minute in response to the Linnet stimulus and a higher, similar mean number of songs per minute in response to both Cyprus and Sardinian Warbler stimuli (Fig. 3.7b).

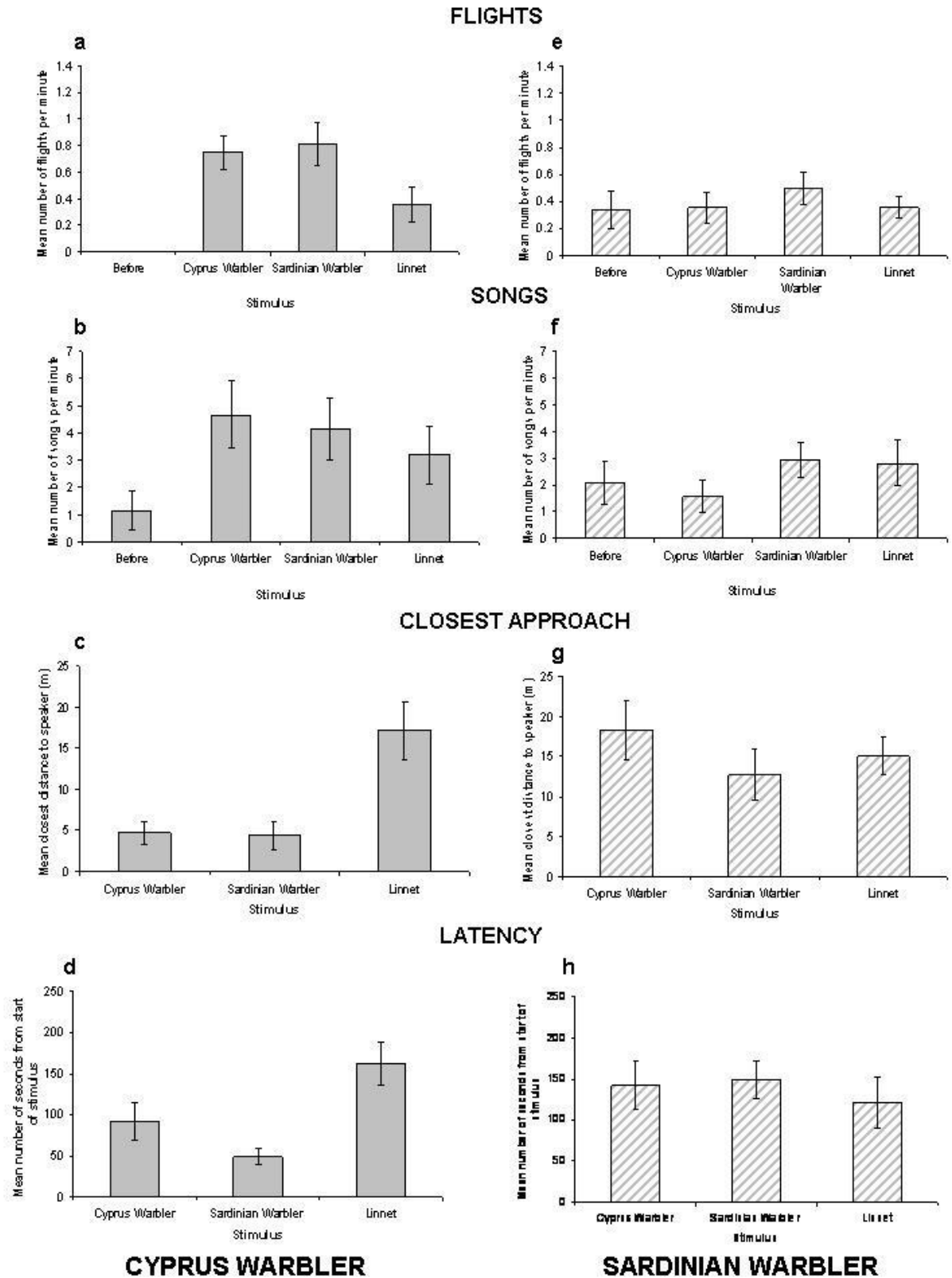


Figure 3.7 Four measures of responses by twelve male Cyprus Warblers (a-d) and twelve Sardinian Warblers (e-h) in zone 2 to playback of Cyprus Warbler, Sardinian Warbler and Linnet (control) song. Bars represent mean $\pm$ SE for responses before (a,b,e and f only), during and post-playback (4 min).

For the ‘closest approach’ and ‘latency to approach’ measures of response (Fig. 3.7c & d), the comparison is between the three stimuli with no pre-stimulus period, as both of these measures were recorded from the start of each stimulus. With the ‘latency to approach’ measure Cyprus Warblers approached the speaker most rapidly in response to Sardinian Warbler stimulus, slightly less rapidly in response to Cyprus Warbler stimulus and were relatively slow in responding to Linnet stimulus.

Wilcoxon test for differences in response to stimuli	Flights		Songs		Closest approach		Latency	
	Z	P	Z	P	Z	P	Z	P
Cyprus : Sardinian	9.00	0.844	24.5	0.719	12.0	0.953	15.0	0.064
Cyprus : Linnet	9.50	0.042	22.0	0.365	2.00	0.001	7.00	0.037
Sardinian : Linnet	11.0	0.044	9.00	0.088	0	<0.001	1.00	<0.001
Pre : Cyprus	0	<0.001	1.50	0.003	-	-	-	-
Pre : Sardinian	0	<0.001	1.00	0.008	-	-	-	-
Pre : Linnet	0	0.031	5.00	0.047	-	-	-	-

Table 3.6 Post-hoc Wilcoxon tests for difference in response of 12 Cyprus Warbler males to different stimuli during playback experiments.

Post-hoc Wilcoxon tests (Table 3.6) found no significant difference between Cyprus Warbler responses to Cyprus and Sardinian Warbler stimuli for any of the measures. With the exception of Cyprus Warbler song responses, responses to both Cyprus and Sardinian Warbler stimuli were significantly stronger than responses to Linnet stimulus for all measures. In addition, for flight and song, responses during all stimuli were significantly stronger than those recorded pre-stimulus.

Zone 2 Sardinian Warbler response to playback

For Sardinian Warblers, no significant difference was found between responses to the different stimuli for any of the four measures: number of flights per minute (Friedman: $X^2=1.18$, d.f.=3, $p=0.659$; Fig. 3.7e), number of songs per minute ($X^2=2.58$, d.f.=3, $p=0.418$; fig. 3.7f), closest approach to the speaker ($X^2=2.38$, d.f.=2, $p=0.274$; Fig. 3.7g), or latency to approach the speaker ($X^2=0.67$, d.f.=2, $p=0.656$;

Fig. 3.7h). In fact the level of flight and song activity occurring pre-stimulus was similar to that recorded with stimuli.

Close approach of Cyprus Warblers during zone 2 playback

For Cyprus Warbler neither stimulus (Binomial GLMM: $X^2=1.95$, d.f.=1, $p=0.163$; Fig. 3.8) nor order ($X^2=0.66$, d.f.=2, $p=0.720$) were found to have a significant effect on whether or not Cyprus Warblers approached to within 5 m of the speaker. This indicates that there was no significant difference in Cyprus Warbler close approach in response to conspecific versus congeneric stimuli.

For Sardinian Warblers, neither stimulus ($X^2=0.27$, d.f.=2, $p=0.602$) nor order ($X^2=0.66$, d.f.=2, $p=0.719$) were found to have a significant effect on approach to within 5 m of the speaker (Fig. 3.8).

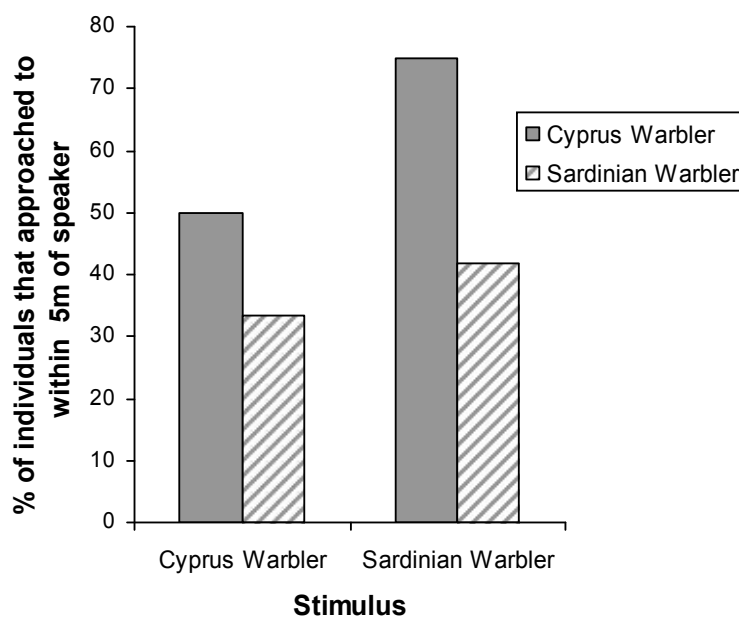


Figure 3.8 Percentage of zone 2 Cyprus Warblers (n=12) and Sardinian Warblers (n=12) that approached to within 5 m of the speaker when presented with conspecific and congeneric stimuli during playback experiments.

Zone 3 Cyprus Warbler response to playback

After sequential Bonferroni adjustment, zone 3 Cyprus Warblers showed a significant difference in number of flights made in response to the different stimuli (Friedman:

$X^2=13.4$, d.f.=3, $p=0.002$; Fig. 3.9). Pairwise comparisons showed that the number of flights performed by zone 3 Cyprus Warblers was not significantly different in response to conspecific and congeneric stimuli (Wilcoxon: $Z=8$, $p=0.688$). There was a significant difference between number of flights performed pre-stimulus and during Cyprus Warbler stimulus ($Z=0$, $p=0.031$), pre-stimulus and during Sardinian Warbler stimulus ($Z=0$, $p=0.031$) and during Sardinian Warbler versus Linnet stimuli ($Z=0$, $p=0.031$).

No significant difference was found between responses to the different stimuli for number of songs per minute ($X^2=2.85$, d.f.=3, $p=0.400$), closest approach to the speaker ($X^2=5.33$, d.f.=2, $p=0.055$) or latency to approach the speaker ($X^2=4.08$, d.f.=2, $p=0.119$).

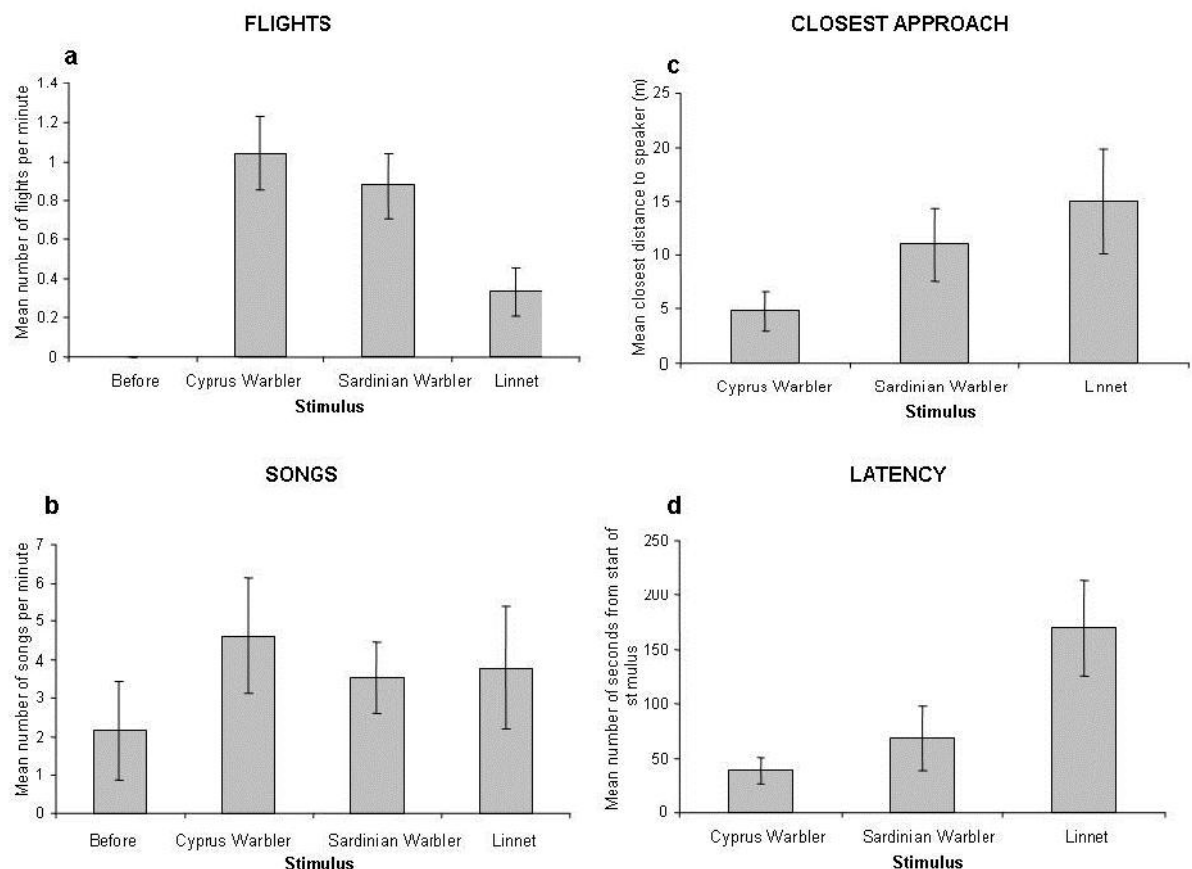


Figure 3.9 Four measures of response of male Cyprus Warblers ($n=6$) in zone 3 to playback of Cyprus Warbler, Sardinian Warbler and Linnet (control) song. Bars represent mean $\pm$ SE for responses before (a and b only), during and post-playback (4 min).

Comparison of Cyprus Warbler response to playback in zones 2 and 3

I tested whether or not there were differences in Cyprus Warbler approach to within 5 m of the speaker with conspecific and congeneric stimuli in the two zones. There was no significant effect of zone (Binomial GLMM: $X^2=0.22$, d.f.=1, $p=0.640$), stimulus ($X^2=0.13$, d.f.=1, $p=0.718$) or order ($X^2=0.86$, d.f.=2, $p=0.652$) on whether or not Cyprus Warblers approached to within 5 m of the speaker. There was a marginally non-significant interaction between zone and stimulus ($X^2=3.23$, d.f.=1, $p=0.072$).

Although the sample size and therefore the statistical power was small, the pattern of responses of Cyprus Warblers in zone 2 (Fig. 3.7) was slightly different from that in zone 3 (Fig. 3.9). For all four response measures zone 2 Cyprus Warblers tended to respond equally strongly to conspecific and congeneric song, or more strongly to congeneric song, while for every behavioural measure, zone 3 Cyprus Warblers responded more strongly to conspecific playback than to congeneric playback.

Although there was no statistical difference between Cyprus Warbler approach to within 5 m in the two zones, the pattern of response (Fig. 3.10) differed between the two zones in the same respect as for the four behavioural measures (Fig. 3.9). In zone 2, the pattern indicated a higher percentage of individuals approaching within 5 m when played congeneric than conspecific song, whereas in zone 3, a higher percentage of individuals approached closely in response to conspecific than to congeneric song.

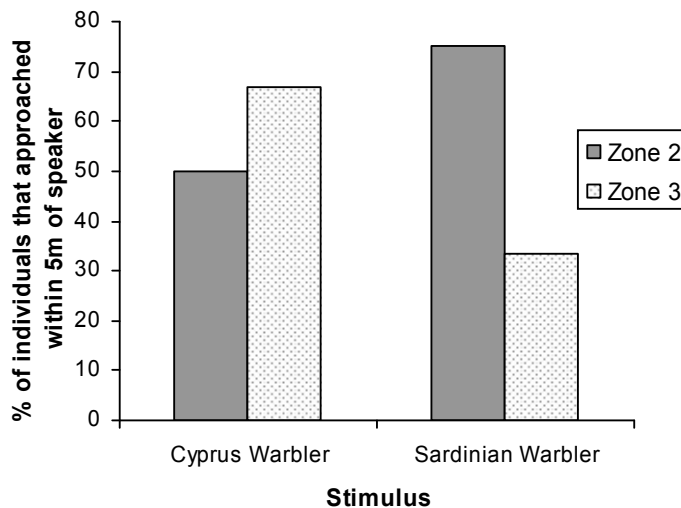


Figure 3.10 Percentage of zone 2 (n=12) and zone 3 (n=6) Cyprus Warblers that approached to within 5 m of the speaker when presented with conspecific and congeneric stimuli during the playback experiments.

Results 3: Behavioural observations

Aggressive behaviour observed is summarised in Table 3.7. More conspecific chases were recorded between Sardinian Warblers than between Cyprus Warblers, but in congeneric interactions, slightly more Cyprus Warblers were recorded chasing Sardinian Warblers than vice versa and twice as many Cyprus Warblers were recorded chivvying Sardinian Warblers than vice versa. No physical fights were recorded between the two species and there were nine recorded incidents of a Cyprus Warbler and a Sardinian Warbler within 2 m of one another with no apparent reaction from either.

Behaviour	Cyprus→ Cyprus	Cyprus→ Sardinian	Sardinian→ Sardinian	Sardinian→ Cyprus	Not identified
Chase	15	6	24	4	-
Chivvy	6	8	3	4	-
Fight	3	-	2	-	1

Table 3.7 Summary of aggressive behaviour observed during 2003-2005 breeding seasons with initiator listed first. Chase – one individual pursuing another in flight. Chivvy – low level aggression usually involving one individual slowly pursuing another through vegetation, sometimes with vocalisation. Fight – one individual physically attacks another. Any one interaction is listed as either chase, chivvy or fight.

Discussion

Home-range size

Cyprus Warbler breeding density varied between plots in this study, but was generally towards the higher limit of the 5-170 pairs/km² (previously reported on Cyprus (Shirihai *et al.* 2001). The highest density of 223 Cyprus Warbler pairs/km² recorded at Kouklia Hives in 2004 exceeds the previous maximum density estimate. Mean pair home-range size for Sardinian Warblers by 95% MCP area or the circle method was an order of magnitude smaller than has been recorded for radio-tracked male Sardinian Warblers during the breeding season in Spanish shrubland (Bas *et al.* 2005). In addition, the densities of up to 559 Sardinian Warbler pairs/km² recorded in this study far exceeded the 76-93 pairs/km² recorded in favourable habitat in France (Shirihai *et al.* 2001).

Both Cyprus and Sardinian Warblers clearly breed at high density in the scrub habitat represented by my study plots. This suggests that either this habitat is particularly favourable for both species or it reflects the fact that no other *Sylvia* breed sympatrically with Cyprus and Sardinian Warbler in Paphos District, Cyprus. In contrast, in Spain and France three other *Sylvia* species may occur syntopically with Sardinian Warblers.

Although Cyprus Warbler home-ranges tended to be slightly larger, once the effect of site was removed, there was no significant difference between home-range sizes (using either method) for Cyprus and Sardinian Warbler. This seems to be in contrast to Cody's (1979) findings for the *Sylvia* community on Sardinia, where Sardinian Warbler was the more dominant, aggressive species with a more generalised feeding ecology, broader niche and, in any particular habitat type, much larger territories than its 'more specialised and presumably more efficient congeners'. It may be that Cyprus Warblers, having evolved with few sympatric *Sylvia* species has similarly generalised feeding ecology, and this will be investigated further in Chapter 6.

Interspecific home-range distribution

If Cyprus and Sardinian Warblers were interspecifically territorial, we would expect nearest neighbours to be a similar distance away, whether conspecific or congeneric. In fact, for both species, conspecific nearest-neighbour distances were significantly larger than congeneric nearest-neighbour distances, indicating that the two species are not interspecifically territorial. The maps show considerable overlap between home-ranges of the two species. Martin & Thibault (1996) found that Marmora's Warblers and Sardinian Warblers overlapped extensively with no particular pattern of spatial segregation. They found that the greatest overlap occurred in the most heterogeneous vegetation and lowest overlap occurred when the vegetation was homogeneous. It would be interesting to test whether this was the case between Cyprus and Sardinian Warblers across a range of different habitats.

Does the apparent lack of interspecific spatial segregation reflect a lack of interaction or does either species exhibit aggressive behaviour towards the other? Given their spatial relationship, one would predict that both species should show stronger responses to conspecific playback than congeneric playback.

Relative strength of responses to playback

The fact that Sardinian Warblers responded to playback relatively weakly and did not show any difference between their behaviour prior to the start of playback and their behaviour during any of the stimuli is surprising. Perhaps they perceived all playback as unnatural and therefore did not react to it. If this is the case it is difficult to explain why Cyprus Warblers did react.

Cody (1979) found that, in Sardinia, Sardinian Warbler was dominant over the other *Sylvia* (Dartford Warbler *S. undata* and Marmora's Warbler) with which it interacted, even chasing and fighting. However, it overlapped other species in this habitat or the same species in other habitats without exhibiting aggression. Cody also noted that in Morocco, where Sardinian Warbler overlaps with three *Sylvia* species without interaction, Sardinian Warblers failed to respond to playback of heterospecific song.

Sardinian Warbler is a generalist species which regularly coexists with other *Sylvia* species in other parts of its range. The provenance of the breeding population on Cyprus is not yet known, but my morphometric measurements (Appendix 1) indicate that these birds belong to the subspecies *Sylvia melanocephala melanocephala*. The only ringing recovery of a Sardinian Warbler in Cyprus (March 1974) came from Turkey (Flint & Stewart 1992) and the closest breeding population of this subspecies is in southwest Turkey, where Sardinian Warblers occur sympatrically with at least five other breeding *Sylvia* species (Shirihai *et al.* 2001). The genus *Sylvia* exhibits its highest species diversity in the Mediterranean region, so whether Cyprus's breeding population of Sardinian Warbler originated in Turkey, Greece, or elsewhere in the Mediterranean, it must have evolved in the company of other breeding *Sylvia*. In contrast, Cyprus Warbler has evolved on an island which, like many islands, is rather depauperate in breeding species. Apart from Cyprus and Sardinian Warbler, the only other *Sylvia* to breed on Cyprus is Spectacled Warbler which is found largely on the central plain and is therefore largely non-sympatric with Cyprus Warbler. Thus, Cyprus and Sardinian Warbler are likely to have evolved under quite different selective pressures. Sardinian Warbler may have adapted not to react strongly to congeneric song, while Cyprus Warbler, which until recently, did not have to coexist with other *Sylvia* during the breeding season, reacts more strongly.

Asymmetric responses to playback in species pairs are relatively common. Mirroring the situation in the present study, Willow Flycatcher (*Empidonax traillii*) has recently expanded its range into areas historically occupied by Alder Flycatcher (*E. alnorum*). In contrast to findings of the present study, during playback experiments Willow Flycatcher responded more aggressively than Alder Flycatcher to both conspecific and congeneric playback (Prescott 1987). Catchpole (1978), studying sympatric Sedge (*Acrocephalus schoenobaenus*) and Reed Warblers (*A. scirpaceus*) in the UK and sympatric Reed and Marsh Warblers (*A. palustris*) in Germany, found that only one member of each sympatric species pair reacted to playback of the other species' song. In both cases, the species which reacted was the first to arrive and establish territories at the start of the breeding season. Martin & Martin (2001a) found that the larger and earlier arriving Orange-crowned Warbler (*Vermivora celata*) was aggressive towards the later arriving Virginia's Warbler (*V. virginiae*), while Virginia's

Warbler avoided the speaker during playback of Orange-crowned Warbler song. Well-established males are often dominant and later arriving species are often submissive in interspecific interactions (Murray 1971). Cyprus Warbler is a partial migrant, and a proportion of male Cyprus Warblers remains on the breeding home-range over-winter. A proportion of breeding Sardinian Warblers now also remains on the breeding home-range over winter (pers. obs.). To investigate whether one species had an advantage over the other by settling earlier, I carried out early morning counts of singing males of both species at the mixed sites Ineia, Choli and Lysos from the end of February until the beginning of April in 2004. These counts indicated that males of both species had settled by early March and the relative proportions of the two species singing during this period tended to simply reflect the proportion of the two species that later bred on the study plot (Appendix 2).

Cyprus Warblers showed a definite reaction to playback as is evident from the significant differences between their behaviour pre-stimulus and during stimuli for all of the measures. The fact that Cyprus Warblers tended to respond equally strongly to conspecific and congeneric song in all the behavioural measures is very interesting. In general, male birds react more strongly to playback of conspecific song than heterospecific song (Catchpole & Slater 1995). Sardinian Warblers therefore show the pattern of behaviour one might expect, with more individuals approaching closely in response to conspecific song than to congeneric song, and fewest responding to the control. Catchpole (1978) suggested that proximity to the speaker gives the clearest indication of an individual's level of aggression. In real conspecific or congeneric encounters observed in this study, close approach often preceded a chase (pers. obs.). Therefore the fact that zone 2 Cyprus Warblers closely approached the speaker in response to both congeneric and conspecific stimuli is particularly interesting. Behavioural observations in the field support the findings of the playback experiment, showing more incidents of interspecific aggression instigated by Cyprus Warblers on Sardinian Warblers than vice versa. This finding contrasts with that of Martin and Thibault (1996) who studied four *Sylvia* species in Sardinia. They observed nine direct antagonistic interactions; in all nine cases Sardinian Warbler was the aggressor, other species being attacked in seven of these cases. Considering the high degree of congeneric home-range overlap, interspecific

aggression was relatively rare compared to conspecific aggression. Highly aggressive activities like chasing and fighting were considerably more common between conspecifics than congeners and it appears that interspecific aggression was more likely to take the form of low level chivvying behaviour.

Mistaken identity?

It may be that Cyprus Warblers are unable to discriminate between the two songs and therefore reacts strongly to both, effectively mistaking Sardinian Warbler song for conspecific song. Murray (1981) suggested that interspecific territoriality essentially arises from misdirected intraspecific aggression, because through common ancestry, convergence or chance, individuals of different species possess traits in common that stimulate intraspecific aggression. At first sight this appears a reasonable explanation for the aggression Cyprus Warblers show towards Sardinian Warblers in zone 2. The two species' songs are quite similar and Cyprus Warblers have not evolved in circumstances where they were breeding syntopically with other *Sylvia* species; they have therefore not had long to evolve discrimination (breeding Sardinian Warblers have only gradually spread across zone 2 from the Akamas since 1992). Selection should favour those males which are able to or learn to discriminate, because it is maladaptive to waste energy responding unnecessarily to congeneric song. Similarly, there should be strong selective pressure acting on female Cyprus Warblers to distinguish conspecific from congeneric males, as choosing an appropriate mate is critical to an individual's fitness. The fact that no mixed species pairs were found during the course of this study indicates that both species are capable of making the distinction. Of course discrimination by either sex may be based on learning to associate multiple traits, some of which may be visual (Gill & Murray 1972, Grant & Grant 1997, Irwin & Price 1999). It is possible that in a natural situation Cyprus Warbler males respond to Sardinian Warbler song, mistaking it for conspecific song, but cease to react once they have the opportunity for visual identification.

However, the songs of the two species, while similar, are sufficiently different for the experienced fieldworker to be able to distinguish the two species accurately more than 90% of the time. In addition, birds are generally extremely good at learning to distinguish subtle differences even within conspecific song to, for example, recognise

neighbours from strangers (Fisher 1954, Weeden & Falls 1959, Falls & Brooks 1975, Godard 1991). Among *Sylvia* warblers, Blackcaps (*S. atricapilla*) have been found to differentiate between conspecific and congeneric song, associate heterospecific song with heterospecific plumage and retain this information long-term (Matyjasiak 2005). All of this suggests that it is unlikely that Cyprus Warblers are simply unable to distinguish between Cyprus and Sardinian Warbler song.

An adaptive response?

If Cyprus Warblers in zone 2, which occur syntopically with breeding Sardinian Warblers are unable to distinguish between Cyprus and Sardinian Warbler song and are misdirecting intraspecific aggression, we would expect zone 3 Cyprus Warblers, which have little or no experience of breeding Sardinian Warblers, to have even poorer discrimination and therefore also to react equally strongly to conspecific and congeneric playback. No significant difference was found between zone 3 Cyprus Warblers' responses to conspecific and congeneric stimuli. However, the very small sample size meant that any statistical tests from playback experiments on zone 3 Cyprus Warblers had very low power. The pattern which emerged was that zone 3 Cyprus Warblers reacted more strongly to Cyprus than to Sardinian Warbler stimuli for all behavioural measures. This could indicate that Cyprus Warblers can in fact discriminate, but that Cyprus Warblers in zone 2 have learned to, or are under selective pressure to, react aggressively to Sardinian Warbler song. It would be interesting to compare responses of a larger sample of Cyprus Warblers in zone 2 and zone 3 to investigate this further.

Other researchers have found evidence that interspecific aggression is not simply misdirected intraspecific aggression with behaviour to heterospecific stimuli differing either in nature or strength (Catchpole & Leisler 1986, Prescott 1987, Martin & Martin 2001a). Sedlacek (2004) found that Black Redstart (*Phoenicurus ochuros*) responded almost as strongly to Redstart (*P. phoenicurus*) playback as to conspecific playback and were also dominant in natural encounters. They suggested that regular interbreeding between the two species (which have segregated territories) means that heterospecific males may represent male competitors, and interspecific aggression could therefore operate as a pre-copulation barrier. Although Cyprus and

Sardinian Warblers are relatively closely related, there are no confirmed cases of hybridisation; therefore, this is unlikely to explain Cyprus Warbler aggression.

The context of playback has proven very important in determining response, with several other studies also finding much stronger reactions to congeneric playback in areas where the two species occur syntopically in sympatry than in allopatry (Emlen 1975, Catchpole & Leisler 1986, Prescott 1987). It is notable, however, that in many of these cases the two species concerned also exhibited interspecific territoriality. Fascinatingly, some authors have actually found that those individuals that respond to heterospecific song are those whose territories adjoin a heterospecific, implying that individual learning is the key (Catchpole & Slater 1995).

The data from the present study may allow an ecological explanation. Cyprus Warblers in zone 2 may have learned to react aggressively to Sardinian Warblers, because they are a competitor. Learning is known to involve heritable elements, and it is possible that selection is taking place in zone 2, such that those individuals that have successfully learned to respond to Sardinian Warbler song achieve higher breeding success.

Choice of control

For most of the response measures, Cyprus Warblers reacted significantly more strongly to conspecific and congeneric stimuli than in response to the control (Linnet), as we might expect. However, Cyprus Warblers did not sing significantly more in response to conspecific and congeneric song than in response to control song (Linnet) and Sardinian Warblers generally reacted more than expected to the control song. This could mean that Linnet was not an ideal choice as a control. Since nestling diet of Linnets has not been studied in Cyprus, it remains possible that Linnets do compete with Cyprus and Sardinian Warblers for nestling insect food, and this could explain the response of both Cyprus and Sardinian Warblers to Linnet playback. It is interesting to note, however, that Cyprus Warblers flew significantly less, were considerably slower to approach the speaker and approached it significantly less closely in response to Linnet playback than in response to congeneric or conspecific stimuli. This indicates that, while Cyprus Warblers may be

stimulated to sing in response to Linnet song, their agonistic response in physically approaching the 'intruding Linnet' is much weaker than with conspecific or congeneric playback. It would be interesting to try the experiment again using a different species as a control.

Conclusions

Previous studies have used the terms 'interspecific territoriality' or 'interspecific territorialism' to mean both aggressive behaviour directed towards a heterospecific, and the defence of mutually exclusive territories. This use of terms implied that the two aspects of behaviour are inextricably linked. Many previous studies have examined either one or the other aspect of interspecific territoriality. Studies where both aspects have been examined have generally shown lack of interspecific spatial segregation to be accompanied by little or no response to heterospecific playback (Reed 1982, Robinson & Terborgh 1995) and/or interspecific spatial segregation accompanied by a strong response to heterospecific playback (Garcia 1981, Reed 1982, Garcia 1983, Prescott 1987, Robinson & Terborgh 1995, Sedlacek *et al.* 2004). The case of Cyprus and Sardinian Warblers may demonstrate asymmetric interspecific aggression in the absence of mutually exclusive territories. Martin & Martin's (2001a) study of Wood Warblers may provide a parallel with the present study; Orange-crowned Warblers reacted strongly to Virginia's Warbler playback, yet the two species have completely overlapping breeding territories.

The strong response of zone 2 Cyprus Warblers to Sardinian Warblers may be in some way adaptive. The most obvious possibility with two congeners of similar size is that the two species compete for food and this will be explored further in Chapter 6. If this is the case, why don't Cyprus and Sardinian Warblers exhibit interspecific spatial segregation to avoid competition? Minot (1981) found that Great Tit and Blue Tit (*Parus caeruleus*) territories may overlap completely, especially in high density years, with no suggestion of interspecific territoriality, even though the two species compete for nestling food. Clearly, defending a territory against heterospecifics as well as conspecifics carries energetic costs, so interspecific territoriality would only be expected to occur where the benefits exceed these costs, i.e. where the costs of food competition are very high. However, even in the absence of interspecific territoriality,

one would expect two species with overlapping territories and similar diet to suffer some level of cost through competition for food. It may not be sufficient to provoke evolution of interspecific territoriality, but could still have a negative impact on either species. This will be explored further in Chapter 6.

A second possible explanation for Cyprus Warbler aggression is that overlap with Sardinian Warblers results in a negative impact on breeding through increased predation. This possibility will be investigated in Chapters 4 and 5.

It would be interesting to test both of these ecological explanations for Cyprus Warbler aggression by providing supplemental food in some areas to investigate whether this lessened interspecific aggression in playback experiments. The predation hypothesis could potentially be tested by playing predator calls, for example calls of Magpie (*Pica pica*) or Great Spotted Cuckoo (*Clamator glandarius*), in some areas to see whether this increased the level of interspecific aggression shown by Cyprus Warblers.

It must be borne in mind that the coexistence of Cyprus and Sardinian Warblers during the breeding season is relatively recent and we may simply be observing a 'snapshot' of ongoing evolution. One can imagine a situation where, initially, one species reacts with aggression to the other, possibly even stimulating a niche shift or character displacement (Brown & Wilson 1956, Lack 1971), which would, in turn, reduce competition, relaxing the selective pressure for interspecific aggression. Likewise, relationships which began in the same way could eventually result in defence of mutually exclusive interspecific territories, with continued interspecific aggression, but this may also not be a static state.

Orians & Willson (1964) suggested that interspecific aggression may be expected where populations of two species come into contact for the first time. In the present study we may be witnessing the very early stages of species coexistence; currently the two species may occupy similar niches and this may be resulting in interspecific aggression in areas where Cyprus and Sardinian Warblers overlap. Interspecific territoriality, differentiation of foraging behaviour, or character shift allowing

coexistence are possible outcomes of the selective pressure exerted by coexistence. We do not yet know what the outcome of the interaction between these two species will be.

Situations like the present study, where new relationships are forming between previously allopatric breeding species, provide a fascinating insight into what drives interspecific aggression. Understanding the dynamic nature of interspecific relationships will become increasingly important as habitat alteration and climate change continue to change the nature of bird communities, and range changes bring new contacts between hitherto allopatric species.

Chapter 4

A comparison of nest-site selection and home-range habitat characteristics in Cyprus and Sardinian Warblers

Introduction

Habitat selection can occur on numerous spatial scales. All bird species are to some extent restricted in the range of habitats they use, because of species-specific requirements for nest-sites, food and other resources (Wiens 1989). At a broad scale, therefore, a species may be confined to a subset of habitat types, while at a medium scale, a population may be confined to a particular area of habitat. At a fine-scale, individuals or pairs locate their home-range within an area of habitat, which may comprise many small patches of different types of vegetation. The scale at which observations are made is important in influencing understanding of ecological processes (Kelt *et al.* 1999, Moura *et al.* 2005).

Pomeroy and Walsh (2002) found Cyprus Warblers (*Sylvia melanothorax*) and Sardinian Warblers (*Sylvia melanocephala*) at varying densities in a wide range of habitats at a broad scale across Paphos District, including coastal juniper, pine forest, scrub, grassland, cultivated groves, abandoned farmland and arable crops. As they point out, there are few large areas of pure habitat in Paphos District and the landscape is a relatively fine scale mosaic of different habitats.

Fine-scale vegetation composition of warbler home-ranges

The scrub habitat on which I have chosen to focus this study is very heterogeneous, consisting of a mosaic of maquis and garrigue within which there are some patches of trees and some very open areas more closely resembling phrygana (Chapter 2). In Chapter 3, I established that Cyprus Warblers and Sardinian Warblers exhibit considerable interspecific overlap of home-ranges in this habitat, which suggests that,

at a basic level, the same scrub habitat is suitable for both species. However, even with interspecific home-range overlap, it is possible for species to have different habitat preferences at the patch scale (Martin & Thibault 1996). Cyprus and Sardinian Warblers could differ in their fine-scale habitat selection, and the overlap observed could occur because some patch types are selected by both species. Determining whether home-ranges of the two species are qualitatively different is important in informing the overall question of whether the two species are likely to be competing.

In Chapter 3 I showed that the density of breeding pairs varied considerably between study plots. Since there are energetic costs to defending a large home-range, birds normally only defend the area required to supply sufficient resources (Brown 1964). For insectivorous species which glean from vegetation, the height of vegetation contained within a home-range might predict the amount of food resources available. In this chapter I investigate whether density of breeding pairs is related to vegetation height on different study plots.

Do Cyprus and Sardinian Warblers choose similar nest-sites?

The fact that Cyprus and Sardinian Warblers overlap in home-range also raises the possibility that the two species could compete for nest-sites. Nest-site competition has been found commonly in bird species which nest in holes or nest boxes (Newton 1994), but interspecific exclusion from preferred nest-sites has also been found in some open cup-nesting species (Martin & Martin 2001b). Predation is the most important cause of nest failure in many avian species (Ricklefs 1969, Safford 1997, Grant *et al.* 1999, Donald *et al.* 2002). Choice of nest-site is known to be an important factor influencing predation rates of nests in passerine species (Martin & Roper 1988). Therefore any differences between Cyprus and Sardinian Warblers in choice of nest-site could affect breeding success and consequently, population trend.

Five main questions will be addressed in this chapter:

- Do Cyprus and Sardinian Warblers show differences in fine-scale habitat preferences at the home-range level?
- Is breeding density of warbler pairs related to vegetation height?
- Do the two species select particular nest bushes or simply use them in proportion to their availability?
- Do the two species differ in their choice of nest-site and in the structure of their nests?
- Are any nest-site characteristics associated with risk of predation?

Methods

Vegetation transects in home-ranges

Vegetation transects were carried out after the 2004 breeding season on all 2004 breeding home-ranges of Cyprus and Sardinian Warblers at all sites. Home-ranges of breeding pairs were mapped and the GPS coordinates for the centre point of each home-range were noted (Chapter 3). On each territory four 20 m transects were marked with a measuring tape radiating out north, south, east and west from the centre point. Conspecific home-range centres of Cyprus and Sardinian Warblers were on average separated by 63.3 and 54.2 m respectively (Chapter 3), so the 40 m span of the transects covered the majority of the home-range in most cases. The vegetation intersected by the tape was recorded in 0.5 m sections. The species of plant lying under the majority of each section was recorded (Viney 1994, Tsintides et al. 2002) and the height, length and breadth of the whole plant were measured. Rarely, the vegetation clearly comprised distinct layers (e.g. a tree overhanging other plants) and so the composition of the two layers was recorded separately; for simplicity only the upper layer was included in analysis. Where transects intersected rock, earth or sparse herbs, this was recorded as 'open ground'.

Nest-site characteristics

Measurements were taken at every Cyprus and Sardinian Warbler nest found once young had fledged or the nest had failed. In all years characteristics recorded included: nest bush species, nest height, nest bush height, nest bush breadth, nest bush length and nest distance from bush edge. In 2003 and 2004 nest dimensions were also measured and an index of nest visibility (defined below) was calculated for all nests.

Nest height was measured from the ground beneath the nest to the base of the nest. Nest bush height was measured from the ground to the highest point of the bush. Nest bush length was measured between the extremities of the longest axis of the bush. Nest bush breadth was measured on the axis perpendicular to the length axis. Nest distance from bush edge was measured as the shortest distance between the outer rim of the nest and the edge of the nest bush. Nest external diameter was the diameter across the outer rim of the nest. Nest internal diameter was the diameter across the inner rim of the nest cup. Nest external depth was the vertical distance between the external nest base and the rim. Internal nest depth was the vertical depth of the nest from the base of the cup to the rim. Two measures of nest thickness were obtained. The first, thickness of rim, was obtained by subtracting the internal diameter from the external diameter of the nest cup. The second, thickness at base, was obtained by subtracting internal depth from external depth of the nest. Where nests were clearly elliptical, two measurements were taken for internal and external diameter (across the longest axis and then at a right-angle to the longest axis) and the average of each was used.

Three measurements of nest visibility were also recorded, using a thin 12 cm stake bearing 13 luminous red dots at 1 cm intervals. With the observer 1 m from the nest, the number of dots visible was recorded with the stake in three different positions around the nest (Fig. 4.1). With the stake in positions 1 and 2 (shown below), the observer viewed the stake from 1 m away on whichever side of the nest was closest to the bush edge. In position 3, the observer viewed the stake from 1 m above the nest. The number of dots visible in the three positions was summed to provide an index of visibility, with high scores representing highly visible nests.

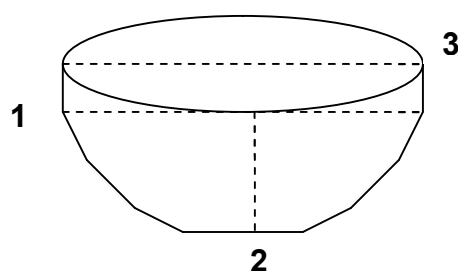


Figure 4.1 Measurement of nest visibility, using a stake bearing luminous dots placed in three positions around a nest, as indicated by the dotted lines.

Aspect of the nest was measured as the bearing of the nest from the central trunk of the bush.

Data analysis

Vegetation composition of warbler home-ranges

A number of vegetation measures were selected for analysis; for each 20 m transect these were mean height of the vegetation, number of transitions, number of species, number of sections intersecting bushes (less than 3 m in height), number of sections intersecting trees (more than 3 m in height), along with the number of sections intersecting nine key bush species (the nine most commonly recorded species on the seven study plots; Table 4.1). Number of transitions was established by counting the number of times that vegetation category (categories being the different plant species and open ground) changed between sections on a 20 m transect. For illustration, a 20 m transect comprising 20 0.5 m sections of *Genista sphacelata* followed by 20 0.5 m sections of *Calycotome villosa* would include only one transition, whereas a 20 m transect comprising 10 sections of *G. sphacelata* followed by 10 sections of *C. villosa*, another 10 sections of *G. sphacelata* and finally 10 more sections of *C. villosa* would include three transitions. For every home-range each vegetation measure value was the mean from the four 20 m vegetation transects.

Comparisons of Cyprus and Sardinian Warbler home-range vegetation were only made for sites with a minimum of three home-ranges for each species. To allow vegetation measures to be pooled across sites while controlling for differences in

vegetation between sites, data for each home-range were converted to deviations from the site mean (by simply subtracting the site mean for a particular habitat measure from the figure recorded for each home-range). Independent samples t-tests were then conducted comparing means of these deviations for Cyprus and Sardinian Warblers for each vegetation measure. Principal Component Analysis (PCA) or Explanatory Factor Analysis (EFA) are commonly used tools for collapsing a large number of variables into a smaller number of components. However, these techniques are most effective with large 'subject to item ratios'; in this case, a large sample sizes of home-ranges compared to the number of vegetation measures. However, since the vegetation composition differed between sites, a separate PCA would be necessary for each site, leaving the subject to item ratio short of the 5:1 ratio recommended as a minimum by some authors for EFA (Gorusch 1983, Hatcher 1994) and the 5:1 to 10:1 subject to variable ratio recommended for PCA (Nunnally 1978).

Nest bush use compared with availability

Sizes and species of bushes intersecting transects were recorded to compare nest bush selection with availability of bushes of different sizes and species on the site (as measured in 2004). For nest bush selection and nest dimension analysis only those nests which were laid in were included. To avoid confounding effects of individual pair preferences, only a pair's first nest of the season was included and, where the same female nested in different years, one year was randomly selected for inclusion in statistical analysis. Only sites with at least three pairs of each species were used for comparison on Cyprus and Sardinian Warbler nest bush selection.

Compositional analysis is often appropriate for examining use versus availability (Aebischer *et al.* 1993). Unfortunately, since both the species and size composition of bushes available was unique to each study plot, sample sizes of nest bushes used on the same plot were small, even with the three years' data combined. I did not consider it instructive to compare a sample of 350-1000 bushes representing what was available on a study plot with a sample of just 6-19 nest bushes used by Cyprus Warblers or 3-28 nest bushes used by Sardinian Warblers on a given plot. Instead, I graphed the results for both species and size to allow visual inspection of the data.

Bush volume was calculated from bush height x bush length x bush breadth. In order to see whether the two species chose nest bushes of different sizes, I ran a linear mixed model (LMM) with nest bush volume rank as the dependent variable (since nest bush volume data could not be transformed to meet the assumptions of an LMM, ranks were used instead), bird species and year as fixed factors and site as a random factor.

Nest-site characteristics

In order to investigate whether the two species differed in the height at which they nested, how far from the edge of the bush they located their nests, or nest visibility, separate LMMs were run with either nest height (log-transformed to fit the assumptions of a LMM) or nest distance from bush edge as the dependent variable, bird species and year as fixed factors and site as a random factor.

Nest structure

Independent samples t-tests were performed to compare measurements of Cyprus Warbler and Sardinian Warbler nest structure. Nest volume was calculated by simplifying nest shape into a cylinder and calculating the volume of the cylinder, with external nest diameter as the cylinder's diameter and external nest depth as the cylinder's depth.

Nest-site characteristics and predation

To test whether particular features of nest-sites were associated with increased or decreased likelihood of predation, I first removed from analysis any nests known to have failed for reasons other than predation. I then ran a GLMM with binomial error structure; whether or not the nest was predated was the binomial response, nest bush volume, whether or not the bush was spiny, height of the nest, distance of the nest from the bush edge, nest visibility and nest volume as fixed factors and site as a random factor. Bush species were split into two classes, those species armoured with spines versus those species without spines as follows:

Spiny	Not spiny
<i>Genista sphacelata</i>	<i>Pistacia lentiscus</i>
<i>Calycotome villosa</i>	<i>Lithodora hispidula</i>
<i>Rhamnus oleoides</i>	<i>Cistus creticus</i>
<i>Sarcopoterium spinosa</i>	<i>Cistus salvifolius</i>
<i>Quercus coccifera</i>	<i>Cistus monspelliensis</i>
<i>Olea europea</i>	<i>Teucrium creticum</i>
	<i>Onosma fruticosa</i>

Results

Vegetation composition of warbler home-ranges

Although the different study plots appeared to differ in percentage cover of open ground, bushes and trees, the broad-scale vegetation structure within territories of the two species in any one plot was very similar (Fig. 4.2).

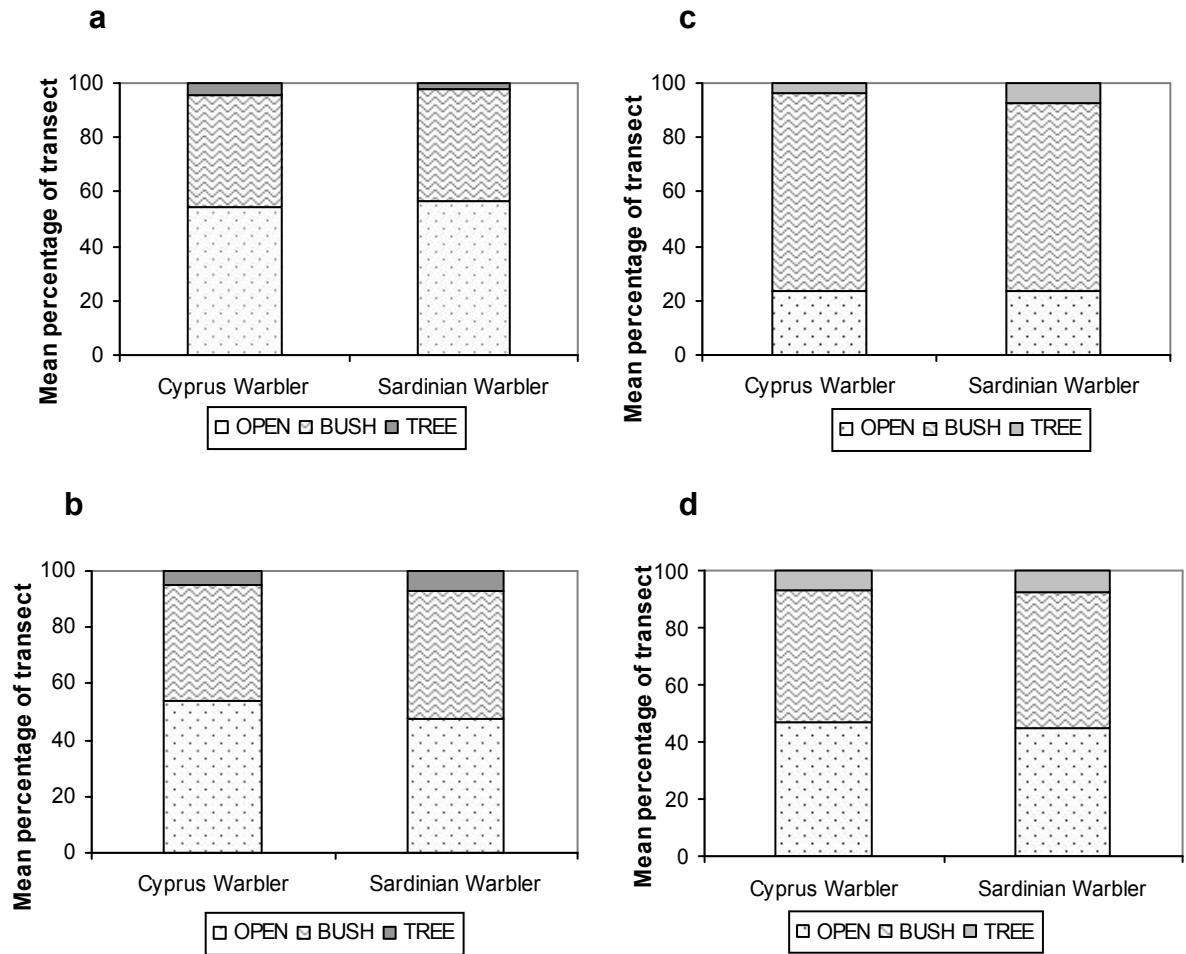


Figure 4.2 Percentage of open ground, bushes and trees on Cyprus Warbler and Sardinian Warbler home-ranges at a) Akamas 2, b) Ineia, c) Choli, d) Lysos in 2004. Means first calculated for each home-range, then across all home-ranges for the species on that site. Sample sizes for Cyprus Warbler home-ranges: a-4, b-7, c-6, d-4. Sample sizes for Sardinian Warbler home-ranges: a-7, b-6, c-8, d-13.

Vegetation transects were used to compare fine-scale vegetation characteristics between Cyprus and Sardinian Warbler home-ranges at Akamas 2, Ineia, Choli and Lysos. No significant differences were found between the vegetation characteristics of Cyprus Warbler and Sardinian Warbler home-ranges for any of the measures, even without Bonferroni correction (Table 4.1).

Vegetation measure	Mean of average deviations from site means		t-test results (d.f.=53)	
	Cyprus Warbler	Sardinian Warbler	t	p
Mean height (cm)	-3.82 ± 6.69	2.36 ± 6.654	-0.620	0.539
Mean no. transitions	-0.0351 ± 0.727	0.0217 ± 0.521	0.0600	0.948
Mean no. species	-0.0434 ± 0.157	0.1574 ± 0.153	0.300	0.762
Mean no. bushes	-0.118 ± 0.870	0.0729 ± 0.914	0.140	0.888
Mean no. trees	-0.3162 ± 0.380	0.195 ± 0.466	-0.850	0.399
Mean no. <i>Cistus</i> spp.	0.110 ± 0.383	-0.0679 ± 0.416	0.290	0.772
Mean no. <i>Genista sphacelata</i>	0.129 ± 0.824	-0.0795 ± 0.658	0.200	0.845
Mean no. <i>Pistacia</i> spp.	-0.580 ± 0.498	0.358 ± 0.373	1.520	0.134
Mean no. <i>Calycotome villosa</i>	0.498 ± 0.731	-0.308 ± 0.420	1.03	0.308
Mean no. <i>Sarcopoterium spinosum</i>	-0.181 ± 0.301	0.112 ± 0.236	-0.760	0.488
Mean no. <i>Thymus integer</i>	-0.00359 ± 0.160	0.00222 ± 0.120	-0.0300	0.977
Mean no. <i>Lithodora hispidula</i>	0.0492 ± 0.151	-0.0304 ± 0.134	0.380	0.704
Mean no. <i>Rhamnus oleoides</i>	-0.0713 ± 0.0497	0.0440 ± 0.0590	1.360	0.180
Mean no. <i>Teucrium creticum</i>	0.230 ± 0.344	-0.142 ± 0.315	0.770	0.446

Table 4.1 Mean ± SE of deviations from site means for all vegetation measures on Cyprus and Sardinian Warbler home-ranges. Average vegetation measures for Akamas 2, Ineia, Choli and Lysos were established from all warbler home-range transects at that site, then data for each home-range were converted to deviations from the site mean. Sites were then pooled and independent samples t-tests conducted comparing deviations for Cyprus (n=21) and Sardinian Warbler (n=34) home-range vegetation for all measures.

There was no significant correlation between the mean height of vegetation on plots and the density of Cyprus Warbler pairs supported by that plot (Fig. 4.3).

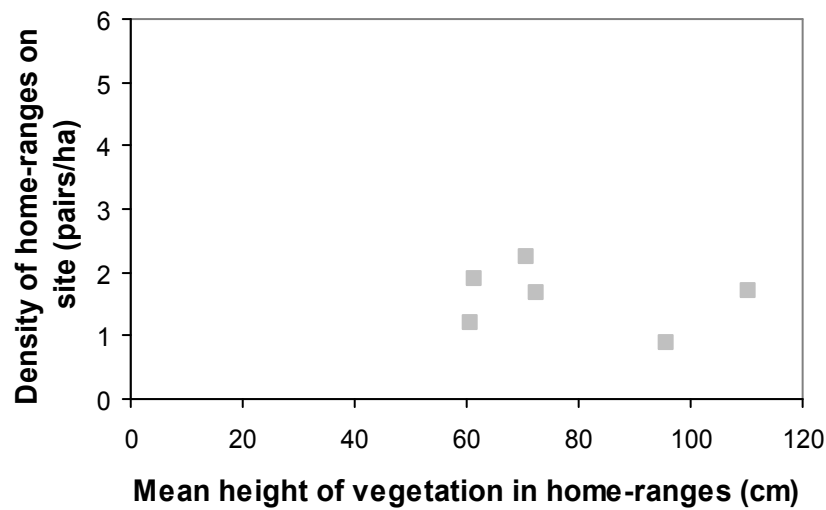


Figure 4.3 Relationship between mean height of vegetation on Cyprus Warbler home-ranges and density of Cyprus Warbler pairs occupying that site in 2004 breeding season ($r=-0.237$, $d.f.=4$, $p=0.652$).

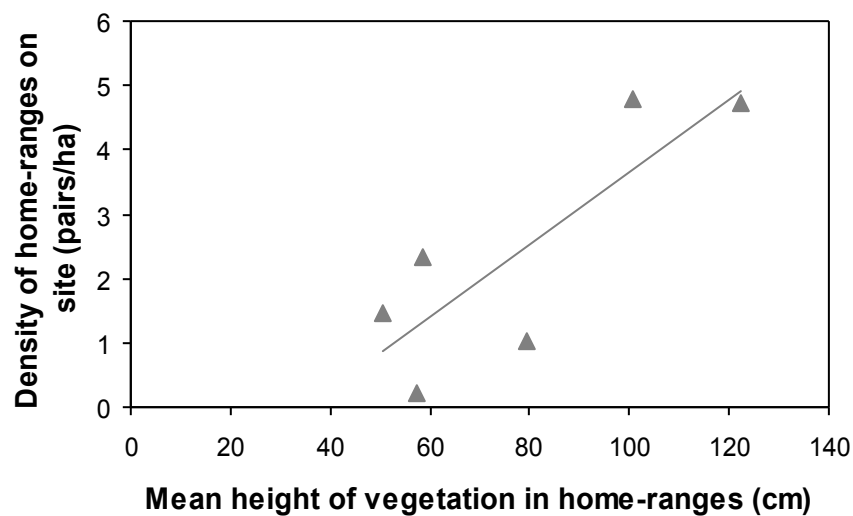


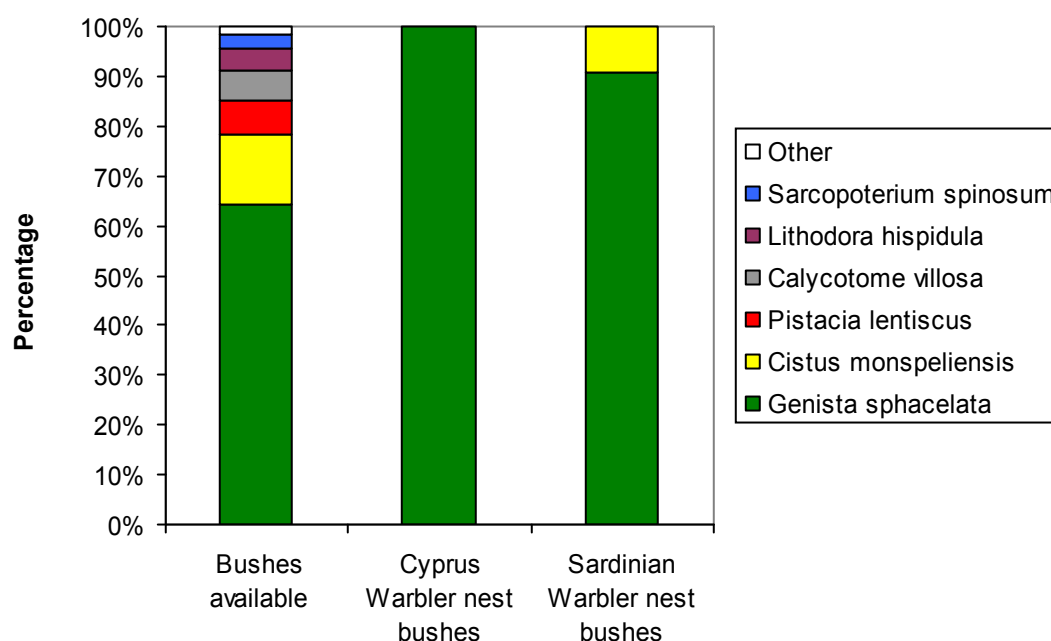
Figure 4.4 Relationship between mean height of vegetation on Sardinian Warbler home-ranges and density of Sardinian Warbler pairs occupying that site in 2004 breeding season ($r=0.828$, $d.f.=4$, $p=0.042$).

There was a significant positive correlation between the mean height of vegetation on Sardinian Warbler home-ranges and the density of Sardinian Warbler pairs supported by that plot (Fig. 4.4). This indicates that Sardinian Warbler pairs on plots with taller vegetation occupy smaller home-ranges.

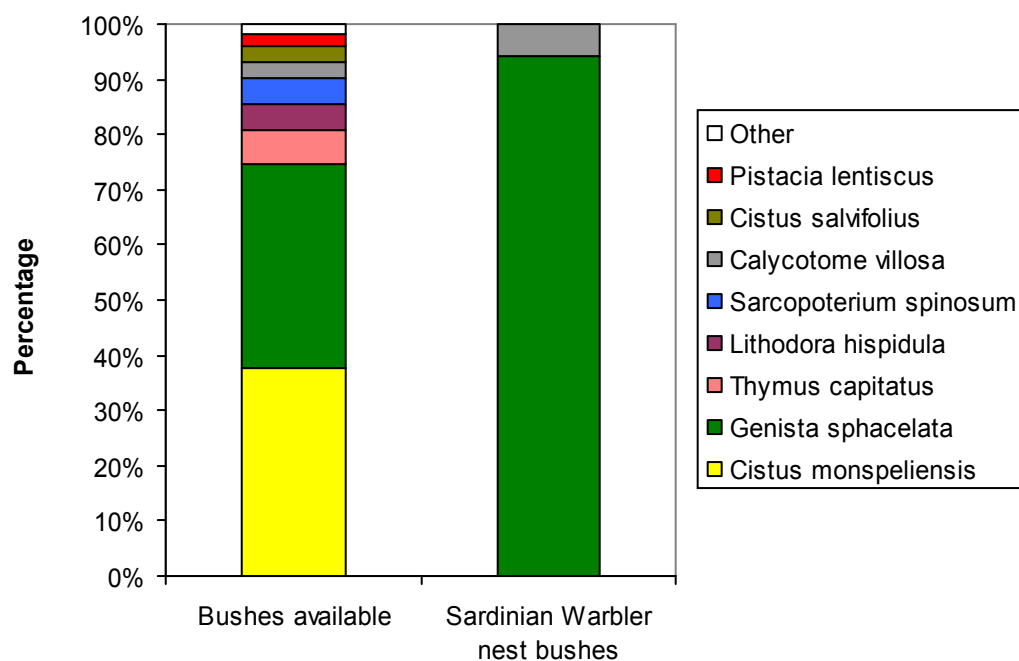
Nest bush use compared with availability

Figure 4.5 indicates that Cyprus and Sardinian Warblers select particular bushes for nesting. Cyprus Warblers at Ineia, Kouklia Hives and Kouklia 3, used *Genista sphacelata* three times more often than expected from its availability and *Rhamnus oleoides*, four to 15 times more frequently than expected from its availability on the sites. At Akamas 2 and Akamas Pines both Cyprus and Sardinian Warblers used *G. sphacelata* almost exclusively despite 36 % and 63 % of vegetation comprising other bush species. At Ineia and Lysos *Calycotome villosa* was used by Cyprus Warblers three and 15 times more frequently than predicted from its availability on the sites. At Choli, Lysos and Kouklia Hives *Lithodora hispidula* was used two to nine times more frequently than expected. Choli was the only site where *Teucrium creticum* was available and both Cyprus and Sardinian Warblers on this site nested in it three times more often than expected from availability. In general nest bush preferences of Sardinian Warblers were similar to Cyprus Warblers', but at Ineia, Choli and Kouklia Hives some Sardinian Warblers used *Pistacia lentiscus*, a bush species in which Cyprus Warblers were never recorded to nest. Sardinian Warblers also nested more frequently than Cyprus Warblers in *Cistus* species, but in contrast to Cyprus Warblers, were never recorded nesting in *R. oleoides*.

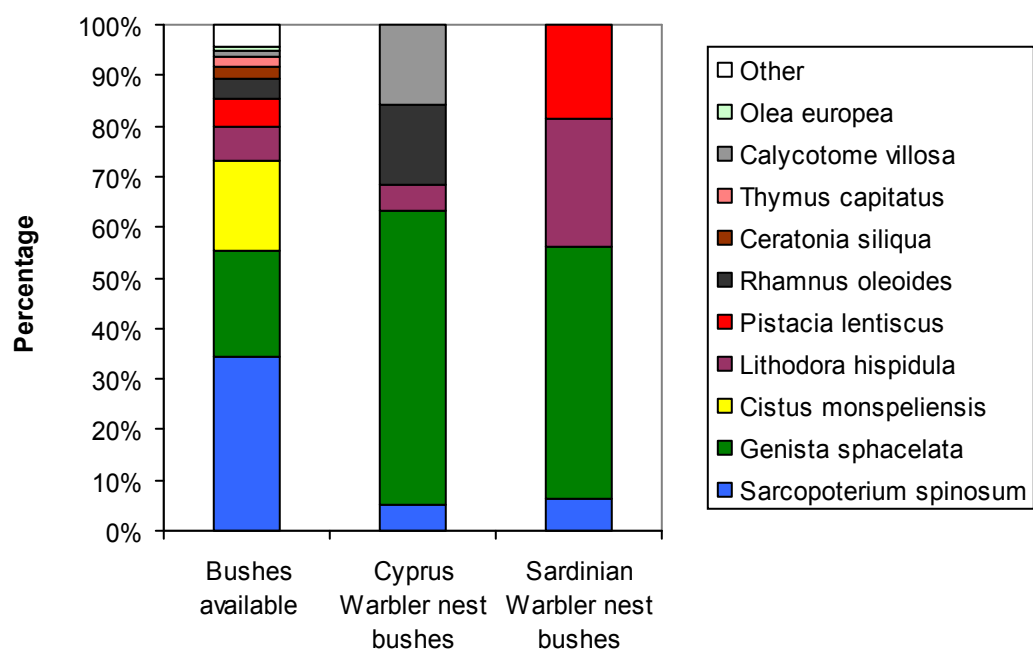
a Akamas 2 (n=472, n=6, n=11)



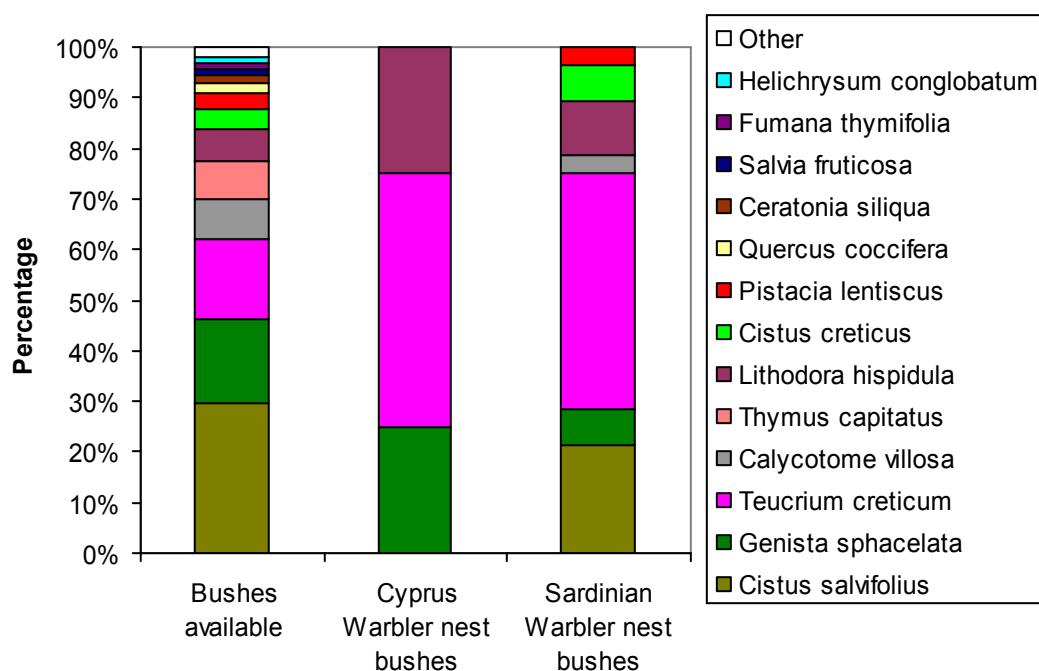
b Akamas Pines (n=363, n=17)



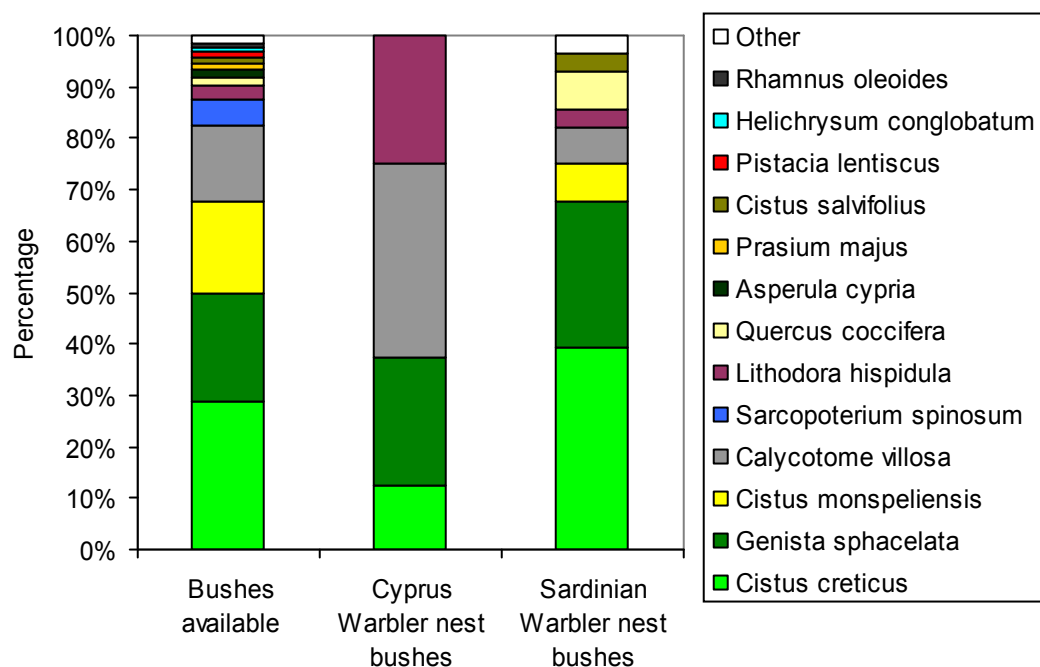
c Ineia (n=573, n=19, n=16)



d Choli (n=923, n=8, n=28)



e Lysos (n=751, n=8, n=28)



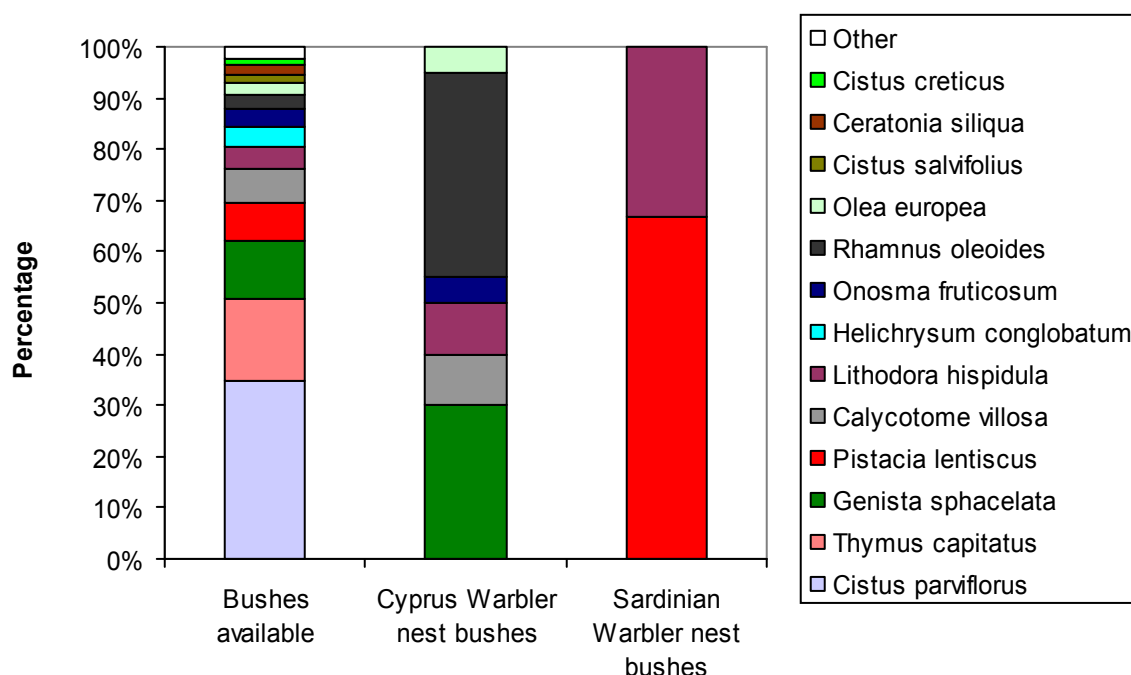
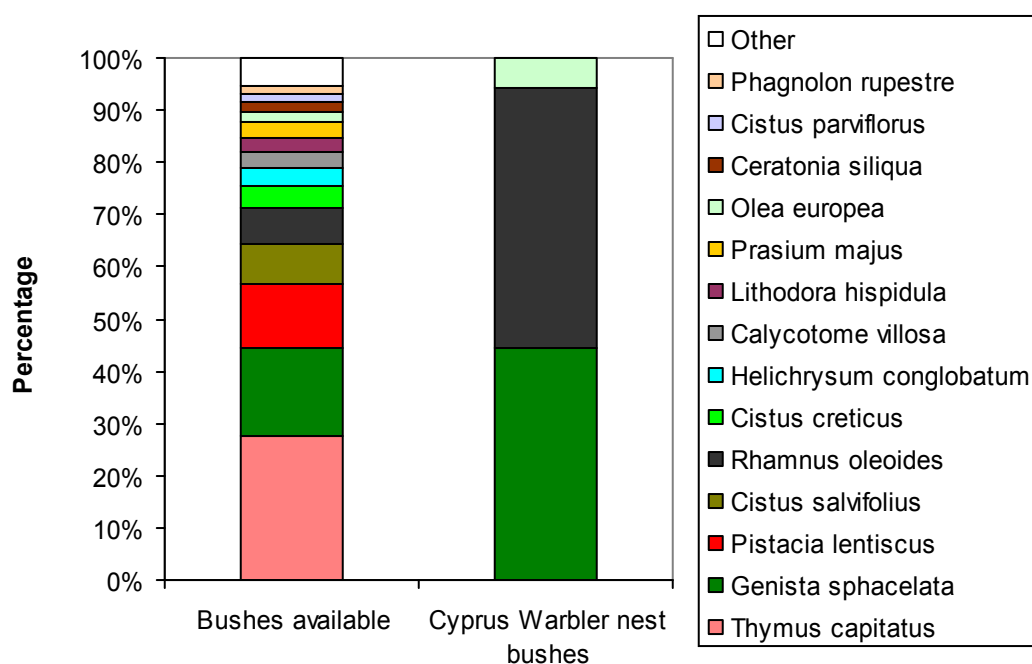
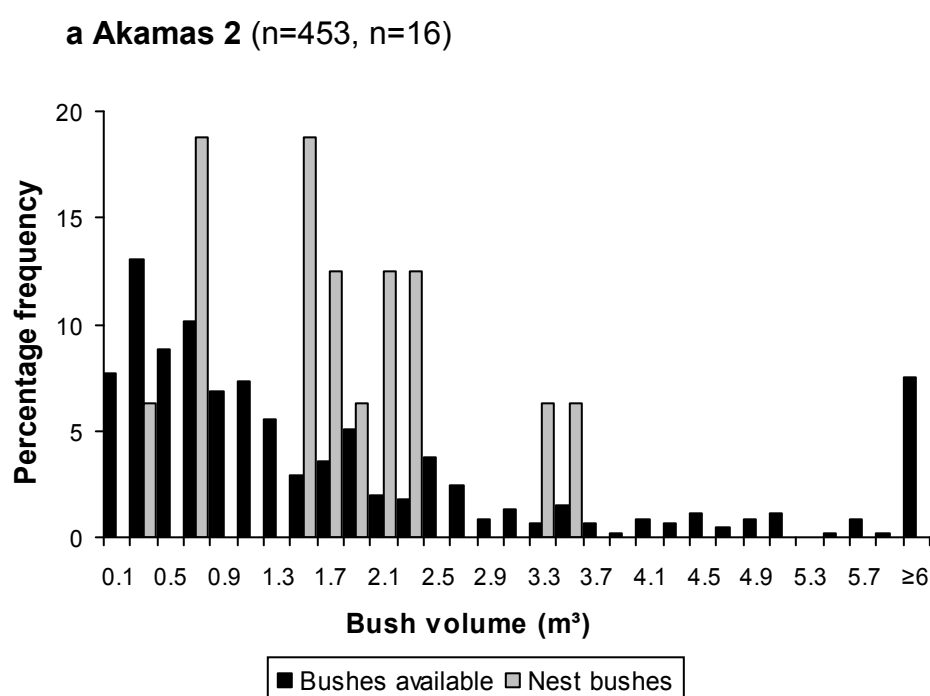
f Kouklia Hives (n=587, n=20, n=3)**g Kouklia 3 (n=386, n=18)**

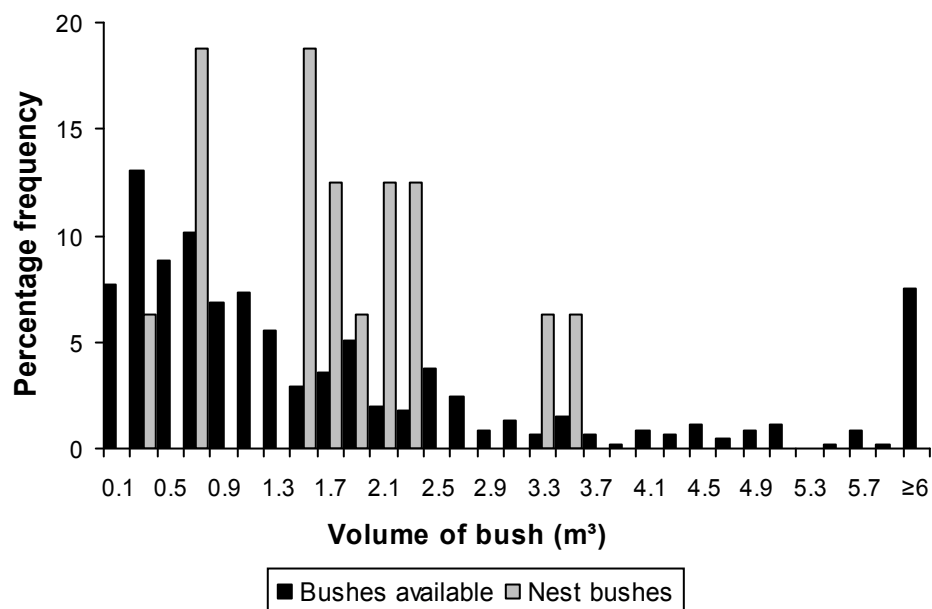
Figure 4.5 Cyprus and Sardinian Warbler nest bush selection in breeding seasons 2003-2005 compared with availability of bush species sampled at different sites during 2004 breeding season. Sample sizes given for the number of bushes sampled on transects, followed by the number of nest bushes used by Cyprus and Sardinian Warblers at that site.

Cyprus Warbler nest bushes were not significantly different in volume from those used by Sardinian Warblers ($X^2=1.19$, d.f.=1, $p=0.276$), nor was there any difference between years in the volume of nest bushes used ($X^2=5.08$, d.f.=2, $p=0.079$).

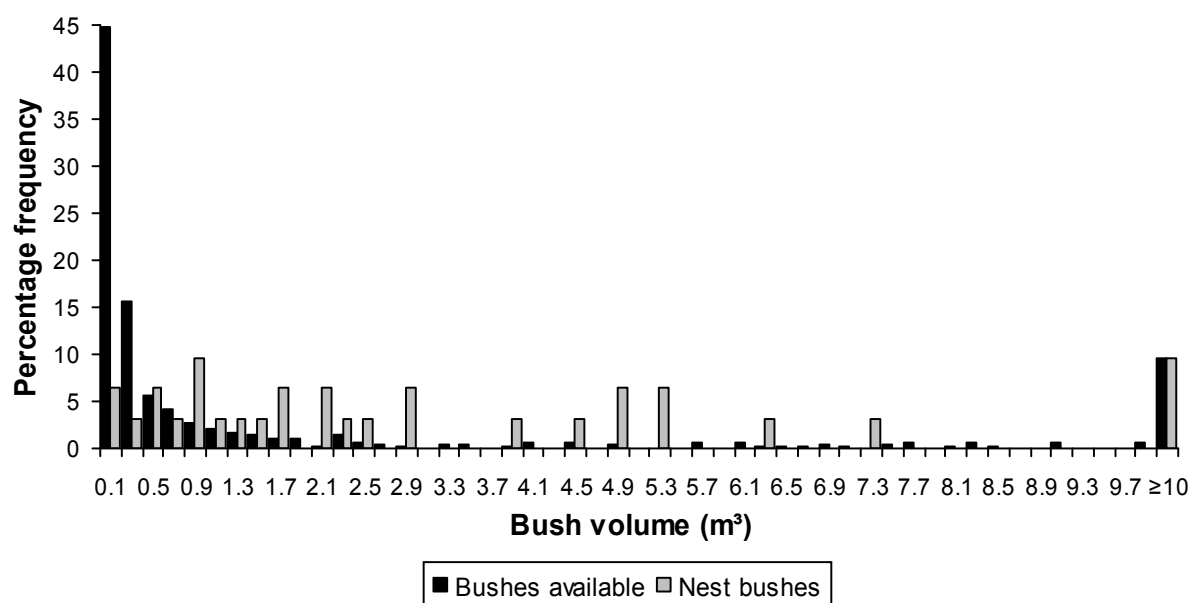
Since nest bush volume was not found to differ significantly between Cyprus and Sardinian Warblers, the two species were pooled to compare the size (volume) of bushes used for nesting with the size of bushes available on the site (Fig. 4.6).



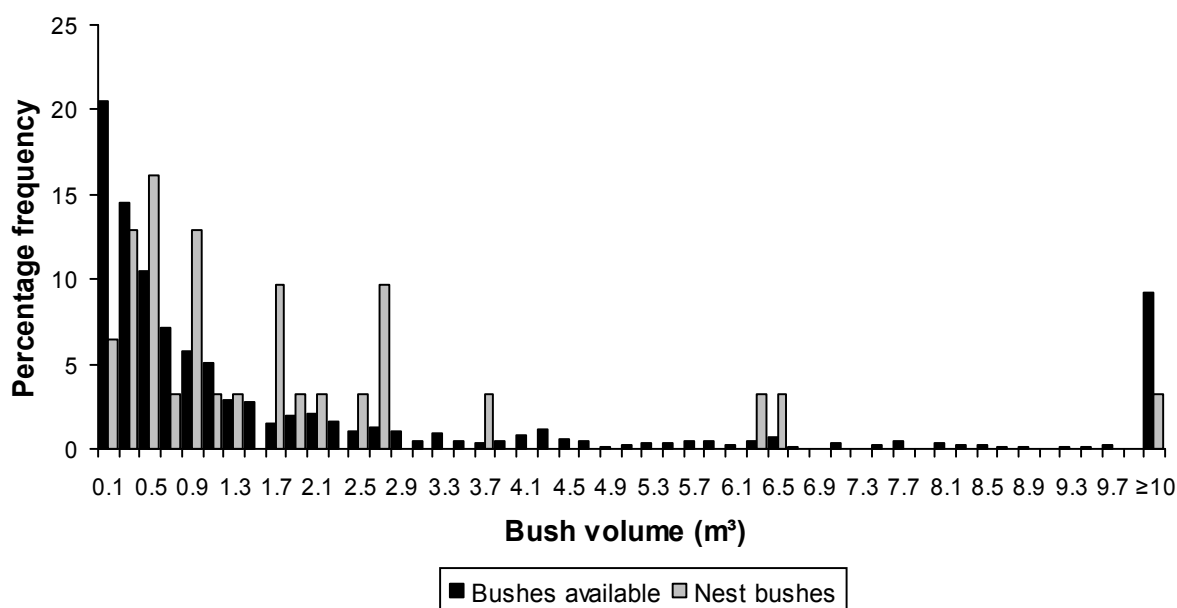
b Akamas Pines (n=363, n=17)



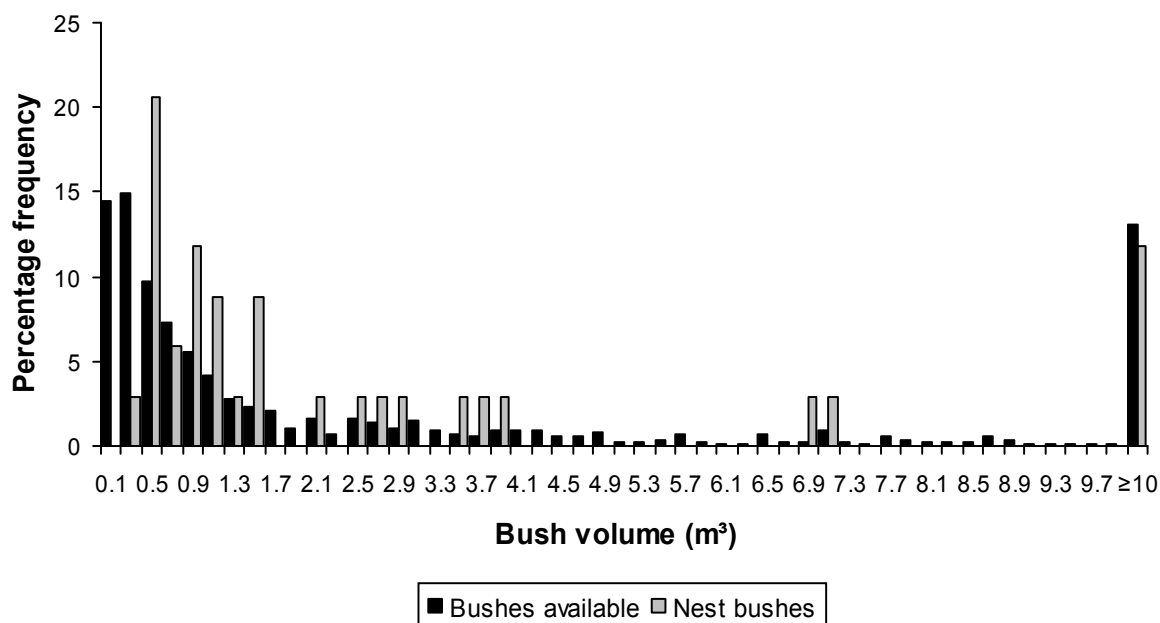
c Ineia (n=573, n=31)



d Choli (n=888, n=31)



e Lysos (n=751, n=34)



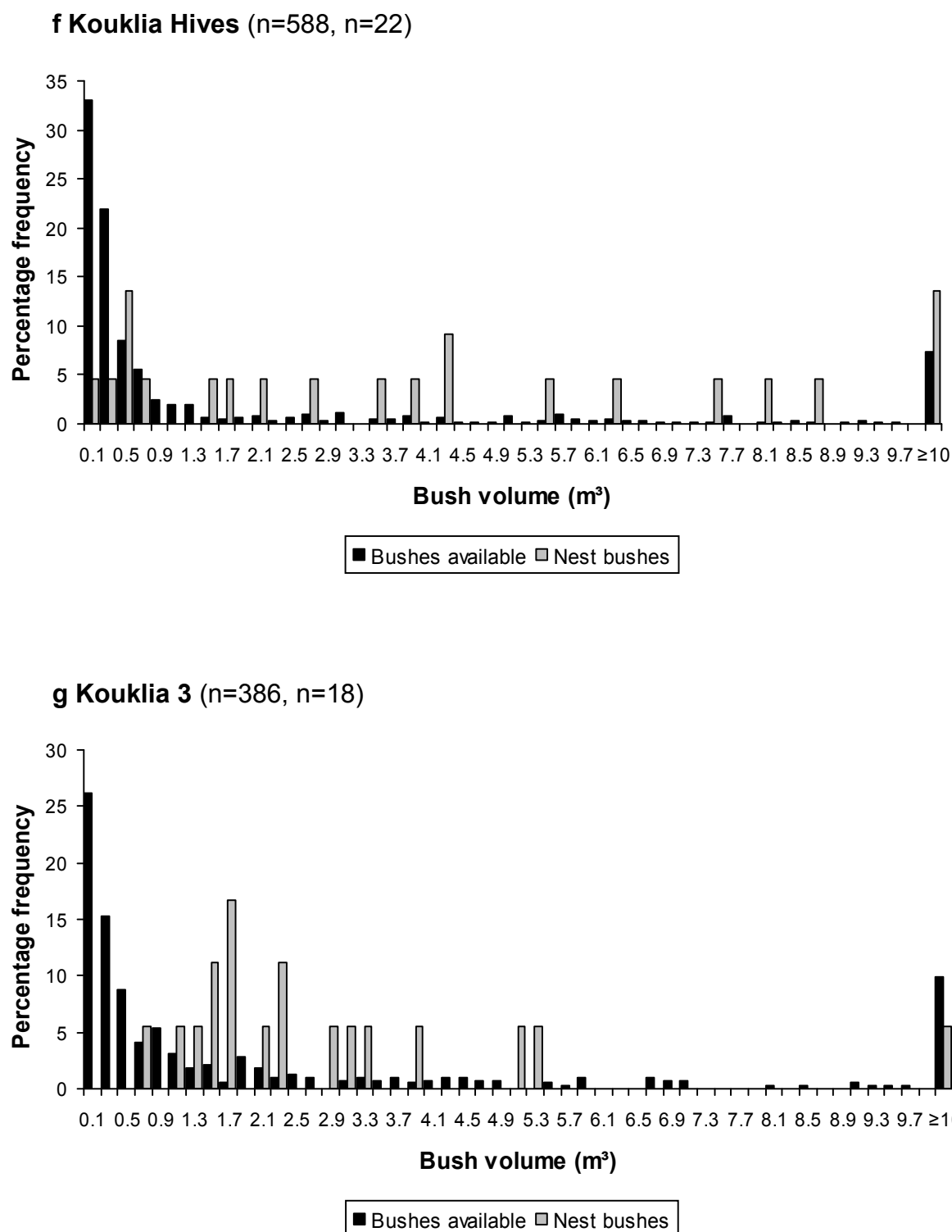


Figure 4.6 Bush size availability compared with nest bush use by warblers of both species nesting on study plots during 2003-2005 breeding seasons. Sample sizes for bushes available and nest bushes used are given in brackets.

In general, Cyprus and Sardinian Warblers appeared to nest in very small bushes

(< 0.5 m³) less than expected from their availability, but otherwise they used bushes of different sizes broadly in proportion to their frequency at a given site.

Nest-site characteristics

There was no significant effect of bird species ($X^2=0.11$, d.f.=1, $p=0.736$) or year ($X^2=2.41$, d.f.=2, $p=0.299$) on nest height. There was a significant effect of bird species ($X^2=6.44$, d.f.=1, $p=0.011$) on distance of nest from bush edge, which indicated that Sardinian Warblers nest closer to the edge of the bush than Cyprus Warblers (Fig. 4.7). This difference remained significant after sequential Bonferroni adjustment. There was no significant effect of year ($X^2=3.78$, d.f.=2, $p=0.276$) on distance of nest from bush edge.

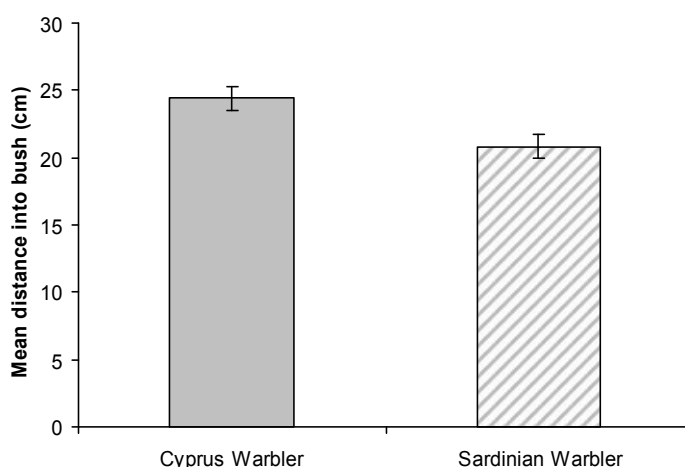


Figure 4.7 Mean $\pm$ SE distance of Cyprus (n=78) and Sardinian Warbler (n=90) nests from the bush edge in 2003-2005 breeding seasons.

There was no significant effect of either bird species ($X^2=0.50$, d.f.=1, $p=0.479$) or year ($X^2=0.92$, d.f.=1, $p=0.336$) on visibility of nest.

Nest structure

Cyprus and Sardinian Warbler nests found during breeding seasons 2003-2005 were open cups formed predominantly from grasses and herbaceous plant stems, leaves and cobweb and lined with finer grass, hair or soft vegetative matter like thistle-down (Plates 4.1 and 4.2).

**Plate 4.1** Cyprus Warbler nest**Plate 4.2** Sardinian Warbler nest

Cyprus and Sardinian Warbler nest dimensions were compared (Table 4.2). There were no significant differences between the two species for any of the measures after sequential Bonferroni adjustment.

Mean nest measurements	Cyprus Warbler	Sardinian Warbler	t-test results		
			t	d.f.	p
Internal diameter of cup (cm)	5.61 ± 0.0840 (n=50)	5.69 ± 0.0720 (n=53)	-0.66	101	0.514
External diameter of nest (cm)	9.26 ± 0.105 (n=50)	8.95 ± 0.105 (n=54)	1.87	102	0.064
Internal depth of cup (cm)	3.89 ± 0.0920 (n=48)	3.98 ± 0.105 (n=49)	-0.64	95	0.522
External depth of nest (cm)	6.52 ± 0.116 (n=52)	6.96 ± 0.157 (n=52)	-2.29	94.1	0.025
Thickness at rim (cm)	3.64 ± 0.116 (n=50)	3.25 ± 0.112 (n=53)	2.42	101	0.017
Thickness at base (cm)	2.93 ± 0.171 (n=48)	3.04 ± 0.197 (n=50)	-2.14	86.9	0.035
Nest volume (cm ³)	439.7 (n=50)	442.4 (n=52)	-0.13	100	0.896
Aspect (°)	141.2 ± 15.8 (n=39)	148.6 ± 12.5 (n=42)	-0.370	79	0.710

Table 4.2 Mean ± SE measurements of Cyprus and Sardinian Warbler nests from 2003 and 2004 breeding seasons, with results of independent samples t-tests comparing dimensions of the two species' nests. Sample sizes given in brackets. None of the tests were significant after sequential Bonferroni adjustment.

Nest-site characteristics and predation

I tested whether any features of nest-site were associated with likelihood of predation (Table 4.3). For Cyprus Warbler nests, of the terms tested only bush volume had a significant effect on whether or not nests were predated, with likelihood of predation being higher for nests in larger bushes (Fig. 4.8).

Explanatory terms	Cyprus Warbler			Sardinian Warbler		
	F	df	<i>p</i>	F	df	<i>p</i>
Bush volume	5.23	1	0.022	0.08	1	0.775
Bush spiny or not	2.34	1	0.126	2.54	1	0.111
Height of nest	1.60	1	0.206	0.06	1	0.804
Distance to bush edge	1.29	1	0.257	0.01	1	0.906
Visibility	1.14	1	0.463	2.51	1	0.113
Volume of nest	0.54	1	0.463	4.99	1	0.025
Minimal model	Effect size		SE	Effect size		SE
Constant	-1.188		0.301	-1.202		0.401
Bush volume	0.260		0.114			
Volume of nest				0.00838		0.00375

Table 4.3 Binomial GLMM with whether or not Cyprus and Sardinian Warbler nests (from 2003, 2004 and 2005) were predated as the response, the explanatory terms listed as fixed factors and site as a random factor. Nests known to fail for reasons other than predation were removed from this analysis. Significant terms highlighted in bold. Effect sizes given for significant terms only.

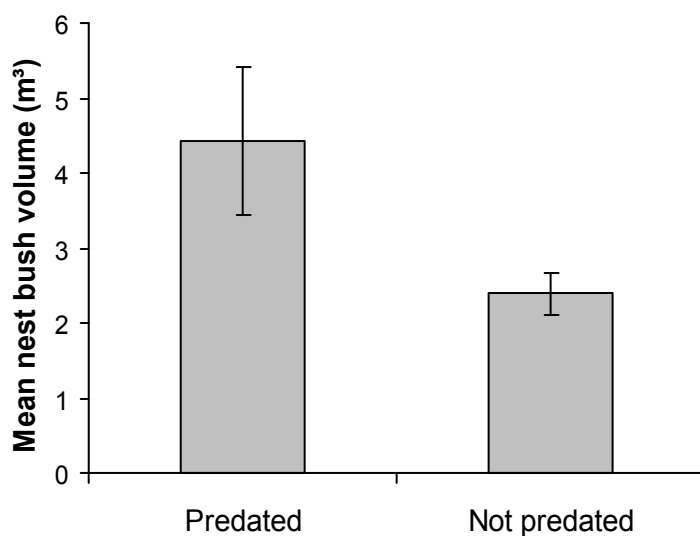


Figure 4.8 Mean $\pm$ SE volume of Cyprus Warbler nest bushes comparing nests which were predated (n=16) with those not predated (n=53) during 2003-2005 breeding seasons. Nests known to fail for reasons other than predation were excluded.

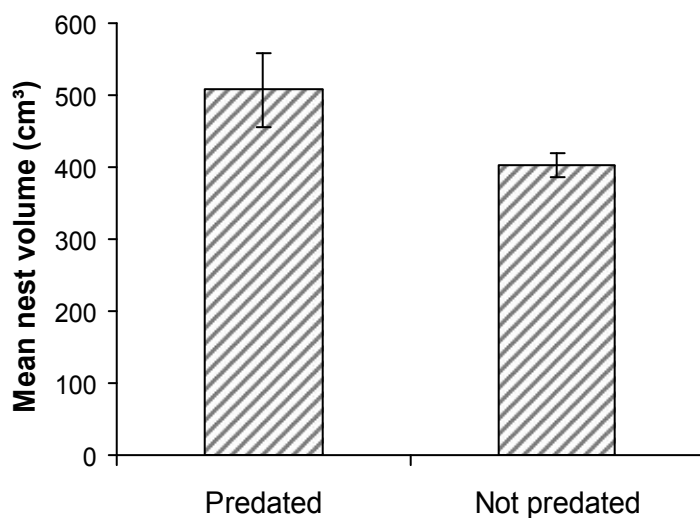


Figure 4.9 Mean $\pm$ SE volume of Sardinian Warbler nests which were predated (n=9) or not predated (n=37) during 2003-2005 breeding seasons. Nests known to fail for reasons other than predation were excluded.

For Sardinian Warbler nests, of the terms tested, only volume of the nest had a significant effect on whether or not nests were predated, with larger nests having a higher likelihood of predation (Fig. 4.9).

Discussion

Vegetation composition of warbler home-ranges

In Chapter 3 I showed that the home-ranges of Cyprus and Sardinian Warblers overlap. In this chapter I have found no evidence that the two species' home-ranges have different fine-scale habitat composition within scrub study plots. Therefore it appears that, within the study plots, areas suitable for one species are also suitable for the other. Martin and Thibault (1996), studying coexistence of four Mediterranean *Sylvia* species, found that Sardinian Warbler was the most generalist in terms of habitat patch selection. In addition they found that the four species overlapped considerably in patch selection, but that they segregated ecologically and behaviourally while foraging. Time constraints precluded investigation of foraging behaviour in this study, but it would be interesting to see whether Cyprus and Sardinian Warblers differ in habitat utilisation.

Vegetation height and warbler breeding density

The positive correlation found between density of Sardinian Warbler pairs and mean height of vegetation on their home-ranges at different study plots has interesting implications. Although the concept of a home-range is often simplified into two dimensions (and this may adequately reflect resources available to ground-based species), in volant birds it is clearly more appropriate to consider the home-range as a three-dimensional space. In general birds only defend the home-range area required to support their needs, because larger home-ranges carry increasing costs of defence (Brown 1964). These results suggest that in taller vegetation, Sardinian Warbler pairs are able to support their needs in a smaller area. This may reflect a positive relationship between the availability of their arthropod food and volume of vegetation and reflect the relatively broad habitat preferences of Sardinian Warblers (Shirihai *et al.* 2001).

The lack of significant relationship between Cyprus Warbler home-range vegetation height and density of Cyprus Warbler pairs supported may indicate that there are differences in habitat utilisation between the two species; perhaps Cyprus Warblers

are not well adapted to utilising taller vegetation and are more specialised in their use of habitat or in their diet. Habitat utilisation was not investigated in this study, but would be interesting to pursue. The diet of Cyprus and Sardinian Warblers will be investigated in Chapter 6.

Neither Cyprus nor Sardinian Warblers appeared to select nest bushes in proportion to their availability. It is not surprising that both Cyprus and Sardinian Warblers appeared to avoid nesting in very small bushes as these would be unlikely to provide sufficient support, shading, concealment or protection from predation. In addition flocks of goats and sheep regularly browse the scrub of the study plots and any nests in small bushes would be very vulnerable to trampling. Cyprus Warblers and, to a lesser extent Sardinian Warblers appeared to favour spiny species like *G. sphacelata*, *R. oleoides* and *C. villosa*, which would be expected to offer greater protection from predation. The strong preference shown by both nesting warbler species for *T. creticum* at Choli is more difficult to explain since this species lacks spines. However, at Choli many warbler pairs nested in areas where *T. creticum* grows at high density, effectively forming a thicket of stems, among which it is presumably difficult for predators to find nests. *L. hispidula*, which was used by both species, also lacks spines, but its leaves provide good concealment. Neither *Cistus* species nor *P. lentiscus* have any protective spines, but larger *Cistus* bushes offer relatively good concealment and nests in *P. lentiscus* tended to be very well concealed by foliage from the sides and above.

It is interesting that for Cyprus Warblers, nests in larger bushes were more likely to be depredated; this is contrary to what one might intuitively expect. Since there were no significant interactions between terms, the result is not explained by bush species (for example the bush species that grow largest could have less dense foliage and therefore provide less concealment). It may be that large bushes are used as refuges by potential predators, rendering any nests in such bushes more vulnerable to predation by ground-based predators like snakes and rodents. For Sardinian Warblers larger nests were more likely to be depredated. This makes intuitive sense; larger nests would be more easily seen, from any angle. The fact that neither nest height, visibility of the nest nor distance of the nest from the bush edge appeared to

have an effect on likelihood of predation in either species, is perhaps surprising. Hatchwell *et al.* (1996) and Hoover (1998) both found that visibility was higher for failed nests, while Burhans and Thompson (1998) and Holway (1991) found that visibility did not differ between predated/parasitised and unpredated/unparasitised nests. Murphy (1983) suggested that since predation was the primary cause of nest failure, it should be the key factor influencing selection of nest-sites. However particular nest characteristics could theoretically make the same nest more vulnerable to depredation by one type of predator, but less vulnerable to another (Filliater *et al.* 1994). For example, a nest built high up in a bush might be more vulnerable to avian predators, but less vulnerable to snakes. A lack of effect of nest height and visibility could reflect the existence of a suite of different predators, each subjecting warbler nest-site choice to different selective pressures.

Implications of nest-site similarity in coexisting species

Overall, Cyprus and Sardinian Warblers nested at similar heights in bushes of similar species and sizes. Cyprus Warblers tended to position their nests slightly further from the bush edge than Sardinian Warblers. This did not appear to make nests less visible, and distance from the bush edge was not a variable found to influence likelihood of predation in the present study.

The advantage of nest spacing which results from intraspecific territoriality may be reduced where two species overlap. Martin (1996) found that predation rates were higher where two bird species coexisted than where each occurred alone and also that predation rates increased more when species were similar in nest placement than when they differed. From a predator's perspective nests might be twice as common in overlap areas, doubling the potential success rate of random searching. In addition, the similarity in Cyprus and Sardinian Warbler nest-site and nest structure could be detrimental to both species because after finding a number of one prey type predators may learn to look in the same type of microhabitats (Royama 1970) or develop a 'search image' for prey which they commonly encounter (Tinbergen 1960). Although originally conceived as a visual phenomenon, the search image concept can be applied to other senses (Nams 1991) and a similar search blue-print might be formed by more olfactory predators like snakes, which are thought to be important

predators of Cyprus and Sardinian Warbler eggs and nestlings. A number of studies have found that corvids found proportionately more prey as prey density increased (Tinbergen *et al.* 1967, Goransson *et al.* 1975, Andersson & Wiklund 1978). Crows may return to areas of past success (Tinbergen *et al.* 1967) and spend more time hunting in areas following successful foraging (Sugden & Beyersbergen 1986). In the latter study, density dependent nest predation began to operate at about one nest per hectare, which is well below the density of warbler nests to be found in the scrub habitat of the present study during the main breeding season (Chapter 3).

Magpies (*Pica pica*), Woodchat Shrikes (*Lanius senator*) Masked Shrikes (*L. nubicus*) and Red-backed Shrikes (*L. collurio*) were regularly seen perching on vantage points within plots, watching the activities of warblers, and it is possible that they are able to locate nests using the same visual cues as we used to find nests (Erikstad *et al.* 1982). Cyprus and Sardinian Warblers could be disadvantaged not only because of the similarities in their nest-site, but also because, as congenics, their behaviour around the nest is very similar. A predator could therefore easily apply experience of behavioural cues in one warbler species to locate nests of either species. Since Sardinian Warblers more frequently have two broods per season, starting to breed slightly earlier and finishing slightly later than Cyprus Warblers, the warbler breeding season is extended. This could disadvantage Cyprus Warblers further, because predators could potentially be 'primed' to search for warbler nests by the time Cyprus Warblers begin breeding. In Chapter 5 I will investigate whether there is any indication that coexistence results in higher nest predation rates for either warbler species.

Competition for nest-sites?

Martin & Martin (2001b) found that Orange-crowned Warblers (*Vermivora celata*) aggressively interfered during nest-site selection and nest building by Virginia's Warblers (*V. virginiae*), causing them to use different nest-sites where the two species coexisted. Where Orange-crowned Warblers were removed, Virginia's Warblers used nest-sites indistinguishable from those used by Orange-crowned Warblers. Despite having overlapping home-ranges, it is unlikely that Cyprus and Sardinian Warblers are competing for nest-sites. Most of the bush species and sizes

used for nesting were relatively common on any given home-range and no aggressive interference behaviour was ever observed, despite the two species sometimes nesting simultaneously within 5 m of one another. Conspecific neighbours were never observed nesting simultaneously in such close proximity to one another.

According to the competitive exclusion principle (Gause 1934), ecologically similar species using the same set of limited resources cannot coexist at equilibrium. Cyprus and Sardinian Warblers in scrub habitat do not appear to differ in fine-scale home-range habitat composition, their home-ranges overlap and their nest-sites are very similar. I have not yet found any evidence that competition for resources has stimulated ecological segregation. However a species' niche is a multi-dimensional concept and it is possible that Cyprus and Sardinian Warbler differ in aspects of their ecology which have not yet been addressed. Even within the same habitat patch, the two species could utilize the habitat differently, have different foraging behaviour or differ in diet. The former was not studied in detail, but during field observation no clear differences were noted between Cyprus and Sardinian Warblers' foraging behaviour. The possibility that Cyprus and Sardinian Warblers differ in diet will be examined in Chapter 6.

Chapter 5

A comparison of breeding biology, productivity and nest survival in Cyprus and Sardinian Warblers

Introduction

In a simple, closed system, population dynamics reflect the balance between productivity and mortality. Poor reproductive success is often found to be important in driving bird population declines (Norris 1947, Moss *et al.* 2000, Rogers 2006, Watson *et al.* 2006). Sardinian Warbler (*Sylvia melanocephala*) does not appear to be having a negative impact on Cyprus Warbler (*Sylvia melanothorax*) through direct aggression (Chapter 3) or competition for nest-sites (Chapter 4). In this chapter I will compare the breeding biology of the two species and investigate whether there are any differences in various parameters of breeding success which might help to explain the apparent decline in the Cyprus Warbler population and continued expansion of the Sardinian Warbler population in parts of Paphos District. Sardinian Warbler breeding biology has been studied elsewhere in its range (Gibb 1951, Gauci & Sultana 1980), but it has not been studied in Cyprus. Current knowledge of Cyprus Warbler breeding biology is largely based on anecdotal reports or studies of a small number of nests (McNeile 1948-1955, Ashton-Johnson 1961, Castell 2001).

Many prior studies have found negative effects of one species on another coexisting species' breeding success (Gustafsson 1987, Ellis & Good 2006). Martin and Martin (2001b) used removal experiments to show that Virginia's Warblers (*Vermivora virginiae*), whose home-ranges normally overlapped with Orange-crowned Warblers (*V. celata*), increased their feeding rates during incubation and nestling periods when Orange-crowned Warblers were removed. In addition, in comparison with control plots, each species enjoyed reduced predation rates on plots where the other was removed. This situation differs from that of Cyprus and Sardinian Warblers in two

important respects. Firstly Orange-crowned Warbler displays overt aggression towards Virginia's Warbler, whereas I have found little evidence for overt aggression between Cyprus and Sardinian Warblers (Chapter 3). Secondly, Orange-crowned Warbler is known to exclude Virginia's Warblers from preferred nest-sites, whereas I have found no evidence for such interference in this study (Chapter 4).

In Chapter 1 I discussed the possibility that the decline in Cyprus Warblers abundance in western Paphos District had resulted from some effect of climate change. Where conditions are becoming drier and warmer in Europe, we expect species' climate envelopes to shift northwards (Thomas & Lennon 1999). More locally we might expect species distributions to shift onto higher ground (Pounds *et al.* 1999). Therefore if climate change is a factor in Cyprus Warbler decline we might predict that conditions would be more suitable for breeding Cyprus Warblers on higher altitude plots. In this chapter I investigate whether productivity measures provide any evidence to support climate change as a potential cause of Cyprus Warbler decline.

Given the similarity in their choice of nest-site (Chapter 4) it is likely that Cyprus and Sardinian Warblers share the same nest predators. The increased nest density that results from home-range overlap between the two species could result in 'apparent competition' (Holt 1977, Holt 1984, Hoi & Winkler 1994, Holt & Lawton 1994), where predators shared by two species respond to increased prey density by increasing in numbers or altering their behaviour to target a common prey type (Tinbergen *et al.* 1967, Goransson *et al.* 1975, Andersson & Wiklund 1978, Sugden & Beyersbergen 1986). In this way both Cyprus and Sardinian Warbler could suffer reduced breeding success as a result of coexistence.

As closely related species of similar size, one might reasonably expect Cyprus and Sardinian Warbler to share a similar diet (this will be explored in Chapter 6). The fact that Cyprus and Sardinian Warblers overlap in home-range (Chapter 3) could, therefore, potentially result in negative effects on both species through interference or exploitation competition for the same food resources during the breeding season.

In this chapter the breeding ecology of the two species will be described and four main questions will be addressed:

- Are there any differences in breeding biology between Cyprus and Sardinian Warblers?
- Do the two species differ in various parameters of productivity?
- Is productivity in either species' influenced by study plot altitude?
- Do the two species have different rates of nest survival?
- Is there any evidence that aspects of breeding are influenced by the presence of the congener?

Methods

Breeding data collection

During the 2003, 2004 and 2005 breeding seasons, all breeding attempts found were monitored regularly at all seven sites. Breeding attempts were found at different stages from nest prospecting to late nestling stage. Frequency of monitoring was a compromise between maximizing information gained while minimizing disturbance and risk of abandonment. During incubation, it was often possible to check that the nest was still active and determine which sex was incubating while the bird remained on the nest. Where clutch size needed to be confirmed or hatching was anticipated, observers waited until the parent left the nest, before checking it. By four to five days after hatching, both parents were usually engaged in feeding chicks, so nests could be checked when no parent was present.

Where un-hatched eggs remained in the nest several days beyond hatching, they were opened and the contents were inspected for signs of embryo development. Where nests failed between visits, it was often difficult to determine the cause. In some cases there were signs at the nest following predation, such as egg shell fragments, droppings (reptile) in the nest or damage to the nest and nest bush. However, frequently the contents of the nest were gone and there was no obvious sign of predation. In these cases it was impossible to determine the cause of failure,

but several species of snake (known to include eggs and small birds in their diet) were seen frequently on the study plots and snakes often depredate nests cleanly (Stake *et al.* 2005).

Every effort was made to catch and ring the adults at each nest, so that data could be collected on subsequent nests and adult survival. This was generally attempted on day six, when the nestlings were usually ringed. A short V-shaped net was set around the nest bush and the adults could sometimes be caught as they brought food to the nest. If the adults were not caught within 45 minutes, the net was removed. At nests which were not well shaded, netting of adults was restricted to early morning to prevent nestlings from over-heating in the absence of a parent.

Data analysis

Approach to productivity

I approached analysis of productivity by focusing on success of the first nest of the season and the success of any genuine second nesting attempts. The first nesting attempt of each pair in a given season was used in calculations of success/failure, mean clutch size and mean number of nestlings surviving (first nests of pairs which had formed after one member had already had a breeding attempt with another partner were not included). I was interested in comparing breeding productivity per attempt between species, and the first attempt of the season is a clearly comparable element. I could have chosen randomly a single nesting attempt for each pair (including some renests after failure), but this approach would have been complicated by seasonal changes in productivity.

In 2003, observations began later than in 2004 and 2005; sample sizes were relatively small because fewer birds were ringed at the start of the project than in 2004 and 2005 and observers were less experienced in nest finding. No genuine second nesting attempts were found for known breeding pairs, which may mean that some first attempts were missed and their first known attempt was actually their second. However, for some analyses the 2003 data were used and treated as first nesting attempts. Only 2004 and 2005 data were used for any investigation of proportion of pairs initiating a second attempt and for calculation of overall output per season.

Clutch initiation, size and hatching success

Where nests were discovered after laying was complete, clutch initiation dates were calculated using a 13 day incubation period for both species, assuming one egg was laid per day, with incubation commencing on the day the last egg was laid. Only clutches found prior to hatching were used in the calculation of mean clutch size. Cases of clutch size reduction during the incubation period were very rare and therefore the number of eggs in complete clutches found prior to hatching was assumed to be the number laid. Only clutches of known size which survived to the point of hatching were included in hatching success. For each first nesting attempt where clutch size was known, hatching success was calculated as the percentage of eggs which successfully hatched. Percentage hatching success was then averaged for each species in a given year and compared.

Defining success

Ideally one would visit nests regularly in order to confirm fledging, which is often used to define success. However, following nests at seven study sites imposed logistical constraints such that, while all nests were visited when nestlings were aged 5 or 6 days (for ringing), not all nests could necessarily be visited again prior to fledging. The state of the nest could not be used to indicate whether chicks had fledged or been predated, as many presumed predation events left no sign at the nest. An attempt was therefore considered successful if one or more nestlings were known to reach 5 days. This definition of success almost certainly overestimated actual breeding success, because failures could have taken place at nests which were not checked between 5 days and fledging. However, I was primarily interested in comparing breeding success in Cyprus and Sardinian Warblers and I applied the same criteria to both species.

Data for mean number of chicks surviving to 5 days could not be transformed to meet the assumptions of parametric tests, so non-parametric analyses were performed. Date of first clutch initiation was log-transformed for inclusion in the GLMM (with binomial error structure) investigating variables associated with success or failure of first nesting attempts.

Second nesting attempts

In calculating what percentage of pairs with first nesting attempts went on to make a second nesting attempt, it was important to distinguish between renesting after failure and renesting after success within a single breeding season. Therefore breeding attempts following the first of the season were only considered 'second breeding attempts' if the first had succeeded (by the 5-day definition) and was not known to have failed subsequently. Since this method could have overestimated the frequency of genuine second nesting attempts for both species, I also recorded the minimum percentage of pairs having second nesting attempts, by including only those pairs whose first attempt nestlings were observed to have survived to within one day of fledging. In cases where one member of the pair had changed between first and second nesting attempts, both attempts were excluded from analysis. For the GLMM with binomial error structure investigating which factors had an effect on whether or not a second nesting attempt was initiated, clutch initiation date was log-transformed to achieve normality prior to inclusion in the model.

Nestling output per pair per season

To calculate chick output per pair per season, I added together the number of chicks surviving to 5 days from each nesting attempt by the pair. Occasionally, breeding attempts were missed and ringed adults were seen with unringed fledglings. In these cases the minimum number of fledglings seen was added to the output of any other nests in calculating output for the pair that season. A GLM with chick output per pair per season as the dependent variable and species, year and zone (and their interactions) as fixed factors was run to investigate whether there were significant differences in chick output between years, species or zones. Separate GLMs were then run for Cyprus and Sardinian Warblers in 2004 and 2005 to investigate whether lay-date of first clutch, species of nearest neighbour, distance to nearest neighbour or zone had an effect on chick output per pair per season. Lastly, I used mean values for number of chicks surviving to 5 days in the first nesting attempt, the minimum probability of initiating a second nesting attempt and the mean number of chicks surviving to 5 days in any second nesting attempts to calculate what the chick output would have been for an average pair of either species in 2004 and 2005.

Nest survival

I calculated nest survival using the Mayfield (1961, 1975) method, which takes into account not only whether or not a nest failed during the period through which it was observed, but also how long the nest was exposed to risk, thus avoiding overestimation of nest survival. Estimated daily nest survival was calculated by $1 - \text{Nu}/\text{E}$ (where Nu is the number of nests which failed and E was the total number of exposure days). Nest survival probabilities could then be calculated for any period by $(1 - \text{Nu}/\text{E})^h$ where h is the total number of days over which each nest is exposed. Standard errors for daily nest survival probabilities were calculated using the method of Johnson (1979). I analysed the egg and nestling periods separately, because they may have different survival rates. Nest survival probabilities for laying/ incubation and nestling periods could then be multiplied together to obtain overall nest survival probabilities. Exposure period from laying to hatching was calculated for each year and species separately by adding the mean incubation period for that year to the mean clutch size for first nesting attempts in that year minus one (because incubation generally begins on the last day of laying). Over the three years few nestling periods could be quantified exactly; it was more common to find that nestlings fledged between two visits. However the length of the nestling period was generally 11 days for Cyprus Warblers and 12 days for Sardinian Warblers and there was no indication that it differed between years. These values were therefore used as the exposure periods from hatching to fledging for the two species in Mayfield calculations.

For nests which failed, the number of exposure days was recorded as the mid-point between the last visit where the nest was active and the date it was discovered to have failed. For nests with uncertain fate (for example where a brood could have reached fledging age between visits and the state of the empty nest gave no obvious indication of whether the chicks had fledged or been predated during the period between visits), a conservative approach was taken and the number of exposure days was recorded as the number of days until the last visit that took place within the potential nestling period.

Survival analysis is a well-established tool used in biomedical studies to compare survival of patients under different treatment regimes. In biology it is often used for examining survival of marked or radio-tagged populations and can be a useful tool for

assessing nest survival, because it incorporates measures to deal with nests that have ambiguous fates. For the main analysis of breeding success the Mayfield method was used in preference because survival analysis requires that the age of the nest be estimated at the time that it enters the study; in this study a number of nests were found with the clutch complete and were then depredated before hatching. Omitting these nests would have biased results, so my use of survival analysis was limited to generating survival curves for the nestling period only (treating day of hatching as day 0) using the Kaplan-Meier method (Kaplan & Meier 1958). Survival analyses use time-to-failure data and for these analyses the lifetime of a failed nest is known and is not 'censored', while the lifetimes of successful nests or those with ambiguous fates are considered unknown (because they haven't failed) and are therefore censored (Nur *et al.* 2004). In Kaplan-Meier survival curves this difference is represented by the curve changing only when deaths occur; censored observations are individually marked to show the point beyond which we have no further information on a particular nest.

Binomial GLMMs were used to examine whether there were any differences in survival between Cyprus and Sardinian Warbler nests in different years. Survival during the egg stage and the nestling stage were analysed separately. The binomial outcome was whether a nest was known to have failed (1) or not (0) during the period of observation and the number of days the nest was exposed (observed) for was included as a factor in the model, along with species and year. Site was included as a random factor.

Results

Behaviour

In both species, both male and female were involved with building breeding nests. Male Sardinian Warblers sometimes built cock nests prior to pairing. These were nests which were built but not lined. This behaviour was seen less often in Cyprus Warbler males.

In general both species appeared to commence incubation on the last day of laying. However, there was some variation, and in a number of five-egg clutches, the fifth chick hatched a day later than the other four, suggesting that incubation began with laying of the fourth egg. I did not study incubation and brooding behaviour in detail, but as a rough guide, I collated data from nest checks where the sex of the parent on the nest was recorded in 2003 (Table 5.1).

Species	Egg stage		Nestling stage	
	Male	Female	Male	Female
Cyprus Warbler	3	9	1	5
Sardinian Warbler	3	5	1	8

Table 5.1 Sex of parent on the nest as recorded during checks made on Cyprus (n=14) and Sardinian Warbler (n=14) nests in 2003 breeding season. For any one nest only the first check made at egg stage and nestling stage is included.

Although this only provides a ‘snapshot’ it appears that, in both Cyprus and Sardinian Warblers, females incubate more than males and females do the majority of brooding. In both species ‘change-overs’ were regularly seen where the female flew off to forage leaving the returning male to cover the eggs. Although the female generally did more brooding in the first days after hatching, in both species provisioning of nestlings aged 5-7 days was split roughly equally between male and female (Chapter 6). For Cyprus Warbler the nestling period was usually 11 (range 9-12) days, while for Sardinian Warbler it was usually 12 (range 11-13) days.

Young of both species usually fledged several days before being able to fly capably, rendering them vulnerable to predation. Several incidents of snakes preying on newly fledged young were witnessed. In both species parents continued to feed fledglings for at least two weeks post-fledging, and family parties stayed together for several weeks beyond this. For both species clutch initiation for second nesting attempts occurred 4-8 weeks after clutch initiation for successful first nests (5-day definition), which means that in some pairs of both species females began second clutches while males were still feeding fledglings.

Both species normally stayed with the same partner for all breeding attempts within a breeding season. There were occasional cases of 'divorce' in Sardinian Warblers, where both members of the pair re-paired with other individuals after a first nesting attempt together. In Cyprus Warblers and Sardinian Warblers there were occasional cases where more than one male was seen building a single nest, attending the nest, feeding nestlings or feeding fledglings. I consider it likely that these were cases where males were contributing to breeding attempts where they had obtained extra-pair copulations. Indeed, one Cyprus Warbler extra-pair copulation was witnessed. There was only one recorded case of natal philopatry in each species, where offspring ringed in their year of hatching were recorded on or near the same study plot in the following year.

Of 238 nests laid in over three years (93 Cyprus Warbler and 145 Sardinian Warbler), I noted no cases of Cyprus and Sardinian Warblers pairing with one another. Furthermore, I witnessed no interspecific disputes around nests even though the two species sometimes nested within 5-10m of one another.

Cyprus and Sardinian Warblers were seen harassing or scolding the following species: Magpie (*Pica pica*), Red-backed Shrike (*Lanius collurio*), Masked Shrike (*L. nubicus*), Great Spotted Cuckoo (*Clamator glandarius*), Scops Owl (*Otus scops*) and Montpellier Snake (*Malpolon monspessu lanus*). Scops Owls are nocturnal and mostly insectivorous and so are not considered a likely predator, but the other species are likely to be potential predators of warbler eggs, nestlings or adults. Mixed species groups of birds (including both Cyprus and Sardinian Warblers) sometimes gathered to harass predators.

Return rates of ringed breeding birds

On average 50.0 % of ringed Cyprus Warbler males went on to breed on the same study plot the following year, while on average 41.3 % of Sardinian Warbler males did so (Tables 5.2 and 5.3). Two Cyprus Warbler males bred on the same plots in all three years, but no Sardinian Warbler males bred in all three years.

Returns of ringed breeding birds	Cyprus Warbler	Sardinian Warbler
No. of ringed breeding males alive in 2003	6	8
No. of ringed males with ringed female in 2003	5	4
No. of 2003 ringed males breeding again in 2004	3	3
No. of 2003 males paired with the same ringed female in 2004	1	0
No. of 2003 males known to change partner for 2004	0	1
No. of 2003 males known to change partner for 2004 with original female still known to be alive	0	0

Table 5.2 Return of ringed breeding males and their partners to study plots between 2003 and 2004.

Only one Cyprus Warbler male and no Sardinian Warbler males were known to pair with the same female in consecutive years (Tables 5.2 and 5.3).

Returns of ringed breeding birds	Cyprus Warbler	Sardinian Warbler
No. of ringed breeding males alive in 2004	17	21
No. of ringed males paired with ringed female in 2004	7	15
No. of ringed males breeding again in 2005	9	10
No. of ringed males paired with the same ringed female as previous year	0	0
No. of ringed males known to change partner for 2005	3	8
No. of ringed males known to change partner for 2005 with original female still known to be alive	0	2

Table 5.3 Return of ringed breeding males and their partners to study plots between 2004 and 2005.

Resighting of all ringed birds

Including all ringed adults ever resighted on study plots (Tables 5.4 and 5.5), resighting rates were higher for Cyprus Warbler males than Sardinian Warbler males. Females of both species appeared to have lower resighting rates than males and Cyprus Warbler females had considerably lower resighting rates than Sardinian Warbler females.

	Cyprus Warbler			Sardinian Warbler		
	No. ringed birds alive 2003	No. resighted 2004	Percentage resighted	No. ringed birds alive 2003	No. resighted 2004	Percentage resighted
Adult males	20	15	75.0	18	5	27.8
Adult females	14	2	14.3	10	4	40.0

Table 5.4 Resighting rates for ringed adult Cyprus and Sardinian Warblers on all seven study plots for 2003-2004.

	Cyprus Warbler			Sardinian Warbler		
	No. ringed birds alive 2004	No. resighted 2005	Percentage resighted	No. ringed birds alive 2004	No. resighted 2005	Percentage resighted
Adult males	27	15	55.6	38	15	39.5
Adult females	11	1	9.1	35	7	20.0

Table 5.5 Resighting rates for ringed adult Cyprus and Sardinian Warblers on all seven study plots for 2004-2005.

Nesting phenology

In 2004 and 2005 clutches of both species were initiated over a two-month period from early March to early June (Fig. 5.1). In all three years Sardinian Warblers finished breeding one to three weeks later than Cyprus Warblers, and in 2004 and 2005 they also started breeding one to three weeks earlier. In 2003 fieldwork started late and nesting almost certainly began earlier than is indicated. In 2003 Cyprus Warbler last clutches were initiated at the end of May, but the last Sardinian Warbler clutch was initiated in mid-June, considerably later than in 2004 or 2005.

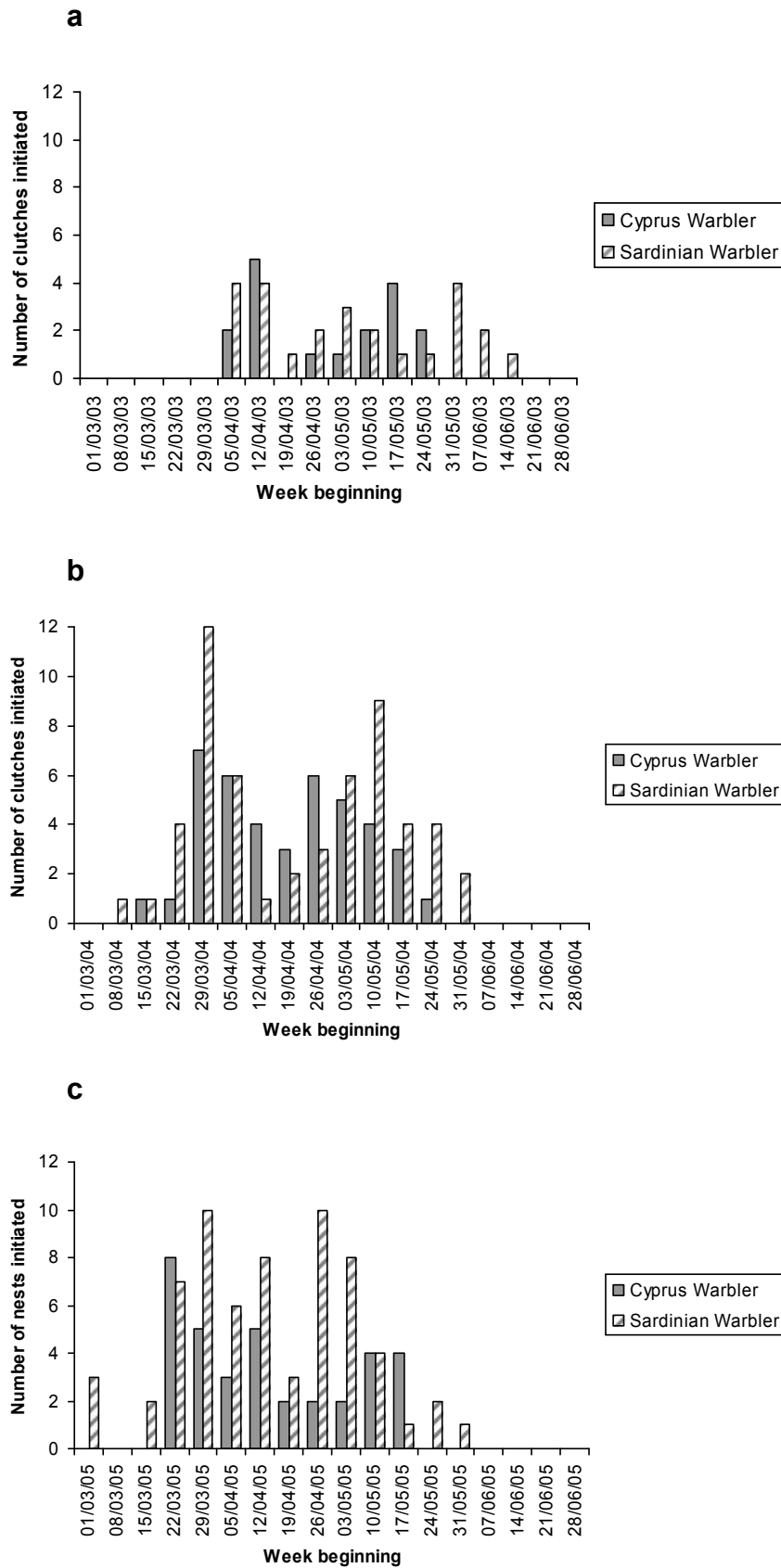


Figure 5.1 First-egg dates for nests laid in by Cyprus Warblers and Sardinian Warblers in a) 2003 (n=17, n=25), b) 2004 (n=41, n=55) and c) 2005 (n=35, n=65) breeding seasons.

Clutch size and hatching success

When data for the three years' first nesting attempts were pooled, Cyprus Warbler mean clutch size was 3.98 ± 0.10 (range 3-5, $n=40$), while Sardinian Warbler mean clutch size was 3.89 ± 0.10 (range 2-5, $n=56$). For first nesting attempts Cyprus Warblers (95.8 ± 1.94 %, $n=24$) had slightly higher hatching success than Sardinian Warblers (86.9 ± 3.07 %, $n=45$). Although consistent between years, the difference between the two species was not significant (Mann-Whitney U test: $U=428$, $p=0.080$). Across all nests that were laid in during the three breeding seasons 7 % of Cyprus Warbler and 18 % of Sardinian Warbler nests contained one or more eggs that failed to hatch where other eggs in the clutch hatched successfully. Such remaining eggs were usually found to be infertile.

Incubation

Exact incubation periods were only obtained for a relatively small sub-sample of nests (Fig. 5.2). Mean incubation periods for Cyprus Warbler and Sardinian Warbler were 12.9 ± 0.39 days ($n=9$) and 13.4 ± 0.30 ($n=21$) days respectively. There was some variation between years, with median incubation for both Cyprus and Sardinian Warblers lasting one day longer in 2004 than in the other years. The difference between years was not significant for Cyprus Warbler (GLM: $F=1.242$, $d.f.=2$, $p=0.354$) or Sardinian Warbler ($F=1.181$, $d.f.=2$, $p=0.330$), and therefore 13 days was used as the standard incubation period for both species when calculating laying dates for any nests found after hatching.

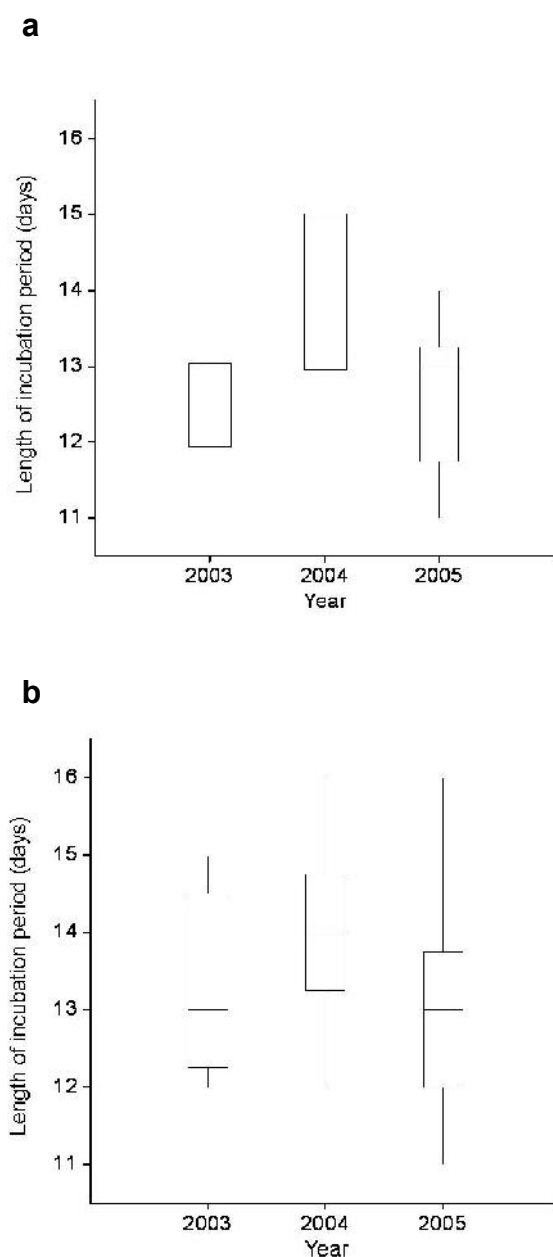


Figure 5.2 Box plots (horizontal line - median value, box - interquartile range, whisker - largest and smallest value within 1.5 interquartile ranges of top and bottom). Length of (a) Cyprus Warbler ($n=2$, $n=2$, $n=5$) and (b) Sardinian Warbler ($n=3$, $n=7$, $n=11$) incubation periods recorded during 2003, 2004 and 2005 breeding seasons. Only nests where exact incubation periods were recorded are included.

Productivity of first nesting attempts

Averaging means for first nesting attempts over the three years, overall mean number of Cyprus Warbler chicks surviving to 5 days was 2.51, while mean number of Sardinian Warbler chicks surviving was 2.67. Despite some variation between years

(Fig. 5.3), there was no significant difference between years in the mean number of chicks surviving to 5 days during first nesting attempts for either Cyprus Warbler (Kruskal-Wallis: $H=2.116$, $d.f.=2$, $p=0.318$) or Sardinian Warbler ($H=1.740$, $d.f.=2$, $p=0.394$). In addition, there was no significant difference in number of chicks surviving to 5 days between the two species in 2003 (Mann-Whitney U: $U=198.5$, $p=0.612$), 2004 ($U=591.0$, $p=0.727$) or 2005 ($U=389.5$, $p=0.574$).

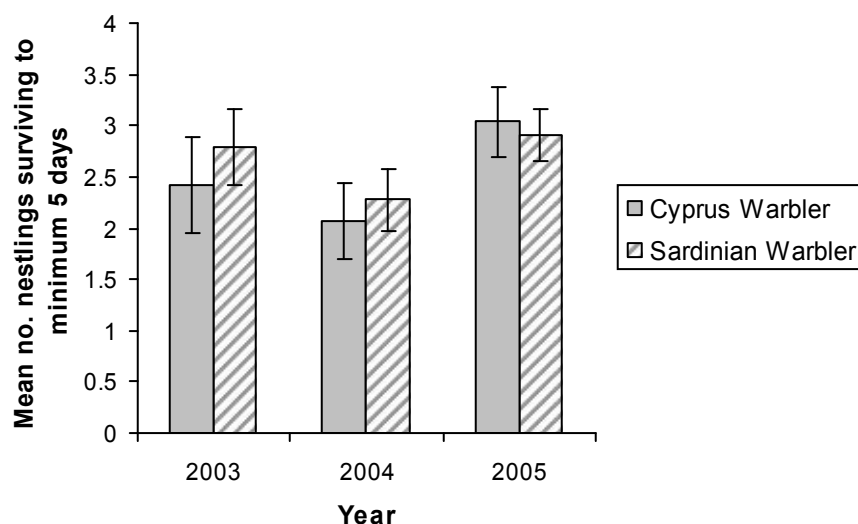


Figure 5.3 Mean number of nestlings surviving to minimum 5 days during first known nesting attempts for Cyprus and Sardinian Warbler pairs during 2003 ($n=19$, $n=23$), 2004 ($n=31$, $n=40$) and 2005 ($n=25$, $n=34$) breeding seasons.

There were no consistent patterns between years for number of chicks surviving to 5 days at different sites (Table 5.6).

Site	2003		2004		2005	
	Cyprus Warbler	Sardinian Warbler	Cyprus Warbler	Sardinian Warbler	Cyprus Warbler	Sardinian Warbler
Akamas 2			3.25 ± 1.18 (n=4)	2.14 ± 0.77 (n=7)	(n=2)	(n=2)
Akamas Pines	(n=1)	3.67 ± 0.67 (n=3)		2.57 ± 0.69 (n=7)	(n=1)	3.50 ± 0.56 (n=6)
Ineia	2.25 ± 1.32 (n=4)	1.75 ± 0.85 (n=4)	1.60 ± 0.98 (n=5)	1.33 ± 0.72 (n=6)	3.14 ± 0.60 (n=7)	1.50 ± 0.96 (n=4)
Choli	(n=2)	2.88 ± 0.67 (n=8)	0.75 ± 0.75 (n=4)	1.60 ± 0.68 (n=5)	(n=2)	2.54 ± 0.43 (n=13)
Lysos	2.25 ± 0.75 (n=4)	2.88 ± 0.69 (n=8)	4.33 ± 0.67 (n=3)	2.62 ± 0.58 (n=13)	(n=1)	3.57 ± 0.37 (n=7)
Kouklia Hives	1.17 ± 0.75 (n=6)		2.14 ± 0.77 (n=7)	(n=1)	2.83 ± 0.91 (n=6)	(n=2)
Kouklia 3	(n=2)		1.50 ± 0.73 (n=8)	(n=1)	3.00 ± 0.63 (n=6)	
All sites	2.42 ± 0.47 (n=19)	2.78 ± 0.37 (n=23)	2.07 ± 0.38 (n=31)	2.28 ± 0.30 (n=40)	3.04 ± 0.34 (n=25)	2.91 ± 0.26 (n=34)

Table 5.6 Mean ± SE number of Cyprus and Sardinian Warbler nestlings surviving to minimum 5 days at different sites during first nesting attempts in 2003, 2004 and 2005 breeding seasons. Means given only where there were three or more observations for that species on the plot. Sample sizes in brackets.

In general, in each year a higher percentage of Cyprus Warblers produced no chicks in their first breeding attempt than Sardinian Warblers (Fig. 5.4). Sardinian Warblers more commonly had one or two chicks surviving to 5 days than did Cyprus Warblers, while Cyprus Warblers more commonly had first nesting attempts where 5 chicks survived than did Sardinian Warblers. The frequency distributions indicate that for both species the frequency of failure was highest in 2004 and lowest in 2005.

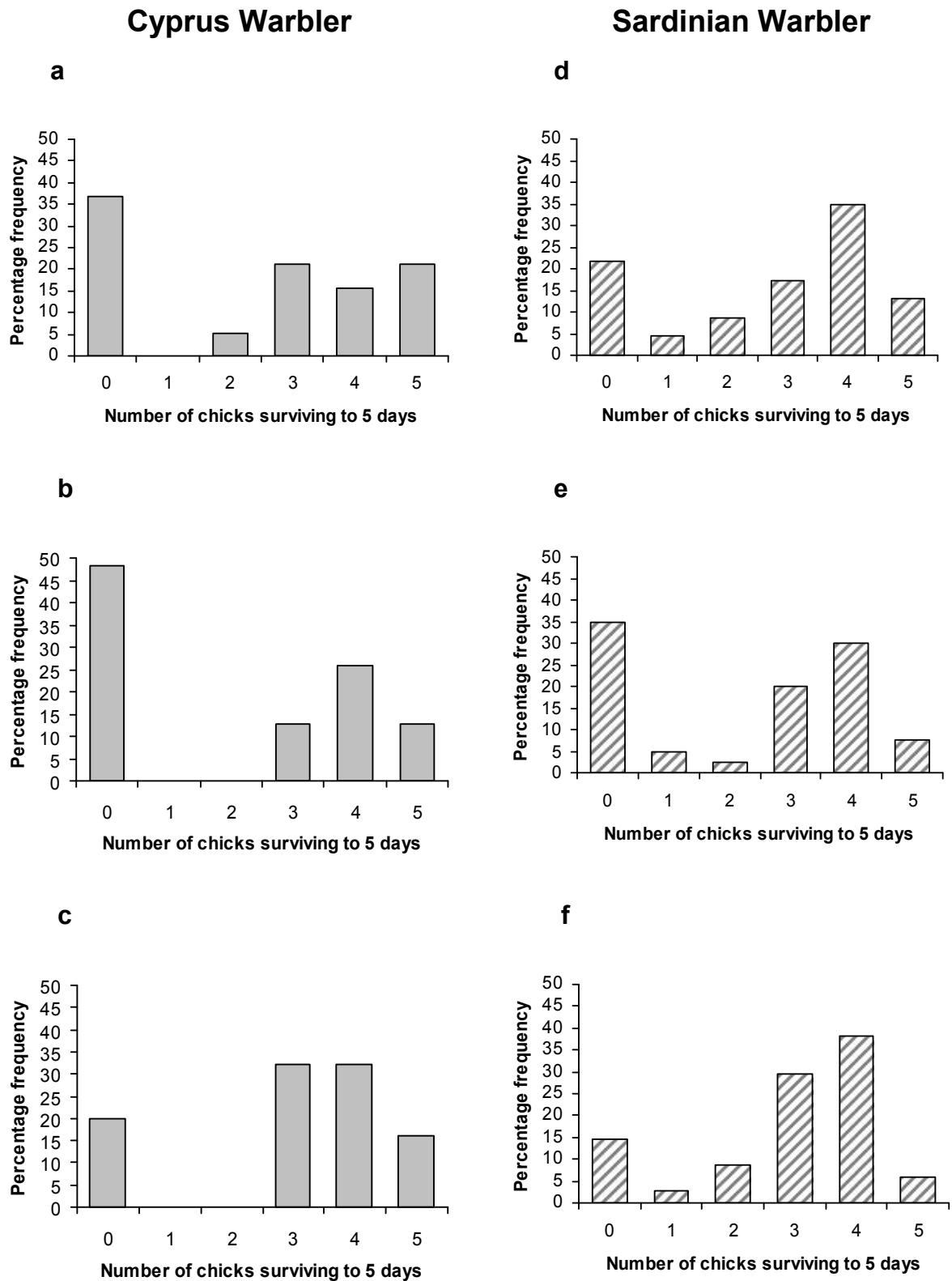


Figure 5.4 Frequency with which different numbers of Cyprus and Sardinian Warbler chicks survived to 5 days during first nesting attempts in a & d) 2003 (n=19, n=23), b & e) 2004 (n=31, n=40) and c & f) 2005 (n=25, n=34).

When success (defined as a minimum of one nestling surviving to 5 days) or failure (no nestlings surviving to 5 days) of Cyprus and Sardinian Warbler first nests in 2004 and 2005 was modelled as a binomial response (Table 5.7), only year was found to have a significant effect on success, with more first nests having nestlings surviving to 5 days in 2005 than in 2004. There was no significant difference in success between the species.

Explanatory terms	F	df	p
Year	9.32	1	0.002
Species	0.99	1	0.320
First clutch initiation date	1.87	1	0.171
Species of nearest neighbour	0.21	1	0.651
Distance to nearest neighbour	0.00	1	0.967
Minimal model	Effect size	SE	
Constant	0.349	0.292	
Year	1.316	0.431	

Table 5.7 Results of a binomial GLMM investigating factors affecting whether or not Cyprus and Sardinian Warbler nests succeeded in 2004 and 2005. Success (min. 1 nestling surviving to 5 days) or failure (0 nestlings surviving to 5 days) was the response, the explanatory terms listed were fixed factors and site was a random factor. Significant terms highlighted in bold. Effect sizes given for significant terms only.

Incidence and productivity of second nesting attempts

In 2004 3.2-9.7 % of Cyprus Warbler pairs had a second nesting attempt following a 'successful' first attempt compared with 12.5-25.0 % of Sardinian Warbler pairs (minimum estimate based on ≥ 1 chick surviving to minimum 5 days post-hatching, maximum estimate based on ≥ 1 chick surviving to within 1 day of fledging). In 2005 16.0-28.0 % of Cyprus Warblers had a second nesting attempt, compared with 30.0-40.0 % of Sardinian Warbler pairs (Fig. 5.5). In both years Sardinian Warblers were more likely to make a second nesting attempt, but in neither 2004 (Binomial GLM: $F_{1,70}=2.15$, $p=0.142$) nor 2005 ($F_{1,54}=1.52$, $p=0.218$) was there a significant difference between species in the minimum number of pairs making a second nesting attempt.

For Cyprus Warblers the minimum number of second nesting attempts was not significantly different between years ($F_{1,55}=2.88$, $p=0.090$). However, Sardinian Warbler pairs had significantly more second nesting attempts in 2005 than in 2004 ($F_{1,67}=4.64$, $p=0.031$).

Mean $\pm$ SE number of days between initiation of first and second breeding attempts (5-day definition) was 39.8 ± 5.0 ($n=4$) for Cyprus Warbler and 41.8 ± 2.2 ($n=9$) for Sardinian Warbler in 2004 and 38.9 ± 3.7 ($n=7$) for Cyprus Warbler and 36.8 ± 1.8 ($n=12$) for Sardinian Warbler in 2005. There was no significant difference between Cyprus and Sardinian Warbler inter-clutch intervals in either 2004 (Independent samples t-test: $t=-0.44$, $d.f.=11$, $p=0.668$) or 2005 ($t=0.55$, $d.f.=17$, $p=0.590$).

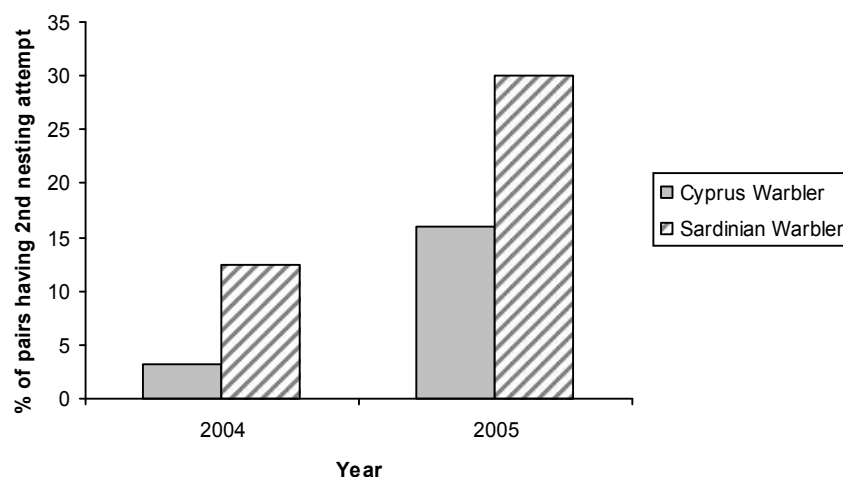


Figure 5.5 Minimum percentage of Cyprus and Sardinian Warbler pairs making a second nesting attempt in 2004 and 2005 (after nestlings from their first attempt survived at least to within 1 day of fledging).

For those Cyprus and Sardinian Warbler pairs in 2004 and 2005 where first nests were found, I examined which factors had an effect on whether or not a second nesting attempt was initiated (Table 5.8).

Explanatory terms	Cyprus Warbler 2004		Sardinian Warbler 2004		Cyprus Warbler 2005		Sardinian Warbler 2005	
	F	p	F	p	F	p	F	p
Species of nearest neighbour	0.00	0.977	0.45	0.503	1.26	0.262	0.040	0.845
Distance to nearest neighbour	0.77	0.381	0.66	0.416	0.17	0.679	2.56	0.109
Clutch initiation date for first attempt	3.19	0.074	4.68	0.031	4.56	0.033	5.14	0.023
Minimal model	Effect size	SE	Effect size	SE	Effect size	SE	Effect size	SE
Constant			-0.924	0.766	-0.443	0.536	-0.471	1.016
Clutch initiation date for first attempt			-8.063	3.729	-9.371	4.386	-17.40	7.677

Table 5.8 Binomial GLMM with whether or not Cyprus and Sardinian Warbler pairs initiated a second nesting attempt (by 5-day measure of first attempt success) in 2004 and 2005 as the response, the explanatory terms listed as fixed factors (d.f.=1) and site as a random factor. Significant terms highlighted in bold. Effect sizes given for significant terms only.

Date of first clutch initiation had a significant effect on whether or not a second nesting attempt was initiated for Cyprus Warblers in 2005 and for Sardinian Warblers in 2004 and 2005. In both years for both Cyprus and Sardinian Warbler, pairs which had a second nesting attempt had initiated their first clutch earlier than those that did not (Fig. 5.6).

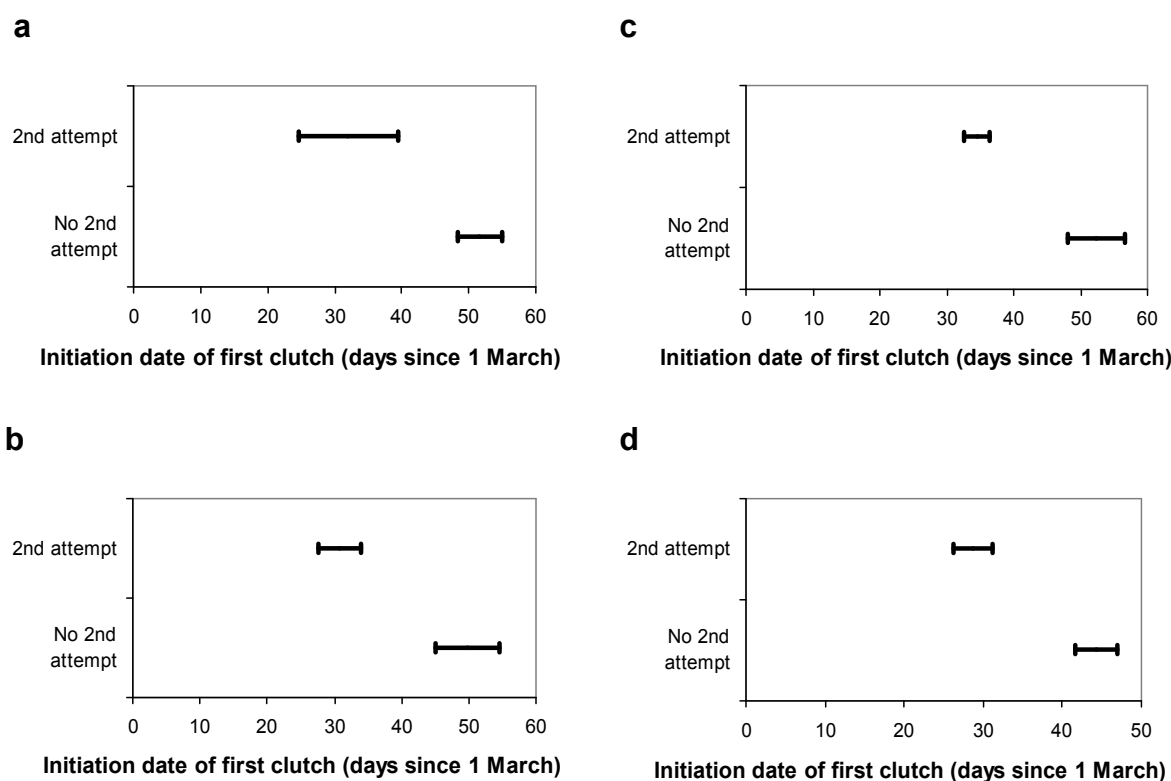


Figure 5.6 Standard errors of mean first clutch initiation dates for a) Cyprus Warbler 2004 (n=30), b) Cyprus Warbler 2005 (n=23), c) Sardinian Warbler 2004 (n=37) and d) Sardinian Warbler 2005 (n=29) pairs which did or did not initiate a second nesting attempt (after their first nest reached 5-day nestling stage).

Mean number of chicks per second attempt surviving to 5 days in 2004 was 2.33 ± 0.33 (n=3) for Cyprus Warbler and 2.20 ± 0.51 (n=10) for Sardinian Warbler, while in 2005 it was 2.86 ± 0.63 (n=7) for Cyprus Warblers and 3.25 ± 0.429 (n=12) for Sardinian Warblers. There was no significant difference between the two species in the mean number of chicks surviving to 5 days in second broods in either 2004 (Mann-Whitney U: $U=13.0$, $p=0.706$) or 2005 ($U=36.0$, $p=0.630$).

For those pairs which had a second nesting attempt, I compared mean number of chicks surviving to 5 days for the pair's first and second broods. For Cyprus Warbler pairs in 2004, there was no significant difference between number of chicks surviving to 5 days in first and second attempts (Wilcoxon test: $Z=0$, $p=0.250$). In 2005 slightly fewer chicks survived in the second nesting attempt than the first, but the difference was marginally non-significant ($Z=0$, $p=0.063$). Sardinian Warbler first broods yielded

significantly more surviving chicks than second broods in 2004 ($Z=4.5$, $p=0.047$), but not in 2005 ($Z=13.5$, $p=0.797$).

Total nestling output per pair

Mean nestling output (Fig. 5.6) over the 2004 breeding season was 2.66 ± 0.41 (range 0-8) for Cyprus Warbler pairs and 3.18 ± 0.41 (range 0-9) nestlings to 5 days for Sardinian Warbler pairs. Over the 2005 breeding season mean nestling output was 3.83 ± 0.54 (range 0-9) nestlings to 5 days for Cyprus Warbler pairs and 4.49 ± 0.42 (range 0-10) nestlings to 5 days for Sardinian Warblers.

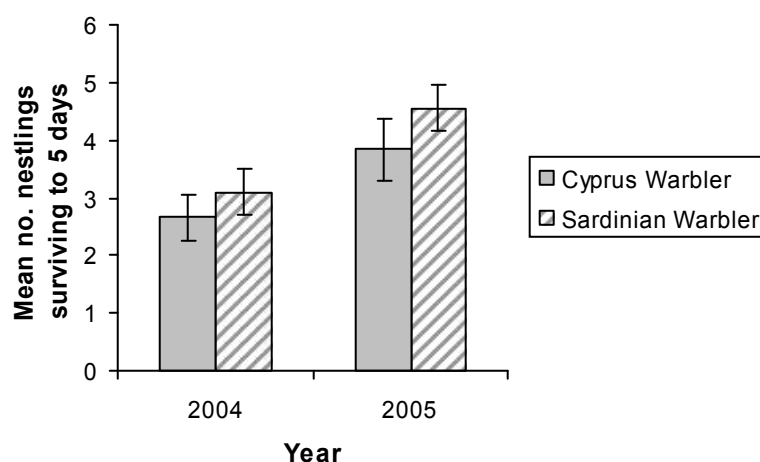


Figure 5.6 Mean number of Cyprus ($n=32$, $n=24$) and Sardinian Warbler ($n=39$, $n=33$) nestlings per pair surviving to minimum 5 days over the course of the breeding season in 2004 and 2005.

Nestling output per season was 19.5 % higher for Sardinian Warbler pairs than Cyprus Warbler pairs in 2004 and 17.2 % higher for Sardinian Warbler pairs than Cyprus Warbler pairs in 2005.

Explanatory terms	F	df	p
Species	1.74	1	0.187
Year	8.29	1	0.004
Zone	0.80	2	0.669
Minimal model	Effect size		SE
Constant	2.944		0.294
Year - 2004	0.000		0.000
Year - 2005	1.267		0.440

Table 5.9 GLM with data from both Cyprus and Sardinian Warbler nesting attempts in 2004 and 2005. Dependent variable: chick output per pair per season and explanatory terms listed as fixed factors. Significant terms highlighted in bold. Effect sizes given for significant terms only.

A GLM with chick output per pair per season as the dependent variable and species, year and zone as factors (with their interactions) showed no significant effect of species or zone on total chick output for the season (Table 5.9). However there was a significant effect of year, with 2005 having significantly higher chick output per pair than 2004.

Site	2004		2005	
	Cyprus Warbler	Sardinian Warbler	Cyprus Warbler	Sardinian Warbler
Akamas 2	4.00 ± 1.68 (n=4)	3.33 ± 1.20 (n=6)	(n=2)	4.75 ± 1.03 (n=4)
Akamas Pines		2.57 ± 0.69 (n=7)	(n=1)	4.20 ± 1.16 (n=5)
Ineia	2.00 ± 0.89 (n=5)	3.00 ± 1.10 (n=6)	3.71 ± 0.92 (n=7)	3.67 ± 0.88 (n=3)
Choli	0.75 ± 0.75 (n=4)	2.40 ± 0.68 (n=5)	(n=2)	3.83 ± 0.53 (n=12)
Lysos	5.00 ± 0 (n=3)	3.69 ± 0.91 (n=13)	(n=1)	5.29 ± 1.32 (n=7)
Kouklia Hives	3.29 ± 0.61 (n=7)	(n=1)	3.40 ± 1.40 (n=5)	(n=2)
Kouklia 3	2.0 ± 0.82 (n=9)	(n=1)	4.30 ± 1.17 (n=6)	

Table 5.10 Mean ± SE number of Cyprus and Sardinian Warbler nestlings (surviving to minimum 5 days) produced over all nesting attempts per pair in breeding seasons 2004 and 2005 at different sites. Means given only where three or more observations for that species on the site. Sample sizes in brackets.

There were no obvious patterns between years in chick output per pair for different sites, although Lysos appeared to be the most consistently productive site for both species (Table 5.10).

Explanatory terms	2004			2005		
	F	df	p	F	df	p
Lay-date of first clutch	10.52	1	0.001	5.90	1	0.015
Species of nearest neighbour	0.27	1	0.606	0.71	1	0.400
Distance to nearest neighbour	0.08	1	0.782	0.31	1	0.578
Zone	1.01	2	0.602	3.13	2	0.209
Minimal model	Effect size		SE	Effect size		SE
Constant	2.833		0.3629	4.136		0.493
Lay-date of first clutch	-0.0674		0.0208	-0.0665		0.0274

Table 5.11 GLMs for 2004 and 2005 Cyprus Warbler chick output per pair with the explanatory terms listed as fixed factors. Significant terms highlighted in bold. Effect sizes given for significant terms only.

Explanatory terms	2004			2005		
	F	df	p	F	df	p
Lay-date of first clutch	9.17	1	0.002	14.06	1	<0.001
Species of nearest neighbour	0.34	1	0.562	0.89	1	0.345
Distance to nearest neighbour	1.53	1	0.216	3.72	1	0.054
Zone	0.00	2	0.999	0.25	2	0.881
Minimal model	Effect size		SE	Effect size		SE
Constant	3.361		0.382	4.531		0.357
Lay-date of first clutch	-0.0564		0.0186	-0.0898		0.0239
(Distance to nearest neighbour)				0.457		0.0237

Table 5.12 GLMs for 2004 and 2005 Sardinian Warbler chick output per pair with the explanatory terms listed as fixed factors. Effect sizes given for significant terms. Effect size also given for the marginally non-significant variable: distance to nearest neighbour (2005).

GLMs showed no significant effect of species of nearest neighbour, distance to nearest neighbour or zone on Cyprus Warbler or Sardinian Warbler chick output per pair during 2004 or 2005 breeding seasons (Tables 5.11 and 5.12). However lay-date

of the first clutch had a significant effect on Cyprus and Sardinian Warbler chick output in both 2004 and 2005. Pairs which initiated first nesting attempts earlier had higher chick output (Fig. 5.7). For Sardinian Warbler in 2005 there was a marginally non-significant effect of distance to nearest neighbour on chick output for the season.

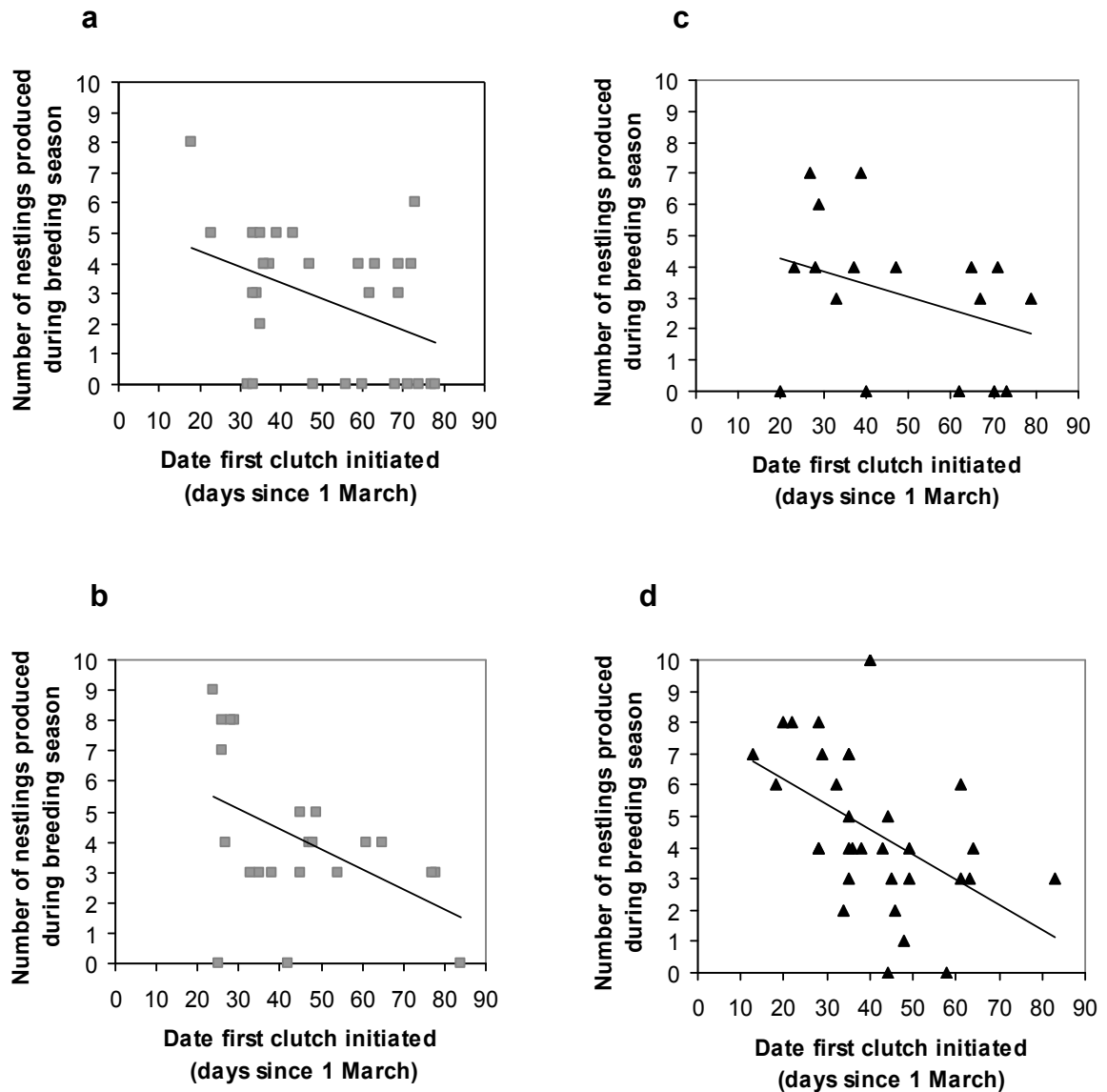


Figure 5.7 Total number of chicks surviving to 5 days over all breeding attempts for Cyprus Warbler pairs in a) 2004 (n=30) and b) 2005 (n=22) and Sardinian Warbler pairs in c) 2004 (n=36) and d) 2005 (n=32) in relation to date of first clutch initiation.

Species	Year	Mean chick output per pair per season		
		Zone 1	Zone 2	Zone 3
Cyprus Warbler	2004	4.00 ± 1.68 (n=4)	2.33 ± 0.64 (n=12)	2.56 ± 0.54 (n=16)
	2005	5.67 ± 1.76 (n=3)	3.20 ± 0.73 (n=10)	3.91 ± 0.87 (n=11)
Sardinian Warbler	2004	2.92 ± 0.65 (n=13)	3.25 ± 0.57 (n=24)	4.00 ± 0.00 (n=2)
	2005	4.44 ± 0.75 (n=9)	4.27 ± 0.52 (n=22)	7.00 ± 1.00 (n=2)

Table 5.13 Mean Cyprus and Sardinian Warbler chick output per pair per season in the three zones (zone 1-predominantly Sardinian Warbler, zone 2- both Cyprus and Sardinian Warbler, zone 3-predominantly Cyprus Warbler) during 2004 and 2005.

There were too few Cyprus Warbler pairs in zone 1 and Sardinian Warbler pairs in zone 3 for proper comparison between chick output in the 3 zones, but both species' productivity appeared to be highest in the zone in which the species was rarest (Table 5.13).

Mean chick output per pair appeared to increase with the altitude of the study plot for both Cyprus and Sardinian Warbler in 2004 and for Sardinian Warbler in 2005 (Fig. 5.8). However there was no significant relationship between mean chick output per pair and study plot altitude for Cyprus Warbler in 2004 (Spearman rank correlation: $r_s=0.754$, d.f.=4, $p=0.084$). There were too few plots with a minimum of three Cyprus Warbler pairs to be able to analyse 2005 data. For Sardinian Warbler there was a significant positive relationship between mean chick output per pair and study plot altitude in 2004 ($r_s=0.900$, d.f.=3, $p=0.037$), but not in 2005 ($r_s=0.400$, d.f.=3, $p=0.505$).

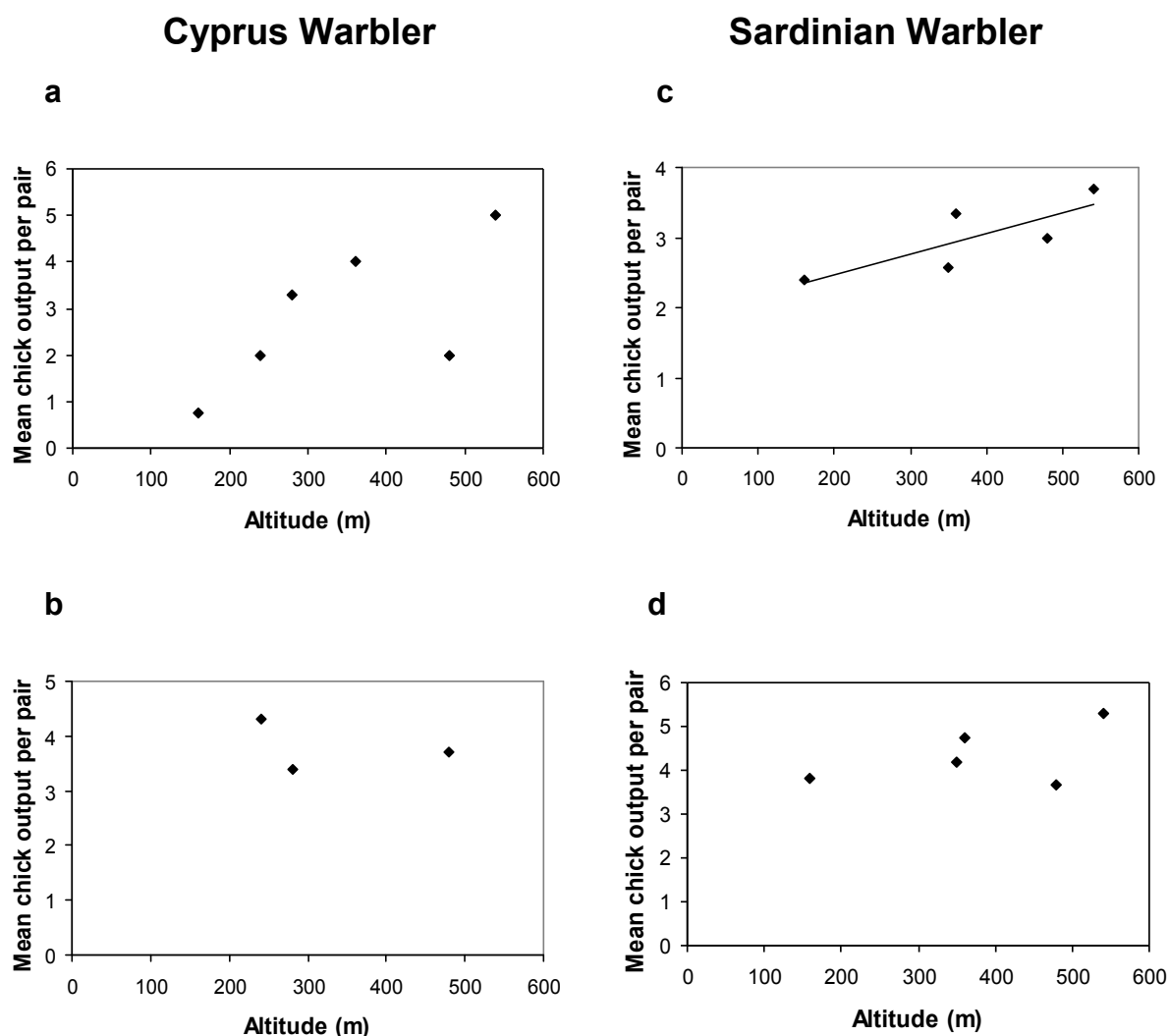


Figure 5.8 Mean chick output of Cyprus and Sardinian Warblers during 2004 (a & c) and 2005 (b & d) at study plots of different altitudes. Trend-line shown for significant r_s . Mean chick output was only calculated for plots with ≥ 3 pairs of the species concerned.

Total nestling output per average pair

Using a more or less conservative figure for proportion of Cyprus and Sardinian Warblers initiating a second nesting attempt could affect results for nestling output of Cyprus and Sardinian Warblers. Therefore nestling output for the average pair of each species in each year was calculated using both minimum (Table 5.14) and maximum (Table 5.15) probabilities of initiating a second attempt.

Formula	Mean no. chicks produced from 1 st nesting attempts	+	Minimum probability of initiating a 2 nd nesting attempt	x	Mean no. chicks produced from 2 nd nesting attempts	=	Mean output
Cyprus Warbler 2004	2.07 ± 0.38	+	0.0323	x	2.33 ± 0.33	=	2.15
Sardinian Warbler 2004	2.28 ± 0.30	+	0.125	x	2.20 ± 0.51	=	2.56
Cyprus Warbler 2005	3.04 ± 0.34	+	0.160	x	2.86 ± 0.63	=	3.50
Sardinian Warbler 2005	2.91 ± 0.26	+	0.300	x	3.25 ± 0.43	=	3.89

Table 5.14 Calculation of minimum mean output for the average Cyprus or Sardinian Warbler pair in 2004 and 2005.

Formula	Mean no. chicks produced from 1 st nesting attempts	+	Maximum probability of initiating a 2 nd nesting attempt	x	Mean no. chicks produced from 2 nd nesting attempts	=	Mean output
Cyprus Warbler 2004	2.07 ± 0.38	+	0.0968	x	2.33 ± 0.33	=	2.30
Sardinian Warbler 2004	2.28 ± 0.30	+	0.250	x	2.20 ± 0.51	=	2.83
Cyprus Warbler 2005	3.04 ± 0.34	+	0.280	x	2.86 ± 0.63	=	3.84
Sardinian Warbler 2005	2.91 ± 0.26	+	0.400	x	3.25 ± 0.43	=	4.21

Table 5.15 Calculation of maximum mean output for the average Cyprus or Sardinian Warbler pair in 2004 and 2005.

The earlier analysis summarised in Table 5.9 showed no significant effect of species on total chick output per pair for the season. Table 5.15 shows that whether minimum or maximum probability of a second nesting attempt is used, Sardinian Warblers, on

average appear to produce slightly, but not significantly, more chicks per season than Cyprus Warblers.

Nest survival

Overall, for both species nest survival was highest in 2005 and lowest in 2004 (Table 5.17).

Year	Phase	Cyprus Warbler	Sardinian Warbler
2003	Daily nest survival probability-laying & incubation	0.949 ± 0.231 (n=10)	0.968 ± 0.239 (n=8)
	Probability of nest survival-laying to hatching	0.441	0.595
	Daily nest survival probability-nestling phase	0.974 ± 0.187 (n=12)	0.977 ± 0.181 (n=17)
	Probability of nest survival-hatching to fledging	0.746	0.754
	Overall probability of nest survival from laying to fledging	0.329	0.448
2004	Daily nest survival probability-laying & incubation	0.966 ± 0.152 (n=21)	0.986 ± 0.0922 (n=29)
	Probability of nest survival-laying to hatching	0.557	0.790
	Daily nest survival probability-nestling phase	0.919 ± 0.177 (n=22)	0.947 ± 0.130 (n=33)
	Probability of nest survival-hatching to fledging	0.394	0.521
	Overall probability of nest survival from laying to fledging	0.220	0.411
2005	Daily nest survival probability-laying & incubation	0.978 ± 0.146 (n=15)	0.994 ± 0.0619 (n=25)
	Probability of nest survival-laying to hatching	0.705	0.914
	Daily nest survival probability-nestling phase	0.991 ± 0.0974 (n=22)	0.974 ± 0.118 (n=29)
	Probability of nest survival-hatching to fledging	0.906	0.727
	Overall probability of nest survival from laying to fledging	0.639	0.665

Table 5.16 Mayfield nest survival probabilities for first Cyprus and Sardinian Warbler nests of 2003, 2004 and 2005 breeding seasons. Daily nest survival probabilities ± SE shown separately for laying and incubation and nestling periods, along with the overall probability of nests surviving from laying to the point of fledging (sample sizes in brackets). Exposure periods from laying to hatching: Cyprus Warbler=15.8 days in 2003, 16.8 days in 2004, 15.5 days in 2005 and Sardinian Warbler=16.2 days in 2003, 16.7 days in 2004, 16.1 days in 2005 (see data analysis section of methods). Exposure periods from hatching to fledging in all years: Cyprus Warbler=11 days and Sardinian Warbler=12 days.

There was no significant effect of species or year on survival of Cyprus and Sardinian Warbler nests from laying to hatching (Table 5.17).

Explanatory terms	F	df	p
No. days nest exposed	20.89	1	<0.001
Species	1.55	1	0.212
Year	3.64	2	0.162
Minimal model	Effect size		SE
Constant	-0.857		0.281
No. days nest exposed	-0.229		0.050

Table 5.17 Binomial GLMM with whether or not Cyprus and Sardinian Warbler nests from 2003, 2004 and 2005 survived from laying to hatching as the response, the explanatory terms listed as fixed factors and site as a random factor. Significant terms highlighted in bold. Effect sizes given for significant terms only.

There was no significant effect of species on survival of nests from hatching to fledging, but there was a significant effect of year, with highest survival in 2005 and lowest survival in 2004 (Table 5.18).

Explanatory terms	F	df	p
No. days nest exposed	12.53	1	<0.001
Species	0.88	1	0.347
Year	7.01	2	0.030
Minimal model	Effect size		SE
Constant	-1.621		0.578
No. days nest exposed	-0.381		0.108
Year - 2003	0.000		0.000
Year - 2004	1.128		0.021
Year - 2005	-0.221		0.022

Table 5.18 Binomial GLMM with whether or not Cyprus and Sardinian Warbler nests from 2003, 2004 and 2005 survived from hatching to fledging as the response, the explanatory terms listed as fixed factors and site as a random factor. Significant terms highlighted in bold. Effect sizes given for significant terms only.

I plotted Kaplan-Meier curves in order to visualise survival over time for the nestling phase in different years (Fig. 5.8). In 2004, Cyprus Warbler nestling survival dropped relatively sharply at 3 days, and again at 8 days.

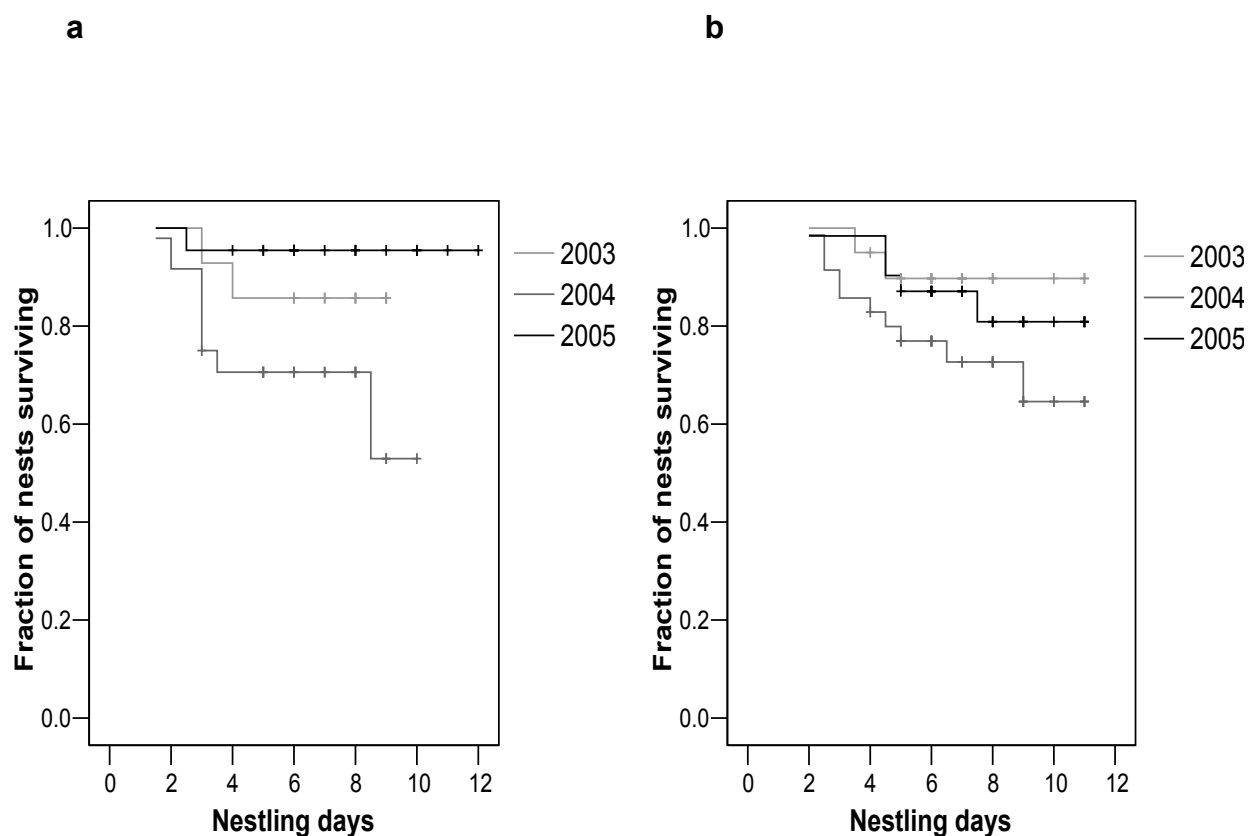


Figure 5.8 Kaplan-Meier cumulative survival functions showing a) Cyprus Warbler first nesting attempts from hatching to fledging in 2003 (n=14), 2004 (n=24) and 2005 (n=22) and b) Sardinian Warbler first nesting attempts from hatching to fledging in 2003 (n=20), 2004 (n=35) and 2005 (n=31). Censored observations are marked with a vertical line (See methods for description of censoring procedure).

I removed any nests known to have failed for reasons other than predation (leaving in any nests where cause of failure could not be determined) and then tested for any relationship between the resulting Mayfield nest survival probabilities and the number of warbler nests laid in over the breeding season, expressed as a density per hectare for each site. There was no significant correlation between density of nests at a site and Mayfield nest survival probabilities in 2004 for Cyprus Warblers ($r_s = 0.600$, d.f.=3, $p=0.285$), or Sardinian Warblers ($r_s = -0.400$, d.f.=3, $p=0.505$), or in 2005 for Sardinian

Warblers ($r_s = -0.400$, d.f.=2, $p=0.600$). There were too few sites with ≥ 3 pairs to carry out a correlation for Cyprus Warbler in 2005.

Discussion

Breeding behaviour

Cyprus and Sardinian Warblers have very similar breeding biology and behaviour, as one might expect from closely related congeners, but it is important to note that no mixed species pairs were found during the three-year study. Cyprus Warbler, Sardinian Warbler and Menetries Warbler (*Sylvia mystacea*) have all been considered to be a single species (e.g. Meinertzhagen 1930) or a superspecies (Cramp & Perrins 1994) in the past. The lack of hybridisation in this study supports the finding from mitochondrial DNA-sequencing that the two species are distinct (Shirihai *et al.* 2001). Cyprus Warbler was previously described as ‘apparently single brooded’ (Shirihai *et al.* 2001), but in this study I have shown that a proportion of pairs do have two nesting attempts in a breeding season. Sardinian Warblers appeared to start breeding slightly earlier and finish breeding slightly later than Cyprus Warblers and this was probably related to the fact that a higher percentage of Sardinian Warblers had two genuine nesting attempts in a breeding season. Intervals recorded between first and second nesting attempts suggest that some pairs of both Cyprus and Sardinian Warbler initiated a second clutch while still feeding recently fledged offspring from their first brood. This has been recorded in many other species including Spectacled Warbler (*Sylvia conspicillata*) (Guerrieri *et al.* 1998). Natal philopatry was recorded only once in each species in the present study, but was recorded in three cases in Sardinian Warblers on Malta (Gauci & Sultana 1980).

Resighting rates of adult warblers

The resighting rate of adult Cyprus Warbler males was relatively high. This may reflect good survival or high site fidelity. The particularly low resighting rate for Cyprus Warbler females is a potential cause for concern, although it may simply reflect lower site fidelity among females than among males. If it is a true reflection of survival, then it may be related to females being at higher risk of predation during the breeding

season because they spend more time on the nest. It could also reflect a higher proportion of females than males migrating and therefore being subject to higher mortality (Sillett & Holmes 2002, Jones *et al.* 2004). Among Sardinian Warblers the difference between male and female resighting rates was less marked.

Productivity

The two species had similar mean clutch sizes for their first nesting attempts and Sardinian Warbler mean clutch sizes were comparable with those reported in previous studies of the species in Malta, Morocco, Sicily and France (Shirihai *et al.* 2001). Cyprus Warbler had slightly higher hatching success than Sardinian Warbler, but otherwise, Sardinian Warbler appears to be slightly more productive in all respects, with slightly more chicks surviving to 5 days in first nesting attempts, slightly more chicks surviving on average in second attempts and a considerably higher proportion of pairs initiating a second nesting attempt. All of these elements result in Sardinian Warblers producing on average 18 % more chicks to 5 days than Cyprus Warblers over the course of a breeding season. Number of chicks surviving to 5 days is not, of course, as good a measure of success as number of chicks fledging, and actual nesting success for both species is likely to be lower than the 5-day measure indicates. However, there is no reason to suspect that relative survival of chicks beyond 5 days is different between the two species and as a relative measure of productivity it is likely to reflect accurately the disparity between the two species.

The finding that pairs with earlier clutch initiation dates were more likely to have second breeding attempts and also have higher chick output over the season, was consistent between species and years and may be related to pair quality. In passerines and other birds, older, more experienced or higher quality males often establish breeding territories of higher quality and begin breeding earlier (Brooke 1979, Bibby 1982, Lozano *et al.* 1996). Age, arrival time, quality and experience are likely to be interrelated. Aebischer *et al.* (1996) found that early-arriving Savi's Warbler (*Locustella luscinioides*) males secured higher quality territories and were able to achieve higher breeding success by fledging more broods in a breeding season.

Productivity and population trends

Differences in productivity between the two species could be contributing to the different population trends of Cyprus and Sardinian Warblers in Paphos District (Chapter 2). Productivity has many different components and differences between the species in any one of clutch size, hatching success, number of chicks surviving in first and second nesting attempts and probability of making a second nesting attempt could have effects at the population level. Of course one cannot deduce the effect of productivity on population trends without also having good information on survival. While I have information on resighting rates, this is unlikely to correspond to survival. The small size of my study plots meant that any birds returning, but settling just a short distance away would have been missed. Shirihi (2001) stated that in general, a pair of *Sylvia* needs to produce about 2.5 fledglings per breeding season in order to compensate for mean mortality rates. If mortality rates for both species were average for the genus then both species would have effected a population increase in 2005. However, in 2004, while on average Sardinian Warblers would have compensated for mortality or even increased slightly, taking into account that my 5-day definition of success almost certainly overestimates output, Cyprus Warblers would have failed to compensate for mortality. If in all years, Sardinian Warblers have higher productivity than Cyprus Warblers, it is easy to see how the population could be increasing in good years and at least 'breaking even' in poor years. In contrast, Cyprus Warbler populations might be increasing (albeit at a slower rate) in good years, but declining in poor years.

An effect of climate on productivity?

In Chapter 6, I will investigate what made 2004 a 'poor' year. If poor years are related to higher temperatures and lower rainfall, for example, climate change in the Mediterranean region could be negatively affecting productivity in both species but impacting more on Cyprus Warbler. Perhaps the influence of altitude on productivity could help to elucidate what effect climate change might have on Cyprus and Sardinian Warblers in the future. Although in this study the relationship between productivity and altitude was only significant for Sardinian Warblers in 2004, there was a weak positive relationship for both species in 2005. It is unclear what mechanism might generate such a pattern, but rainfall tends to correlate with altitude and this could in turn affect warblers by influencing the availability of arthropod food.

While preliminary, these results suggest that climate change should not be ruled out as a potential cause of Cyprus Warbler decline. In this study, the plots were located within a relatively narrow band of altitudes; it would be interesting to investigate the pattern further for a wider range of altitudes.

Productivity by zone

Although sample sizes were too small to allow statistical comparison of productivity from all three zones, in both years both species appeared to enjoy higher productivity in the zone where their species was scarcest. This could reflect an advantage in having fewer conspecific pairs to compete with. However if the Cyprus Warbler population is declining in zone 1, it is perhaps surprising that pairs that continue to breed there should enjoy high productivity. One explanation might be that any decline of the Cyprus Warbler population in this area is driven by increased adult mortality. Under such conditions the most successful life history strategy might be to invest in maximising productivity in the current breeding season.

No evidence for effects of Sardinian Warbler on Cyprus Warbler productivity

In the present study I found no evidence that species of nearest neighbour or distance to nearest neighbour had a significant impact on the breeding success of either Cyprus or Sardinian Warbler. The marginally non-significant result for Sardinian Warblers in 2005 suggests there may be some weak effect of distance to nearest neighbour but I found no evidence that Cyprus Warbler suffered negative effects on productivity from having a Sardinian Warbler nearest neighbour. Confer *et al.* (2003) found that clutch sizes of Golden-winged Warblers (*Vermivora chrysoptera*) were reduced with closer proximity of Blue-winged Warblers (*V. pinus*), but did not establish the causal link. In this study, effects of differing proportions of the two species, differing vegetation and differing density of breeding pairs on different plots may confound interpretation of observational data. Reciprocal experimental removal of the two species is often used to evaluate the effects of coexistence. Sillet *et al.* (2004), studying the Black-throated Blue Warbler (*Dendroica caerulescens*), found that the number of young fledged per territory, territory size, proportion of pairs having two broods and the proportion of time males spent foraging were greater on territories around which conspecific neighbour density was experimentally reduced,

compared to control territories. Experimental reduction of neighbour density for Cyprus and Sardinian Warbler could be illuminating.

Cyprus and Sardinian Warbler nest survival

Cyprus Warbler and Sardinian Warbler appear to have similar nest survival to one another, and Mayfield daily nest survival rates observed in this study are comparable with those observed in other studies of breeding *Sylvia* (Weidinger 2000, Stoate & Szczur 2001). During the nestling phase, daily nest survival in both species was lower in 2004 than in the other years, yet this was not the case during the laying and incubation phase. This might either suggest that food availability was poorer in 2004 causing more nests to fail through nestling starvation or that predators were particularly abundant during 2004 and were aided in locating nests by the extra activity during the nestling phase. Food availability and body condition of adults and chicks in the three years will be examined further in Chapter 6, but some findings of the current chapter are consistent with the idea of poorer food availability in 2004. For example the incubation period of both species was a day longer in 2004 than in 2003 and 2005. In both Cyprus and Sardinian Warbler the female appears to incubate the majority of the time and in neither species is she fed by the male during incubation. Thus under conditions of low food availability incubating females may need to spend longer off the nest in order to satisfy their own nutritional requirements, meaning that development of the embryo is slowed. Moreno (1989) found that Wheatear (*Oenanthe oenanthe*) incubation periods were longest during the least favourable years and that provisioned females were able to shorten incubation periods. In addition 2004 was the year where, for both species, fewest nests succeeded, first nesting attempts had lowest output and a considerably lower percentage of pairs of both species attempted second nests than in 2005. Furthermore chick output from second attempts and overall output per pair were both lower for Cyprus and Sardinian Warblers in 2004 than in 2005.

The drop-offs in survival which occurred three days and eight days into the Cyprus Warbler nestling period in 2004 (Fig. 5.8) may simply be an artefact of relatively low sample size; however the three-day drop-off could also be biologically meaningful. Both species generally brood nestlings more or less continuously for the first two or three days after hatching and the reduction in survival could coincide with lower

attendance at the nest, with both parents needing to forage in order to meet the nestlings' requirements in a poor food year.

There was no sign that either species had lower nest survival on plots with a higher overall density of warbler nests and therefore I found no evidence of 'apparent competition' (Hoi & Winkler 1994) occurring, with predators responding behaviourally or predator populations increasing in response to higher nest density. Any relationship between predation rate and nest density could of course be obscured by differences between plots in food availability, because hungry chicks tend to beg more and this may increase their likelihood of being predated (Haskell 1994, Leech & Leonard 1997).

In this chapter I have focused on how differences between Cyprus and Sardinian Warblers in the number of offspring produced per breeding season could be contributing to their differing population trends. However in the absence of evidence of interspecific competition between the two species, the decrease in Cyprus Warbler abundance in western Paphos District could be unrelated to the increase in Sardinian Warbler abundance. In Chapter 6 I will investigate whether there is any evidence that Cyprus and Sardinian Warbler might be competing for food resources, and how this might relate to the quality of offspring produced.

Chapter 6

Food availability, diet and nestling condition in Cyprus and Sardinian Warblers

Introduction

Food availability is a key factor influencing bird populations (Lack 1966, Perrins *et al.* 1991, Newton 1998). Intraspecific competition for food may be important in regulating population size in bird species and, where sympatric species have similar diets, interspecific competition for food may occur (Wiens 1989). It is therefore important to assess food availability and diet when investigating potential impacts of species coexistence.

Cyprus Warblers (*Sylvia melanothorax*) and Sardinian Warblers (*Sylvia melanocephala*) have overlapping home-ranges during the breeding season (Chapter 3) and their home-ranges have very similar vegetation composition (Chapter 4), so there is potential for the two species to compete for food. Minot (1981) suggested that interspecific overlap in home-ranges may result in greater food competition between heterospecifics than occurs between conspecifics, which are spatially separated by intraspecific territoriality. To investigate whether food competition could be having a negative impact one must first establish whether the two species concerned overlap in diet and secondly, establish whether food is a limited resource during the period under scrutiny.

As closely related congeners of similar size, we might expect Cyprus and Sardinian Warblers to have similar diets. *Sylvia* warblers are primarily insectivorous and forage almost exclusively by gleaning (Shirihai *et al.* 2001). Elsewhere in its range, Sardinian Warbler has been found to feed chiefly on insects (Debussche & Isenmann 1983), but also fruit, which may be an important component of the diet outside the breeding

season and is also taken opportunistically during the breeding season (Herrera 1984). Cyprus Warbler diet has not been studied previously. In this chapter I investigate whether Cyprus and Sardinian Warblers occupying the same study plot have similar adult and nestling diets and thereby assess the potential for food competition between the two species.

Faecal analysis was chosen as the method with which to investigate Cyprus and Sardinian Warbler diet because, unlike neck-collars (Poulsen & Aebischer 1995, Moreby & Stoate 2000) and emetics (Prys-Jones *et al.* 1974, Carlisle & Holberton 2006), it is non-invasive. Concerns have been raised about differential digestibility of food items biasing results of faecal analysis (Hartley 1948, Ralph *et al.* 1985), but this is more problematic when attempting to quantify accurately different elements of the diet than when broadly comparing the diets of two species.

Nestling survival and growth rates are usually highest for broods reared under conditions of high food availability and temporal variation in food supply has frequently been suggested to account for variation in breeding success (Brinkhof 1997, Siikamäki 1998). In Chapter 5, I measured breeding success as number of offspring surviving. However, not all offspring are equal; there is evidence to suggest that both quality and quantity of offspring may be important in maximizing a parent's fitness (Smith & Fretwell 1974, Sinervo *et al.* 2000). Body condition indices attempt to determine the mass of the individual after correcting for structural body size (Schulte-Hostedde *et al.* 2005) and are often used as a measure of offspring quality. Higher offspring body condition is known to be associated with increased survival rates (Ricklefs 1984, Millar & Hickling 1990, Tinbergen & Boerlijst 1990, Hochachka & Smith 1991, Linden *et al.* 1992) so associations between food availability and nestling body condition can have impacts at the population level.

Food availability can be difficult to quantify and, as Wiens (1989) pointed out, many studies simply assume that food is a limiting resource. Some researchers have experimentally reduced food supply and demonstrated a negative impact on chick body condition (Boatman *et al.* 2004, Morris *et al.* 2005), while others have experimentally increased food supply and demonstrated a positive effect on chick body condition (Crossner 1977, Simons & Martin 1990, Richner 1992, Brinkhof &

Cave 1997). In this chapter I investigate whether food supply could be limiting during the breeding season by monitoring seasonal changes in food supply on the study plots and examining whether these changes have an effect on Cyprus and Sardinian Warbler nestling body condition. I then go on to investigate whether measures of nestling body condition provide any evidence for negative effects of coexistence on either species.

When food is limiting, parents could respond by feeding all nestlings less food. However there is much evidence to show that, particularly when food is less plentiful, nestlings compete for resources and this tends to result in stronger members of the brood receiving more than their share of available food and weaker nestlings receiving less than their share (Trivers 1974, Cotton *et al.* 1999). In this way one might expect to see increased variation in the body condition of brood members when food availability is low. In this chapter, I examine whether differences in variation of body condition within broods are associated with food availability and investigate whether there is any evidence from variation in within brood body condition for food competition occurring between Cyprus and Sardinian Warblers.

Nestling provisioning rates are often used as a surrogate for nestling food intake. If either species is having a negative impact on the other through food competition, one might expect to see an effect on provisioning rates. Accordingly I examine nestling provisioning rates at Cyprus and Sardinian Warbler nests to investigate whether rate of provisioning correlates with measures of brood body condition and to determine whether there is any evidence that coexistence has a negative impact on chick provisioning rates.

In summary, in this chapter I will address the following questions:

- Are the diets of Cyprus and Sardinian Warbler adults and nestlings similar?
- Does food availability have an effect on nestling provisioning rates, nestling body condition or variation in nestling body condition within broods?
- Is there any evidence that either species suffers negative effects on nestling quality through food competition with the other species?

Methods

Rainfall

Precipitation data for Polis in 2003-2005 were obtained from the Cyprus Meteorological Service. Polis weather station lies within 15 km of five of the seven sites and was therefore likely to closely reflect the amount of precipitation occurring on the sites themselves.

Arthropod availability

Arthropod sampling (using four water traps at each site) was undertaken at all sites between April and the end of July 2003 and March and the end of June in 2004 and 2005. Mapping of the study plots (see general methods) had resulted in each plot being divided into a number of rows of marked grid-points. I selected one grid-point from each of four rows at random to determine the grid point where each trap would be placed. The trap was then positioned 4 m south of the selected grid-point. Of each study plot's four insect traps, two were situated 80 cm above the ground and two 10 cm above the ground. Trap height was random with respect to site row. The trap consisted of a 500 ml clear plastic container mounted on a cane. Traps were filled with water containing a standard amount of detergent to reduce surface tension and were collected every 5-9 days.

Contents were strained and stored in 70 % alcohol. Each sample was later examined at x 12 power under a dissection microscope. Individual arthropods were counted and measured in 1 mm size categories using graph paper placed underneath the Petri dish. Protruding structures such as mandibles, antennae, ovipositors and forceps were not included in the body length measurement.

A general length-weight regression equation was applied, such that biomass could be calculated from the length of arthropods captured. Hodar (1996) developed such an equation based on a sample of arthropods sampled from the Gaudix-Baza Basin in Granada Province, south-eastern Spain. Since this region has the same Mediterranean climate as Cyprus, and arthropod body types vary between regions

with different bioclimates, this was the most appropriate index to use of those available.

For each site, groups of four traps were left out for a varying number of days. All four traps did not always provide a sample, as they were sometimes knocked over by livestock or high wind. Occasionally, other animals like rodents or lizards became trapped in them, in which case the sample was discarded as it tended to attract large numbers of Diptera. I used an index of arthropod availability to account for different numbers of samples and exposure for different numbers of days. Arthropod availability was expressed as:

$$\frac{x}{yz}$$

where: x=total number or biomass (mg) of arthropods
 y=number of traps collected on that date
 z=number of days trap was left out for

This gave the index: mean number of arthropods or mean biomass (mg) per station per day.

Feeding behaviour

The feeding behaviour of the two species was not specifically studied. Since both species tend to glean arthropods as they move through bushes, the birds remain out of sight for long periods, making it difficult to record feeding behaviour in any detail. However during normal fieldwork, observations of feeding birds were recorded opportunistically.

Diet

Faecal samples produced during ringing of adults and nestlings were collected and stored separately in 70 % alcohol. To avoid the potential problem of different sites supporting slightly different prey assemblages, faecal sample analysis was confined to material collected between February and July over the three breeding seasons at Ineia, which had roughly equal numbers of Cyprus and Sardinian Warblers. Since

nestlings from the same brood are not independent samples, one faecal sample from each brood was randomly selected for analysis in order to avoid pseudoreplication.

Faecal samples from adult birds were gently broken up using fine forceps and then sieved through a 0.2 mm sieve to remove small pieces of organic material and unidentifiable fragments of chitin. The sample was then washed into a 50 mm Petri dish and examined using x 12 to x 50 magnification under a dissection microscope. The higher uric acid content and larger size of nestling faecal sacs required them to be prepared slightly differently from adult faeces. Nestling faecal sacs were emptied into a Petri dish and approximately 10 ml of 20 % potassium hydroxide was added. The faecal sample was then gently teased apart and large lumps of uric acid were broken up. The sample was then left to stand for 15 min to allow the potassium hydroxide to dissolve away some of the fine organic matter and hard lumps of uric acid. The sample was then sieved and placed in an 80 mm Petri dish for examination.

Samples were systematically searched for recognisable parts of food items; these included heads, mandibles, fangs, legs, wings, pieces of shell and elytra of arthropods as well as berry stones. Where possible, arthropod prey parts were identified to order with the aid of several publications (Pearson Ralph *et al.* 1985, Moreby 1988, Chapman & Rosenberg 1991, Shiel *et al.* 1997) and by comparison of prey parts with the collection of arthropods from the study plots, which was used to examine food availability (see below). Results were expressed as percentage frequency of occurrence.

Body condition

Nestlings were measured during ringing when aged 5–7 days. Nestling right and left wing lengths were measured to the nearest 0.5 mm using a wing-rule and the lengths of both tarsi were measured to the nearest 0.1 mm using callipers. Maximum tarsus length (Redfern & Clark 2001) was measured with the tarsus at right angles to the tibia and the foot at right angles to the tarsus. The measurement was then taken from the foot to the distal point of the 'knee' (not to the notch). Weight was recorded to the nearest 0.1 g using a 30 g spring balance. To ensure consistency, I was the only person who carried out measurements and I usually measured each chick twice,

once before ringing and once after. The mean of the two measurements was then used in body condition calculations.

Nestling provisioning

During the 2004 breeding season, watches were carried out at each nest to determine the rate of nestling provisioning and to clarify whether or not the sexes contributed equally. Nestling age was standardised as far as possible and most watches were carried out when chicks were 5-7 days old.

During provisioning watches the observer found a good vantage point more than 20 m away, from which the nest could be watched readily without causing disturbance. The observer remained still for 15 min after arrival before starting to record activity in order to allow the birds to settle. The nest was then watched for one hour, noting down the time of all visits to the nest and which parent was involved. Sometimes it was obvious that a visit had taken place, but the parent was not seen well enough to be sure of the sex; in these cases the visit was noted and the visiting bird marked down as unidentified.

Data analysis

Although both abundance and biomass of arthropods were recorded, only arthropod biomass was used in analyses, because it was considered the measure most relevant to chick condition. High arthropod abundance in samples sometimes consisted of many very small arthropods (0-2mm) which I considered warblers were unlikely to collect for chicks.

In order to compare biomass available between years where sampling began and ended at different times, I restricted the data set to day 65 (4th May) to day 110 (18th June), the period which was covered by sampling in all years. I then compared biomass available at each site in different years by summing mean biomass per station per day for different collection dates between day 65 and day 110, and dividing by the number of collection dates.

Sample sizes for faecal analysis were too small for chi-squared analysis, and frequency of occurrence data do not sum to one; a sample containing Coleoptera

may also contain Hemiptera and Araneida for example. This meant that the data were also unsuitable for compositional analysis (Aitchison 1986, Aebischer *et al.* 1993). Formal statistical analysis was not therefore carried out on diet data.

Only those nests for which nestlings were measured between 5 and 7 days were included in analysis of body condition. Over this age range, there was a straight line positive relationship between log mass and tarsus length (Fig. 6.1).

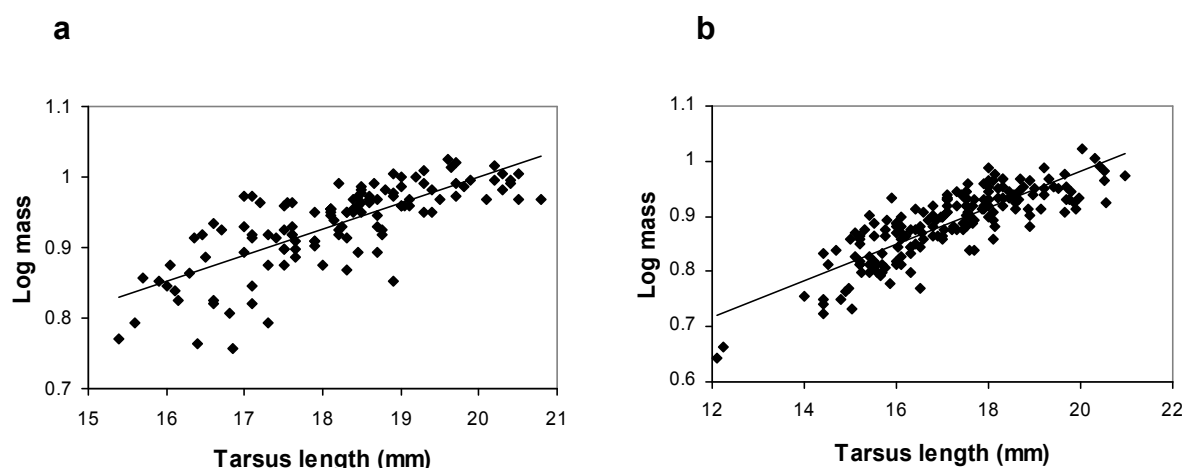


Figure 6.1 Relationship between log mass and length of right tarsus for a) Cyprus Warbler and b) Sardinian Warbler nestlings aged 5-7 days

I examined which factors affected nestling body condition separately for the two species, pooling 2004 and 2005 data. I excluded 2003 because data were relatively sparse and several potentially important explanatory variables were not measured in 2003. I also excluded nests where measurements were not obtained from all the nestlings. In addition, two outlying Sardinian Warbler broods were excluded because one or more chicks was moribund and so very under-weight when measured, and residuals of the model did not conform to normality when these data points were included. I used log mass as the response, but included tarsus length as a covariate and brood identity as a random factor in the linear mixed models (LMMs). In this way, in a single step, I was able to examine weight in relation to structural size, while accounting for the fact that nestlings from the same brood were not independent data points. Each brood was linked to arthropod biomass available on the study plot during the period between hatching and measuring. This was represented by the mean of

whichever set of four insect samples had come from traps exposed for most of the period between hatching and measuring. Arthropod biomass and date were log-transformed to meet the assumption of normality before LMMs were carried out.

For the two species separately, variation in chick body condition was calculated using a two step process. First, I used the residuals of a linear regression with tarsus as the predictor and log mass as the response, as a measure of each nestling's body condition. I then calculated variation in body condition within broods using the 'coefficient of variation' (standard deviation/mean value of set), a dimensionless index allowing comparison of variation in body condition between broods of different physical size. LMMs were then carried out separately for each species (pooling 2004 and 2005 data,) using arcsine square-root transformed coefficient of variation (CV) as the dependent variable. A number of factors were included in the model; arthropod biomass and date were log transformed to achieve normality.

To investigate whether Cyprus and Sardinian Warbler mean chick output per pair per season (from Chapter 5) on each plot was related to arthropod food availability, I carried out Spearman rank correlations on pooled data for 2004 and 2005. The measure of plot arthropod availability used was the restricted data set (4th May-18th June) as described above (start of data analysis section).

For analysis of nestling provisioning data (collected in 2004 only), only nests containing chicks aged 5-7 days were included and where provisioning data for several nests of the same pair were available, only the first surviving nesting attempt was included. Body condition of all nestlings in a brood (as calculated previously from the residuals of a regression of tarsus as a predictor of log mass) were averaged to provide a single data point for each brood for inclusion as a variable in provisioning rate analyses. Sample sizes for nestling provisioning data were relatively small and some variables were not normally distributed, so I conducted analysis as a series of parametric (Pearson's) and non-parametric (Spearman rank) correlations. When testing whether high biomass samples contained a higher proportion of large arthropods, those longer than 6 mm were classified as large. The vast majority of arthropods trapped were less than 5 mm in length and I considered a 6 mm long prey item as large in relation to the 12-14 mm bill length of the two warbler species.

Results

Rainfall

In 2003 there was a peak in rainfall in February, but rainfall then declined gradually to a low point in May. In contrast to the other two years, there was some rain in June, then none until October. In 2004, there was very high rainfall in January and some in February, but virtually no rainfall from March until October. In 2005 there was relatively low rainfall in January. Rainfall in subsequent months declined gradually and remained very low from May until October (Fig. 6.2).

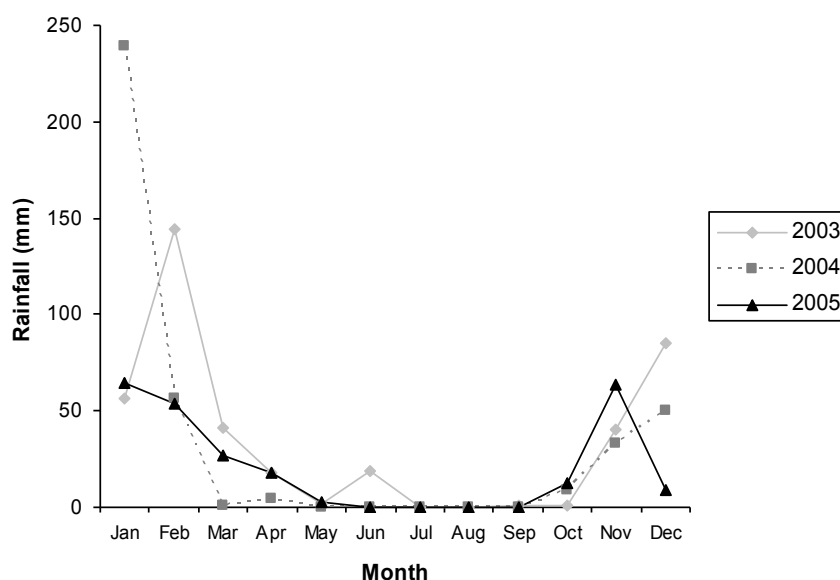


Figure 6.2 Rainfall in Paphos District throughout years 2003, 2004 and 2005, measured at Polis Chrysochous MET station.

Insect availability

In general, arthropod availability, whether measured as abundance or biomass, peaked between 70 and 90 days from the start of March, which is mid to late May (Figs. 6.3-6.9). The exception to this was Kouklia Hives, where peak arthropod availability occurred in June. At almost all sites, the peak was particularly pronounced in 2005 and arthropod availability was relatively low throughout the season in 2004.

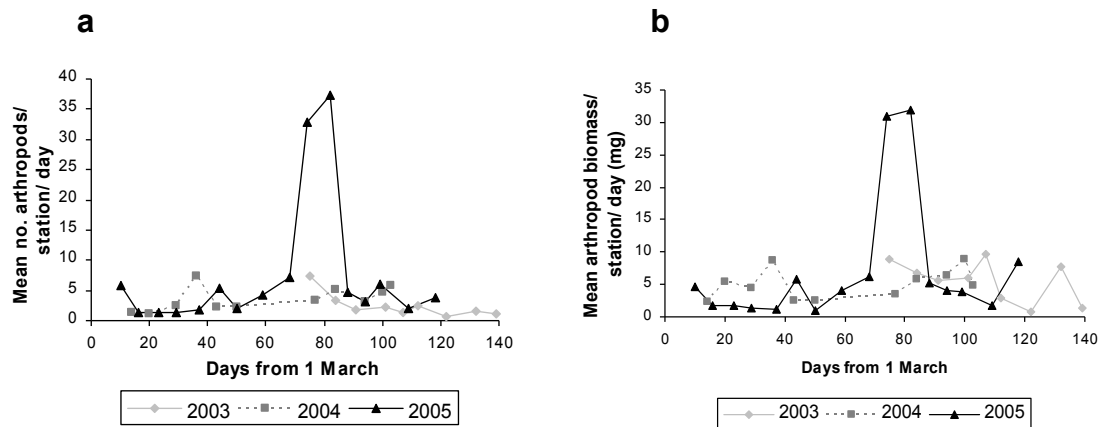


Figure 6.3 Arthropod a) abundance and b) biomass from water traps at Akamas Pines in 2003, 2004 and 2005 breeding seasons, measured as mean per station per day.

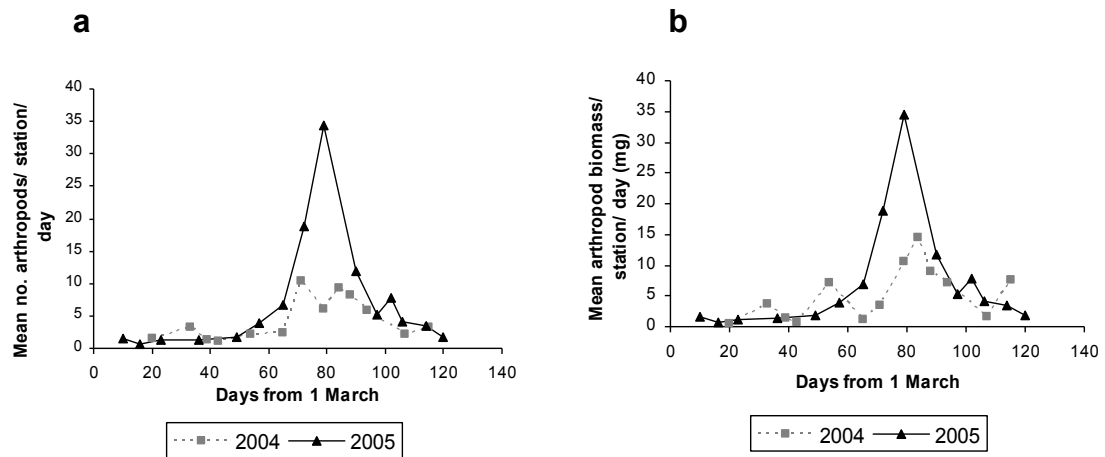


Figure 6.4 Arthropod a) abundance and b) biomass from water traps at Akamas 2 in 2004 and 2005 breeding seasons, measured as mean per station per day.

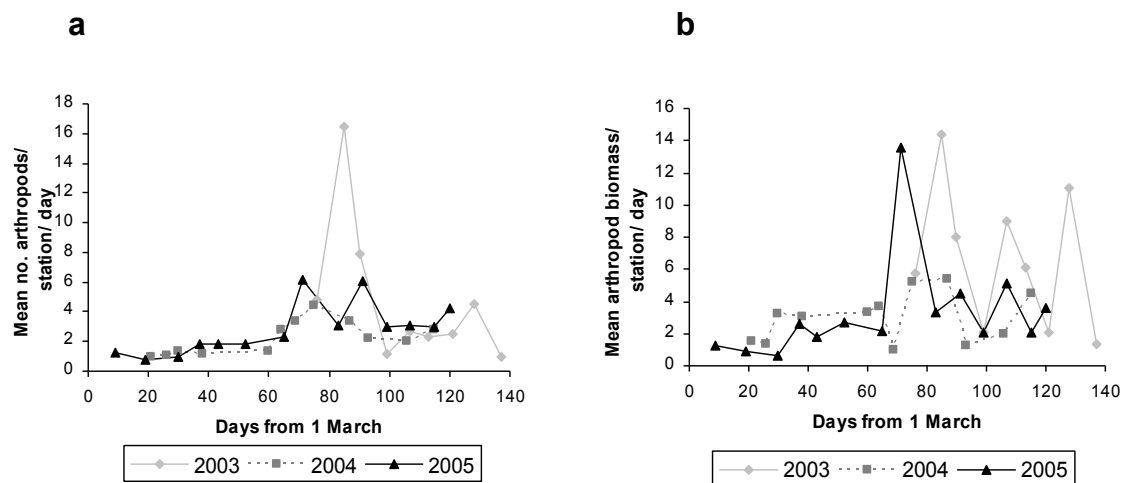


Figure 6.5 Arthropod a) abundance and b) biomass from water traps at Ineia in 2003, 2004 and 2005 breeding seasons, measured as mean per station per day.

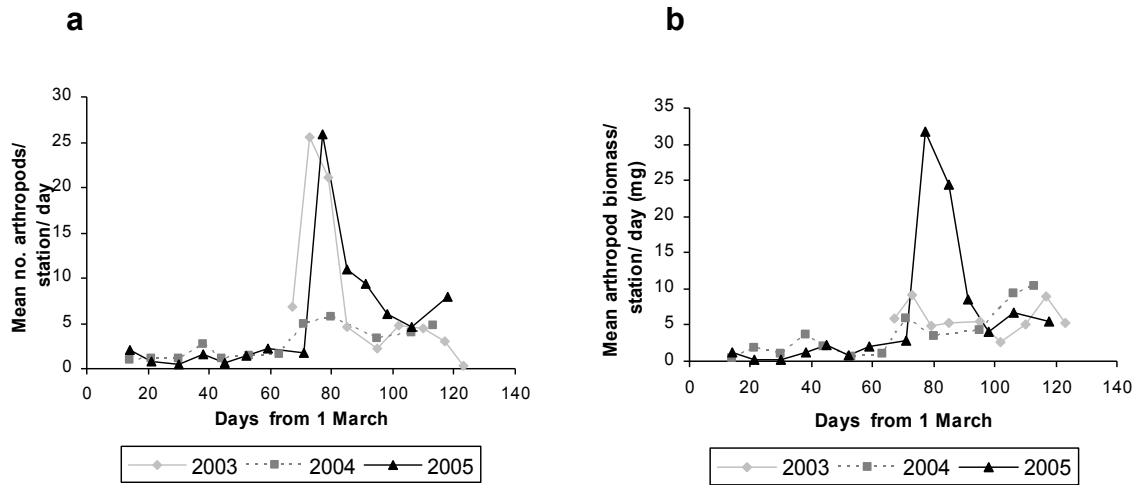


Figure 6.6 Arthropod a) abundance and b) biomass from water traps at Choli in 2003, 2004 and 2005 breeding seasons, measured as mean per station per day.

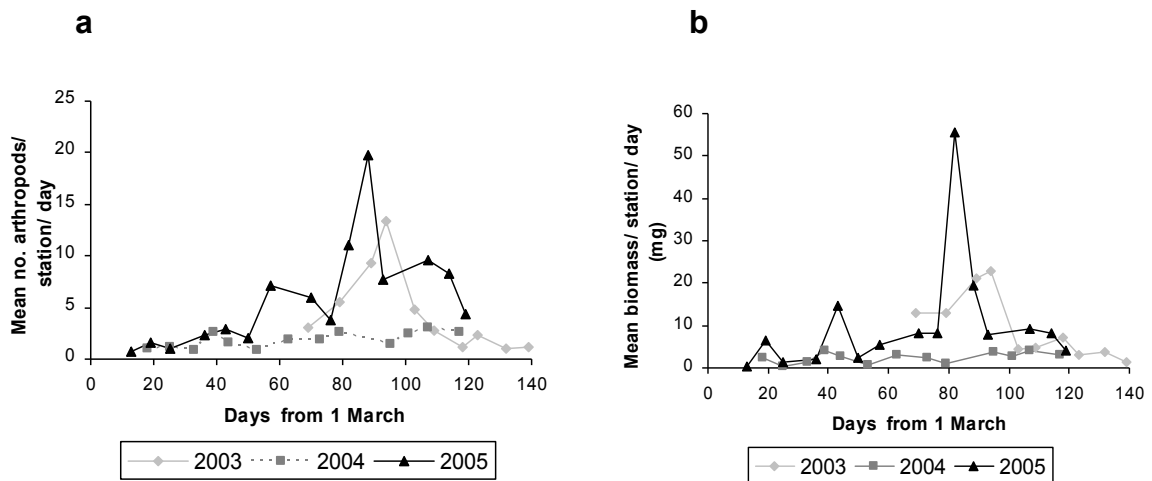


Figure 6.7 Arthropod a) abundance and b) biomass from water traps at Lysos in 2003, 2004 and 2005 breeding seasons, measured as mean per station per day.

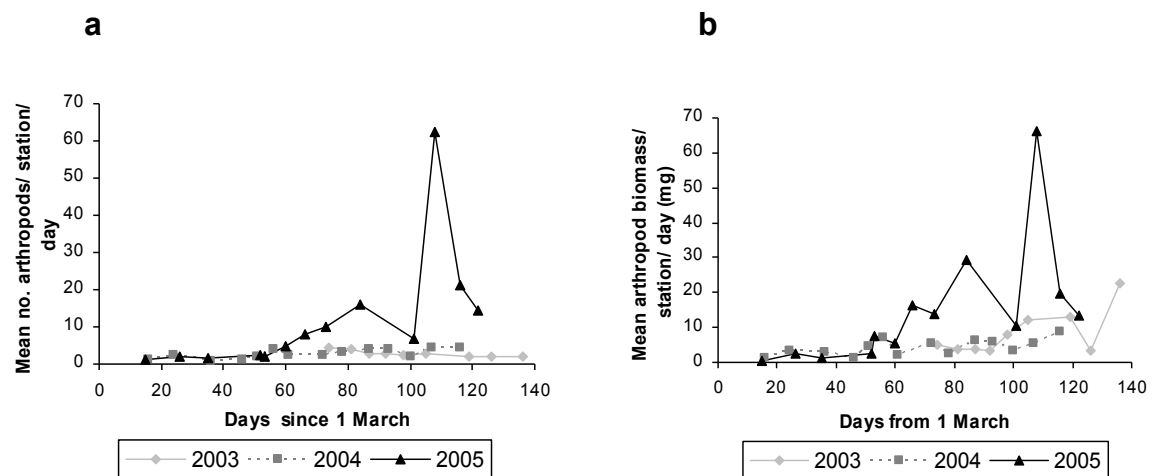


Figure 6.8 Arthropod a) abundance and b) biomass from water traps at Kouklia Hives in 2003, 2004 and 2005 breeding seasons, measured as mean per station per day.

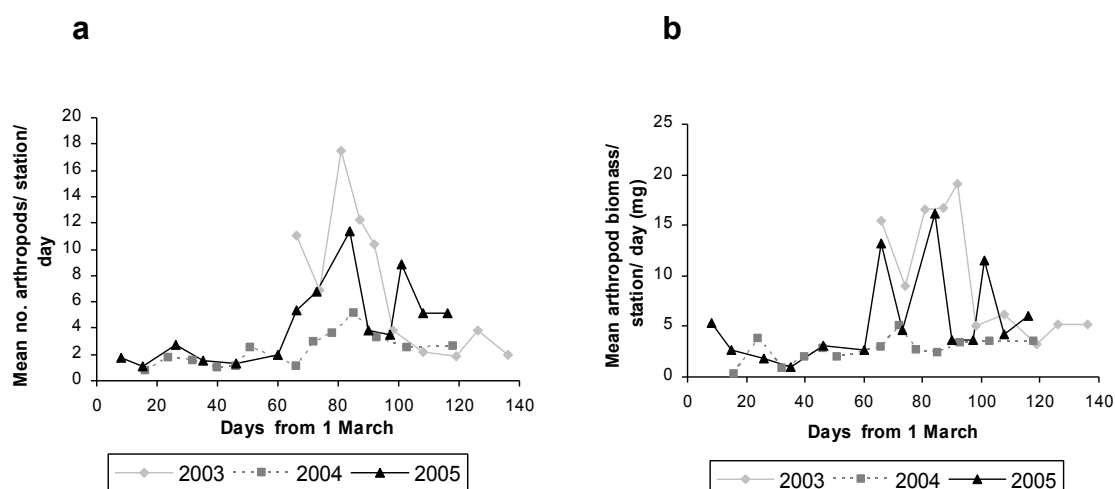


Figure 6.9 Arthropod a) abundance and b) biomass from water traps at Kouklia 3 in 2003, 2004 and 2005 breeding seasons, measured as mean per station per day.

There was a significant difference in arthropod biomass available between years (GLM: $F_{2,113}=13.55$, $p<0.001$). Post-hoc tests indicated that 2003 had significantly higher biomass than 2004 (Independent samples t-test: $t=4.37$, $d.f.=70.0$, $p<0.001$), and 2005 also had significantly higher biomass than 2004 ($t=-4.84$, $d.f.=73.1$, $p<0.001$). There was no significant difference in arthropod biomass available between 2003 and 2005 ($t=-1.15$, $d.f.=72.3$, $p=0.253$). At five out of the seven sites, biomass of arthropods sampled was highest in 2005. There was no consistent pattern of biomass availability between sites (Fig. 6.10).

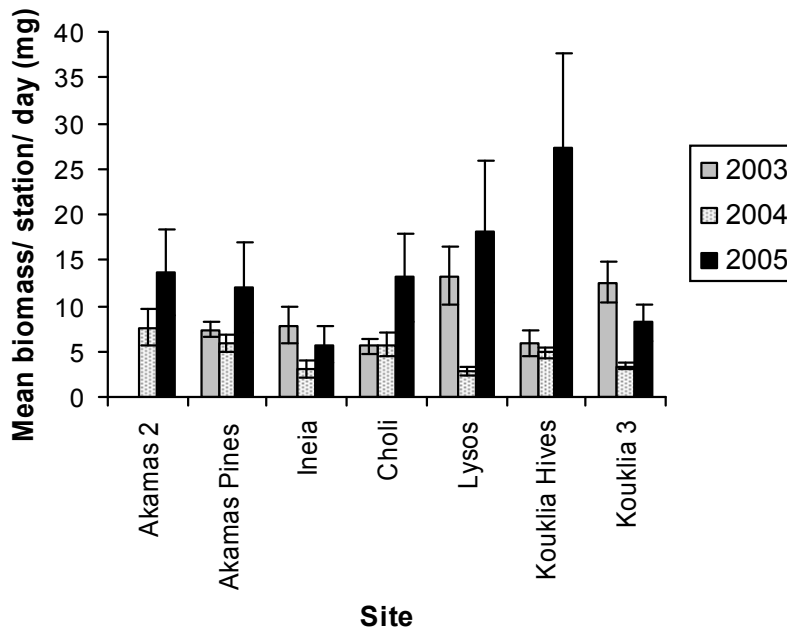


Figure 6.10 Mean $\pm$ SE arthropod biomass recorded at different sites in 2003 (n=35), 2004 (n=37) and 2005 (n=42) between 4 May and 18 June (see data analysis section for explanation).

Feeding behaviour

Both Cyprus and Sardinian Warblers foraged primarily by gleaning. However both species were also occasionally seen fly-catching small insects in mid-air. In addition, both species were frequently observed feeding on the nectar of *Prasium majus* while it was in flower early in the breeding season.

Diet analysis

Faecal analysis clearly indicated that the two species ate largely the same food items at Ineia during the breeding season. In both adult (Fig. 6.11) and nestling (Fig. 6.12) faecal samples, different food groups occurred with similar frequency for Cyprus and Sardinian Warblers.

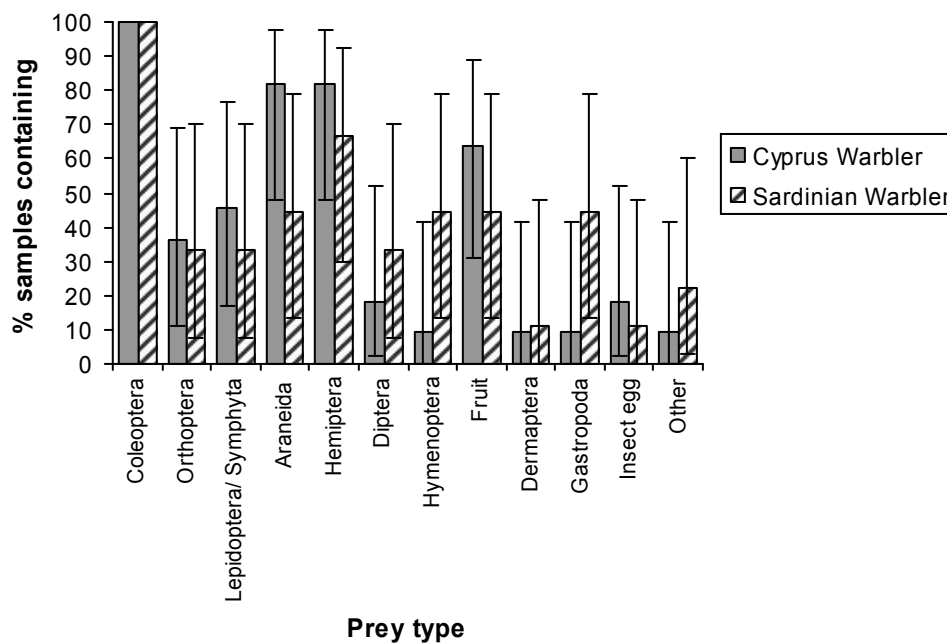


Figure 6.11 Percentage of 11 Cyprus Warbler and 9 Sardinian Warbler adult faecal samples which contained remains of different prey types. All samples were collected from Ineia during the breeding season (February to July) in 2003, 2004 and 2005. 95% confidence limits calculated using the method of Zar (1996).

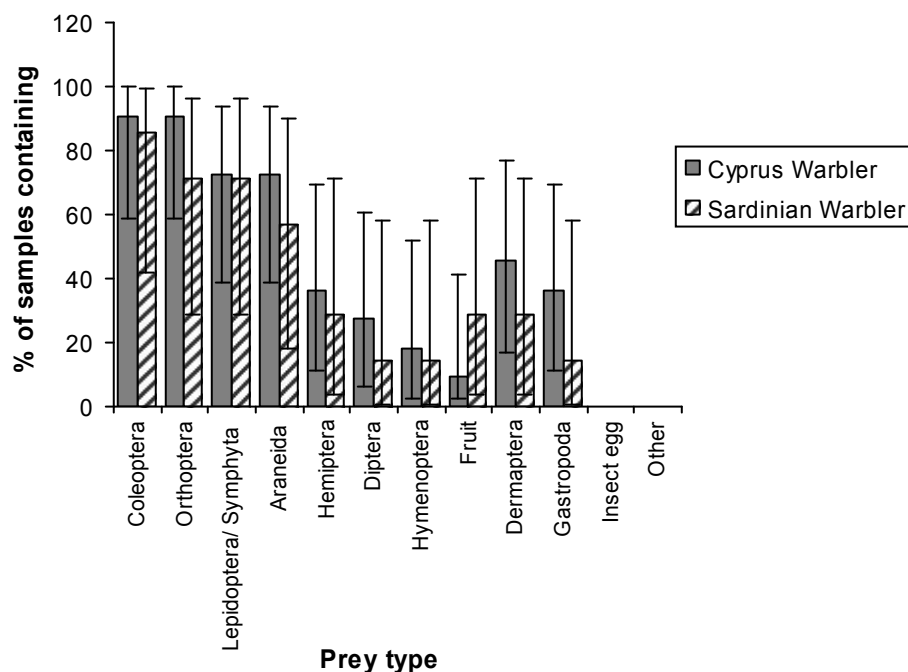


Figure 6.12 Percentage of 11 Cyprus Warbler and 7 Sardinian Warbler nestling faecal samples which contained remains of different prey types. All samples were collected from Ineia during the breeding season (February to July) in 2003, 2004 and 2005. 95% confidence limits calculated using the method of Zar (1996).

In both species, fruit was an important component of adult diet but was less commonly fed to nestlings. In both species Orthoptera, Lepidoptera/ Symphyta larvae and spiders occurred in nestling samples much more commonly than adult samples, while conversely, Hemiptera were considerably more common in adult than nestling samples. It is interesting that Cyprus Warbler had a slightly higher percentage frequency of occurrence for nine out of ten categories of food in nestling faecal samples. This may simply result from the fact that Cyprus Warbler nestlings tended to be ringed at one day older than Sardinian Warbler nestlings (because Sardinian Warblers develop the tendency to 'explode' from the nest when disturbed at an earlier age than Cyprus Warblers). Older nestlings produce more faecal material in a sac, and different food groups are more likely to be found in larger sized samples.

Chick body condition results

For Cyprus Warblers tarsus length, brood size when measured, distance to nearest neighbour, date and zone were all found to have a significant effect on chick body mass (Table 6.1). Year, species of nearest neighbour, arthropod biomass available and age when measured had no significant effect on chick body mass.

Explanatory terms	Cyprus Warbler			Sardinian Warbler		
	F	df	p	F	df	p
Length of tarsus	141.90	1	<0.001	419.27	1	<0.001
Year	1.14	1	0.285	17.16	1	<0.001
Brood size	21.19	3	<0.001	6.40	4	0.171
Species of nearest neighbour	0.01	1	0.935	0.09	1	0.766
Distance to nearest neighbour	6.24	1	0.012	0.03	1	0.871
Date when measured	5.58	1	0.018	6.70	1	0.010
Arthropod biomass	0.74	1	0.390	0.54	1	0.461
Zone	17.26	2	<0.001	3.02	2	0.221
Age	2.87	2	0.238	1.68	2	0.433
Minimal model	Effect size		SE	Effect size		SE
Constant	1.014		0.0295	0.907		0.00581
Length of tarsus	0.0353		0.00296	0.0358		0.00175
Year - 2004				0.000		0.000
Year - 2005				-0.329		0.00795
Brood size – 2	0.000		0.000			
Brood size – 3	-0.0814		-0.0273			
Brood size – 4	-0.111		0.0277			
Brood size – 5	-0.109		0.0308			
Distance to nearest neighbour	-0.000620		0.000248			
Date when measured	-0.101		0.0429	-0.0704		0.0272
Zone - 1	0.000		0.000			
Zone - 2	0.00614		0.0124			
Zone - 3	0.0462		0.0134			

Table 6.1 Linear mixed model with 2004 and 2005 Cyprus Warbler and Sardinian Warbler log chick mass as the response, the explanatory terms listed as fixed factors and brood identity as a random factor. Only the first surviving nesting attempt for each pair in 2004 and 2005 is included. Significant terms highlighted in bold. Effect sizes given for significant terms only.

For Cyprus Warbler, tarsus length increased with chick mass. Cyprus Warbler chick body mass decreased with increasing distance to nearest neighbour and at later

dates. Cyprus Warbler chick mass tended to decrease with increasing brood size (Fig. 6.13).

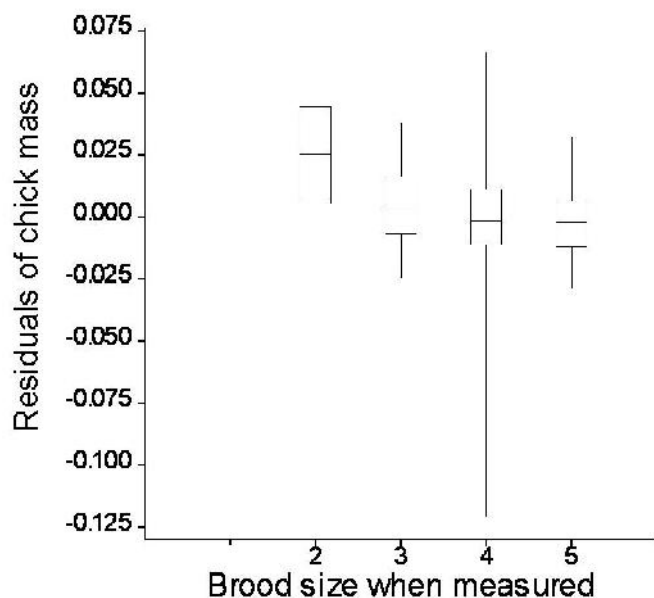


Figure 6.13 Box plots (horizontal line - median value, box - interquartile range, whisker - largest and smallest value within 1.5 interquartile ranges of top and bottom). Cyprus Warbler chick body condition for different brood sizes (2004 and 2005 data) derived from LMM in Table 6.1. For graphical illustration, residuals were generated by running LMM with Cyprus Warbler chick mass as the dependent variable and the significant terms: tarsus length, distance to nearest neighbour, date and zone as fixed factors and brood identity as a random factor, but without including brood size as a fixed factor.

For Cyprus Warblers chick mass increased slightly with zone such that body condition of chicks was lowest in zone 1 and highest in zone 3 (Fig. 6.14).

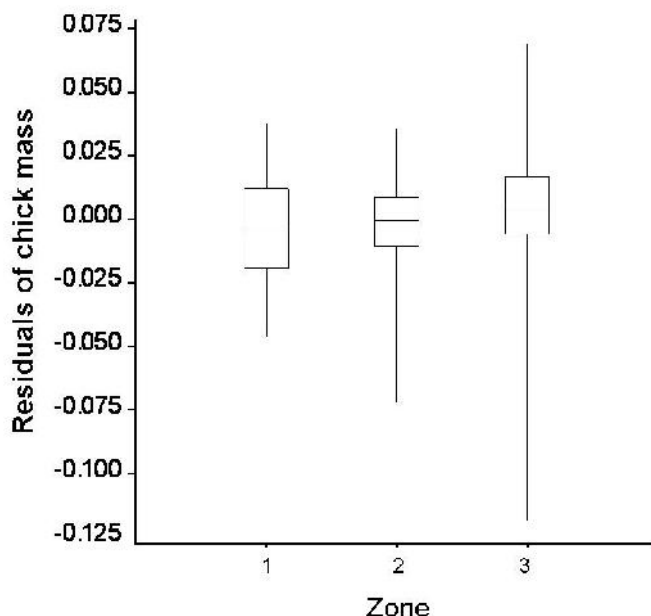


Figure 6.14 Box plots (horizontal line - median value, box - interquartile range, whisker - largest and smallest value within 1.5 interquartile ranges of top and bottom). Cyprus Warbler chick body condition in the three zones (2004 and 2005 data) derived from LMM in Table 6.1. For graphical illustration, residuals were generated by running LMM with Cyprus Warbler chick mass as the dependent variable and the significant terms: tarsus length, brood size, distance to nearest neighbour and date as fixed factors and brood identity as a random factor, but without including zone as a fixed factor.

For Sardinian Warbler chicks tarsus length, year and date when measured all had a significant effect on chick mass (Table 6.1). Brood size, species of nearest neighbour, distance to nearest neighbour, arthropod biomass and chick age all had no significant effect on chick mass. Sardinian Warbler chick mass increased with increasing tarsus length. Chick mass was greater in 2004 than in 2005 and earlier in the breeding season. There was no significant effect of species of nearest neighbour or biomass of arthropods available on Sardinian Warbler chick mass.

Explanatory terms	Cyprus Warbler			Sardinian Warbler		
	F	df	p	F	df	p
Year	1.41	1	0.235	2.05	1	0.152
Brood size	3.14	3	0.371	3.72	3	0.294
Species of nearest neighbour	0.01	1	0.928	12.54	1	<0.001
Distance to nearest neighbour	2.73	1	0.098			
Arthropod biomass	0.16	1	0.691	2.97	1	0.085
Date when measured	1.06	1	0.302	1.80	1	0.180
Zone	1.12	2	0.570	2.56	2	0.278
Age	2.07	2	0.355	10.66	2	0.005
Brood size * Distance to nearest neighbour				16.33	3	<0.001
Minimal model	Effect size		SE	Effect size		SE
Constant				11.23		1.736
Distance				-0.244		0.101
Distance to nearest neighbour * Brood size - 2				0.000		0.000
Distance to nearest neighbour * Brood size -3				0.274		0.117
Distance to nearest neighbour * Brood size - 4				0.215		0.108
Distance to nearest neighbour * Brood size - 5				0.825		0.209
Brood size – 2				0.000		0.000
Brood size – 3				-1.953		1.751
Brood size – 4				-2.415		1.674
Brood size – 5				-0.100		2.069
Species of nearest neighbour– Cyprus Warbler				0.000		0.000
Species of nearest neighbour– Sardinian Warbler				3.348		0.945
Age– 5 days				0.000		0.000
Age– 6 days				2.802		1.075
Age– 7 days				3.733		1.242

Table 6.2 GLM with coefficient of variation of body condition within Cyprus and Sardinian Warbler broods in 2004 and 2005 as response and the explanatory terms listed as fixed factors. Only the first surviving nesting attempt of each pair within a year was used, any nests missing measurements from one or more chicks were excluded. Significant terms highlighted in bold. Effect sizes given for significant terms only.

For Cyprus Warbler broods in 2004 and 2005, none of the explanatory terms tested had a significant effect on coefficient of variation (CV) of within brood body condition (Table 6.2).

For Sardinian Warbler broods species of nearest neighbour, age when measured and the interaction between brood size and distance to nearest neighbour all had a significant effect on CV of within brood body condition (Table 6.2). CV of Sardinian Warbler brood body condition was highest when the nearest neighbour was a Sardinian Warbler pair rather than a Cyprus Warbler pair (Fig. 6.15).

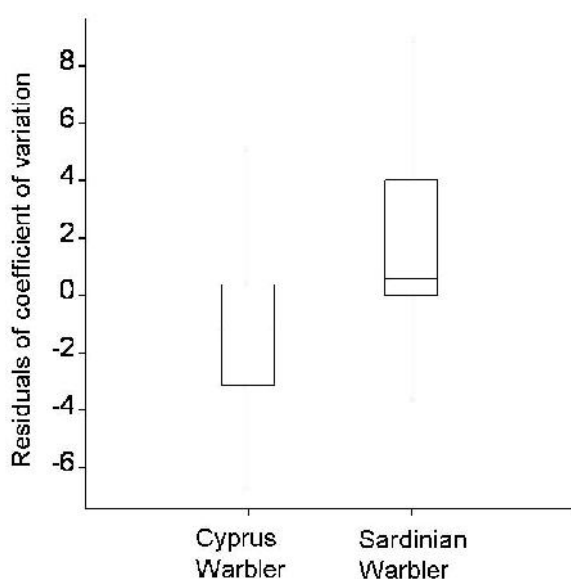


Figure 6.15 Box plots (horizontal line - median value, box - interquartile range, whisker - largest and smallest value within 1.5 interquartile ranges of top and bottom). Coefficient of variation of chick body condition in Sardinian Warbler broods, with Cyprus or Sardinian Warbler nearest neighbour derived from GLM in Table 6.2. For graphical illustration, residuals were generated by running GLM with arcsine square-root coefficient of variation as the dependent variable and the significant terms: chick age and brood size*distance to nearest neighbour as fixed factors, but without including species of nearest neighbour as a fixed factor.

For Sardinian Warbler chicks there was no relationship between CV of body condition and distance to nearest neighbour for brood sizes of three or four, but for brood size two, CV declined with increasing distance to nearest neighbour, while for brood size five, CV increased with increasing distance to nearest neighbour.

Productivity and arthropod biomass

As Fig. 6.16 indicates, there was no significant relationship between mean productivity (chick output for the breeding season) and mean arthropod biomass available on study plots in 2004 and 2005 for Cyprus Warbler (Spearman rank correlation: $r_s=0.113$, d.f.=7, $p=0.781$). However there was a positive relationship between mean chick output and arthropod biomass available on study plots for Sardinian Warbler ($r_s=0.673$, d.f.=8, $p=0.033$).

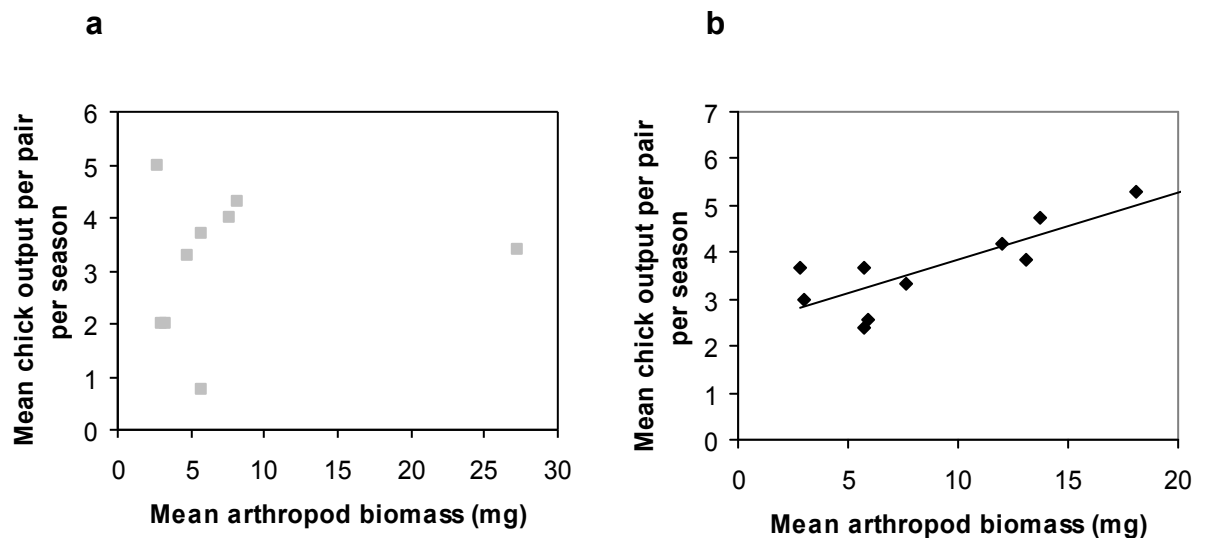


Figure 6.16 Mean chick output per season for a) Cyprus Warbler and b) Sardinian Warbler pairs compared with mean arthropod biomass available on study plots (2004 and 2005 data included). Trend-line shown only for significant Spearman-rank correlation. Mean chick outputs only included for plots with three or more pairs of that species. For each study plot in each year arthropod biomass available was calculated between 4 May and 18 June (see data analysis section).

Nestling provisioning

There was no significant difference between male and female provisioning rates at the nest (Fig. 6.17) for either Cyprus (Wilcoxon's : $Z=49$, $n=14$, $p=0.820$) or Sardinian Warblers ($Z=122.5$, $n=25$, $p=0.284$).

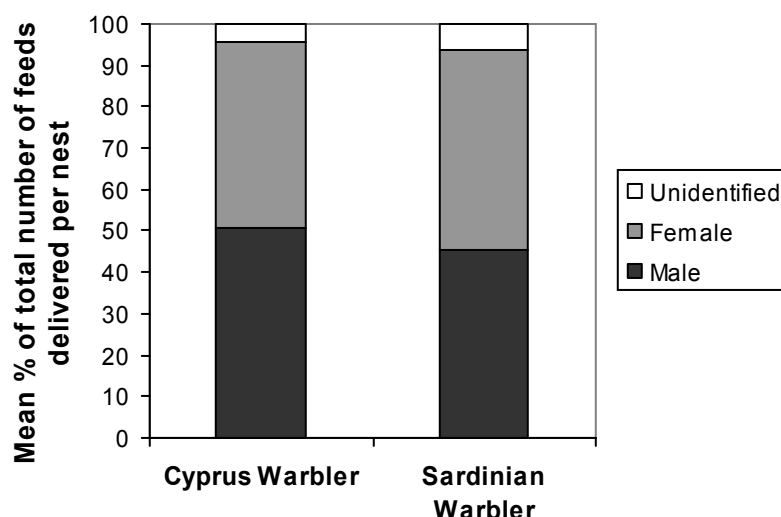


Figure 6.17 Mean percentage of total number of feeds which were delivered by the male or female parent at Cyprus ($n=15$) and Sardinian Warbler ($n=28$) nests containing nestlings aged 5-7 days in 2004.

For Cyprus Warbler there was no significant correlation between provisioning rate for nest and brood size (Spearman rank correlation : $r_s=0.357$, d.f.=13, $p=0.192$) or provisioning rate per chick and brood size ($r_s=-0.397$, d.f.=13, $p=0.143$). There was no significant correlation between provisioning rate per chick and mean brood body condition (Pearson's correlation : $r=0.102$, d.f.=10, $p=0.751$), date ($r=-0.75$, d.f.=13, $p=0.791$), distance to nearest neighbour ($r=0.117$, d.f.=11, $p=0.703$) or biomass of insects available ($r_s=0.075$, d.f.=13, $p=0.790$).

For Sardinian Warbler there was a significant positive correlation between provisioning rate at the nest and brood size (Fig. 6.18) (Spearman rank correlation : $r_s=0.644$, d.f.=26, $p<0.001$), but no significant correlation between provisioning rate per chick and brood size ($r_s=0.322$, d.f.=26, $p=0.095$).

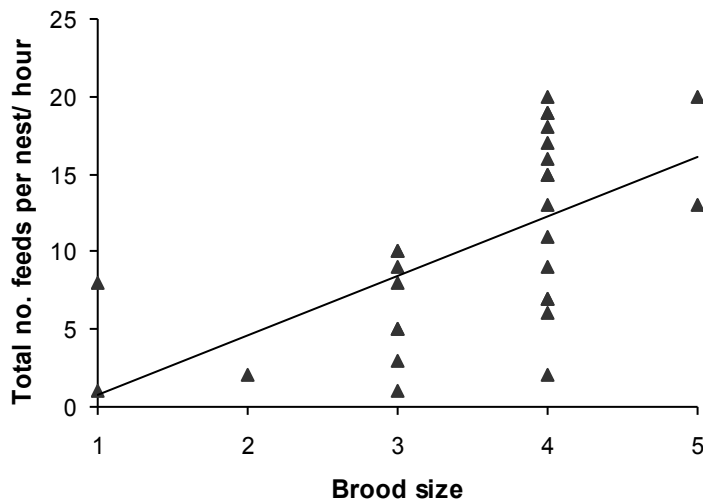


Figure 6.18 Relationship between number of feeds delivered during one hour and brood size for Sardinian Warbler nests containing chicks aged 5-7 days in 2004 (n=28).

There was no significant correlation between provisioning rate per chick and mean brood body condition for Sardinian Warbler (Pearson's correlation : $r=0.140$, d.f.=19, $p=0.545$).

There was a significant negative correlation between provisioning rate per chick and date for Sardinian Warbler (Fig. 6.19 : $r=-0.420$, d.f.=26, $p=0.026$).

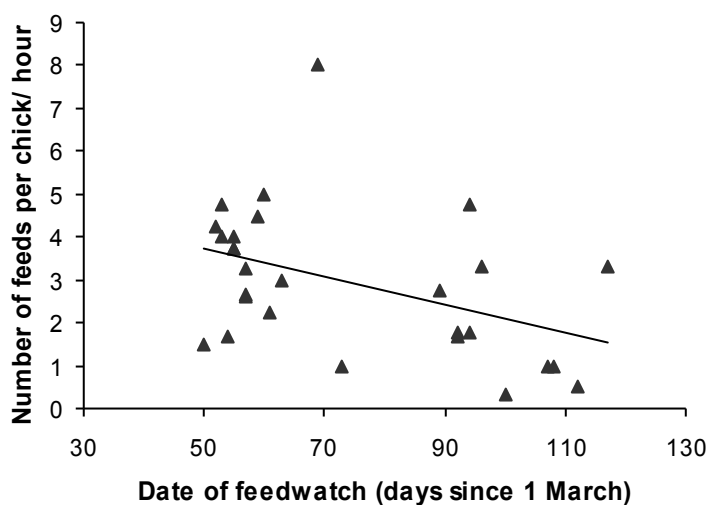


Figure 6.19 Relationship between provisioning rate per chick and date at Sardinian Warbler nests containing chicks aged 5-7 days during 2004 (n=28).

There was no significant correlation between provisioning rate per chick and distance to nearest neighbour ($r=-0.082$, d.f.=18, $p=0.730$). There was a significant negative correlation between provisioning rate per chick and arthropod availability when arthropod biomass was used as the measure (Fig. 6.20 : Spearman rank correlation: $r_s=-0.404$, d.f.=26, $p=0.033$), but this did not hold when abundance was used as the measure of arthropod availability ($r_s=-0.316$, d.f.=26, $p=0.102$).

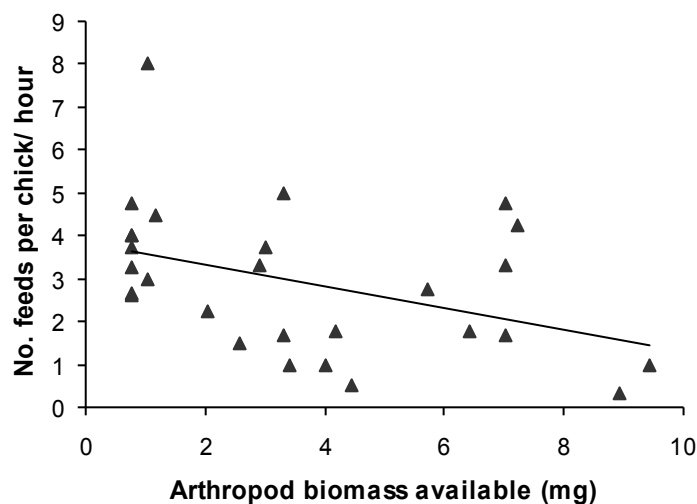


Figure 6.20 Relationship between provisioning rate per chick and arthropod biomass available for Sardinian Warbler nests containing chicks aged 5-7 days during 2004 (n=28).

I tested whether this result might have arisen because parents were bringing larger food items where arthropod biomass available was high. There was a positive correlation between the proportion of arthropods which were more than 6 mm long in samples and biomass of samples in 2003 (Pearson correlation: $r=0.289$, d.f.=54, $p=0.031$), 2004 ($r=0.550$, d.f.=86, $p<0.001$) and 2005 ($r=0.222$, d.f.=99, $p=0.026$).

Discussion

Are the diets of Cyprus and Sardinian Warblers similar ?

Although the method used did not allow in-depth enumeration of diet composition or size class of prey items taken, faecal analysis showed considerable overlap in the

diets of Cyprus and Sardinian Warblers. The frequency with which different food types occurred in both adult and nestling faecal samples was very similar in the two species. However adult and nestling diets differed. For both species Orthoptera were more commonly found in nestling than adult samples. Orthoptera are large, nutritious prey items, but their hard, serrated hind legs could be dangerous to feed to nestlings. Orthopteran prey appear to be processed prior to delivery to nestlings, because no Orthopteran hind legs were recovered in any faecal samples and two Orthoptera samples dropped by adults caught in mist-nets surrounding their nest had had their hind legs removed. Lepidoptera and Symphyta larvae and spiders probably occurred more frequently in nestling than adult samples because they are soft items easily digested by nestlings. Indeed one might expect diets of adults and nestlings to be complementary to some extent, with adults eating less nutritious, smaller prey themselves, but returning to the nest with larger protein-rich prey which represent a good investment of the time and energy required to fly back to the nest (Brooke 1983). Both fruit (berries) and Hemiptera occurred more frequently in adult than nestling diets. Fruit is less protein-rich than arthropod prey and the large stones present in berries may make them unsuitable for nestling consumption. Hemiptera are generally small, with a tough exoskeleton and some may produce toxic substances, making them less suitable food for nestlings.

There is little information on Sardinian Warbler nestling diet from elsewhere in the species' range, but my results for adult diet are broadly in accordance with the findings of a study of diet from stomach contents of Sardinian Warbler in France (Debussche & Isenmann 1983).

The overlap found in diet suggests potential for exploitation competition between Cyprus and Sardinian Warbler, given that the two species have overlapping home-ranges. Sardinian Warblers have slightly larger bills than Cyprus Warblers (Appendix 1), but the difference is less than 0.5 mm in all dimensions. In any case one might expect insectivore bill morphology or gape size to be less closely linked to prey size than is the case for frugivores or granivores, as insects are often soft-bodied, or can be processed prior to consumption (Wiens 1989). It is possible, however, that although diet is similar at the scale of arthropod orders consumed, the two species utilise slightly different sizes or species of prey. It would be interesting to extend the

diet study to measure prey size and identify arthropods to a finer scale to see whether this is the case. In this study I have not examined foraging behaviour in depth and it remains possible that, even with similar diet, the two species are able to reduce food competition through subtle differences in foraging behaviour (MacArthur 1958, Morse 1978, Alatalo 1982). This may be more difficult to achieve in structurally simple scrub habitat than is the case in more complex habitats.

What is the temporal pattern of arthropod availability ?

The relatively low arthropod availability in 2004 may be related to the unusually high rainfall in January. Rainfall is known to have a variety of direct and indirect effects on arthropod populations (Speight *et al.* 1999) and the high rainfall could have caused high mortality of over-wintering stages. In general, arthropod availability followed a similar pattern whether measured as abundance or biomass. The pronounced peak in mid to late May appeared to be related to hatching or maturation of small Diptera and Coleoptera.

Nestling provisioning rates

It is surprising that none of the variables tested had a significant effect on Cyprus Warbler nestling provisioning rates. It is possible that some unmeasured factor, such as parent quality, has a much larger impact on feeding rates than any of the variables measured. The fact that there was a significant positive correlation between Sardinian Warbler provisioning rate at the nest and brood size, but not between provisioning rate per chick and brood size indicates that Sardinian Warbler parents were able to increase their effort in proportion to brood size to ensure that each chick is adequately fed. The lack of correlation between provisioning rate per chick and mean brood body condition is perhaps surprising, as is the negative correlation between provisioning rate and arthropod biomass available. Both of these results may indicate that provisioning rate is a poor surrogate for nestling biomass intake. The positive correlation between proportion of larger insects in a sample and biomass of the sample from water trapping indicates that, at times of high biomass availability, parents may also be more likely to encounter larger prey. In addition, when food availability is high birds may be more selective (Krebs *et al.* 1977). It may therefore be that when biomass of available food is high, both increased availability of and greater selectivity for large food items allow parents to provide for the chicks'

nutritional needs in fewer trips. Grundel (1987) found that less than half the variation in daily prey volume delivered to nestling Mountain Chickadees (*Parus gambeli*) was explained by provisioning rate. To understand provisioning rates properly, one would need to set up nest cameras so that the volume of prey items being delivered could be estimated.

Arthropod availability and nestling quality and quantity

The lack of significant effect of arthropod biomass available on chick condition or CV in chick condition for either species is perhaps surprising. One possibility is that during the breeding season there is plenty of food available for both species and food is therefore not a limiting factor. Cyprus has fewer syntopic *Sylvia* than many other Mediterranean islands (Chapter 2), so it is possible that food is not limiting during the breeding season. Alternatively the range of arthropods trapped might not have been what the warblers were eating. For example, the water traps caught very few Lepidoptera or Symphyta larvae, which were an important component of nestling diet in both species. In addition I did not attempt to measure availability of non-animal food such as fruit, which occurred in the faecal samples of nestlings. My measures of food availability may also have been too coarse to predict nestling condition at the level of individual pairs. Sampling food availability within each home-range, while very time consuming, might be more instructive than the broader plot-wide measures I used in this study.

At the plot scale, the positive correlation between Sardinian Warbler chick output and arthropod availability suggests that my measure of food availability may have reflected what Sardinian Warblers were eating, or at least have been positively related to another variable of importance to Sardinian Warblers. It is difficult to know why food availability would have a positive effect on breeding output for one species and not the other, given the similarity of Cyprus and Sardinian Warbler diets.

No evidence for negative impacts of coexistence on chick quality

I found no evidence for an effect of species of nearest neighbour on Cyprus Warbler chick condition or within brood CV. It is difficult to explain why Cyprus Warbler nestling body condition decreased with increasing distance from the nearest neighbour; one might expect the opposite pattern. The finding may have resulted

from home-ranges being more widely spaced on plots where habitat was poorer quality, which could also have resulted in chicks being in poorer condition.

CV in Sardinian Warbler chick body condition was higher when the nearest neighbour was a Sardinian Warbler, suggesting that conspecific neighbours have a more negative impact on chick quality than congeneric neighbours. This could be because the two species are using slightly different food resources or it could have a behavioural basis. Time and energy are expended defending the home-range from conspecifics not only to safe-guard resources but also to prevent neighbouring males from obtaining extra-pair copulations (Catchpole & Slater 1995). Thus with a conspecific nearest-neighbour, males may devote less time to chick provisioning. The interaction between Sardinian Warbler CV in chick body condition and distance to nearest neighbour may simply be a result of very small sample sizes for brood sizes three and five, since there was no relationship between CV in chick body condition and distance to nearest neighbour for the most common brood sizes of three and four.

Effects of brood size, date and age on chick condition

The decline in Cyprus Warbler nestling body condition with increasing brood size indicates that parents find it increasingly difficult to provision each chick sufficiently with larger broods. This might be because there is in fact a limit to food availability and parents must spend time searching for each food item and bringing it to the nest; therefore a limited number of prey items can be brought to the nest within a given period of time.

In both Cyprus and Sardinian Warbler nestling body condition was higher earlier in the breeding season. This could be related to the tendency for higher quality or more experienced pairs to breed earlier (Brooke 1979, Bibby 1982, Aebischer *et al.* 1996). Such pairs may be higher quality individuals which are in better body condition themselves, or may defend high quality home-ranges with plentiful food. They may produce nestlings of high body condition through a combination of genetics and provisioning.

CV in Sardinian Warbler within brood body condition increased with the age at which chicks were ringed, but this is likely to be an artefact of decisions made on when to ring chicks. Broods which were growing rapidly and were in good condition were likely to be ringed at a younger age, in order to avoid chicks ‘exploding’ from the nest (which was a danger at a younger age for Sardinian Warblers than for Cyprus Warblers). Thus broods which were not thriving well were more likely to be ringed when older and such broods were also likely to have a higher CV in within brood body condition.

A trade-off between offspring quantity and quality ?

That body condition of Cyprus Warbler nestlings increased slightly with zone is very interesting, because the pattern opposes that recorded for productivity (Chapter 5). The two results together indicate that Cyprus Warblers produce more nestlings of lower quality in zone 1 (the zone in which they are declining) and fewer nestlings of higher quality in zone 3 (the predominantly Cyprus Warbler zone). Any breeding organism might be expected to trade-off the number and size of offspring produced against their own fitness (Smith & Fretwell 1974). Producing a higher number of lower quality offspring is the life-history strategy we might expect in zone 1 if adult mortality was relatively high for some reason. At present, little is known about causes of adult mortality, but it would be interesting to investigate this pattern further.

For Sardinian Warbler nestlings, body condition was poorer in 2005 than in 2004. This is the opposite of what might be expected from my measures of food availability, which suggested that 2004 was the poorer year. However, since Sardinian Warbler productivity was higher in 2005 (Chapter 5) this result may also reflect the trade-off between number and quality of offspring.

Overall, through comparative methods, I have found no evidence that chick body condition or CV in within brood body condition is affected by species of nearest neighbour and therefore no evidence that coexistence has negative effects on chick quality in either species. However, it would be interesting to carry out a removal experiment to see whether a different approach produces the same result.

Chapter 7

General discussion

Summary of main findings

Cyprus Warblers (*Sylvia melanothorax*) and Sardinian Warblers (*Sylvia melanocephala*) both established home-ranges without reference to the other species, resulting in considerable interspecific home-range overlap (Chapter 3). This has important implications, because it indicates that (at least in scrub habitat, over the 13 year period since Sardinian Warblers began to breed) competition between the two species has been insufficient to drive the evolution of interspecific territoriality. It has been suggested that interspecific territoriality (in the sense of spatial segregation) is more likely to occur in structurally simple habitats in which there is insufficient structural complexity to allow niche divergence to occur in terms of foraging behaviour, diet etc. (Orians & Willson 1964). The scrub habitat of my study could be considered to be structurally less complex than many of the other habitats in which Cyprus Warblers are found. I therefore consider it unlikely that spatial segregation occurs between Cyprus and Sardinian Warblers in other habitats.

The playback experiment (Chapter 3) indicated that Cyprus Warblers responded equally strongly to Cyprus and Sardinian Warbler song in zone 2, but less strongly to Sardinian Warbler song in zone 3. This suggested that Cyprus Warblers might be beginning to develop an antagonistic response to Sardinian Warblers. However behavioural observations of natural interactions did not indicate that either species was behaviourally dominant over the other and displays of aggression, like chasing, were much less frequent in interspecific interactions than among conspecifics.

The vegetation composition of Cyprus and Sardinian Warbler home-ranges was very similar (Chapter 4) and I found no evidence that the two species were selecting different vegetation patch types for inclusion in their home-ranges. Cyprus and

Sardinian Warblers nests and nest-sites were also very similar, but the two species did not appear to compete for nest-sites; both species generally nested in widely available bush species.

Nest survival was similar for Cyprus and Sardinian Warblers (Chapter 5) and there was no indication that the similarity of the two species' nest-sites, or the elevated nest density which resulted from interspecific home-range overlap had led to apparent competition via shared predators. As would be expected from members of the same genus, Cyprus and Sardinian Warblers had similar breeding biology. The main difference between the two species was that Sardinian Warblers had a higher frequency of second nesting attempts and this resulted in higher chick output per pair per year than was achieved by Cyprus Warblers.

Cyprus and Sardinian Warbler diets were very similar (Chapter 6). The positive relationship between arthropod food availability and chick output at the plot level for Sardinian Warbler suggests that productivity is influenced by food availability at least to some degree. Productivity was lower for both species in the year with lowest arthropod availability, but even in this year there was no significant effect of species of nearest neighbour. Cyprus Warblers had highest nestling body condition in zone 3 and lowest in zone 1, but productivity followed the opposite pattern, so this may simply reflect the trade-off between offspring number and quality. There was no negative impact of either species on the number or condition of nestlings produced over the course of a breeding season.

At the home-range scale I have found no evidence that having a congeneric nearest neighbour influenced the number or quality of offspring produced. At the broader scale of zone, if interspecific competition during the breeding season had caused the decline in Cyprus Warblers, we might expect their productivity to be lowest in zone 1 where they were out-numbered by their putative competitors. The finding that both Cyprus Warblers and Sardinian Warblers had the highest productivity in the zone in which they were rarest might suggest that intraspecific competition is more important than interspecific competition in regulating productivity. Similarly Sardinian Warblers had higher variation in within-brood body condition where their nearest neighbour

was conspecific, again suggesting that intraspecific effects might be more important than interspecific effects.

Since breeding Sardinian Warblers were first noted in Cyprus in 1992 (Frost 1994), the breeding population has extended in range from the Akamas eastwards, at least as far as the south-eastern limit of Paphos District. From their point of arrival in southern Cyprus, breeding Sardinian Warblers have spread at least 50 km in 13 years. This corresponds to a rate of breeding range extension of 3.8 km per year. If the Akamas was the sole point from which the breeding population was expanding one would therefore expect Sardinian Warblers to be breeding across Cyprus within the next 40 years. Given that a second breeding population has established in northern Cyprus, Sardinian Warbler populations may expand to cover the whole island more rapidly than that.

If there was a causal link between the increase in Sardinian Warblers and the decline of Cyprus Warblers, the results of such an expansion in the Sardinian Warbler breeding range on Cyprus could be very serious for the Cyprus Warbler. However, while on a proximate level the difference in productivity between Cyprus and Sardinian Warblers might be contributing to their differing population trends, in the absence of evidence for interspecific resource competition between the two species and with no spatial segregation of home-ranges (Chapter 3), I have found no evidence for a competitive mechanism by which the presence of breeding Sardinian Warblers might be causing the decline in Cyprus Warblers.

Analysis of my approach

In this study, I investigated interspecific competition at two different scales, the zone and the home-range. Carrete *et al.* (2005) used a similar distance-to-neighbour approach when investigating interspecific competition between several eagle species. They found that proximity to other eagle species' territories negatively affected productivity of both species, which they suggested resulted from both aggressive interference and resource depletion.

Although fine-scale, my nearest-neighbour approach may not have captured all the relevant information. For example, in my study, a pair's closest nearest neighbour could be conspecific, yet a proportion of the pair's home-range could still be overlapped by one or more neighbouring congeneric pairs. My approach only considers the closest (and therefore arguably the most influential) neighbouring pair, whereas pairs are in fact likely to be affected to some degree by pairs on all surrounding home-ranges. The closest nearest-neighbour approach also takes no account of home-range shape; two home-range centres could be very close, but the configuration of the home-range could mean there was very little overlap. A measure like percentage of home-range overlapped by congeners might better represent the degree to which a pair is likely to be impacted by congeners. However, this approach would require collection of a large number of observations of each marked pair which, given the cryptic nature of the species, would require a very large time investment, restricted to just one or two study plots. It was not possible to achieve this in the current project without compromising other aims of the study, but it could be a useful approach for a smaller-scale study in the future.

This study was restricted to scrub habitat and it is therefore difficult to extrapolate my findings to other habitats. Judging from the high population densities achieved in scrub, this appears to be a very productive habitat for both species, but Cyprus is a fine-scale mosaic of many different habitats. It would be very interesting to examine relative abundance, spatial arrangement and home-range size of the two species in other habitats and compare the measures of productivity and condition with those obtained in this study.

Coexistence and competition

Seminal early experiments in interspecific competition examined the phenomenon in single celled organisms (Gause 1934) and in beetles in a laboratory setting (Park 1948). While this work was very important in developing our understanding of the potential end-points of the process of interspecific competition, there is an important difference between what a process can do in theory or in a laboratory and how that process operates in a natural setting. While Park's results have been cited for fifty

years as demonstrating competitive exclusion, it is less well known that one pair of *Tribolium* species in his experiments was able to coexist in the long-term.

The structural simplicity of the early study systems and the fact that species interactions have often been studied at a local scale (for obvious logistical reasons) have resulted in the commonly held view that interspecific interactions are unvarying. The principle of competitive exclusion is itself based on species coexisting in a stable environment. However most natural systems are in constant flux and work on a variety of taxa in natural systems has shown that the intensity of interspecific competition may be greater in certain seasons (Prins *et al.* 2006), in years of food shortage (Dunham 1980) at different population densities (Gustafsson 1987, Forsman *et al.* 2002) or in different geographic locations. Even in the well-known example of Red Squirrels (*Sciurus vulgaris*) suffering through competition with introduced congeneric Grey Squirrels (*S. carolinensis*), the situation is not clear cut. For example there are woodlands in the UK where replacement has occurred within five years of Grey Squirrel arrival and other woodlands where Red Squirrels have apparently persisted despite the presence of Grey Squirrels (Bryce *et al.* 2002).

Coexisting species do not always compete (Wiens 1989, Caughley & Sinclair 1994). There are many kinds of interspecific relationships, including positive ones (Monkkonen *et al.* 1990, Dickman 1992). Indeed, relationships between species can switch from negative to positive along an environmental gradient (Forsman *et al.* 2002) and interspecific competition, where it does occur, tends to vary in intensity both temporally and spatially. Wang *et al.* (2002) developed a model with four possible outcomes of interspecific competition, depending on the intensity of competition. Their model showed that an inferior and superior competitor, or two strongly competing species can never stably coexist, but that two weak competitors (even if they are very similar species) may coexist in the long-term in heterogeneous environments. Cyprus and Sardinian Warblers may be an example of a weakly competing pair of species.

The relative paucity of *Sylvia* species breeding on Cyprus (Chapter 3), in comparison to other islands in the Mediterranean, raises the possibility that the community is not saturated and that the Sardinian Warbler could simply have filled an empty niche.

Island species often have broad niches in comparison to their mainland counterparts (Grant 1966, MacArthur *et al.* 1972, Martin 1992), and in other Mediterranean communities Sardinian Warbler is considered the most generalist *Sylvia* species (Cody & Walter 1976). It is therefore possible that both Cyprus and Sardinian Warblers have quite broad fundamental niches, which might facilitate their coexistence. However, although both species occur in a wide range of habitats, there is some evidence that the two species may have slightly different habitat preferences, with Cyprus Warblers occurring at higher densities than Sardinian Warblers in regenerating vegetation and agro-ecosystems and Sardinian Warblers prevailing in coastal juniper and pine forest habitats (Pomeroy & Walsh 2000). If the two species have slightly different habitat preferences at a broad-scale this would promote their long-term coexistence.

This study represents an unusual situation in the sense that while coexistence of the two species during the breeding season is relatively recent, the two species have coexisted in winter previously. It is therefore possible that they have previously evolved mechanisms which reduce interspecific competition between them. Interspecific competition can generate selective pressure promoting niche divergence which may result at a broad scale from habitat segregation (Lamprey 1963), or on a finer scale, in divergence in diet, which may or may not be associated with morphological divergence (Brown & Wilson 1956, Schoener 1965), or divergence in habitat utilisation (MacArthur 1958, Alatalo *et al.* 1985). At a coarse scale, I found no evidence that the two species differed in diet at the scrub study plot examined, but it would be interesting to study foraging behaviour in detail to see whether there is any evidence of niche divergence between Cyprus and Sardinian Warblers in scrub and other habitats, and particularly, whether any divergence in habitat utilisation increases in winter.

What may have caused the decline in Cyprus Warbler?

In this study, I have found no evidence to suggest that interspecific competition with Sardinian Warbler during the breeding season is likely to have caused the observed Cyprus Warbler decline in western Paphos District. Once the first pairs of Sardinian

Warblers began to breed at the western tip of Cyprus eastward expansion was likely; the subsequent increase in Sardinian Warbler abundance is what we would expect in the early years of a new breeding species establishing. However if interspecific competition during the breeding season has not caused the decline of Paphos District Cyprus Warblers, what might be responsible?

Food competition in winter

This study has concentrated on the breeding season. Over-wintering population dynamics of Cyprus and Sardinian Warbler are poorly understood, but some Sardinian Warblers that breed on Cyprus are now over-wintering on their breeding home-ranges. It is possible that the proportion of Cyprus Warblers which remain on their home-range over winter are negatively impacted, either by higher numbers of Sardinian Warblers over-wintering (if we assume that the new breeding population of Sardinian Warblers is of different provenance to the population that previously wintered on Cyprus), or by overlapping Sardinian Warbler pairs (which did not pose a threat during the breeding season when food was abundant) becoming winter competitors with an equal stake in resources in the area of overlap. Given the likely importance of fruit (berries) in the winter diet of both species (Shirihai *et al.* 2001) and the relative scarcity of fruiting shrubs, it is not difficult to imagine how interspecific over-winter food competition could occur between Cyprus and Sardinian Warblers. Increased resource competition on Cyprus could prompt a higher proportion of Cyprus Warblers to migrate. If migrating warblers are subject to higher mortality, as has been found in other species (Silllett & Holmes 2002, Jones *et al.* 2004) than those which remain on Cyprus then a shift in the balance of migrants versus residents could also cause a decline at the population level.

Disease

Apparent competition through the influence of a shared predator or pathogen causes responses in the prey/ host population which are indistinguishable from resource competition. While I have found no evidence for apparent competition occurring through predation (Chapter 5), the possibility remains that disease could have caused the observed decline in Cyprus Warblers.

Parasites and pathogens can represent potent ecological forces. Bowers and Turner (1997) showed how, theoretically, shared infection and interspecific competition could act in combination to determine community structure. Avian blood parasites and the infectious diseases they can transmit can cause significant morbidity (Garvin *et al.* 2006) and mortality (Warner 1968) in wild bird populations. In Europe the range of the Melodious Warbler (*Hippolais polyglotta*) has been expanding over the past few years, while simultaneously, the range of its parapatric congener, the Icterine Warbler (*H. icterina*) has been contracting. Faivre and Auger (1993) suggested that differing predation risk among the two species could explain this pattern. However Reullier *et al.* (2006) suggested that asymmetric transmission of blood parasites from the expanding host to the receding host along the narrow zone of sympatry could be influencing the population dynamics of the two warbler species.

Results of my pilot study of frequency of infection with blood parasites (Appendix 3) show that the same species of blood parasite infected Cyprus and Sardinian Warblers. Cyprus Warbler incidences of infection of 56-67 % are high compared to other *Sylvia* (Hauptmanova *et al.* 2006), and considerably higher than incidence of 11-33% recorded for Sardinian Warbler. It is interesting that infection levels were highest for Cyprus Warbler and lowest for Sardinian Warbler in zone 1, where Cyprus Warblers have declined. Cyprus Warblers may have lower resistance to blood parasites than Sardinian Warbler, but the parasites involved are general to many *Sylvia* species. Since Sardinian Warblers have always wintered in Cyprus, and at least eight other species of *Sylvia* pass through Cyprus on migration, it is unlikely that breeding Sardinian Warblers have introduced blood parasites that Cyprus Warblers had not already been exposed to. However it is possible that the increased density of hosts that results from coexistence of two *Sylvia* species at high density during the breeding season (when transmission is highest) may have promoted higher rates of infection, and that this has had a disproportionate effect on the less resistant Cyprus Warbler population. The interesting results from this pilot study suggest that the possibility that disease is contributing to the decline of Cyprus Warblers may be worth pursuing.

Climate change

Climate change could have prompted the range change that brought breeding Sardinian Warblers to Cyprus. As mentioned in the introduction, climate might explain reduced Cyprus Warbler populations in western Paphos District if, as Flint and Stewart (1992) suggest, Cyprus Warblers are unable to cope with dry conditions. The Akamas area where the decline was first noted is lower-lying and drier than inland areas. Rainfall was not measured in individual plots, and study plots covered a relatively narrow range of altitudes, but weak positive relationships between breeding productivity and plot altitude for both species (Chapter 5) suggest that it would be worth further investigating Cyprus and Sardinian Warblers' responses to physical parameters. Both species might be negatively affected by climate change. However, elsewhere in their range, Sardinian Warblers are considered to be a species of lower elevations (Cramp & Perrins 1994), known to be adapted to a regime of summer drought (Caughley & Sinclair 1994). Therefore the Sardinian Warbler may be better able to cope with the effects of climate change than is the Cyprus Warbler. Changing conditions could even have prompted the Sardinian Warbler to begin breeding on Cyprus and the opposing population trends of Cyprus and Sardinian Warblers in Paphos District could reflect conditions becoming more suitable for Sardinian Warblers and less suitable for Cyprus Warblers. Pomeroy and Walsh (2002) found that the relationship between count-site altitude and bird abundance was positive for Cyprus Warbler, but negative for Sardinian Warbler, which provides some support for this idea. The lower arthropod availability in the driest year of this study suggests that arthropod availability could be affected by the gradual decline in precipitation and increase in temperature that characterises climate change in the Mediterranean and this is one possible mechanism via which climate change could affect Cyprus Warblers.

Habitat degradation

This study has not attempted to examine habitat degradation as a possible cause of Cyprus Warbler decline. However the differing relationship between pair density and vegetation height in the two species suggests that there could be subtle differences in Cyprus and Sardinian Warbler utilisation of scrub habitat. If this were the case then subtle but widespread changes in scrub habitat through, for example, changes in grazing pressure, could potentially have benefited Sardinian Warblers, but had a

negative impact on Cyprus Warblers. This possibility would be worth investigating further.

Conservation in Cyprus

The Cyprus Warbler is one of only two bird species endemic to the island of Cyprus. The work of Pomeroy and Walsh (2000, 2002) and Hellicar (2004) suggests that low intensity agricultural land is important habitat for Cyprus Warbler. With Cyprus's entry into the EU in 2004, there are fears that intensification of agriculture could lead to habitat degradation or loss. Scrub habitat is also under threat in Paphos District from development for tourism resulting in the loss of habitat which could support a high density of Cyprus Warblers, but is also important for many bird species on passage. Mediterranean island economies are particularly reliant on tourism which leads to strong economic incentives for coastal development with little consideration given to the long term impact of habitat destruction on natural heritage. In Cyprus much coastal scrub has already been built on and the best hope of conserving scrub habitat for breeding bird species may be inland. The Akamas peninsula where the Cyprus Warbler has been declining is not yet protected by legislation despite its importance for a host of species (Terra_Cypria 2006). It may take time to discover exactly what has caused the decline of this endemic species, but there is no doubt that giving the Akamas and other important scrub areas some protection from development for tourism and eliminating illegal trapping of songbirds would help the situation.

Future directions

The opposing population trends noted by Pomeroy and Walsh (Pomeroy & Walsh 2000, 2002) suggested that there might be a causal link between the arrival of breeding Sardinian Warblers and the population decline of Cyprus Warblers in western Paphos District. However, Thompson (2006) urged caution in making assessments of invasion impact on the basis of spatial or temporal correlations between abundance of invasive and native species. There is little doubt that research is required to clarify causes of decline and to gain understanding of the mechanisms

by which one species impacts another. I have found no evidence that competition with Sardinian Warbler for limited resources during the breeding season is likely to have caused the decline in Cyprus Warblers. Now it is important to investigate further the other possibilities of resource competition in winter, apparent competition through shared pathogens and climate change.

Meanwhile it is critical that population monitoring be continued in Paphos District and preferably, extended to include a range of habitats across the island. TSC counts will not be the ideal method for monitoring these two species in the future. Transect counts have been used to supplement TSC monitoring in Paphos District since 2004 (Pomeroy pers. comm.) and I would suggest that future monitoring of Cyprus and Sardinian Warblers in Paphos District and elsewhere on the island uses transect counts in preference to TSCs. An expanded monitoring programme would help to determine whether the observed trend is short-term and local to western Paphos District or represents a more widespread problem across all habitat types on the island. Fortunately monitoring (Pomeroy & Walsh 2000, 2002) has allowed early detection of the potential problem, buying time to investigate what has caused it. If climate change is involved we need to anticipate where the Cyprus Warblers climate envelope (Berry *et al.* 2002, Huntley *et al.* 2004) may be located 20, 50 or 100 years from now and ensure that sufficient habitat is protected in the right areas to secure the species' future.

Acquiring basic knowledge of a species' natural history and ecological requirements is essential in helping to diagnose causes of decline and I hope that this study will provide a basis for further research to contribute towards this process. Moreover, we need a better understanding of the mechanisms which allow species to coexist, and the circumstances in which invasions (natural and human-induced) are likely to have a negative impact on native species, in order to help predict and manage the conservation consequences of introductions and the many new coexistences likely to be generated by global climate change.

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Appendix 1

Morphometric measurements of Cyprus and Sardinian Warblers

Morphometric measurements were recorded for Cyprus and Sardinian Warbler adults captured during 2003, 2004 and 2005 breeding seasons.

Methods

<i>Wing</i>	Maximum length measured (to the nearest 0.5 mm) using wing-rule.
<i>Tail</i>	Length measured (to the nearest 0.5 mm) using ruler slid under base of tail feathers.
<i>Tarsus</i>	Maximum length (Redfern & Clark 2001) measured (to the nearest 0.1 mm) using callipers, with the tarsus at right-angles to the tibia and the foot at right angles to the tarsus. The measurement was taken from the foot to the distal point of the 'knee' (not to the notch).
<i>Bill length</i>	Measured (to the nearest 0.1 mm) from skull to tip using callipers.
<i>Bill depth</i>	Measured (to the nearest 0.1 mm) at the distal end of the nostrils.
<i>Bill width</i>	Measured (to the nearest 0.1 mm) at the distal end of the nostrils.
<i>Fat score</i>	Measured using the BWG system, described by Gosler (1996).
<i>Weight</i>	Measured (to the nearest 0.1 g) using a spring-balance.

Only one set of measurements is included for each bird. For birds that were re-trapped, the first complete set of adult measurements was used.

Measurements	Male			Female		
	Mean ± SD	Range	Sample size	Mean ± SD	Range	Sample size
Wing (mm)	60.4 ± 1.0	58.0-62.5	43	58.5 ± 1.2	56.5-61.0	36
Tail (mm)	57.0 ± 1.8	50.8-60.0	42	54.8 ± 2.0	50-59	33
Tarsus (mm)	20.9 ± 0.7	18.4-21.9	43	20.9 ± 0.7	18.7-22.0	35
Bill length (mm)	13.3 ± 0.5	12.0-14.7	43	13.4 ± 0.6	11.8-14.5	35
Bill depth (mm)	2.7 ± 0.1	2.1-3.6	42	2.7 ± 0.2	2.1-3.6	35
Bill width (mm)	2.5 ± 0.2	2.1-2.8	16	2.6 ± 0.2	2.3-2.9	13
Fat score (B)	2.1 ± 1.1	0-4	42	2.6 ± 0.9	1-4	34
Weight (g)	10.7 ± 0.7	9.4-12.2	42	11.3 ± 1.1	9.3-14.9	36

Table 1 Cyprus Warbler (*Sylvia melanothorax*) morphometrics from 2003-2005 breeding seasons (February-July).

Measurements	Male			Female		
	Mean ± SD	Range	Sample size	Mean ± SD	Range	Sample size
Wing (mm)	58.4 ± 1.5	56-62	69	57.6 ± 1.4	54-60	62
Tail (mm)	58.4 ± 2.1	54-63.5	66	56.8 ± 2.1	51-62	57
Tarsus (mm)	21.6 ± 0.6	20.2-22.9	65	21.5 ± 0.5	20.4-23.3	62
Bill length (mm)	13.6 ± 0.6	12-15.2	67	13.5 ± 0.5	12.2-14.7	59
Bill depth (mm)	2.8 ± 0.2	2.1-3.1	67	2.8 ± 0.1	2.1-3.0	60
Bill width (mm)	2.6 ± 0.1	2.4-2.8	18	2.6 ± 0.2	2.3-3.0	21
Fat score (B)	2.5 ± 1.0	0-4	66	3.0 ± 0.8	1-4	60
Weight (g)	11.7 ± 0.7	10.5-14.3	69	11.6 ± 0.7	10.1-13.5	59

Table 2 Sardinian Warbler (*Sylvia melanocephala*) morphometrics from 2003-2005 breeding seasons (February-July).

Appendix 2

Early breeding season counts of Cyprus and Sardinian Warblers at study plots in zone 2

I carried out counts of singing Cyprus and Sardinian Warbler males during the early breeding season in 2004 in order to determine whether either species began defending breeding home-ranges earlier than the other.

Methods

In order to investigate when the two species established their breeding territories, counts of singing males were made between 8 a.m. and 11 a.m. at all zone 2 sites during the early part of the breeding season. The observer walked at a steady pace along each row of grid-points on the study plot, taking one hour in total. Any singing males of either species were recorded.

Date	Cyprus Warbler	Sardinian Warbler
08/03/2004	3	1
14/03/2004	4	3
21/03/2004	2	1
26/03/2004	4	2

Table 1 Counts of singing Cyprus and Sardinian Warbler males at Ineia during early 2004 breeding season.

Date	Cyprus Warbler	Sardinian Warbler
25/02/2004	3	4
11/03/2004	3	3
17/03/2004	4	1
30/03/2004	4	3

Table 2 Counts of singing Cyprus and Sardinian Warbler males at Choli during early 2004 breeding season.

Date	Cyprus Warbler	Sardinian Warbler
03/03/2004	0	6
12/03/2004	1	1
25/03/2004	2	6
02/04/2004	1	4

Table 3 Counts of singing Cyprus and Sardinian Warbler males at Lysos during early 2004 breeding season.

Appendix 3

Incidence of blood parasites in Cyprus and Sardinian Warblers

Methods

A few drops of blood were taken from the brachial veins of 22 Cyprus Warblers (*Sylvia melanothorax*) and 36 Sardinian Warblers (*Sylvia melanocephala*) captured between February and July in Paphos District, Cyprus. Blood smears were prepared using standard techniques and then analysed by Dr M.A. Peirce. Blood parasites present were identified but not counted.

Date sampled	Zone	Site	Sex	Age	Blood smear analysis
04/03/2005	1	Akamas Pines	Male	6	<i>Trypanosoma everetti</i>
15/05/2005	1	Akamas Pines	Male	6	<i>Haemoproteus sylvae</i>
15/05/2005	1	Akamas Pines	Female	5	nps
07/04/2005	2	Choli	Male	6	nps
09/03/2005	2	Ineia	Male	6	nps
27/06/2005	2	Lysos	Male	5	<i>Leucocytozoan phylloscopus</i>
07/05/2005	2	Ineia	Female	5	nps
15/05/2005	2	Ineia	Female	5	<i>H. sylvae</i>
11/05/2005	2	Ineia	Female	6	<i>T. everetti</i>
07/06/2005	2	Ineia	Female	6	<i>Trypanosoma</i> sp. (possibly <i>T. macfie?</i>)
01/03/2005	3	Kouklia 3	Male	5	nps
15/03/2005	3	Kouklia 3	Male	6	<i>L. phylloscopus</i>
17/04/2005	3	Kouklia 3	Male	6	<i>L. phylloscopus</i>
12/05/2005	3	Kouklia 3	Male	6	<i>H. sylvae</i> + <i>L. phylloscopus</i> + <i>T. everetti</i>
05/05/2005	3	Kouklia Hives	Male	6	nps
30/06/2005	3	Kouklia Hives	Male	6	nps
22/05/2005	3	Kouklia 3	Female	5	nps
26/03/2005	3	Kouklia Hives	Female	6	<i>L. phylloscopus</i>
17/04/2005	3	Kouklia Hives	Female	6	<i>L. phylloscopus</i> + <i>Trypanosoma</i> sp. (possibly <i>T. macfie?</i>)
29/04/2005	3	Kouklia Hives		1J	nps
30/06/2005	3	Kouklia Hives		3J	nps
30/06/2005	3	Kouklia Hives		3J	nps

Table 1 Blood parasites identified from Cyprus Warbler blood smears collected during the breeding season in 2005. Infections of more than one parasite species are denoted by +. nps - no parasites recorded.

Date sampled	Zone	Site	Sex	Age	Blood smear analysis
13/04/2005	1	Akamas Pines	Male	5	nps
19/04/2005	1	Akamas Pines	Male	5	<i>H. sylvae</i>
06/05/2005	1	Akamas Pines	Male	6	nps
18/05/2005	1	Akamas 2	Female	5	nps
28/06/2005	1	Akamas 2	Female	6	nps
07/05/2005	1	Akamas Pines	Female	5	nps
13/04/2005	1	Akamas Pines	Female	6	nps
19/04/2005	1	Akamas Pines	Female	6	nps
06/05/2005	1	Akamas Pines	Female	6	nps
14/03/2005	2	Choli	Male	5	nps
14/03/2005	2	Choli	Male	5	nps
28/04/2005	2	Choli	Male	6	nps
24/05/2005	2	Choli	Male	6	nps
30/03/2005	2	Ineia	Male	6	<i>T. everetti</i>
01/06/2005	2	Ineia	Male	6	<i>Trypanosoma</i> sp. (probably <i>T. macfieii</i> ?)
12/04/2005	2	Lysos	Male	6	nps
24/05/2005	2	Choli	Female	5	<i>H. sylvae</i> + <i>L. phylloscopus</i>
28/04/2005	2	Choli	Female	5	nps
14/03/2005	2	Choli	Female	6	nps
25/04/2005	2	Choli	Female	6	<i>L. phylloscopus</i>
01/05/2005	2	Choli	Female	6	<i>L. phylloscopus</i>
01/06/2005	2	Ineia	Female	5	nps
25/04/2005	2	Ineia	Female	6	nps
10/05/2005	2	Ineia	Female	6	nps
26/04/2005	2	Lysos	Female	5	nps
27/06/2005	2	Lysos	Female	5	nps
23/04/2005	2	Lysos	Female	6	<i>L. phylloscopus</i>
28/06/2005	2	Ineia		3J	nps
28/06/2005	2	Ineia		3J	nps
29/06/2005	2	Ineia		3J	<i>T. everetti</i>
29/06/2005	2	Ineia		3J	nps
27/06/2005	2	Lysos		3J	nps
08/03/2005	3	Kouklia 3	Male	5	nps
11/03/2005	3	Kouklia Hives	Male	6	nps
02/06/2005	3	Kouklia area	Male	5	<i>L. phylloscopus</i>
30/06/2005	3	Kouklia Hives		3J	nps

Table 2 Blood parasites identified from Sardinian Warbler blood smears collected during the breeding season in 2005. Infections of more than one parasite species are denoted by +. nps - no parasites recorded.

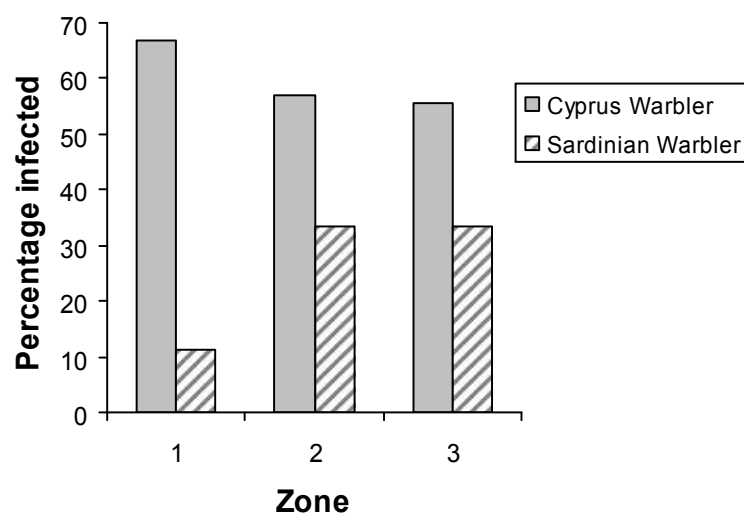
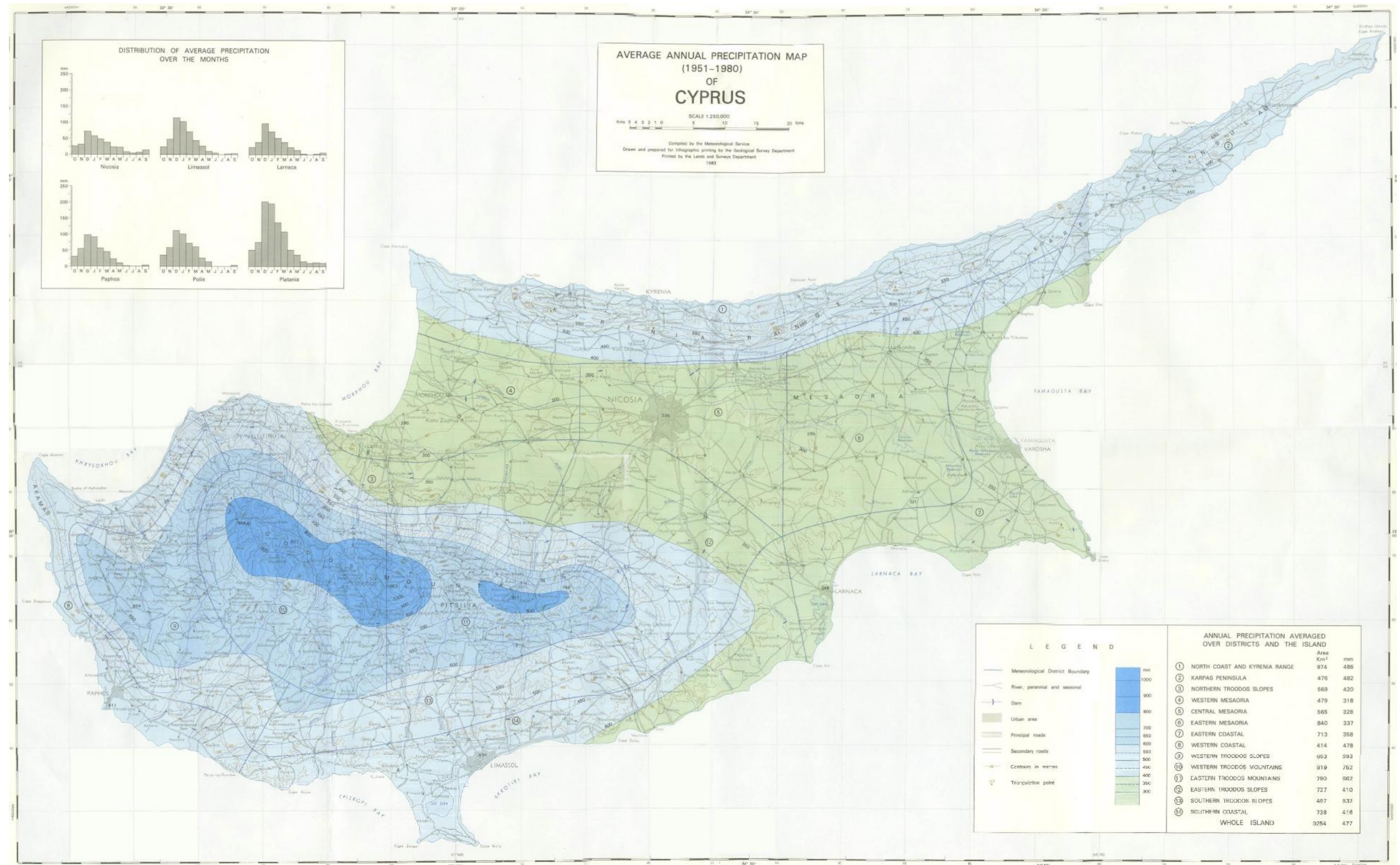


Figure 1 Incidence of blood parasites in blood smears taken from 19 Cyprus Warbler and 30 Sardinian Warbler adults from different zones, during the 2005 breeding season.

Appendix 4

Precipitation map of Cyprus



Average annual precipitation in Cyprus (1951-1980) reproduced from the Cyprus Meteorological Service, Ministry of Agriculture and Natural Resources, Government of Cyprus.