## **Is the Sardinian Warbler** Sylvia melanocephala **displacing the endemic Cyprus Warbler** S. melanothorax **on Cyprus?**

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We firstly describe the history, status, distribution and habitats of the two species on the island. In the light of this the evidence for a decline in Cyprus Warbler numbers in the areas colonised by Sardinian Warbler is assessed and is found to be compelling. Possible reasons for this decline are examined; they are apparently complex, but primarily Cyprus Warbler appears to have stronger interspecific territoriality than Sardinian Warbler and may treat the latter territorially at least to some extent as a conspecific, with some tendency to avoid its home-ranges, especially their centres. Other important factors may be interspecific aggression from Sardinian Warbler (where its population density is high) which might reduce Cyprus Warbler's ability to establish breeding territories; and competition from Sardinian Warbler for food and for autumn/winter territories. Also, Sardinian Warbler appears to be more efficient in exploiting the habitats of the endemic species, which may have reached a stage in its evolution as an island endemic where it is vulnerable to such an apparently fitter invading congener from the mainland. The changing climate on the island may also be a factor. We conclude that Sardinian Warbler does appear to be displacing Cyprus Warbler, and we recommend that the latter's conservation status be re-assessed.

## INTRODUCTION

Sardinian Warbler Sylvia melanocephala, previously known only as a winter visitor, was found breeding on Cyprus in 1992 (Frost 1995) and is rapidly spreading through the island (eg Cozens & Stagg 1998, Cyprus Ornithological Society (1957)/BirdLife Cyprus annual reports and newsletters, Ieronymidou et al 2012) often breeding at high densities within the same areas as the endemic Cyprus Warbler S. melanothorax (eg Pomeroy & Walsh 2002, 2006, Jones 2006, Pomeroy et al in prep). Where this happens Cyprus Warblers decline and may cease to be recorded (eg Pomeroy 1999, Pomeroy & Walsh 2002, Pomeroy 2009, Richardson 2011, Pomeroy et al in prep). However, Ieronymidou et al (2012) stated that no significant decline had yet been recorded and that the perceived decline was unlikely to be attributed to interspecific competition; suggesting instead that Sardinian Warbler has exploited a different niche from Cyprus Warbler, rather than displacing it. Whether or not the presence of breeding Sardinian Warbler is causing the decline in Cyprus Warbler is clearly worthy of closer examination. Here we present a review: firstly looking at the history, status, phenology, distribution, breeding habitats, densities and altitudes asl, and taxonomy and biometrics, of the two species on the island, something not previously attempted in such detail and which we believe is fundamental to an understanding of their relationship. We also briefly look at the third breeding Sylvia species on Cyprus, Spectacled Warbler S. conspicillata. We then present the historical and recent evidence, including our own observations, for a decline in Cyprus Warbler numbers in the areas occupied by breeding Sardinian Warblers and finally examine possible reasons for any such decline.

#### CYPRUS WARBLER (Plates 1–5)

#### Breeding status and distribution

A very common and widespread endemic breeder on Cyprus, occurring on the Karpas peninsula, in the Kyrenia mountain range and adjacent coastal lowlands, and in the Troodos mountain range (to 1400 m) and adjacent coastal lowlands (Figure 1). Although widespread it was not known to occur where the 1941–1970 average annual rainfall (Figure 2) was less than *c*340 mm (Flint & Stewart 1992) and its then limits of distribution closely





Plate I. Cyprus Warbler Sylvia melanothorax male, Petra tou Romiou, Cyprus, 24 April 2013. © Alison McArthur Plate 2. Cyprus Warbler Sylvia melanothorax unusually dark and presumably old male, Happy valley, Episkopi, Cyprus, early April 1985. © Stuart Allen

Plate 3. Cyprus Warbler Sylvia melanothorax female, Mavrokolymbos, Cyprus, I March 2013. © Alison McArthur

Plate 4. Cyprus Warbler Sylvia melanothorax over-wintering female, Anarita, Cyprus, 27 November 2006. © Alison McArthur

Plate 5. Cyprus Warbler Sylvia melanothorax male on territorial song post, Yialousa, Karpas, Cyprus, 21 April 2013. © Steve Cale

followed the 340–350 mm isohyets around the central plain, from which it was unrecorded as a breeding bird except for eastern coastal areas (Stewart & Christensen 1971, Flint & Stewart 1992). Rainfall has decreased since (Rossel 2001) and the southern 340 mm isohyet has moved slightly southwards (Figure 2), but essentially the same pattern of distribution is shown by subsequent records in Cyprus bird reports and by the mapped distribution in Ieronymidou et al (2012). We are aware of only one breeding season record, one bird west of Nicosia on 5 June 2013 (Cypriaca recording site at www.worldbirds.org), from an area where recent average annual rainfall is significantly less than 340 mm. The species has been recorded from Athalassa park, Nicosia (eg BirdLife Cyprus 2012/6) but recent average annual rainfall there has been 342 mm (Meteorological Service 2013a); the area also has scrub and water. Cyprus Warbler's absence from the central plain may be due to that region's aridity (low rainfall and summer temperatures 4°C higher than coastal areas, Meteorological Service 2013a), combined with the largely unsuitable habitat of extensive cereal fields (Plate 6) and a natural vegetation of mainly grassland/herbage, with relatively little scrub. Possible competition from the congeneric Spectacled Warbler, which is present on the plain, may also be a factor.



**Figure 2** (redrawn from Meteorological Service 1972). Average annual rainfall in mm for the years 1941–1970 (there is no data from the north of the island after 1973). Rainfall has declined since and the red line shows the approximate position of the southern 340 mm isohyet, calculated from the 1960–1990 map for the south of the island, the current position of the northern 340 mm isohyet is not known but is believed to have moved slightly northwards since 1941–1970.



**Figure 3.** Distribution of Paphos Blue *Glaucopsyche paphos* on a UTM 10 km grid (Eddie John in litt). This Cyprusendemic butterfly occurs only where its food plants, thorny gorse *Genista sphacelata* and thorny broom *Calycotome villosa*, are present, and is absent where they are not. The map thus also shows their distribution. These two species are often major components of the scrub which forms the core habitat of Cyprus Warbler *Sylvia melanothorax* and the map, apart from a small peripheral area in the southeast of the central plain, corresponds well with the latter's distribution.

#### Breeding habitat (Plates 7-14, 34-39, 41) and altitude

Our use of the term scrub includes maquis and garrigue (Polunin 1980) and their many intergrades and variations, all of which are semi-natural, ie modified by browsing and grazing, cutting and burning, etc. Other habitat terms are those used by the authors cited. In the south and west of the island there have been several surveys of habitat utilisation by Cyprus Warbler. In 1977–1978 near Episkopi the highest densities were in tall maquis of juniper Juniperus phoenicea, myrtle Myrtus communis and carob Ceratonia siliqua, in low isolated clumps of rock-rose Cistus spp and Pistacia without trees, and in bushes among carob and olive Olea europaea (S Fulford in Cramp 1992). H-H Bergmann (in Cramp 1992) found it near the coast in scattered low thorny scrub with carobs, at 1000 m in phrygana on mountain slopes and at 1400 m in undergrowth of open pine Pinus brutia woodland. None was found above 1530 m on Troodos in a nine month survey from April 1975 (Mason 1980), though there have since been occasional records up to 1750 m (eg BirdLife Cyprus 2010/7) perhaps reflecting the warming climate (see below). Bacon & Bacon (1986) found it absent from wide expanses of wheat fields, dense high forest (Troodos) and unvegetated areas, but otherwise occurring in almost all regions containing even traces of Cistus. The latter is one of the most prominent shrubs on the island, often prevalent over large areas and an important constituent of garrigue, maquis and forest to c1700 m (Holmboe 1914, Chapman 1949, Meikle 1977, Thirgood 1987). Bacon & Bacon (1986) found the highest density of warblers in areas of dense *Cistus* and provided a formula for calculating warbler density from % Cistus cover, though also considered thorny gorse Genista sphacelata and thorny broom Calycotome villosa to be of importance-both are common constituents of maquis and forest (Chapman 1949) and of the thorny scrub which forms one of the core habitats of Cyprus Warbler. Both are also food plants of the endemic Paphos Blue butterfly Glaucopsyche paphos which occurs where they are present and is absent where they are not (Eddie John pers comm). A map of its distribution (Figure 3) thus also shows theirs, and apart from small areas in the southeast, corresponds well with the distribution of Cyprus Warbler.

Pomeroy (2004), during 1997–2003, in Paphos District (= Paphos administrative district) (Figure 1) found Cyprus Warbler at 39 of 40 sites between sea level and 800 m, *ie* at 14 of 15 natural sites (mainly open forest), at 15 of 15 semi-natural sites (mainly browsed/ grazed scrub with trees) and at 10 of 10 agricultural sites (orchards, vines and arable with boundary walls, hedges, trees *etc*). Of the 33 breeding species monitored by him, only Cyprus Wheatear *Oenanthe cypriaca* had a wider habitat occupancy rate. Pomeroy & Walsh (2006) found Cyprus Warbler most numerous in scrub, forest and permanent crops, its density in the first being more than four times that in any other habitat. Ieronymidou *et al* (2012) also found it to have a wide habitat range but to be strongly associated with scrub. They also found it, outside the Sardinian Warbler's range, to be more associated with olive and carob and boundary features, though this may reflect habitat differences across the island.

Within the central Kyrenia mountain range in 1999 (outside the area populated by breeding Sardinian Warblers, see below), it occurred primarily in low to medium height dense scrub, with the highest density of warblers where there was also very open forest or scattered trees. High densities were also found in open forest with a good understory of strawberry tree *Arbutus andrachne* and *Cistus*, and in areas of burnt and cleared forest with four years regeneration of *Cistus*, carobs and wild olives. Within forest, areas of young pines were particularly favoured. No warblers were found in the limited areas of dense forest with no understory (Flint 2000). In the east of the Kyrenia range (within the Sardinian area), breeding habitats appeared similar to those occupied by it in the centre of the range (PF). Elsewhere in the north of the island, high densities were found in low-





lying areas near the coast with scrub (Orga to Liveras, Ayia Irini forest, cape Elea and near Kyrenia), sometimes also where there were scattered trees or very open pine forest (Kuşkor 1999–2003, PF).

#### Breeding density and population size

Within its favoured dense scrub habitats densities are usually high with 3 or 4 singing males often heard from one point: in Paphos District 1–2.2 pairs/hectare (Jones 2006, Pomeroy & Walsh 2006), in the Kyrenia mountain range a mean of 1.7 pairs/ hectare (Flint 2003), and near the north coast 2 or 3 singing males/hectare (Kuşkor 1999). Exceptionally, there are occasional small areas where Cyprus Warblers are at

#### Legend to plates on facing page and this page

**Plate 6.** Extensive cereal fields on the central plain (Mesaoria) with the Kyrenia mountain range in the distance, Cyprus, 2 February 2004. © Peter Flint

**Plate 7.** Cyprus Warbler Sylvia melanothorax habitat on Akamas north coast with thorny scrub, juniper and isolated pine, Cyprus, 23 April 2013. © Alison McArthur

Plate 8. Cyprus Warbler Sylvia melanothorax habitat near Petra tou Romio with eucalyptus, lentisc and thorny scrub, Cyprus, II May 2013. © Alison McArthur

**Plate 9.** Cyprus Warbler *Sylvia melanothorax* high density habitat: hillside above Kouklia, Paphos District, with thorny scrub, wild olive and carob, Cyprus, 12 May 2013. © *Alison McArthur* 

Plate 10. Cyprus Warbler Sylvia melanothorax high density habitat at Pissouri headland east with thorny scrub, thyme, *Cistus* and occasional olive and carob, Cyprus, 6 December 2013. © Alison McArthur

**Plate 11.** Cyprus Warbler Sylvia melanothorax habitat in Souni forest with pine, *Cistus*, thyme and a little thorny broom, Cyprus, 29 April 2013. © Alison McArthur

**Plate 12.** Cyprus Warbler *Sylvia melanothorax* habitat near Vasilia at the western end of the Kyrenia mountain range, in this area hawthorns are often used as song posts, Cyprus, early April 2013. © *Clive Walton* 

Plate 13. Cyprus Warbler Sylvia melanothorax habitat near Yialousa, Karpas, male territory in low open scrub, Cyprus, 21 April 2013. © Steve Cale

**Plate 14.** Cyprus Warbler Sylvia melanothorax habitat near Yialousa, Karpas, nest site area with herbage, grasses and scattered low shrubs, Cyprus, 20 April 2013. © Steve Cale

densities of 4, 5 or 6 singing males/hectare (AM, see below). Within dense *Cistus* in the south, Bacon & Bacon (1986), found densities to be often quite similar from sea level up into the higher Troodos, *ie* 1.4 singing males/hectare at 50 and 80 m, 1.7 at 150 m (at Agios Theodoros in Larnaca District), 0.9 at 300 and 350 m, 1.0 at 500 m, 0.9 at 550 m and 1.1 at 1150 m. Their highest survey point was at 1300 m where they obtained a density of 0.23 in sparse *Cistus* with pines.

Except when singing, this species, and Sardinian Warbler, are unobtrusive and easy to overlook, especially in scrub; counts and surveys may underestimate the true numbers present unless designed to account for this. Line transects are commonly used for censusing on Cyprus, but for scrub and forest habitats point counts might be more appropriate and allow slightly more time for detection (Bibby *et al* 2000). For Cyprus Warbler, ten minute point counts achieved higher detectability than five minute counts (Flint 2003). Cyprus Warblers are also easiest to detect earlier in the breeding season, rather than later (PF, AM); an analysis of counts in April and June 2013 in eight  $10 \times 10$  km atlas squares in the south (BirdLife Cyprus newsletters, Cypriaca recording site at www.worldbirds.org) shows a 43% lower detection rate in June compared with April even though the June counts included juveniles. Home-range (the area used by a pair for foraging) sizes in scrub habitats vary from *c*1600 to *c*16 000 m<sup>2</sup> (Fig 3.3 in Jones 2006) with a mean of 5358 m<sup>2</sup> (Jones 2006). The latest population estimate is 60 000–120 000 pairs (BirdLife Cyprus not yet published).

#### Non breeding season habitat, distribution, numbers and phenology

In winter in the southwest, thick maquis with isolated trees on steep hillsides held the highest density of Cyprus Warblers, though other habitats were freely used (S Fulford in Cramp 1992). Winter habitats occupied in the Kyrenia range were similar to those in the breeding season, except that few warblers were found in forest. The highest densities were in open low scrub to 1 m, where 0.3 birds/hectare, and in taller scrub to 2 m with many pines, where 0.6 birds/hectare (Flint 1999).

During the winter it is absent above *c*1000 m and many leave the island (Flint & Stewart 1992); the proportion leaving is unknown and may vary with the severity of the winter. Shirihai *et al* (2001) believed the majority apparently migrate, though the maximum number returning through Israel in spring, *c*2000 (Shirihai 1996), is very low in comparison with the total population. In the Kyrenia mountains in January 2002 and outside the Sardinian breeding area, by using response to Cyprus Warbler song-playback (methods as below) to determine presence or absence, only 5 of 17 (29%) monitored breeding territories were occupied (PF), suggesting most birds from that area may have left the island. Year-round observations in Paphos District 1998–2013 (Richardson in prep) show a reduction in numbers from late January, which may reflect high mortality of overwintering birds; this is followed by a large increase from early March, suggesting the arrival of substantial numbers of migrants.

Occasionally scarce in winter in the past (*eg* Walker 1964, Grieg 1966), but more usually fairly common then, sometimes outnumbering the former wintering Sardinian Warblers, with maximum site counts of 10 and 13 (Flint & Stewart 1992). Since *c*2000, winter numbers have often been as high or higher in breeding areas where Sardinians are absent or have only recently colonised. Examples from the south are Petra tou Romiou, Happy valley, Tunnel beach, Kensington cliffs, Curium, Pissouri bay gorge, Pissouri headland east, Akrotiri village juniper scrub, Germasogia dam and Limassol, all of which have held 8 to 15 birds (BirdLife Cyprus newsletters and database, Cypriaca recording site at www. worldbirds.org). However, none was found on the coastal path between Baths of Aphrodite and Pano Vakhines on the Akamas in December 2012, only Sardinians at a high density (AM).

In the north of the island, birds were very common between Orga and Liveras in late December 1999 and many singing males were near Pentadactylos, Kyrenia range, in late December 2000 and early January 2001 (Kuşkor 2000, 2001, 2003). The high numbers (above) outside Sardinian areas in recent years suggest overwintering may have increased as the winters have become less cold (see below), though previous under recording in winter makes this difficult to determine with any certainty.

Earlier authors (eg Bannerman & Bannerman 1958, Bourne et al 1964, Stewart & Christensen 1971) gave no autumn departure dates for Cyprus Warbler, perhaps because the departure of only part of the population was not obvious. According to Flint & Stewart (1992) departure is mainly in late September and October, but these dates were based on limited evidence and now seem too early. The first birds do not arrive in Israel until late October, with the main arrival there in the second half of November (Shirihai 1996), and as birds probably fly there non-stop from Cyprus these dates should more accurately reflect the main departure period from Cyprus. Relatively few occur in Israel in autumn however, with most migrants apparently making a direct flight from Cyprus to North Africa. Wintering is mainly around the northern and western Red sea, from Egypt to Eritrea, females and first winter birds apparently wintering further south than older males. More return through Israel in spring, where mostly males pass mid February to mid March and mostly females mid March to early April (Shirihai *et al* 2001). As adult males apparently winter further north and return earlier they might be expected to be less migratory than

females. The male/female ratio of 41:54 of returning migrants at Paralimni in 1968 (Horner & Hubbard 1982) might support this, but the warming climate since may have changed the proportions of each sex now migrating. The much lower resighting rate of adult females (9.1–14.3%) in subsequent breeding seasons, compared with adult males (55.6–75.0%) may reflect lower site fidelity among females, but could reflect a higher proportion of females than males migrating and therefore being subject to higher mortality. The difference between Sardinian Warbler male (27.8–39.5%) and female (20.0–40.0%) resighting rates was much less marked (Jones 2006). Recent observations on Cyprus in early winter do not show more Cyprus Warbler males than females present (AM), though some adult females may appear quite similar to first winter males in the field (Shirihai *et al* 2001). To accurately establish the proportions of the sexes/ages now overwintering there should ideally be a long-term study of both species in winter involving ringed birds sexed and aged in the hand.

#### Taxonomy and biometrics

Cyprus Warbler is in the same Mediterranean *Sylvia* warbler sub-group of five species as Sardinian Warbler, but within that sub-group it is closest to Rüppell's Warbler, whereas Sardinian is closest to Ménétries's Warbler *S. mystacea* and then to Subalpine Warbler *S. cantillans* (Shirihai *et al* 2001). Thus Cyprus and Sardinian Warblers are quite closely related but are not each other's closest relatives. Breeding season adult mean wing lengths are: males 60.4 mm n = 43, females 58.5 mm n = 36 (Jones 2006). Breeding season adult mean weights are: males 10.7 g n = 46, females 11.4 g n = 40 (Brimmell *et al* 1998, Jones 2006). All year mean weights are: males 11.2 g n = 61, females 11.5 g n = 42 (Flint & Stewart 1992). Mean bill dimensions in mm are: for males, length 13.3 n = 43, depth 2.7 n = 42, width 2.5 n = 16, and for females length 13.4 n = 35, depth 2.7 n = 35, width 2.6 n = 13 (Jones 2006).

#### SARDINIAN WARBLER (Plates 15-18)

#### Status prior to colonisation as a breeding species

Prior to 1992 Sardinian Warbler was known in Cyprus only as a winter visitor and passage migrant. Earlier authors (Guillemard 1888, 1889, Lilford 1889, Bucknill 1909) did not find it common, but by the start of regular observations on the island in 1956 it was so, suggesting that the source population on the mainland may have increased or spread, increasing the chances of successful colonisation of Cyprus. Winter visitors occurred in variable numbers with apparently more in cold winters but were usually widespread on low ground and in the hills and lower mountains, and were usually fairly common to very common (Flint & Stewart 1992, Cyprus bird reports). Counts were usually <10, but more thorough searches gave higher totals *eg* 20 in the Fontana Amorosa valley, Akamas, November 1960 (Smith 1961), 25 around Buffavento, Kyrenia range, January 1970 (Neophytou *et al* 1971), 29 at Tunnel beach, Episkopi, December 1971 (Neophytou *et al* 1972), 39 around Akrotiri salt lake January–February 1972 and 40 at Liveras on the north coast in January 1972 (Charalambides *et al* 1973). Forty were also at Neo Chorio, Akamas, November 1990 (Charalambides 1994) but with present knowledge this may have included previously overlooked local breeders.

It sometimes and perhaps often outnumbered Cyprus Warbler in winter, *eg* in maquis in the southwest in February and early March 1985 (Hjort *et al* 1986), and by 10 to 1 at Akrotiri in January and February 1963 (Walker 1964) and by 5 to 1 there in January 1964, increasing to 10 to 1 in February after a period of cold weather (Rivers 1965). Some overwintering birds showed site fidelity in subsequent winters (Flint & Stewart 1992). In the past, wintering Sardinians occurred mainly November–March, with peak numbers December–February, frequenting scrub similar to and denser than Cyprus



Plate 15. Sardinian Warbler Sylvia melanocephala male, Anarita, Cyprus, 22 April 2010. © Alison McArthur

Plate 16. Sardinian Warbler Sylvia melanocephala male, Minthis hills, Cyprus, 30 November 2009. © Alison McArthur

Plate 17. Sardinian Warbler Sylvia melanocephala female, Tala, Cyprus, 30 April 2011. © Alison McArthur

Plate 18. Sardinian Warbler Sylvia melanocephala female, Kelokedara ford, Cyprus, 26 October 2009. © Alison McArthur

Warbler inhabits. Passage migrants occurred November and February–March (Stewart & Christensen 1971, Flint & Stewart 1992). Occasional birds seen April–May were presumed to be late migrants or late departing winter visitors, and while most of them probably were such, this may have prevented the earlier discovery of breeding.

The presence of the residents makes it difficult to determine the size of the current population of winter visitors but it is apparently much smaller now *eg* year-round observations in Paphos District 1998–2013 (Richardson in prep) show no evidence of a significant winter influx. The warming climate in Turkey (Tayanç *et al* 2009) has perhaps caused more to now winter closer to or within their breeding range. However, some winter visitors still occur with up to 15 at sites in the southeast, mainly mid winter (*eg* Richardson *et al* 2012). An influx in the west after northerly winds and storms in late November 2012 (AM) was also probably of birds from the mainland. Apparent passage migrants also still occur *eg* 33 at cape Greco 28 October 2005 reducing to 13 the next day (Richardson *et al* 2006), and 30 there 2 November 2012, reducing to 3 by the 30th (BirdLife Cyprus 2012/11).

Winter visitors and passage migrants are of the nominate race and believed to be from Turkey (Vaurie 1959, Cramp 1992), which has the only breeding population north of Cyprus (Svensson *et al* 2009). Possibly a few originate from further northwest, *ie* Romania and Bulgaria. The only Cyprus recovery originated from the Black sea coastlands of northwestern Turkey (Flint & Stewart 1992). Wing lengths of winter visitors and passage migrants (Flint & Stewart 1992) are close to those of nominate *melanocephala* from western Turkey (Roselaar 1995).

#### Breeding colonisation history and breeding distribution (Figure 4)

In April 1992 a population of at least ten territorial males, plus three females carrying food, was discovered on the Akamas peninsula, and in April and May 1993 breeding was confirmed at six sites there (*eg* Plate 19), plus another seven territorial males. This population was between Baths of Aphrodite and the plain 2.5 km to the northwest, at Smyies and at Neo Khorio (Frost 1995). No detailed search was made in either year and these totals could represent only part of the population then present. In view of the size and extent of the breeding population when discovered in 1992 it seems likely that earlier breeding there had been overlooked (the peninsula was previously little visited) but when it began is not known. Of the few earlier records from there: two birds, Baths of Aphrodite, in April 1980 and 1984 could have been breeders or migrants/winter visitors,



Figure 4. Sardinian Warbler Sylvia melanocephala breeding distribution on Cyprus. The map shows UTM 10 km grid squares and their co-ordinates. Dots indicate the I km squares in which the species has been recorded at least once during April-August since 1993; dark green dots show records for 1993-1999, mid green for 2000-2009 and yellow for 2010–2013. A small proportion (7%) of the dots come from casual records which, by necessity, have used the nearest village as the reporting point, some of these will have an accuracy of less than 1km. A few February and March records where there is evidence of breeding are included. Excluded are several records from the south and southeast which probably involved migrants or post-breeding dispersing birds rather than breeders. Yellow triangles indicate the centres of BirdLife Cyprus 10 km atlas survey squares in which the species was recorded in 2013 (BirdLife Cyprus newsletters, Cypriaca recording site at www.worldbirds.org), this survey is based on a grid offset c4 km south and west from the UTM grid); we have included these records only for peripheral areas and where there are no 1km records. The two original breeding areas are shown by the dense clusters of dots on the Akamas peninsula in the extreme west, and at Kantara on the north coast at the base of the Karpas peninsula. The map is based upon the published and unpublished sources mentioned in the text and acknowledgements and on our own observations. Within the two main areas now colonised (the southwest and the north), blank areas on the map will more likely indicate absence of observations rather than absence of birds. This is especially so for the north of the island, where we believe the distribution on the Karpas peninsula, along the north coast and in the Kyrenia range, is denser and more widespread than shown here (see text).

but one, Akamas, 29 August 1984 (Charalambides & Charalambides 1985, 1989) would be exceptionally early for the latter and fits better with an over-summering breeder. Records from 1988 onwards almost certainly do refer to breeding birds: a singing male, Baths of Aphrodite, 29 April 1988 (Flint & Stewart 1992), a pair in breeding display, Smyies, 7 May 1989 (Bennett 1990), a male, Baths of Aphrodite, 11 June 1990 (Bennett 1991), one, Smyies, 8 April 1991 (Frost 1995) and a pair, Baths of Aphrodite, 1 May 1991 (Bennett 1994). Earlier breeding may also have been overlooked elsewhere: a probably reliable report of a breeding pair at Episkopi in the late 1970s was not taken seriously at the time and was not investigated (Frost 1996, PF).

The rate of increase and spread of the Akamas population was extremely rapid: in spring 1995 at least 50 pairs were present (Frost 1996) and in 1997 its numbers and extent were found to have markedly further increased. In the latter year a peninsula-wide survey mapped 162 Sardinians (compared with 49 Cyprus Warblers), and outside the Akamas birds were found as far as Pyrgos (*c*38 km to the east-northeast and near the ceasefire line), and c10 km south to Lara (Cozens & Stagg 1998). Since then, this population has spread southeastwards, between the coast and the higher Troodos, throughout and beyond Paphos District until it now covers most of the southwest of the island, including coastal areas west of Limassol (Pomeroy & Walsh 2000, 2002, BirdLife Cyprus reports, newsletters and database, Ieronymidou *et al* 2012, AM).

In May 2001 a separate population was discovered in the northeast of the island, *c*150 km from that on the Akamas. This population, centred on Kantara (Plates 37, 38), extended westwards for 37 km from the base of the Karpas peninsula along the eastern Kyrenia mountain range, covering both sides of the mountain ridge and extending down to the north coast (this mountain range is low, with a typical ridge height of 600–800 m, Lands and Surveys 1980). The density was high and an estimated 6000 pairs were present (Kuşkor 2003). This population had clearly existed undiscovered for many years, probably since at least 1990, when two males were at Kantara in May (Bennett 1991). It appears to represent a separate colonisation event from that on the Akamas, though apparently occurring at about the same time and probably for the same reasons. Also in 2001–2004, a few pairs were found near Vouni and Soli, to the south of Morphou bay and *c*45 km east of the Akamas, from where they were presumed to have spread across the ceasefire line (Kuşkor 2003, PF).

By 2004 the Kyrenia range population had extended a further 25 km westward along the mountain ridge and adjacent slopes (PF). This rapid spread, c8 km/year and twice the rate in the southwest (Jones 2006), coincided with three years of above average rainfall and subsequently slowed, perhaps because the next four years were all of below average rainfall and included a year of severe drought (Meteorological Service 2013b). The present distribution in the north of the island is poorly known compared with the south, due to a lower level of observer coverage. Nevertheless, it is clear that Sardinians now breed throughout most of the north (apart from the central plain), from the tip of the Karpas peninsula in the east to the Kormakiti peninsula in the west; at both these more visited sites they are increasing and apparently considerably more numerous than Cyprus Warblers. They are widely distributed on the Karpas where they also appear to outnumber Cyprus Warblers in some areas. There are relatively few records from the western Kyrenia range, probably due to a lack of coverage in this little visited area. The population in the north has merged around Morphou bay with that spreading eastward from the Pomos/ Vouni/Soli area. Birds from the north have also spread southwards down the east coast to Salamis and Silver beach but apparently not yet as regular breeders to cape Greco. General comments on status suggest that the distribution and density in the north of the island are much greater than indicated in Figure 4 (the summary of current status in the north of the

island of this paragraph is based on records from Damla Beton, Steve Cale, Wayne Fuller, Nick Pegler, Robin Snape and Clive Walton; BirdLife Cyprus reports, newsletters and database; Kuşkor sightings group at http://groups.yahoo.com; Mark Easterbrook, Johannes Honold and Colin Richardson).

The original Akamas breeding population appears to have been discrete, with few birds outside it (Frost 1996, Pomeroy & Walsh 2000, 2002). The above 1997 record from Pyrgos is anomalous with this, and fits better with the 2001 records from nearby Vouni and Soli. There had been an extensive forest fire in this region in 1998 (Cyprus Mail 8 July 1998); some of the birds near the latter sites were found in pockets of unburnt scrub (PF), and may have been remnants of a formerly larger and more widespread population. This raises the possibility that there had been a separate colonisation in this area. Also anomalous was a record of an adult with young at Nikoklia (Dhiarizos valley) on 9 May 1994 (Sadler 1995), c39 km southeast of the Akamas population. The scattered and widespread nature of the early breeding records: Akamas, Pyrgos, Nikoklia, Kantara and probably Episkopi, suggests that conditions across the whole island were becoming more favourable for the species to breed; rather than colonisation resulting from a single chance event. In the west some adults show breeding site fidelity and the species' range expansion appears to be driven by juvenile dispersal (Jones 2006, Mawson & Holdsworth 2010); eg in late summer 2001 only juveniles were found on the periphery of the Kantara populated area (PF). The recruitment of winter visitors into the breeding population is also a possibility, especially as the breeding population appears to have arisen from former winter visitors (see below).

Sardinian Warbler is not yet recorded breeding from the central plain, perhaps because the habitats and climate are less suitable for it. However, to the west, there are records from coastal areas southwest of Morphou, the driest region of the island where rainfall averages 290–300 mm per annum (Meteorological Service 2013a). In particular a survey there in late May 2013 in the area up to ten km west-southwest from Morphou found 11 males and 3 females, mainly in or near hawthorn bushes/trees. None were found further inland, where there are very few hawthorns (Wayne Fuller pers comm). Cyprus Warblers are not known to breed in the low rainfall area southwest of Morphou and none were detected in that survey. This suggests that Sardinian may be able to breed in areas of lower rainfall than the endemic species. It is noteworthy that in Israel subspecies *momus* breeds at high density down to *c*400 mm annual rainfall and at low density down to *c*300 mm (Shirihai 1996).

It is also possible that Sardinian Warbler has a better tolerance of high ambient temperatures than Cyprus Warbler, sometimes being seen and heard throughout hot spring days (*c*35°C), whereas the latter species is usually not, except in shadier forest areas (AM). Recent 2013 atlas count results in Limassol District also suggest this may be so: in the Vasa area the Sardinian/Cyprus Warbler numbers were 10/18 in April but 23/6 in June; and in the Gerasa area the numbers were 8/29 in April but 7/9 in June (BirdLife Cyprus newsletters). This needs to be investigated further, but if it is so it may partly explain Sardinian's ability to breed later in spring and to be most successful at lower altitudes; temperatures are higher in both situations.

#### Breeding habitat (Plates 19-39)

In the initial breeding area on the Akamas, Sardinian Warbler was found to share *Cistus* habitats with Cyprus Warbler (Brimmell *et al* 1998). In spring 2013 they were found in almost all available habitat in Paphos District, including extensive thorny scrub, isolated scrub, juniper maquis, open pine forest with shrub understorey, forest and field margins, scrub in forest breaks, areas of strawberry trees with pines, strawberry trees with golden oak, olive and citrus plantations with scrub and herbaceous margins, cereal crop margins,



#### Legend to plates on facing page

Plate 19. One of the first confirmed Sardinian Warbler Sylvia melanocephala nest sites, an isolated lentisc bush among cereals and carobs, Neo Khorio, Akamas, Cyprus, 22 April 1993. © Robert Frost estate

Plate 20. Sardinian Warbler Sylvia melanocephala habitat near Baths of Aphrodite, Akamas, with juniper, spiny burnet, *Cistus* and thyme, Cyprus, 9 December 2012. © *Alison McArthur* 

Plate 21. Sardinian Warbler Sylvia melanocephala habitat near cape Arnaoutis, Akamas, with low stunted juniper and thorny broom plus Cistus, Cyprus, 23 April 2013. © Alison McArthur

Plate 22. Sardinian Warbler Sylvia melanocephala habitat below Pano Vakhines, Akamas, with mature juniper, thorny scrub and occasional lentisc and carob, Cyprus, 9 December 2012. © Alison McArthur

Plate 23. Sardinian Warbler Sylvia melanocephala habitat Akamas south coast with dense juniper, lentisc and thorny scrub, Cyprus, 22 April 2013. © Alison McArthur

Plate 24. Sardinian Warbler Sylvia melanocephala habitat in Xeros valley below Nata with olive grove, vineyard and herbaceous margin, Cyprus, 14 May 2013. © Alison McArthur

Plate 25. Sardinian Warbler Sylvia melanocephala suburban habitat at Queens Gardens, Kato Paphos, Cyprus, 29 April 2013. © Alison McArthur

Plate 26. Sardinian Warbler Sylvia melanocephala habitat in Pikni forest, Peyia, with pine and thorny scrub, Cyprus, 30 April 2013. © Alison McArthur thistle fields and banks with herbaceous cover, and in village and suburban gardens (AM).

Pomeroy & Walsh (2006), also in Paphos District, found that Sardinian, like Cyprus Warbler, occurred in all habitats surveyed by them, but in arable habitats was four times more numerous than the latter, and in grassland was ten times more numerous. Like Cyprus Warbler, its highest densities were in uncultivated scrub habitats, where they were more than four times higher than in any other habitat. Within these uncultivated habitats its mean density was similar to that of Cyprus Warbler where Sardinians were absent. Within scrub habitats, Jones (2006) found that breeding territories were smaller where the vegetation was taller. Ieronymidou et al (2012) in a geographically extensive survey of the habitat associations of the two species, found Sardinian Warbler to be in greater abundance in post-cultivation and semi-natural scrub, but, like Pomeroy & Walsh (2006), found it to be much less strongly associated with scrub than Cyprus Warbler and to have more generalist habitat

associations than the latter species, *eg* being more tolerant of greater tree density and apparently better able to exploit currently managed agricultural landscapes (rotovated vines and fallow land).

In the eastern Kyrenia range in 2001–2004, Sardinian occurred at high density in the same scrub and open forest habitats and in the same areas as Cyprus Warbler (PF). At Akrotiri gravel pits it breeds in isolated tamarisk clumps in a salt marsh, a habitat not known to be used by Cyprus Warbler (Radford 2009). Both species have nested in gardens (*eg* Cramp 1992, Hawkins 1994) but Sardinians are very much more numerous in urban areas, where Cyprus Warblers hardly ever occur, not even in villages (Pomeroy *et al* in prep, AM).

Although Sardinian Warbler has more generalised habitat associations than Cyprus Warbler, by far the highest densities of both occur in scrub habitats. Within such habitats, Jones (2006) found that the broad scale vegetation structure within breeding territories of the two species was similar, with no significant differences for any measure. She found no evidence that the two species' home-ranges have different fine scale habitat compositions either, and that their nesting bush species and sizes are similar. She found that areas suitable for one species are suitable for the other, but also found a significant positive correlation between mean height of vegetation and density of Sardinian Warbler home ranges but no significant relationship for Cyprus Warbler. Where the distribution of the two species overlaps they both occur throughout almost all habitats (Pomeroy & Walsh 2002), and Derek Pomeroy (pers comm) found no evidence for any habitat or site in Paphos District which was better for Cyprus Warblers than Sardinians, which are now more numerous in all Cyprus Warbler habitats than the endemic species (Pomeroy *et al* in prep). Although



#### Legend to plates on facing page

Plate 27. Sardinian Warbler Sylvia melanocephala habitat in Stavros valley with olive grove and cereal crop, Cyprus, 9 May 2013. © Alison McArthur

Plate 28. Sardinian Warbler Sylvia melanocephala habitat in Xeros valley north of Nata with olive, citrus, tamarisk, grass and herbage, Cyprus, 14 May 2013. © Alison McArthur

**Plate 29.** Sardinian Warbler *Sylvia melanocephala* habitat near Arminou with old peach trees, lentisc, thorny scrub and herbaceous understorey, Cyprus, 13 May 2013. © *Alison McArthur* 

Plate 30. Sardinian Warbler Sylvia melanocephala habitat near Evretou dam with thistle field and lentisc, Cyprus, 9 May 2013. © Alison McArthur

**Plate 31.** Sardinian Warbler Sylvia melanocephala habitat at Oreites windfarm with thorny scrub, strawberry tree and lentisc, Cyprus, 12 May 2013. © Alison McArthur

**Plate 32.** Sardinian Warbler Sylvia melanocephala high density habitat above Evretou dam with lentisc, olive, thorny scrub and cereal crop, Cyprus, 24 April 2013. © Alison McArthur

Plate 33. Sardinian Warbler Sylvia melanocephala habitat with grassland and open low scrub, nest bush in the foreground, Yialousa, Karpas, Cyprus, 14 April 2013. © Steve Cale

Plate 34. Sympatric habitat of Cyprus Sylvia melanothorax and Sardinian Warbler S. melanocephala, but mainly the former, near Akrotiri village, with juniper, spiny burnet, thyme, and occasional lentisc and pine, Cyprus, 6 December 2012. © Alison McArthur Sardinians appear to have a preference for taller vegetation and Cyprus Warblers in some areas for lower (Ieronymidou *et al* 2012, AM, Robin Snape pers comm), where the former are long established they are seven to ten times more numerous even in the lowest vegetation (grassland/ phrygana) than the latter species (Pomeroy & Walsh 2006, Pomeroy *et al* in prep). Thus it seems that the more generalised habitat associations of Sardinian might not prevent it from competing with Cyprus Warbler.

#### Foraging behaviour

The more generalised habitat associations of Sardinian and its higher breeding density in taller vegetation suggest that the habitat utilisation or foraging behaviour of the two species may differ slightly (Jones 2006). Jones found no clear differences in foraging behaviour during the breeding season but did not study it in detail, partly because both species spent long periods out of sight among the scrub. Some differences were found during observations in early winter 2012: Sardinian often foraged in long grasses, which were avoided by Cyprus Warbler, and fed from larger-berried shrubs

such as lentisc *Pistacia lentiscus* and hawthorn *Crataegus azarolus* from early winter, whereas Cyprus Warbler only fed from these after box thorn *Lycium schweinfurthii* berries were exhausted. Sardinian also never associated or fed with other species, which Cyprus Warbler occasionally did. However both species took blackberries *Rubus sanctus* (*eg* Plate 18) and regularly foraged in spiny bushes (particularly when fresh growth was emerging), in stink aster *Dittrichia viscosa* and in dumps of pruned branches (AM).

#### Breeding altitudes

Pomeroy & Walsh (2006) did not find Sardinian Warbler above 800 m in Paphos District, though it has now reached over 1000 m there (Derek Pomeroy pers comm). Ieronymidou *et al* (2012) also found it less abundant at higher elevations: the co-ordinates of their survey points (Christina Ieronymidou pers comm) when plotted on Google Earth show the great majority are below 800 m, with only six points higher and the highest at *c*1150 m. A similar breeding season altitudinal distribution is shown by the records in the BirdLife Cyprus database though it includes three July–August records of juveniles at *c*1800 m, possibly post-breeding dispersal. Thus so far Sardinian Warbler on Cyprus seems to be a species of low and middle altitudes, similar to its distribution in southern Turkey, where it breeds primarily in scrub in coastal regions, with an upper elevation of probably *c*1000 m (Kirwan *et al* 2008). In Greece also its highest densities are in low altitude maquis, and it typically occurs up to *c*700 m, though locally to higher elevations and even up to 2000 m on Crete (Handrinos & Akriotis 1997).







On Cyprus, climatological data from Prodromos (1380 m) within the Troodos mountains—a coldest month mean temperature of 3.5°C, an annual temperature sum above 5°C of 2920 degree days (calculated from Meteorological Service 2013a) and an actual to potential evapotranspiration ratio of 0.57:1 (Flint 2011)—indicates that the climate at that altitude would be marginal when compared





**Plate 35.** Sympatric habitat of Cyprus Sylvia melanothorax and Sardinian Warbler S. melanocephala at Souni with *Cistus*, thyme, thorny scrub and oak, Cyprus, 29 April 2013. © Alison McArthur

Plate 36. Sympatric habitat of Cyprus Sylvia melanothorax and Sardinian Warbler S. melanocephala near cape Aspro with ravine and cliff topped by thorny scrub, lentisc and Cistus, Cyprus, 11 May 2013. © Alison McArthur

**Plate 37.** Sympatric habitat of Sardinian Sylvia melanocephala and Cyprus S. melanothorax Warbler: maquis scrub with pines and cypresses, Kantara castle, Kyrenia range, Cyprus, late spring 2001. The site of the initial discovery of the northern breeding population of Sardinians. © Peter Flint

**Plate 38.** Sympatric habitat of Sardinian Sylvia melanocephala and Cyprus S. melanothorax Warbler: low and medium maquis with reafforestation of young pines, east of Kantara, Cyprus; part of the large area of the eastern Kyrenia range occupied by breeding Sardinians by spring 2001. © Peter Flint

**Plate 39.** Sympatric habitat of Sardinian Sylvia melanocephala and Cyprus Warbler S. melanothorax, including *Cistus*, hawthorns, pines and cypresses, near Sina monastery at the western end of the Kyrenia mountain range, Cyprus, early April 2013. © *Clive Walton* 

with the species' known climatic range within Europe (Huntley *et al* 2007), whereas that at Saittas (640 m) is well within. However, as its range expansion appears to be driven by

juvenile dispersal, the high densities and rapid population growth on low ground might push young birds to higher altitudes.

#### Breeding season and productivity

Sardinian Warbler starts breeding 1–3 weeks earlier and finishes breeding 1–3 weeks later than Cyprus Warbler. Sardinian Warbler's breeding season is typically March–June (Jones 2006), but there are records of 'breeding' in February (Hawkins 1994, BirdLife Cyprus 2005/3) and of females carrying food from mid February (Richardson *et al* 2011). It has a higher frequency of double broods and an 18% higher productivity of chicks/pair than Cyprus Warbler (Jones 2006), which could enable it to rapidly build up a much larger population. Triple broods have also been recorded (Richardson 2011).

#### Population density and size

The breeding density of Sardinian Warbler in its favoured scrub habitats is often high or very high. In Paphos District it ranges from 1–2 pairs/hectare (Pomeroy & Walsh 2006, Jones 2006) and 3–4 pairs/hectare (based on spot counts and more prolonged observations at three sites in juniper scrub southeast of Lara, plus in thorny scrub north of Mavrokolymbos dam—areas measured by AM using Google Earth by pinpointing prominent features) to 5.6 pairs/hectare (Jones 2006). Densities in the Kyrenia range have not been calculated but in the Kantara region in 2001 appeared to be high; apparently at least as high as that of Cyprus Warbler elsewhere in the range (PF). Home-range sizes in scrub habitats vary from *c*800 m<sup>2</sup> to *c*6000 m<sup>2</sup> (Fig 3.3 in Jones 2006). The mean of 3244 m<sup>2</sup> is *c*40% smaller than that of Cyprus Warbler, though this difference is not statistically significant (Jones 2006).

The population of Sardinian Warbler in Paphos District 2007–2010 is estimated to be 109 000–152 000 pairs (Pomeroy *et al* in prep). Extrapolation from the size of the Kyrenia range population in 2001 suggests perhaps 20 000–30 000 pairs in the north now. There is no estimate for the population size in Limassol, Nicosia and Larnaca Districts, but from its area (Figure 4) it is probably at least 10 000 pairs. This gives a total for the island of perhaps 140 000–190 000 pairs, which would make Sardinian Warbler the second most numerous species on the island, after House Sparrow *Passer domesticus* (BirdLife International 2004).

## Apparent residence

Southern and island populations of the Sardinian Warbler are more resident than northern and mainland populations (Shirihai et al 2001), suggesting that the population now breeding on Cyprus would be less migratory than its founder population. Also, as Sardinian Warbler was formerly a common winter visitor to Cyprus, it would seem likely that the breeding birds might also overwinter, especially in the now less cold winters, in fact becoming mainly resident, and this does appear to be so. In January 2002, within their breeding area in the Kyrenia range, Sardinians responded to their song-playback at 16 of 17 known breeding territories. But in similar habitat outside the breeding area, none were seen and there was no response to song playback (methods as below) at 11 random sites, suggesting that few if any winter visitors were present and that the birds within the breeding area were overwintering breeders. Those responding within the breeding area included 16 males, 5 females and 2 unsexed, suggesting that the great majority of males at least are present on their territories in winter (PF). This would be in agreement with Shirihai et al (2001) who stated that residents of the species remain on (and defend) their territories all year. Year-round observations in Paphos District 1998-2013 (Richardson in prep) show less difference between winter and early spring numbers than is the case with Cyprus Warbler, suggesting that a larger proportion of Sardinians overwinter. These

observations also show a peak movement in early October which does not correspond with the known late October–November peak movement of passage migrants, suggesting that the former movement involves birds from the breeding population and that some leave the island in autumn. From Shirihai *et al* (2001), the great majority of those leaving are likely to be first winter birds. Given the high numbers of Sardinian Warblers present in winter, the large proportion of males remaining on their territories compared with Cyprus Warbler males, and the earlier start to their breeding season, those leaving seem likely to be a relatively small proportion of the population. The slightly shorter and more rounded wing shape of Sardinian Warbler, when compared with Cyprus Warbler (Shirihai *et al* 2001), also suggests that the former would be less migratory. However, as with Cyprus Warbler, a detailed study is needed to accurately determine the proportion overwintering.

On the Akamas in December 2012, 32 were counted within a strip of dense juniper and thorny scrub covering 4.7 ha (measured from Google Earth using reference points on the ground), a density of 6.8 birds/ha. This is a minimum figure, as many are believed to have been missed in the dense scrub. Many could also be heard calling from a larger adjoining area of similar habitat (AM).

#### Taxonomy and biometrics

The breeding populations on Cyprus are nominate melanocephala (Jones 2006 and see below); they presumably arose from winter visitors remaining to breed. Wings of former winter visitors and passage migrants (Flint & Stewart 1992) average 0.8 mm longer than those of current breeders, if statistically significant this difference may be partly because the primaries of winter visitors would be less abraded than those of breeders in spring/ summer. However, shorter wings may have been a character of the founder population, which may have been shorter-winged than the longer-distance migrants passing through to North Africa. It is noteworthy that birds from Crete and the Greek islands are also shorter-winged than mainland populations (Cramp 1992, Shirihai et al 2001). Breeding season adult mean wing lengths are: males 58.4 mm n = 69, females 57.6 mm n = 62 (Jones 2006), slightly shorter than those of Cyprus Warbler, despite Sardinian's larger body mass. The sexes combined mean wing length of the population breeding in the west of Cyprus, 57.7 mm n = 323 (Cozens 1996, Brimmell et al 1998, Jones 2006), is close to that of melanocephala from southern Greece (Cramp 1992). Wing lengths of the population breeding in the north of the island appear similar, mean 57.8 mm n = 9, sexes combined (Wayne Fuller & Clive Walton pers comm), but the sample size is very small.

There have been several recent reports of melanistic individuals (*eg* Mawson & Holdsworth 2010 and pers comm, Richardson *et al* 2011). This may be a character of the founder population, but melanic or darkened plumages occur in many island birds (Newton 2003) and are shown by the Cypriot endemic avian taxa (Flint & Stewart 1992). Birdlife Cyprus have no confirmed records of the Levantine race *S. m. momus* (Colin Richardson pers comm); examination of hundreds of breeders ringed in the west has revealed only nominate *melanocephala* (Geoff Mawson pers comm) and breeders in the north and south resemble the latter in the field (PF, AM, Clive Walton pers comm). Mean tail lengths of Cyprus breeders, 57.7 mm n = 123, sexes combined (Jones 2006), and mean wing lengths are longer than those of *S. m. momus* (Shirihai *et al* 2001).

Mean weights of adults in the breeding season are: males 11.5 g n = 179, females 11.8 g n = 146 (Cozens 1996, Brimmell *et al* 1998, Jones 2006). Mean weights of former winter visitors and passage migrants are: males 13.3 g n = 93, females 12.2 g n = 81 (Flint & Stewart 1992). Thus during the breeding season Sardinian males average 6.5% heavier than male Cyprus Warblers, and females average 3.5% heavier than female and 10.3% heavier than male Cyprus Warblers. We have been unable to find winter only weights for either species,

but from the data we do have including Cozens *et al* (2000), Sardinian maintains its heavier weight outside the breeding season. It is noteworthy that in Israel the body mass of several small passerines including Sardinian Warbler declined significantly between 1950 and 1999, apparently in response to global warming and in accordance with Bergmann's rule (Yom-Tov 2001). Such a change might be looked for in Sardinian and Cyprus Warblers on Cyprus.

Mean bill dimensions in mm are: for males, length 13.6 n = 67, depth 2.8 n = 67, width 2.6 n = 18 and for females length 13.5 n = 59, depth 2.8 n = 60, width 2.6 n = 21 (Jones 2006). These dimensions are smaller than those of west Mediterranean populations of nominate *melanocephala* given by Shirihai *et al* (2001), but in length are similar to those of birds from Crete (Roselaar 1995). The bill dimensions of Cyprus breeding Sardinians are very close to those of Cyprus Warbler (above).

## SPECTACLED WARBLER (Plate 40)

A common resident in the more arid parts of the island, especially the central plain and adjacent slopes and foothills, where average annual rainfall is less than 400–450 mm. Its typical habitats are garrigue and low maquis, herbage, margins of cultivation and vegetation on salt flats (Flint & Stewart 1992). Although easily overlooked it seems to have extended its range in recent decades, *eg* to the ridge and northern slopes of the





Plate 40. Spectacled Warbler Sylvia conspicillata male, Ayia Napa, Cyprus, 15 April 2011. © Dave Barnes

**Plate 41.** Sympatric habitat of Spectacled Sylvia conspicillata and Cyprus S. melanothorax Warbler: grass, herbage, very low shrubs and scattered pines and hawthorns at Lachin, in the Kyrenia mountains above Bellapais, Cyprus, June 2002. © Peter Flint

Kyrenia range (Kuşkor 2000, 2003), probably because of the increasing aridity of the climate.

It has been present since at least the 19th century, but its similarity to mainland populations despite its apparently sedentary nature suggests it may be a relatively recent colonist. In those parts of its range where the rainfall exceeds 340–350 mm it is sympatric with Cyprus Warbler (*eg* Plate 41). Sardinian Warbler also now breeds in some areas where the other two *Sylvia* species already breed. At 9.4 g n = 10, sexes combined (Flint & Stewart 1992), Spectacled is the smallest of the three species, though this may be an advantage on the hot plain. It will be interesting to see if it also declines where it is sympatric with Sardinian, *eg* on the Kormakiti peninsula, especially in view of the situation on Malta (see below).

# THE EVIDENCE FOR A DECLINE IN CYPRUS WARBLER NUMBERS IN AREAS COLONISED BY SARDINIAN WARBLER

We present the evidence for a decline in Cyprus Warblers in areas colonised by breeding Sardinians to demonstrate the close relationship between these two events. However, while correlation may provide circumstantial evidence of competitive displacement, it does not prove causation. Other factors such as habitat and climate change could be wholly or partly implicated; we later examine and discuss the evidence for these and for competitive displacement. In this section we follow the geographic sequence of the spread of Sardinian Warbler and the accompanying decline of Cyprus Warbler, starting with the Akamas then progressively enlarging the area covered to also include Paphos District, the remainder of western Cyprus and then central and southern Cyprus. We conclude with the Kyrenia mountain range and northern Cyprus.

## Akamas peninsula and Akamas Important Bird Area

There are few records of the status of Cyprus Warbler on the Akamas peninsula prior to its colonisation by Sardinian Warbler. However in April 1988 many male Cyprus Warblers were singing in juniper, *Cistus* and lentisc scrub along the track between Baths of Aphrodite and cape Arnaoutis (PF); suggesting that it was numerous there before Sardinians colonised.

The first indication that colonising Sardinian might be displacing the endemic Cyprus Warbler came in spring 1995 when the latter appeared to be more common in the area where Sardinian numbers were low, compared with the area where they were high (Frost 1996). Although subjective, this comment was based on three weeks observations on the Akamas that spring, including line transects, by a careful and reliable observer. During 1997–1999, ten sites were monitored each year (using timed species counts, Bibby *et al* 2000) in the Akamas/Laona area in three major habitat types: natural (mainly trees), scrub and agricultural. Cyprus Warbler declined over the three years in all three habitat types. By 1999 it was absent from half of the sites, where it had been present in 1997, and all these sites, and many others, now had Sardinian Warblers (Pomeroy 1999). In spring 1997, 49 Cyprus Warblers were mapped at 15 sites at the base of the peninsula, mean 3.3 birds/site, range 1–6 (Cozens & Stagg 1998); but by 2009 they were found in only 1 of 7 transects in the same area (Ieronymidou *et al* 2012).

Analysis of sight records from the peninsula (Neo Khorio and Latchi northwestwards, including Smyies, Agios Minas and Pano Vakhines) for 1993–2012 show dramatic declines in Cyprus Warbler, both in records and in the numbers of individuals recorded (Figure 5). Yearly means of records to numbers of individuals for the three time periods 1993–1999,



Figure 5. Akamas peninsula 1993–2012 sight records of Cyprus Warbler and Sardinian Warbler. The graph shows for each species the mean total number of records/year and the mean total number of individuals recorded/year for the three time periods indicated. See the main text for the area included and the origins of the records.

2000–2009 and 2010–2012 were 14.1:28.0, 3.4:5.5 and 0.7:1.3 respectively. For comparison the equivalent figures for Sardinian were 24.3:86.6, 18.5:97 and 15.0:94.7.

A similar analysis for the about three times larger Akamas IBA (179 km<sup>2</sup>), which includes the peninsula and extends further south to Peyia forest and cape Drepanum (www.globalspecies.org/birdareas/display/25, Figure 1), also shows large declines in Cyprus Warbler records and individuals (Figure 6). Yearly means of records to numbers of individuals for the same three time periods were 20.1:39.9, 7.4:11.6 and 3.0:4.7 respectively. The equivalent results for Sardinian were 29.5:105.0, 31.7:152.7 and 43.0:170.7. The maximum numbers of birds recorded at any one time within the IBA during the three time periods were: for Cyprus Warbler 10, 5 and 2; and for Sardinian 23, 52 and 50 respectively (BirdLife Cyprus newsletters and database, Cypriaca recording site at www.worldbirds.org, AM, Derek Pomeroy pers comm).

The numbers of Cyprus Warblers ringed by expeditions to the Akamas region have also reduced and they are now rarely caught (Geoff Mawson pers comm): *eg* spring 1995, 16 Cyprus and 108 Sardinian (Cozens 1996); spring 1997, 10 and 99 (Brimmell *et al* 1998); autumn 1999, 3 and 95 (Stagg *et al* 2001); spring 2010, 1 and 101 (Mawson & Holdsworth 2010) and spring 2011, none and 127 respectively (Sayer 2011). In 1998 the densities of



**Figure 6.** Akamas IBA 1993–2012 sight records of Cyprus Warbler and Sardinian Warbler. The graph shows for each species the mean total number of records/year and the mean total number of individuals recorded/year for the three time periods indicated. See the main text for the area included and the origins of the records.

Sardinian and Cyprus Warblers on the Akamas peninsula were estimated at *c*40 and *c*20 birds/km<sup>2</sup> respectively (Pomeroy & Walsh 2002). By 2012 Sardinians were present in 100s and Cyprus Warblers were reduced to 1 or 2 pairs/km<sup>2</sup> (Derek Pomeroy pers comm). Richardson (2011) considered the Akamas to now be almost devoid of Cyprus Warblers, which is supported by the above analysis of records.

#### Paphos District (including the Akamas)

During 1997–2001 timed species counts showed that Cyprus Warbler decreased in six out of seven sites colonised by Sardinian Warbler. The probability of this result occurring by chance is 0.0547 or 1 in 18, though not statistically significant at the 5% level (Pomeroy & Walsh 2002). However, closer examination of the results shows that the three sites with the largest decreases (of *c*46, *c*57 and *c*78%) were within or very close to the area where Sardinian was longest established and most numerous, and the one site showing no decrease was where Sardinian numbers were lowest. This pattern of results might be expected if Sardinian was displacing Cyprus Warbler. Furthermore, in the same survey, at a nearby site outside the area colonised by breeding Sardinians, Cyprus Warbler numbers increased by *c*125%; and at another nearby site outside, monitored only in 2001, Cyprus Warbler numbers were higher than at any of the sites within the Sardinian increased in all habitats monitored: forests, semi-natural and agro-ecosystems; and that Sardinian density increases with time.

Using data from Pomeroy & Walsh (2002), plus unpublished timed species count data from those authors for 2002–2005, Jones (2006) found a (non-significant) decrease in Cyprus Warblers for 1997–2005 in the area where Sardinians were longest established and in highest numbers, a gradual (non-significant) decrease in the area more recently colonised by Sardinians, and a gradual (non-significant) increase in the area without Sardinians. However looking only at the results from scrub, the most widespread and most favoured habitat of Cyprus Warbler, which probably holds *c*85% of its population (calculated from Pomeroy & Walsh 2006, see *Changes in breeding population size* below), she found a moderate (significant at the 5% level) decrease in Cyprus Warblers within the area longest colonised by Sardinians, Cyprus Warbler's mean TSC scores falling from more than 3 in 1997 to less than 1 in 2005. The probability of this result occurring by chance is 0.035 or 1 in 28.

Transect counts at 38 sites in Paphos District 2001–2004 produced density estimates for male Cyprus Warblers in birds/km<sup>2</sup> at sites with/without Sardinian Warblers in various habitat types as follows: forest 16.0/22.0, uncultivated (scrub) 40.1/133.9, grassland 2.3/0.0, permanent crops (groves, orchards, vineyards) 12.5/31, arable 5.4/0.0 (Pomeroy & Walsh 2006). Thus in its three most favoured habitats in this survey (forest, scrub and permanent crops) Cyprus Warbler densities were lower at sites colonised by Sardinians, and in its most important habitat, scrub, were only one third of that at sites without Sardinians. The same authors also gave density estimates for males of the two species for the altitude bands <200 m, 200–500 m, 500–800 m and >800 m. The results in birds/km<sup>2</sup> were, for Cyprus Warbler 10.4, 25.6, 14.6 and 32.3; and for Sardinian 90.9, 53.3, 10.6 and 0.0 respectively. Thus the lowest density of Cyprus Warblers was below 200 m, where they were outnumbered 9 to 1 by Sardinians.

There are no similar pre Sardinian Warbler colonisation census data for direct comparison, but before the colonisation by Sardinian, Cyprus Warbler had been common at low altitudes in Paphos District, *eg* in May 1978 singing males were very common in rocky areas with scrub down to sea level in the area north of Paphos to Mavrokolymbos to cape Drepanum, and were still so in April 1988 (PF). The species is now rarely found at cape Drepanum (*eg* BirdLife Cyprus 2009/2, AM). See also other examples of its previous

status above and below. The annual reports of the Cyprus Ornithological Society (founded 1970) also often described Cyprus Warbler as abundant, citing locations near sea level in Paphos District like the Akamas, Lara, Latchi, Polis and Pomos (*eg* Charalambides & Charalambides 1987, 1992). Thus it appears that the decline of Cyprus Warbler has been greatest at low altitudes, where the density of Sardinians is highest.

Colin Richardson (pers comm), mainly in the Paphos area, had 99 sightings of Cyprus Warbler in 2006 but only 52 in 2011 in spite of more frequent field trips in 2011 than in 2006; a reduction in sightings of 47% in five years. In regular visits (>200/year) to the area including the Minthis hills and the Paphos foothills at Armou and Marathounta, the mean number of Cyprus Warblers recorded by him (pers comm) per visit declined from 0.67 in 2004 to 0.09 in 2012; a reduction of 87% in eight years. In late May 2013 no Cyprus Warblers were seen or heard by him (pers comm) during a 2 km transect in the Marathounta hills (c10 km inland from Paphos at c430 m), but Sardinians (22 pairs) were found wherever scrub was present, even small clusters of bushes on the barren hillsides holding pairs. Some visitors are now unable to find Cyprus Warbler, instead finding only Sardinians at previously recommended Cyprus Warbler sites; and tour group leaders are reporting that Cyprus Warbler is increasingly hard to find in spring at sites in Paphos District where it could formerly be relied upon (Colin Richardson pers comm).

In southwest Paphos District in late March–mid May 2013 Cyprus Warblers were still present in good numbers alongside Sardinians in some areas, typically in extensive thorny scrub, with isolated wild olive, carob, *Cistus* and thyme; *eg* east of Peyia in the Xeros valley area, and in the Mavrokolymbos and Asprokremmos dam areas (AM). Cyprus Warblers were also found in some isolated pockets of scrub, with Sardinians nearby in other habitats. However there are other areas of similar habitat to those mentioned above in the Xeros valley *etc*, where Cyprus Warblers were known by AM to be present within the past five years but which now hold only Sardinians *eg* a site in the outer ravine southeast of Lara, the north bank of Mavrokolymbos dam, the area immediately west of Kelokedara ford and a side valley just north of Agios Georgios in the Dhiarizos valley.

#### Western Cyprus (including Paphos District)

Cyprus Warbler was common and widespread in the west prior to its colonisation by Sardinian Warbler, *eg* in April 1978 Cyprus Warbler was very common in open bush habitats with some trees at low altitudes and in the Troodos mountains to nearly 1400 m, with three singing males often heard from one point (H-H Bergmann pers comm), and in late May and early June 1979 singing males and birds carrying food were common in scrub in the south and west and in the Troodos mountains (Flint 1981). During fieldwork for their Cyprus breeding birds atlas in western Cyprus 1995–2002, Whaley & Dawes (2003) found that, apart from some areas colonised by Sardinian Warbler, the Cyprus Warbler population appeared to be stable. They found the highest numbers of Cyprus Warblers in the west, where densities in ideal habitats were up to 100 singing males/km<sup>2</sup>. Their observations also led them to believe that Cyprus Warbler was being displaced, at least in the area of the Sardinian's initial colonisation. Now their impression is that Cyprus Warblers are far less obvious in the west and difficult to see in areas in which they previously were common (David Whaley & Judy Dawes pers comm).

Annual counts 1997–2008 at up to 40 sites, mainly in Paphos District (Pomeroy 2009), show that the "Sardinian Warbler continues its spread, and in the west of the island is becoming very common. Where that happens, Cyprus Warblers decline." The graph in Pomeroy (2009) shows the increase in Sardinians 1997–2008 as *c*475%, and the decrease in Cyprus Warblers as *c*40%, with a decrease every year 2004–2008. These annual counts continued until 2011; a statistical analysis of the results 1998–2011 shows a strong inverse

relationship between the mean abundance of Cyprus and Sardinian Warblers recorded each year: the former showing a significant decrease of 4.7% per year whereas the latter show a significant increase of 27% per year. The probability of these three results occurring by chance is in each case less than 1 in 1000. In 2010–2011 annual data was still being collected at 30 of the sites; Cyprus Warbler had never been recorded at one of these, and at 17 of the remaining 29 it was no longer being recorded. The results also show that on non-grassland sites (*eg* scrub, forest, permanent crops) Cyprus Warbler would be expected to decline after two years of occupancy by Sardinian Warbler (Pomeroy *et al* in prep).

Further compelling evidence of much lower numbers of Cyprus Warblers in the west (where there are many Sardinians) compared with areas further east (where there are few or none), comes from counts in 2013 in BirdLife Cyprus's breeding bird atlas 10 km squares (BirdLife Cyprus newsletters, Cypriaca recording site at www.worldbirds.org). The results from atlas squares in the west (west of the Dhiarizos valley), gave Cyprus/Sardinian Warbler numbers of 0/28, 2/21, 2/15, 0/15 and 0/12. East of this, in the area from cape Aspro to Kolossi and inland to the lower Troodos massif between Arminou and Moniatis, was a 'buffer zone' where both species were present in rather more equal numbers: Cyprus/Sardinian 18/10, 13/22, 8/24, 7/16, 5/27, and 1/20 (*nb* the last two squares were covered late in the breeding season, in mid–late June, when Cyprus Warblers are less obvious). Further east again, counts in squares east, north and northeast of Limassol and immediately east and northeast of Troodos show much higher Cyprus Warbler numbers and few Sardinians: 52/0, 45/1, 39/0, 38/0, 30/1, 28/0, 28/5, 24/0, 17/0, 29/8 and 16/5.

The boundaries of the above 'buffer zone' cut across the rainfall isohyets and altitude contours, rather than running parallel with them; the latter would have been expected if declining rainfall and/or increasing temperatures were responsible for Cyprus Warbler's decline. If Sardinian Warbler is displacing Cyprus Warbler then the eastern boundary of the area where the latter is scarce or absent can be expected to move progressively eastward in future years into the remaining Cyprus Warbler range in the south of the island, as the Sardinian Warbler spreads and the Cyprus Warbler declines in the same areas. Based on events so far, it seems very likely that this will happen.

#### Western, central and southern Cyprus

The areas colonised by Sardinian Warbler in western, central and southern Cyprus were mapped by Ieronymidou *et al* (2012): the main continuous population in the west covers almost all of Paphos District and the western part of Limassol District, with four small outlying areas. In addition they mapped their 202 survey localities (each involving a 500 m transect) showing where Cyprus Warblers were detected or not detected. Their results show a mean of 1.0 Cyprus Warblers detected at each of the 123 survey locations within the Sardinian's breeding range (or a mean of 2.8 at the 43 localities where Cyprus Warblers were detected), and a mean of 1.4 at the 79 survey locations outside the Sardinian's breeding range (or a mean of 3.6 at the 31 locations where they were detected), even though there was less scrub (the prime Cyprus Warbler habitat) in the latter area.

The 79 survey locations outside the Sardinian's breeding range include 24 on the central plain which are also outside the Cyprus Warbler's known breeding range (Flint & Stewart 1992), and when plotted against average annual isohyets (Meteorological Service 2013a) all have rainfall less than c340–350 mm. No Cyprus Warblers were detected at any of these locations. If these 24 are excluded from the 79, the mean number of Cyprus Warblers detected at the 55 survey locations outside the Sardinian's breeding range but within its own known breeding range can be calculated as either ( $1.4 \times 79$ )/55 or ( $3.6 \times 31$ )/55. As these calculations involve the multiplication of numbers rounded to one decimal place the final result will be 2.0 or 2.1, twice the detection rate of that within the Sardinian's

range. Also, as Sardinian Warblers have spread southeastward from the original area of colonisation on the Akamas, the decline in Cyprus Warblers if caused by competition with Sardinians might be expected to be greatest in the northwest (where they have been longest exposed to Sardinians) and lowest in the southeast of the Sardinian's range. From the mapped results of Ieronymidou *et al* (2012) this does appear to be so: of their 114 survey locations within the main breeding range of Sardinian Warbler, Cyprus Warblers were encountered at only 10 of the 57 (17.5%) survey locations in the northwest, compared with 28 of the 57 (49.1%) locations in the southeast. Within the Sardinian's main breeding range leronymidou *et al* (2012) encountered it at a ratio of 5:1 to Cyprus Warbler. A much higher ratio than the 2.3:1 obtained from the 2001–2004 population figures for the two species in Paphos District (Pomeroy & Walsh 2006); suggesting that the ratio in favour of Sardinian had apparently doubled in less than a decade.

Cyprus Warblers are numerous where Sardinians are still in low numbers or absent: *eg* 11 males Germasogeia dam and 11 Curium stadium April 2009; 17 Akrotiri junipers May 2009; 10 Kensington cliffs March 2010; 30+ Pissouri heights (east) May 2010, where it was the commonest breeding bird; 12 Stavrovouni and 13 Lefkara June 2010; 11 males Souni and 18 males Amathus hills March 2011; 15 Pentaschinos river May 2011; 10 pairs Apsiou April 2012; and 15 Kalavasos and 19 Maroni July 2012 (Richardson *et al* 2010, 2011, 2012, BirdLife Cyprus 2012/5,7). Very high densities were also found in April–May 2013; locations and numbers of singing males/area were: Agios Konstantinos church ravine above Kouklia (Plate 9), 5 or 6 in 1.4 ha (no Sardinians within area); Petra tou Romiou headland above restaurant, 6 or 7 in 1.4 ha (no Sardinians within area); and Pissouri headland east basin, 5 or 6 in 1.0 ha (one Sardinian within area). Areas measured on Google Earth, using several reference points at each site (AM).

#### Kyrenia mountain range and northern Cyprus

Earlier records show that Cyprus Warbler was common in the north of the island: eg McNeile (1948–1955) found it common and widespread in the Kyrenia hills and mountains, and Ashton-Johnson (1961) found nesting birds 'extremely common' on the Karpas peninsula. After the discovery of the Kyrenia range Sardinian Warbler population in 2001, PF, aware of the apparent decline of Cyprus Warblers in the area colonised by Sardinians on the Akamas, used response to song playback to look for evidence of a similar decline in the north. Cyprus Warbler song (from Roché 1992) was played through a Sony minidisc and separate small Sony battery-powered speaker; the apparatus was placed, speaker facing up, under small bushes and played at full volume for five minutes. Two observers watched from a car 10-15 m distant and recorded responses, usually birds appearing from cover and approaching the speaker. Sites were >100 m apart and near tracks and minor roads. During the 2001–2002 breeding seasons Cyprus Warblers responded at 12 of 22 (55%) sites within the Sardinian breeding area, compared with at 38 of 40 (95%) sites in similar habitat outside that area. This suggests that the density of Cyprus Warblers within the area colonised by breeding Sardinians may have been lower than outside it, though not of course proving a decline.

Due to a much lower level of observer coverage than in the south the current situation in the north of the island is not well known; annual long-term census counts (similar to those made by Pomeroy & Walsh in the southwest) are needed to accurately determine population levels and trends. Based on the current limited and mainly anecdotal evidence, Cyprus Warblers appear to be declining in some areas, while Sardinians continue to increase. The former are now of patchy distribution; absent from some areas of apparently suitable habitat where only Sardinians are present, and are most encountered where the scrub is lower and denser, and on the southern slopes of the mountain range. In areas of taller scrub (juniper and pines) sometimes now only Sardinians are found (Robin Snape pers comm). Records from the Karpas peninsula are contradictory; they may indicate a very recent decline in Cyprus Warbler numbers. Census counts in several areas in spring 2010 and 2011 found that Cyprus Warblers outnumbered Sardinians by a mean of eight to one, though in spring 2011 other observers reported approximately equal numbers in north Karpas (BirdLife Cyprus newsletters, Cypriaca recording site at www.worldbirds. org). In spring 2012 Steve Cale (pers comm) also found approximately equal numbers on the Karpas (18 Sardinians and 14 Cyprus Warblers), and in spring 2013 he found that Sardinians appeared to outnumber Cyprus Warblers at stops along the Karpas road. At cape Andreas, many singing male Cyprus Warblers and no Sardinians were present in April 2004 (PF), Sardinians had reached there by April 2007 (BirdLife Cyprus newsletters and database), and in April 2011 a 3 km transect along the north coast westwards from the cape found only Sardinians (Kuşkor sightings group at http://groups.yahoo.com). Since 2010, Colin Richardson (pers comm) has recorded only Sardinians at the cape in spring. In April 2013 Cyprus Warblers were difficult to find there (whereas Sardinians were numerous) and not recorded by all visitors (Steve Cale pers comm, BirdLife Cyprus newsletters, Kuşkor sightings group at http://groups.yahoo.com). Along the north coast west from Kantara, only Sardinians are now present in habitat that seems very suited to Cyprus Warbler (Robin Snape pers comm) and where the latter species was present in 2001 (PF). This accords with the experience of Nick Pegler (pers comm) who has noticed in the last two or three years at Agios Amvrosios (on the north coast between Kantara and Kyrenia) that Cyprus Warblers have become more difficult to locate (with none found in autumn 2013), whereas the opposite is the case for Sardinian Warbler. However, he (pers comm) is still finding singing male Cyprus Warblers around Pentadactylos mountain. In the western Kyrenia range and adjacent areas Clive Walton (pers comm) is still encountering Cyprus Warblers in usual numbers. At cape Kormakiti in spring 2012, Steve Cale (pers comm) recorded 5 Cyprus and 11 Sardinian Warblers and in spring 2013 he did not see any Cyprus Warblers there whereas Sardinians were numerous. In early October 2012 Colin Richardson (pers comm) counted 14 Sardinians and no Cyprus Warblers there.

## Changes in breeding population size

We are aware of six whole island Cyprus Warbler population estimates:

- 1994 4000–8000 pairs (Tucker & Heath 1994).
- 1998 c100 000 pairs (Snow & Perrins 1998).
- 2000 180 000 pairs (Flint 2000).
- 2003 120 000–280 000 pairs (Whaley & Dawes 2003).
- 2004 70 000–140 000 pairs (BirdLife International 2004).
- 2013 60 000–120 000 pairs (BirdLife Cyprus, not yet published).

Apart from recent large declines in areas colonised by Sardinian Warbler, there is no evidence to suggest that the Cyprus Warbler has ever been anything other than common and widespread, thus as presented the above widely varying figures clearly do not reliably show changes over time. An examination of the reliability of these estimates, and of the methods and assumptions used to arrive at them (Appendix 1), suggests that the 1994, 1998 and 2004 estimates are too low, that the 2000, 2003 and 2013 estimates are more accurate, and thus that there may have been a decline of more than 30% between 2000/2003 and 2013.

# The evidence against a decline of Cyprus Warbler in areas colonised by Sardinian Warbler

We are not aware of any published or unpublished evidence, from either systematic or non-systematic records, that Cyprus Warbler numbers do not decrease in areas long colonised by Sardinian Warbler. Neither are we aware from such records of any declines in Cyprus Warbler numbers in areas not colonised by Sardinian Warbler. Parts of the middle and lower northern slopes of the Troodos range were poorly covered in past systematic surveys and have few non-systematic records either (*eg* Whaley & Dawes 2003, Pomeroy & Walsh 2000, 2002, 2006, Ieronymidou *et al* 2012, Derek Pomeroy pers comm, Figure 4), probably because of limited access and proximity to the cease fire line. Cyprus Warbler's status in these areas is thus not well known and should be further investigated.

The BirdLife Cyprus database shows an increase in Cyprus Warbler numbers recorded in recent years, *eg* from *c*2322 during 1993–1999, to 12 593 during 2005–2011; this appears to be almost entirely due to increased observer coverage. For example, the 2005–2011 total includes 8193 birds recorded by one observer contributing almost daily records, mainly from the same area; there has also been a 50% increase in the number of contributors, from *c*40 to *c*60, and some previously under-watched sites, outside or marginally within the Sardinian area are now more often covered systematically. In addition, during 1993–1999, *c*6% of records were summarised *eg* 'widespread' or 'many places all month' and these each counted as only one record, whereas during 2005–2011 there were no such records; this will have resulted in a small further increase in the number of records and of the number of birds recorded.

#### The evidence for a decline – conclusions

The evidence presented above is from different observers, often using different methods and covering different areas, and includes both systematic and non-systematic records, and qualitative and quantitative data. However viewed overall it consistently shows that, at least in the west of the island, Cyprus Warbler numbers are lower in areas colonised by Sardinian Warbler, that they decrease in such areas and the longer Sardinian has been present in an area the greater and more serious the decline in Cyprus Warbler is. This does not prove a causal link, but when combined with the fact that Cyprus Warbler numbers remain high outside areas long colonised by Sardinians there is strong circumstantial evidence that one does exist.

The understanding that the Cyprus Warbler is in serious decline in areas colonised by Sardinian Warblers is also shared by Colin Richardson (BirdLife Cyprus recorder 2004–2013), based on his own observations and records and comments submitted to him by resident and visiting observers (Colin Richardson pers comm). The two previous recorders also commented on the decline in Cyprus Warbler numbers in areas colonised by Sardinian Warbler (*eg* Sanders 2000, Gordon *et al* 2004).

## POSSIBLE REASONS FOR THE DECLINE IN CYPRUS WARBLERS: COMPETITIVE DISPLACEMENT

If Sardinian Warbler is displacing Cyprus Warbler, as the circumstantial evidence suggests, then this is liable to be as a result of competition for territories and/or food (competitive displacement), and we here present and discuss the evidence for this. Afterwards, we examine other possible reasons for the Cyprus Warbler's decline: climate and habitat change, and 'apparent competition' due to predators and parasites.

#### Interspecific territoriality within the breeding season

Jones (2006) mapped the home-ranges (the area used by a pair for foraging) of 65 Cyprus and 70 Sardinian Warbler pairs at seven sites in 2004–2005. Both species were present together at five sites in 2004 and at all seven in 2005. She also mapped the mean centre of activity of each pair within its home-range (for Cyprus Warbler these centres are on average 25.4 m distant from their nest sites and for Sardinian 15.5 m distant). She found that the home-ranges of congenerics overlapped more than those of conspecifics and from the raw data found that conspecific nearest-neighbour distances were significantly larger than congeneric nearest-neighbour distances (the actual distances are not given by her). She concluded that the two species are not interspecifically territorial and that both establish home-range without reference to the other species, resulting in considerable interspecific home-range overlap.

This conclusion may be correct, but to us the maps appear to show patterns in the interspecific distribution of the home ranges and their centres, which suggests that some degree of interspecific territoriality may exist, because if there was no territoriality a random distribution would be expected (Newton 1998). Specifically, where congeneric home-ranges overlap, most Cyprus Warbler home-range centres lie outside Sardinian home-ranges, and the minority within are usually close to the edge of the other species' home-ranges; but the reverse is not so with Sardinian. Thus of 42 Cyprus Warbler home-ranges which overlap with Sardinian home-ranges, only 17 have their centres within the home-ranges of the other species, by a mean distance of 8 m. But of 48 Sardinian home-ranges which overlap with Cyprus Warbler home-ranges, 31 have their centres within the home-ranges of the other species, by a mean distance of 15 m. The maps also show that five Sardinian home-ranges lie wholly within Cyprus Warbler home-ranges, but that the reverse is true for no Cyprus Warbler home-ranges.

The often larger home-range sizes of Cyprus Warbler probably partly accounts for these differences, but there are also differences in conspecific home-range overlaps: those of Cyprus Warbler overlapping more than those of Sardinian. Thus of 43 Cyprus Warbler home-ranges which overlap those of other Cyprus Warblers, the centres of ten lie within other home-ranges, but of 39 Sardinian home-ranges which overlap those of other Sardinians, the centres of only two lie within other home-ranges. The ratios of home-range centres lying within overlapping congeneric/conspecific home-ranges are: for Cyprus Warbler 17:10 (1.7:1) and for Sardinian 31:2 (15.5:1). Also, where there is substantial or complete overlap of two or more congeneric home-ranges, their centres never coincide and are usually spaced well apart, this is also so with similar conspecific overlap of Cyprus Warbler home-ranges, eg Figs 3.1a, c–e, h, j–m in Jones (2006). Note, however, that different sites had slightly different vegetation and resulting different mean home range sizes as well as different proportions of Sardinian to Cyprus Warblers; there were also different numbers of observations of each pair. This means that such a re-analysis needs to be treated with caution. Measurements from maps are also subject to inaccuracy, though both authors have independently measured them and obtained the same results.

If our re-analysis is correct, these apparent differences in home-range patterns suggest that Cyprus Warbler may treat Sardinian territorially, at least to some extent, as a conspecific, and may have some tendency to avoid its home-ranges, especially their centres, but that the reverse is apparently much less so with Sardinian, which appears to establish and utilise its home-ranges largely irrespective of those of Cyprus Warbler. Such behaviour would not be inconsistent with the differences in nearest neighbour distances mentioned above. Further evidence of this apparently different territorial behaviour is shown by their responses to recorded song played at the centres of their home-ranges: where the two are sympatric Cyprus Warbler responds equally strongly to conspecific and congeneric song, but Sardinian responds more strongly to conspecific (Jones 2006). Similar differences are also shown in their ratios of incidents of conspecific/interspecific aggression: 24:14 (1.7:1) for Cyprus Warbler and 29:8 (3.6:1) for Sardinian. Looking only at medium level aggression, *ie* chases, the ratios are 15:6 (2.5:1) and 24:4 (6:1) respectively (Jones 2006). The apparent differences in home-range patterns, responses to song playback and interspecific aggression may suggest that Cyprus Warbler has weaker conspecific territoriality than Sardinian, but stronger interspecific territoriality. These apparent differences in territorial behaviour between the two species may have arisen because Cyprus Warbler has apparently evolved in isolation from other breeding *Sylvia* species (apart from limited and perhaps recent sympatry with Spectacled Warbler); whereas the Sardinians have arisen from mainland populations sympatric with five other *Sylvia* species.

#### Interspecific aggression within the breeding season

Jones (2006) recorded 22 incidents of interspecific aggression during the breeding season, and we know of a further nine (Frost 1996, Pomeroy & Walsh 2002, Richardson 2011, BirdLife Cyprus database, PF, AM). These involve chivyying (a close approach or slow pursuit through vegetation, Jones 2006) or chasing, not fights, and all but one are of single incidents. In 20 the aggression came from Cyprus Warbler: these include a record of a male over three days acting aggressively towards a pair of Sardinians with young. It waited in a bush near their nest and chased the adults when they returned with food. Occasionally it entered the bush containing the nest and appeared to attack the nestlings. On the third day the young had fledged (and moved into the Cyprus Warbler's territory) and the aggressiveness continued, particularly towards the male, who was chased relentlessly (AM). In 11 interactions the aggression came from Sardinian Warbler: these include records of one chasing a Cyprus Warbler from its territory (Richardson 2011) and of a male displacing a singing male Cyprus Warbler and singing from the same perch (BirdLife Cyprus database). The last two records were both in late March (in different years), at a time when returning Cyprus Warblers may have been attempting to establish territories among already breeding Sardinians. The number of recorded incidents is low but this is not necessarily evidence of a low level of interspecific territoriality, because Jones (2006) recorded few incidents of conspecific aggression either: only 24 for Cyprus Warbler and 29 for Sardinian, though they tended to be of a higher intensity and included five fights. In passerines song is the primary means of territorial defence in deterring other males; removal and playback experiments showing that song alone can cause surrounding males to avoid a conspecific's territory (Catchpole & Slater 2008). For Cyprus and Sardinian Warblers its effect is intensified by singing and displaying from a prominent perch and, in high intensity situations, by song flights (Cramp 1992), so they may have relatively little need for overt aggression.

Jones (2006) found no evidence of a competitive mechanism during the breeding season, but her results did indicate that within the zone longest colonised by Sardinians that Cyprus Warblers had larger brood sizes of poorer quality, compared with smaller brood sizes of higher quality within the zone where there were few Sardinians. The former pattern is what might be expected if there was a relatively high adult mortality in that zone (Jones 2006).

#### Competition from Sardinian Warbler outside the breeding season

Jones' (2006) study did not cover the winter; she suggested that during that season of relative food scarcity Cyprus Warblers might be negatively impacted by food competition for fruit (berries) with overwintering Sardinian Warblers of the breeding population. The

period after breeding and before departure or overwintering, perhaps June–October, may also be of importance in this respect; especially as before their colonisation, no Sardinian Warblers would have been present during these summer and autumn months. During this period Cyprus Warblers moult and presumably either gain weight for migration or achieve/maintain good condition to face overwintering on the island. Insufficient food due to competition from Sardinian Warblers could leave them in poorer condition, resulting in higher mortality on migration or in winter.

During the breeding season both species on Cyprus eat largely the same food items (Jones 2006); and this is probably so during the post-breeding months when Cyprus Warblers in Sardinian areas will have to compete for food with a denser population of Sardinians which with their fledged young will have roughly doubled in size. This would lead to a faster depletion of food resources than in areas without Sardinians. Arthropods are important in the diet of both species (Shirihai et al 2001, Jones 2006), but arthropod biomass on Cyprus falls to a low level by late June (Jones 2006), and probably remains so throughout what are some of the hottest and driest months of the year. A large range of fruit (berries etc) is taken by Sardinian Warbler, especially in late summer, autumn and winter (Cramp 1992, Shirihai et al 2001), and also by Cyprus Warbler, whose diet was found to contain fruit more frequently than Sardinian (Jones 2006), and which often eats berries during the winter months (AM). The size of fruits/berries which can be swallowed whole (the most efficient method of consuming them) by Sylvia species depends upon their gape/bill width (Shirihai 2001): this dimension is similar in Cyprus breeding Sardinian Warblers and in Cyprus Warbler, suggesting the two probably compete closely for the same fruits. Unlike arthropods, which are thinly spread and gathered by gleaning (Jones 2006), fruiting bushes are a localised food source which can be defended. Such behaviour has been observed in the Cyprus Warbler, males defending blackberry, lentisc and other fruiting bushes in winter and driving away a female Cyprus Warbler and a male Sardinian (AM and see below). The Sardinian Warbler outside Cyprus is also known to defend winter territories containing nectar-rich flowers and/or berries against conspecifics (Cramp 1992).

Cyprus Warbler has always experienced the presence in autumn of millions of small migrant passerines (Flint & Stewart 1992), and in winter of common winter visitors like Robin *Erithacus rubecula*, Black Redstart *Phoenicurus ochruros*, Stonechat *Saxicola torquatus*, Blackcap *Sylvia atricapilla* and Chiffchaff *Phylloscopus collybita* which often share its habitat (Flint 1999, AM) and are probably food competitors. The previously large population of Sardinian winter visitors would also have been food competitors. It isn't known whether that population was smaller than the present resident population, but the former was of variable occurrence with peak numbers December–February, whereas the latter is apparently present throughout the whole of every winter in large numbers; and some winter visitors still occur as well. Thus the presence now of the residents during the winter probably represents additional competition for food.

So far almost all studies of Sardinian Warbler in Cyprus have been in the breeding season, but a seven week study late October–mid December 2012 showed that competition for territories in winter from the heavier and increasingly more numerous Sardinians may be a factor in the decline of Cyprus Warblers (AM). Observations of both species at two mainly scrub sites near Mavrokolymbos and Petra tou Romiou in Paphos District showed little interspecific territorial aggression until early November, but it became frequent thereafter. It was initiated by males and females of both species and sometimes involved prolonged, vigorous and repeated chases; both species apparently trying to establish and hold winter territories and evict the other from them. This activity increased markedly from late November.

At Mavrokolymbos on 21 November a male Cyprus Warbler, over a period of one and half hours, on at least four occasions chased a male Sardinian away from a group of fruiting bushes and up a gulley; although the chases were aggressive and vigorous the latter bird discretely returned each time after 10–15 minutes. An influx of Sardinians occurred on 24 November, and on 1 December there were simultaneous chases there involving up to eight individuals, apparently including two male Cyprus and three male Sardinian Warblers. On the same date there a female Sardinian chased a female Cyprus Warbler on at least three occasions, apparently trying to push her out of the area; similar behaviour occurred on 7 December. This female Cyprus Warbler changed, in a short time, from being easily visible and chasing the female Sardinian, to becoming difficult to see and being chased by the Sardinian. Also, on 7 December no male Cyprus Warblers were seen at this site, and the area defended by one of them on 21 November was now occupied by a male and a female Sardinian, both feeding. At Petra tou Romiou on 8 December a female Sardinian chased a male Cyprus Warbler vigorously; very soon after this he made a short display flight from his song post, but was then almost immediately displaced from the song post by the female Sardinian, who then perched on it herself. An hour earlier she had spent an unusually long period of time sitting on this same bush (AM).

Similar observations were made by AM late October–mid December 2013: the combined results for the two years show >43 instances of territorial aggression (chivvying/chasing); these included nine of Sardinian Warbler aggression against Cyprus Warbler and 18 of Cyprus Warbler against Sardinian Warbler. There were also >13 instances of Sardinian Warbler conspecific aggression (male/male chases were frequent and not all recorded) but only three such for Cyprus Warbler. These results appear to support the observations made in the breeding season in showing different territoriality between the two species, *ie* that Cyprus Warbler has weaker conspecific territoriality than Sardinian, but stronger interspecific territoriality. The observations were from a car on higher ground overlooking the sites and over the two seasons were made on 18 days with an average of *c*3 hours/ day, so *c*54 hours or seven observer days. This early winter territorial aggression seems considerably more frequent than that witnessed in spring by Jones (2006), who recorded only 75 instances in *c*1000 observer days of observations.

After breeding, territory boundaries appear to relax (Jones 2006) and it may be that autumn is the main period in the year when territories are established. This apparently begins earlier than suggested above, as Sardinians have often been seen displaying and chasing in September–October (Colin Richardson pers comm). In these months such behaviour would involve only residents, with that described above in November– December perhaps also involving winter visitors. Such competition for autumn/winter territories from Sardinian has probably increased as its colonisation has progressed and its population has become denser. This could prompt more Cyprus Warblers to migrate than otherwise would have done so and if migrant warblers are subject to higher mortality than those which remain, as has been found in other passerines, this could cause a population decline (Jones 2006).

It seems likely that migrant Cyprus Warblers would suffer high mortality: they are quite often found on limesticks in the traditional migrant bird trapping areas of southeast Cyprus (Edith Loosli pers comm) and, more significantly, many must also winter in or pass through Egypt where trapping of migrant warblers in autumn and winter is extremely common (Olivier 2000, BirdLife International 2006). If females migrate in higher numbers and return later than males they would be more exposed to trapping and to the spring peak trapping season. This may be the main reason for their lower return rate found by Jones (2006). Wintering further south than males they may also experience different trapping/hunting regimes and climates. The climate of Egypt, the Red sea and Israel is also becoming drier and warming rapidly (Met Office 2011); this may be altering the wintering environment of Cyprus Warbler. Conversely, the apparently less migratory Sardinian Warblers would be less exposed to the hazards of migration and would experience milder winters on the island, tending to reduce their mortality. A high density of the earlier breeding and apparently less migratory Sardinian Warblers might also deter some returning Cyprus Warblers from establishing territories among them in spring (Richardson 2011).

There appears to be some difference in the winter territorial behaviour of the two species. Cyprus Warbler sings quite regularly, even song flighting (*eg* Kuşkor 2001), but AM and Colin Richardson (pers comm) have never heard Sardinian Warbler singing in winter, though males fairly commonly chase other males and display. Observations by AM also suggest the Sardinians are often in pairs and that the females participate in defence of territory, but this has not been noticed with the Cyprus Warbler. A systematic study of the autumn and winter relationship and territorial behaviour of the two species would be valuable.

#### Is Sardinian Warbler exploiting its habitat more efficiently than Cyprus Warbler?

Both within and outside Sardinian areas, Cyprus Warbler chick mass declines with brood size, suggesting that the parents find it increasingly difficult to feed each chick sufficiently and that there may be a limit to their food availability (Jones 2006). But for the Sardinian, brood size has no significant effect on chick mass (Jones 2006), suggesting that they are able to feed each chick sufficiently and thus may be more efficient in exploiting their habitat. Their higher density than Cyprus Warbler in all Cyprus Warbler habitats (Pomeroy *et al* in prep) also suggests this. This might explain how Sardinian is able to breed earlier and later in the breeding season than Cyprus Warbler, when arthropod biomass is lower, and allow them to breed more successfully in other conditions of relative food scarcity, *ie* in drought years and in the more arid regions of the island; and partly explain how they are apparently more able to remain on the island in winter, a season of relative food scarcity. From an ability to exploit their habitat more efficiently would follow their greater productivity, probable lower mortality and rapid population growth.

Breeding adult Sardinians have higher mean fat scores than similar Cyprus Warblers: 19% higher for males, 15% for females (Jones 2006). This may be an indication that they are more able than Cyprus Warblers to find sufficient food for themselves, as well as their chicks, during the breeding season. However, it might also be partly a result of the higher percentage of Cyprus Warblers infected with blood parasites (Jones 2006): such infection can result in lower fat scores (Garvin *et al* 2006). On Sardinia, Sardinian Warbler is sympatric with four other *Sylvia* species, which coexist with it partly by being more specialised. There it is the most generalist species, with the widest habitat range and, with the largest territories, it is also the least efficient in exploiting its habitat (Cody & Walter 1976). On Cyprus at locations where it is sympatric with Cyprus Warbler it also has the wider habitat range, but it is Cyprus Warbler which often has larger territories and is apparently less efficient in exploiting its habitat.

## Is Cyprus Warbler especially vulnerable to competition from an invading congener because of its position in its taxon cycle as an island endemic?

Taxon cycles, an evolutionary progression through distinct and recognisable stages (Newton 2003), were originally described for species on archipelagos but can also apply to those on single islands and the mainland. On islands they typically progress from successful newly arrived colonists, indistinguishable from their mainland forms, to endemic speciation, range contraction, habitat specialisation, and final extinction.

Colonisation events between continents and islands are essentially one way, *ie* from the mainland to the island, implying a lower fitness of island endemic forms. The taxon cycle is apparently driven by competition from later colonising species with similar ecological requirements, but which do not have the reduced competitive ability of the island endemic (Newton 2003, Whittaker & Fernández-Palacios 2007). Cyprus Warbler may have reached such a stage in its taxon cycle, and for Sardinian Warbler its greater fitness than Cyprus Warbler may be primarily an ability to exploit the latter's habitats more efficiently. It is noteworthy that on some other Mediterranean islands, several *Sylvia* species co-exist with Sardinian Warbler (Shirihai *et al* 2001), whereas Cyprus Warbler apparently cannot so co-exist for long. Its position in its taxon cycle may be uniquely vulnerable to an invading competitor.

The mainland species from which Cyprus Warbler evolved is believed to be Rüppell's Warbler S. rueppelli (Flint 2001), but the former's distinct morphological differences and its endemic speciation suggest it has been isolated on Cyprus for a long time. Thus it may have progressed through its taxon cycle to a stage where it would be vulnerable to competition from an invading congener. This would lead to population decline and range contraction to relatively competitor free areas; in the case of Cyprus Warbler this might be mountain scrub and forest, which would be typical for a species at a late stage in the taxon cycle (Newton 2003, Whittaker & Fernández-Palacios 2007). The recent loss of 'Balearic' Warbler S. [sarda] balearica from Menorca following the island's colonisation by Dartford Warbler S. undata (Shirihai et al 2001), may be an example of the vulnerability of a Mediterranean island endemic Sylvia to a coloniser from the mainland. These two species are about as closely related to each other as are Cyprus and Sardinian Warblers (Shirihai et al 2001). Sardinian Warbler started breeding on Malta in the 1880s and is now very common and widespread there. It is not known to be responsible for the general and sharp decline in recent decades of the formerly very common and widespread resident Spectacled Warbler (Sultana et al 2011, Joe Sultana pers comm). However Malta is the only country in Europe where Spectacled Warbler is known to be in decline (BirdLife International 2004, Hagemijer & Blair 1997). These two species are less closely related than the previously mentioned two species pairs (Shirihai et al 2001).

It is also worthwhile to look at the example of Rüppell's Warbler and its relationship with Sardinian Warbler. Because of the former's taxonomic closeness to Cyprus Warbler, and its complementary breeding range, similar climatic and altitudinal distribution, and habitats utilised, particularly scrub and open forest, Rüppell's can be considered the mainland counterpart of Cyprus Warbler. Within its breeding range Rüppell's occurs to sea level where Sardinian is scarce or absent, but where Sardinian is common Rüppell's tends to occur on steeper slopes and at higher altitudes (Handrinos & Akriotis 1997, Shirihai et al 2001). Given the latter's restricted east Mediterranean range and the former's much wider and mainly more western range, and its recent population increase and range expansion (Cramp 1992, Hagemijer & Blair 1997), it seems likely that Rüppell's was the original species where both now occur, and that its restriction to steeper slopes and higher altitudes may be a result of competition from Sardinian Warbler. A similar range restriction to higher ground by Cyprus Warbler is apparently starting to occur in parts of western Cyprus. Within the Troodos massif air temperature decreases by 5°C per 1000 m altitude and breeding seasons for small passerines on the higher Troodos are 2–4 weeks later than on low ground (Flint & Stewart 1992). Sardinians breeding at higher altitude would presumably be similarly affected, reducing their percentage of second broods and hence their productivity. Also, the colder winters at altitude would reduce their ability to remain resident throughout the winter; tending to increase their mortality.

Both factors would reduce any competitive advantage Sardinian may have over Cyprus Warbler at higher altitudes. This might enable a population of the latter to survive in the higher mountains, though the area of land above say 1000 m is only *c*300 km<sup>2</sup>; it is also fragmented, very irregular in shape and not all of suitable habitat and thus perhaps inadequate as a refuge from the rapidly growing Sardinian population.

## **OTHER POSSIBLE REASONS FOR CYPRUS WARBLER'S DECLINE**

#### Climate change

During the last century the average annual temperature on Cyprus increased by  $c1^{\circ}$ C, with a more rapid increase of 0.015°C per annum since the 1970s (Meteorological Service 2013b); average minimum temperatures also increased, in winter by up to 1.6°C (Price *et al* 1999) and there was an increase in the frequency and duration of summer heat waves (Hadjinicolaou 2005). If Sardinian Warbler is more tolerant of higher temperatures than Cyprus Warbler (above), this warming may be less disadvantageous to it, especially later in the breeding season, when temperatures are higher.

Precipitation in all regions of Cyprus is mainly in winter; typically increasing rapidly during the autumn to a maximum in either December or January and decreasing more slowly through the spring into a long rainless summer. To cover one 'wet' season, hydrological (rainfall recording) years run from 1st October to the following 30th September. Long-term average annual rainfall has declined: the rate of decrease during the 20th century and at the beginning of the 21st averaged 1 mm/year, with most of the decline in the later years of the 20th century (Meteorological Service. 2013b). A statistical analysis of mean annual rainfall data for the hydrological years 1916/1917 to 1999/2000 (Rossel 2001) shows it can be divided into two periods: up to 1969/1970, and 1970/1971 onwards, with no significant trend in either period but with a step decrease of c80 mm (14.8%) between the two. The decrease in all regions was mainly in January and February; greatest (15-23%) in the Troodos massif and least on lower ground, with the lowest decrease (5.8%) being in northwestern Paphos District, which includes the Akamas. There was no significant difference in the seasonal distribution of mean monthly precipitation between the two periods, and little difference either between the changes in seasonal distribution in northwest Paphos District and the meteorological regions covering approximately southeastern Paphos District and southern Limassol District. During the 30 year recording period 1970/1971-1999/2000 northwestern Paphos District also had the fewest dry years and its proportions of dry, normal and wet years were closer to the norm than in any other region of the island (Rossel 2001). There is nothing in the above analysis to suggest that long-term changes in mean precipitation, either in its amount, or in its seasonal or regional distribution, were implicated in Cyprus Warbler's initial decline in the northwest.

However, Cyprus has a long history of periodic severe droughts (Thirgood 1987) which are becoming more frequent (Meteorological Service 2013b). Cyprus Warbler's absence from the most arid regions suggests it might be sensitive to such droughts, and it is noteworthy that the breeding of its congener Spectacled Warbler was seriously disrupted in the severe drought of 1972/1973 (JME Took in Bennett 1974). The decade which coincided with Sardinian Warbler's colonisation and Cyprus Warbler's initial decline, 1990/1991–1999/2000, was exceptionally dry, the driest on record, with an annual mean of only 434 mm (13.7% lower than the 1961–1990 mean) and included five years of drought, one of which was severe (Meteorological Service 2013a). Also, at Polis which is close to the Akamas and of apparently similar rainfall (Figure 2), during the 15 calendar years 1991–2005 the % decline in mean annual rainfall was greater than in regions further southeast: *ie* the decline at Polis was 16.9% (in comparison with its 1961–1990 mean) to 394 mm, whereas at Paphos the decline was 9.7%, to 387 mm; and at Limassol was 6.3%, to 407 mm

(Meteorological Service 2013a). After the 1990/1991–1999/2000 exceptionally dry decade, national mean annual rainfall in the following decade 2000/2001–2009/2010 recovered to 477 mm; close to the 1970/1971–1999/2000 30 year mean of 463 mm and conforming to Rossel's (2001) step change. Recent (2009/2010–2011/2012) mean rainfall at Polis has also recovered to a high of 551 mm (Meteorological Service 2013a).

Cyprus Warbler has clearly recovered from severe droughts in the past and, where Sardinians are absent or in low numbers, it apparently continues to do so, *eg* it is still numerous in the south (*eg* BirdLife Cyprus newsletters and database, Cypriaca recording site at www.worldbirds.org, AM) despite a severe drought there in 2007/2008 when rainfall there was only 200–300 mm and March–April temperatures were 3–5 °C above normal (Michaelides & Pashiardis 2008). Elsewhere on the island it has also been numerous where average annual rainfall has been <400 mm (Meteorological Service 2013a) *eg* Ayia Irini forest and cape Elea (Kuşkor 1999, 2003, PF) and Mazotos (*eg* Charalambides & Charalambides 1983). However, in the northwest, competition from the high density of Sardinian Warblers, which, from their presence in the more arid regions of the island may be better adapted to drier conditions, may have slowed or prevented the recovery of Cyprus Warbler populations after drought years.

It is not at all clear though that Cyprus Warbler's productivity is adversely affected by drought years. Jones (2006) recorded Cyprus (and Sardinian) Warbler productivity in Paphos District in 2004 and 2005: Cyprus Warbler's mean nestling output/pair in 2004 was 2.66 and in 2005 was 3.83 (for Sardinian Warbler the means were 3.18 and 4.49), and was higher at all three study zones (including the Akamas) in 2005. Yet rainfall had been much higher, both nationally and at Polis, in 2003/2004, *ie* 545 and 425 mm respectively, than in 2004/2005, which was a drought year with only 412 mm nationally, and at Polis only 258 mm, exceptionally low (Meteorological Service *per* Derek Pomeroy). Also, in 2005, despite the lower rainfall total, arthropod biomass was higher at all seven of Jones' study sites, including both on the Akamas, than in 2004.

These differences may have been due to the different monthly rainfall patterns within those two years. At Polis in 2003/2004, 239 mm (56% of the annual total) fell in just one month, January, which was then followed by an exceptionally dry spring: only 6 mm during March–May compared with a 1991–2005 mean of 69 mm. In fact 2003/2004 combined both the highest month's rainfall and the driest spring of any year at Polis during 1991–2005. Whereas in 2004/2005 there was no heavy winter rain and the March–May total was 47 mm (Meteorological Service *per* Derek Pomeroy). Unusually heavy winter rain, as occurred in January 2004, may reduce arthropod availability in the following breeding season (Jones 2006) and perhaps dry springs have a similar effect. Such short-term variations in rainfall pattern are difficult to relate to the long-term decline in Cyprus Warbler, but if Sardinian Warbler is more efficient in exploiting its habitat it might be less disadvantaged by them. Even if arthropod biomass remains high following low rainfall winters it is possible that fruit/berry production would be reduced and this might impact warbler survival rates during the months after breeding.

In addition to a possible increase in the source population of Sardinian Warblers (above), recent climate change on the island may be a factor in its colonisation. Species colonise islands when their recolonisation rate is higher than their extinction rate (MacArthur & Wilson 1967); less cold and less wet winters since the 1970s may have improved the overwinter survival rate of occasionally breeding Sardinians; allowing them to build up viable populations and spread. A year of drought 1989/90 and five more drought years in the following decade (above), may also have reduced possible competition from Cyprus Warbler in the critical early years of the Sardinian's colonisation; increasing temperatures during the spring and summer may also have been to the latter's advantage. Despite the

now generally less cold and less wet winters, frosts, storms and heavy rain still occur (Meteorological Service 2013a & b). In such conditions the larger body mass of Sardinians may allow them to survive better, compared with those Cyprus Warblers remaining overwinter.

By 2071–2100 rainfall on Cyprus is predicted to decrease by a further 20–35%, temperature in summer to increase by  $c5^{\circ}$ C and the number of heat wave days (>35°C) per year to increase by c2 months, compared with 1961–90 averages (Giannakopoulos et al 2010). This would probably make all of low ground too hot and dry for Cyprus Warbler, while making the higher Troodos climatically more suitable for Sardinian. On projected climate change alone, Doswald et al (2009) predict there may be few or no Cyprus Warblers breeding on Cyprus by 2071–2100 (though they do not mention the possibility of altitudinal range shift within the island), and that by then the species will have a simulated potential northward shift in its breeding range of 150–300 km, ie into southern Turkey; though they state that for an island endemic there may be constraints on such a change in distribution. Clearly, even though Cyprus Warbler occurs as a spring overshoot on the south coast of Turkey (Kirwan et al 2008), the chances of it soon colonising the mainland must be remote, especially as five other congeners already breed there, including Sardinian and the closely related Rüppell's Warbler. This difference between the numbers of breeding Sylvia species on Cyprus and in Turkey (and on some other Mediterranean islands) is probably due to biogeographical factors (Flint 2011).

#### Habitat change

In the late 19th century, 800 000 acres (35% of the island) were more or less wooded, of which half was brushwood and the remainder degraded forest or forest (Madon and Kitchener in Thirgood 1987). These areas were further degraded until about the 1950s by cutting, grubbing out, burning and by free-range goats, then began to recover as these factors were controlled and greatly reduced (Thirgood 1987). Forest and other wooded land now covers 42% of the island, of this 18.6% is forest (tree height >5 m, crown cover >10%), 13.6% is maquis (shrubs up to 5 m) and 9.5% is garrigue (subshrubs: 0.5–0.8 m). The extent of forest and other wooded land has greatly increased in the last 50 years or so due to depopulation of mountain and semi-mountainous areas resulting in regrowth of forest and scrub on the abandoned agricultural land (Thirgood 1987, Hadjikyriakou 2005, Department of Forests 2006). This abandonment continues (Ministry of Agriculture 2010) *eg* during 1980–2009 vineyards declined in area by 76% (Bruggeman *et al* 2011). Scrub on such abandoned land is preferred by Cyprus Warblers to cultivation (Symes 2006).

The exclusion of goats from the mountain state forests after 1945–1950 resulted in a rapid regeneration of the shrub understory within three or four years (Thirgood 1987). The Akamas however retained *c*3000 goats (Christodoulou 1959). Goat numbers have increased again in recent decades (Statistical Service 2012) and, although most are now tethered or penned, serious overgrazing/browsing has been a problem in some state forests, *eg* the Akamas and adjacent Peyia forests, where until recently 11 000 goats roamed (Department of Forests 2006, Ioannou 2006). According to the Department of Forests (2006) overgrazing continues to be a severe problem outside the state forests. The seven sites monitored by Jones (2006) in Paphos District, including two on the Akamas, were all regularly browsed by flocks of sheep and goats. However, there are apparently fewer on the Akamas and adjacent areas now, resulting in regrowth of vegetation (Derek Pomeroy & Colin Richardson pers comm, AM). Changes in free-range goat numbers outside forest areas and their impact on such habitats are not well documented, but the apparent reduction in numbers has probably resulted in more of the taller, denser scrub favoured by Sardinian

Warbler (Jones 2006, Ieronymidou *et al* 2012); this may have aided its spread across the island.

Habitat changes resulting from the long term exclusion of goats may not have disadvantaged Cyprus Warblers either. The village areas from which free-range goats were excluded after the Goat Law of 1913 are mapped by Thirgood (1987); by 1920 they included 140 villages and this total later grew to 283 villages, which, including the state forests, meant that free-range goats were excluded from 44% of the island's area. Across the south of the island the map in Thirgood (1987) shows such village areas to be extensive, with no apparent difference in their extent within or outside the area where Cyprus Warbler is declining. Also, in the Kyrenia range in 1999, outside the Sardinian breeding area, Cyprus Warblers were present in forest with a good understory of Arbutus and Cistus at a density of 1.3 birds/hectare (mostly singing males) and in mixed forest/open habitat (trees, many large shrubs and a good understory) at 3 birds/ha (Flint 2000). These areas were free of goats (PF) and had apparently been so for nearly 50 years (Thirgood 1987), but their absence does not appear to have produced habitats unfavourable to the Cyprus Warbler. It is also noteworthy that Cistus, a key shrub for Cyprus Warbler, thrives in the absence of goat browsing (Thirgood 1987). Thus the exclusion of goats may have resulted in some habitat changes favourable to Cyprus Warbler.

In the past *Cistus* and thorny gorse were regularly burnt off by shepherds to improve the grazing (Chapman 1949, Thirgood 1987). Deliberate burning of scrub is apparently less frequent now, though still occurs, as do occasional devastating large forest and scrub fires, *eg* 85 km<sup>2</sup> in one fire in June 1995 (Department of Forests 1996), 40 km<sup>2</sup> in one fire in June 2000 (*Cyprus Mail* 17 June 2000) and 122 km<sup>2</sup> in three fires in June/July 2007 (European Commission 2011). Large fires tend to occur in the increasing areas of forest and scrub on abandoned land, which are not subject to the integrated fire management plan of the state forests (Hadjikyriakou 2000).

*Cistus* usually regenerates quickly after fires and, in the absence of goats, larger shrubs and olive and carob will regenerate as coppice, but pine and cypress are killed by fires and re-establishment of forest may take many decades, resulting in long-term changes in habitat over wide areas (Thirgood 1987, Hadjikyriakou 2000). As Cyprus Warbler has a higher density in scrub than in forest it seems likely that it would benefit from such habitat changes, and its recolonisation of burnt areas can be rapid, *eg* 1.6 birds/ha (mostly singing males) in regenerating scrub, mostly *Cistus*, four years after a severe forest fire (Flint 2000).

Overall, the changes in cutting, burning, grazing and agriculture mentioned above seem likely to have reduced the favoured scrub habitat of Cyprus Warbler up to about the 1950s, and then increased it, so they seem unlikely to be responsible for Cyprus Warbler's decline. There have, however, been recent changes unfavourable to it. Since the later decades of the last century, some natural habitat in coastal areas and the lower hills has been cleared for tourism, retirement and second homes and urban expansion (Ministry of Agriculture 2010). This has resulted in the loss of some prime Cyprus Warbler breeding habitat, *eg* patches of coastal scrub north from Paphos to cape Drepanum (which formerly held a high density, PF) are now largely built up (AM), and ten of thirteen monitored Cyprus Warbler territories in scrub/forest near Kyrenia were lost to housing 2002–2004, as were many other areas of similar habitat along the lower northern slopes of the Kyrenia range (PF).

On some more productive land, agricultural intensification and consolidation of holdings is occurring, resulting in a reduction in fallows, enlarged field sizes and the clearance of stone walls, trees and scrub from field margins (Hellicar 2006, Panayides 2006, AM). Sardinian Warbler is perhaps less disadvantaged by these changes, in contrast to Cyprus Warbler with its stronger association with scrub (Ieronymidou *et al* 2012).

Observations at two sites with scrub in Paphos District where both species formerly bred may support this: Cyprus Warbler ceased to breed at one and declined at the other after the scrub was partly cleared or degraded, whereas Sardinian continued to breed at both (AM).

However, local scrub clearance and agricultural intensification do not seem to be the main reasons for decline of the Cyprus Warbler in Sardinian areas: the Akamas is largely unaffected by them, and so is much of northwest Paphos District, and the changes which have occurred there appear no more extensive than in similar areas further southeast where Cyprus Warbler is still numerous (Ministry of Agriculture 2005, AM, Derek Pomeroy pers comm). In this respect it is worthwhile to compare the Akamas, in particular the area below Pano Vakhines (Plate 22), with that west of Akrotiri village (Plate 34) in the south of Cyprus. Both have remarkably similar habitats: juniper, thyme Thymus capitatus, Cistus, occasional lentisc, pine and carob. Both also are on coastal promontories with generally similar climates (Akrotiri has slightly less rainfall and is south facing, whereas Pano Vakhines is north facing) and not greatly affected by changes in land use. Yet on the Akamas Cyprus Warblers are now scarce or absent, both in the breeding season and in winter, but are still numerous at Akrotiri in both seasons (BirdLife Cyprus newsletters and database, AM). The obvious difference between the two sites is the presence of a high density of Sardinians at Pano Vakhines, in both seasons, but not at Akrotiri, though Sardinians are now starting to colonise the latter area.

Recent habitat changes also seem unlikely to be responsible for the original colonisations by Sardinian Warbler. The initial small population on the Akamas occupied a wide range of habitats: mainly high maquis but also carob parkland with isolated bushes, regularly grazed/browsed by sheep, goats and donkeys; similar habitat but ungrazed and underplanted with cereals; and vegetation around human habitations, including gardens (Hawkins 1994, Frost 1995). Despite recent changes, such habitats had been common on the island for a long time (*eg* Baker 1879, Holmboe 1914, Christodoulou 1959). On the Akamas itself, there also remain extensive stretches of relatively undisturbed natural vegetation, mainly scrub/forest (Rawson *et al* 1956, Thirgood 1987). It is clear from these authors, and from McNeile (1948–1955) that much suitable breeding habitat for Sardinian Warbler has also long existed at the site of the other colonisation, in the Kantara region of the eastern Kyrenia range. Also, the Akamas was heavily browsed by goats until very recently, but the state forests of the Kyrenia range, including Kantara, were free of goats by 1950 (Thirgood 1987), so the absence of goats was apparently not a common factor in the Sardinian's colonisation of the two sites.

#### Apparent competition: predators and parasites

A species may be differentially affected by a predator or parasite in the presence of another prey species; this can produce results which appear similar to those from competition (Newton 1998). There is no evidence of differential predation of nests where Cyprus and Sardinian Warblers are sympatric (Jones 2006). However, the blood parasite infection rate in Cyprus Warbler is higher than that in Sardinian (Jones 2006) and is also high for a European passerine (Scheuerlein & Ricklefs 2004), though similar to some Blackcap populations (Merino *et al* 1997, Hauptmanová *et al* 2006). Overall, 50% (11 of 22) of Cyprus Warblers were infected compared with only 25% (9 of 36) of Sardinians. The greatest difference was on the Akamas, where the rates were 67% (2 of 3) and 11% (1 of 9) respectively; this may be evidence of apparent competition (Jones 2006). The Cyprus Warbler sample is very small though, and it is possible that the Akamas may differ from the two other zones monitored in that survey; perhaps in its peninsular climate, or by having fewer insect vectors or more alternative host species. Also, blood parasites may

be acquired by migratory species on migration and in winter (Marzal 2012), and higher temperatures can lead to a higher prevalence of them (Zamora-Vilchis *et al* 2012). This might explain the higher levels of infection in the Cyprus Warbler: temperatures in its African wintering areas are 6–10°C higher than in western Cyprus (Meteorological Service 2013a, www.climatemps.com). Blood parasite infections can increase mortality in wild birds (Marzal 2012). If Cyprus Warblers in Sardinian areas are in poorer condition for any reason, such as increased competition for food and territories, this might make them more vulnerable to blood parasites.

## CONCLUSIONS

The Cyprus Warbler is faced with a rapidly warming climate, reduced rainfall, increasingly frequent droughts, a higher rate of blood parasite infection than Sardinian Warbler and changing land use. An apparently larger proportion of its population than that of Sardinian Warbler is also faced with the hazards of migration. Nevertheless, it remains numerous except where Sardinian Warbler breeding populations are dense; from this it seems very likely that it is being displaced by the Sardinian Warbler.

We are not able to prove a causal link, but the differences in response to song playback, in territorial aggression and (in our opinion) patterns in the distribution of home ranges and their centres, suggest that the Cyprus Warbler may have stronger interspecific territoriality than Sardinian Warbler and may treat the latter territorially, at least to some extent, as a conspecific, and may have some tendency to avoid Sardinian Warbler home ranges and especially their centres. If the last is so it may be one of the main reasons for Cyprus Warbler's decline. Interspecific aggression from Sardinian Warbler, especially where its population density is high, might also reduce Cyprus Warbler's ability to establish breeding territories.

Contributory and interlinked factors may be competition from Sardinian Warbler for food and for autumn/winter territories, as well as the latter's apparently more efficient exploitation of its habitat, higher productivity, larger size, apparently less migratory nature and lower blood parasite infection rate. Sardinian Warbler's apparently better tolerance of high temperatures and aridity may mean that it is less disadvantaged by the changing climate on the island than Cyprus Warbler; this may have aided its spread across the island. Its colonisation seems at least partly due to climate change; if this is so then Cyprus Warbler may be considered an indirect casualty of such climate change. Changes in land use are a factor in some local Cyprus Warbler declines. Cyprus Warbler may also have reached a stage in its taxon cycle where it is vulnerable to a fitter invading congener from the mainland.

Most examples of apparent competitive displacement in birds have proved difficult to confirm beyond doubt. This is hardly surprising because testing alternative explanations for the patterns is not easy, and anyway one can never be sure that all possible explanations have been identified. Nevertheless it may be unwise to reject compelling circumstantial evidence just because it cannot be checked by empirical tests (Newton 1998). In this case, if the increase and spread of Sardinian Warbler and the decline of Cyprus Warbler continue at their present rates, there may be no Cyprus Warblers well before the end of this century. Currently the conservation status of Cyprus Warbler is IUCN red list least-concern (BirdLife International 2012) and non-SPEC (species of European conservation concern) provisionally secure (BirdLife International 2004). However, because of its continuing and serious decline we believe that its conservation status should be re-evaluated. Given the estimated population decline of >30% in the last ten years, a likely further population decline of 30% or more within the next ten years, the decline in its area of occupancy within its small geographic range, and its solely European breeding range; reassessments

as vulnerable (IUCN red list) and SPEC 1 European species of global conservation concern, might be more appropriate.

Both of which should lead to a species action plan (www.iucn.org) for the Cyprus Warbler. We suggest this should most importantly include island-wide annual census and habitat surveys, similar to those carried out in the southwest (Pomeroy & Walsh 2000, 2002, 2006, Pomeroy *et al* in prep), in order to detect and monitor future population changes. Such surveys might also reveal if there are any areas where Cyprus Warbler is not declining in the presence of Sardinians (we are not aware of any such areas), and help to determine what the characteristics of those areas might be. In addition to transects, such surveys could also include point counts to more accurately determine the numbers and density of warblers present, and hence enable a more accurate estimation of the total population. Finally, a study of the foraging behaviour of the two species and of the fruiting bushes used by them at different seasons; any differences found might enable habitat manipulation in selected areas to make them more suitable for Cyprus Warbler and less so for Sardinian, if the former's decline becomes critical.

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#### Appendix I. CYPRUS WARBLER POPULATION ESTIMATES

1994 estimate: 4000–8000 pairs (Tucker & Heath 1994). This was apparently subjective and was later believed to have been too low (eg Flint 2000, BirdLife International 2004). Because of this estimate the species was given a Conservation Status of SPEC 2.

1998 estimate:  $c100\ 000\ pairs$  (Snow & Perrins 1998). Provided by Peter Stewart and PF, this was an approximation based on a possible mean density of 0.5 pairs/ha in suitable habitats, estimated to be c20% of the island's area (PF). Both density and habitat area are now known to be higher (see below).

2000 estimate: 180 000 pairs (Flint 2000). This was based on a mean density of 0.97 pairs/ha, obtained from point counts in natural habitats (scrub, scrub/forest and forest) in the north of the island, assumed to occur across 20% of the island's area; it did not include an addition for birds breeding in agricultural habitats nor a reduction for the lower densities where Sardinian Warblers were present. Because of the high population figure, reassessment of the species' Conservation Status as SPEC 4 was suggested (Flint 2000). For reasons explained there the densities obtained were believed to be too low; a later census based on refined methods gave a mean density of 1.7 males/ha (Flint 2003).

2003 estimate: 120 000–280 000 pairs (Whaley & Dawes 2003). Based on their extensive atlas surveys, the authors estimated 2000 to 3000 km<sup>2</sup> of suitable habitat in the south of the island (from data in Pomeroy & Walsh 2006 and Ministry of Agriculture 2005 this estimate seems reasonable), with densities of up to 100 singing males/km<sup>2</sup>, and gave an estimated population range there of 80 000 to 200 000 pairs. They also included a figure (from PF) of 40 000 to 80 000 pairs for the north of the island.

2004 estimate: 70 000–140 000 pairs (BirdLife International 2004). The nine contributors included David Whaley, Judy Dawes and PF but although recent high surveys were mentioned in the text, these were apparently subjectively reduced to produce the relatively low published population range.

There is a clear difference between the 2000/2003 estimates and that of 2004; to determine which is likely to be the most reliable the population then can be estimated by two other methods. Pomeroy & Walsh (2006), from annual census counts, estimated the population in Paphos District in 2001–2004 as 28 000 pairs. They also provided mean densities in each habitat type, depending on whether Sardinians were present or absent, together with the areas of each habitat type in the district. From these it can be calculated that, if no Sardinians had been present, the potential population for the district would have been 56 000 pairs. A relatively modest total when compared with the present estimated 109 000–152 000 pairs of Sardinian Warblers there (Pomeroy et *d* in prep). Paphos District represents

only 15% of the island's area, though it contains about a quarter of the climatically suitable and prime Cyprus Warbler habitat in the island (estimated from Ministry of Agriculture 2005). From this it can be calculated that the area of suitable habitat outside Paphos District may have held 168 000 pairs. Sardinians were believed to then be absent from the large areas of Cyprus Warbler habitat in the south of the island outside Paphos District, but a reduction of say 10 000 or 20 000 pairs should be made to allow for possibly lower densities in the then large Sardinian populated area in the north. Combined with the total of 28 000 for Paphos District this would give a whole island figure for 2001–4 of 176 000–186 000 pairs calculated by this method.

Alternatively, it is possible to extend Pomeroy and Walsh's (2006) method to the whole island, ie to multiply their mean densities (pairs/km<sup>2</sup>) in each habitat type by the area (km<sup>2</sup>) of each habitat type in the island (from Ministry of Agriculture 2005). This would give: for scrub,  $133.9 \times 1877 = 250\ 000\ pairs$ ; for forest,  $22 \times 1546 = 34\ 000\ pairs$ ; and for permanent crops  $31 \times 357 = 11\ 000\ pairs$ . The total of 295 000 would have to be reduced as above to allow for lower densities in Sardinian areas, giving 247 000–257 000 pairs. With further reductions for absence from the higher Troodos and from the relatively small areas of scrub on the central plain the final total would probably be at least 200 000 pairs. These two recalculated estimates, arrived at by different means, are reasonably close to that of 2000 and to the mid-range of that of 2003, and suggest that the 2004 estimate is too low.

2013 estimate: 60 000–120 000 pairs (BirdLife Cyprus, not yet published). This population range is based on data sets derived from census counts and upon a lot of expert opinion (Martin Hellicar pers comm). Compared with the 2004 estimate it is 70% higher to 57% lower, with a reduction in the means of 14%. Compared with the 2000 estimate it is at least 33% lower; with the 2003 estimate 0–79% lower; and with the two recalculated 2001–4 estimates at least 32% lower. The different methods and assumptions used to obtain these estimates mean that such comparisons cannot be accurate, though the large population decline suggested by the last three would fit with the known large decline in the southwest of the island within the same period and a perceived decline in parts of the north.