Why has only one wheatear *Oenanthe* species colonised Cyprus?

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Cyprus has only one third as many avian breeding species as nearby Turkey; Flint & Stewart (1992) concluded that the reason for this, and for the absence of many apparently suitable breeding species, was the limitations of island ecology; and that adaptation to island conditions enables fewer species with broader niches to exclude a greater number of specialists. They cited the endemic breeding Cyprus Wheatear *Oenanthe cypriaca* [hereafter *cypriaca*] as an example, which occupies the habitats on Cyprus that in Turkey are occupied by Northern *O. oenanthe*, Black-eared *O. hispanica* (of the subspecies *melanoleuca*), Isabelline *O. isabellina* and Finsch’s Wheatears *O. finschii* [hereafter *oenanthe, melanoleuca, isabellina* and *finschii*], and that the latter four wheatears all commonly occur on Cyprus but have never been known to breed. However, it has recently been implied that competition from *cypriaca* is not the reason for the absence of *melanoleuca, oenanthe* and *isabellina*, as they have different habitat preferences from *cypriaca* and in nearby countries up to four wheatear species coexist (Randler & Crabtree 2010). Of the other large Mediterranean islands, Corsica, Sardinia and Sicily have one breeding wheatear compared with two on the nearest mainland, and Crete, which is quite similar to Cyprus in area, distance from the mainland, latitude and east Mediterranean location, has two, the same as the nearest mainland (Hagemeijer & Blair 1997). So, why does Cyprus have only one when four breed on the nearest mainland?

**FACTORS IMPORTANT TO ISLAND COLONISATION**

Factors important to island colonisation by birds include climate, habitat and food; the distance from the mainland; the numbers of colonists and of subsequent colonists to reinforce earlier ones; breeding success; population growth rate, fluctuations and ultimate size achievable; predation and parasites; and competition with established species, which is regarded as a major factor in preventing many potential colonists from establishing (Newton 2003). A combination of several of these factors is probably responsible for the absence of these other wheatear species from Cyprus, though which factors, and their relative importance, may vary between the species.

Distributions could also arise from chance: those species colonising first developing adaptations to island conditions which enable them to exclude subsequent colonists (Newton 2003), and the more an island differs from the mainland the greater those adaptations may be. This may be so on Cyprus: one of only two Endemic Bird Areas within Europe (Stattersfield et al 1998) with two of the three Mediterranean island endemics (Svensson et al 2009), suggesting either that it has been isolated longer, which is apparently not so (Blondel & Aronson 1999) or that it differs more from the mainland than do the other islands.

Given their distributions in neighbouring countries (Porter & Aspinall 2010), *oenanthe* and *melanoleuca* may well have bred occasionally in the past, and possibly the others also, but have clearly failed to establish populations large enough to be viable in the long term. That is the main problem facing potential island colonists: their low numbers rendering an initial breeding population liable to rapid extinction from random variation in numbers or catastrophe; and if population growth and recolonisation rate are too low to compensate for extinctions, a species may never colonise, however many times it attempts to do so (Newton 2003).
Climate
Huntley et al (2007) examined the distribution of species in Europe in relation to climate and found that high temperatures and aridity often influence their southern breeding boundaries. Those authors used annual temperature sum above 5°C in degree days (GDD5) to represent temperature, and annual ratio of actual to potential evapotranspiration (AET/PET) for aridity, the lower the ratio the drier the climate. On Cyprus GDD5 is c.5000–5600 degree days at low altitude, c.4400 at 640 m in the Troodos massif and c.2900 at 1380 m; and AET/PET is 0.19–0.20 in the southeast, 0.23–0.28 in the coastal south and southwest, 0.43 at 640 m and 0.57 at 1380 m (calculated from data in Met Service 2010b, Water Dev Dept 2010, 2011). Precipitation varies greatly from year to year and droughts are frequent: during 1901/02 to 2007/08 there were 13 years of drought and 7 years of severe drought, sometimes consecutively (Met Service 2010b); severe heat waves also occur (Hadjinicolaou 2005). Such conditions have caused breeding failure of small passerines (Bennett 1975) and could be catastrophic to a small establishing population. The island is also becoming hotter and more arid. Average annual temperature increased by c.1°C during the last century, approximately twice the global increase (Price et al 1999), with a more rapid increase of 0.015°C per annum since the 1970s (Met Service 2010a). Average annual rainfall decreased by c.125 mm (21%) during 1916–2008, with a more rapid decrease again in the later decades (Pashiardis & Michaelides 2008).

Northern Wheatear (Plate 1) is a very common spring migrant mainly mid–late March to mid April (Flint & Stewart 1992, Richardson 2010). It over-summered and may have bred in 1975 (Bennett 1977) and two or three remained into mid–late June 1991 (Bennett 1994). The latitude of the southern boundary of its Eurasian breeding range lies almost entirely north of Cyprus (Cramp 1988); in southern Europe its distribution becomes patchy where temperature or aridity are high (Huntley et al 2007), and in southern Turkey it breeds above 1100 m (Kirwan et al 2008). Thus only the island’s higher mountains might have suitable climate for it to breed, though they are mostly well vegetated or forested and have breeding cypriaca, and oenanthe rarely competes with congeners while breeding (Cramp 1988).

Black-eared Wheatear subspecies melanoleuca (Plates 2 & 3) is a fairly common spring migrant with peak numbers late March–mid April (Flint & Stewart 1992, Richardson 2010). There are several June records and it probably bred in 2009 (Randler & Crabtree 2010), though in May 2010 none were at the 2009 probable breeding site (Alan Crabtree per Derek Pomeroy pers comm). Although some authors consider it might be a scarce

Plate 1. Northern Wheatear Oenanthe oenanthe male, Pano Arodes, Cyprus, 1 April 2004. © David Nye

regular breeder, there are no records of over-summering and it was not found breeding during fieldwork for the Cyprus Breeding Birds Atlas 1995–2002, whose authors commented on its absence, and that of *oenanthe*, *isabellina* and *finschii*, as breeding birds (Whaley & Dawes 2003). Also, Derek Pomeroy (pers comm) found only *cypriaca* in breeding census counts in Pafos district 1997–2011, as did I during widespread breeding surveys in northern Cyprus 1998–2004. In Europe it breeds where GDD5 exceeds 2000 degree days and AET/PET is 0.8 or less (Huntley *et al* 2007). It also breeds on the mainland adjacent to Cyprus (Porter & Aspinall 2010) and in Israel, mainly where annual rainfall is more than 400 mm (Shirihai 1996), so the hills and mountains of Cyprus should be climatically suitable. Its probable breeding in 2009 followed a year of normal rainfall after four years of drought/severe drought (Met Service 2010b) during which *cypriaca* numbers apparently fell (Pomeroy 2009). Perhaps the reduced competition and better conditions encouraged *melanoleuca* to attempt to breed.

**Isabelline Wheatear** (Plate 4) is a common early spring migrant mainly March–early April with no records after mid May nor of breeding (Flint & Stewart 1992, Richardson 2010). It breeds in southeast Europe where GDD5 is 2200–3200 degree days, and AET/PET is 0.8–0.5 (Huntley *et al* 2007), and within Asia almost entirely at higher latitudes than Cyprus (Cramp 1988), where maximum summer temperatures are lower (de Pauw 2008), suggesting that only the higher mountains of Cyprus may be climatically suitable for it to breed.

**Finsch’s Wheatear** (Plate 5) is a locally common winter visitor mainly November–February to open rocky slopes below 600 m; usually all have left by mid–late March, with no records after early May nor of breeding (Flint & Stewart 1992, Richardson 2010). Its Middle Eastern breeding range (Porter & Aspinall 2010) lies mainly north of the latitude of Cyprus, has lower mean annual

temperatures and lower maximum summer temperatures and is mainly less arid (de Pauw 2008). Also it breeds in high mountain ranges in Syria and Lebanon (Shirihai 1996), and largely above 500 m in Turkey (Kirwan et al. 2008). Thus on Cyprus only the higher mountains might be climatically suitable for it to breed.

**Cyprus Wheatear** (Plates 6 & 7) is a summer visitor arriving mainly mid–late March into April (Flint & Stewart 1992, Richardson 2010); females on average arrive c8 days later than males (Horner & Hubbard 1982). It is one of the most numerous bird species on the island with a population of c90 000–180 000 pairs (BirdLife International 2004). Numbers apparently reduce on low ground in summer and it is believed by some that an altitudinal movement takes place at this time (Flint & Stewart 1992). In the hottest and driest areas in summer it seems most frequent near fresh water (Kuşkor 1999–2003). It is the smallest West Palearctic wheatear (Cramp 1988), averaging 15.6 g for March–May males; on Cyprus March–May males of *melanoleuca* are c7% heavier, and of *oenanthe* c50% heavier as are unsexed *isabellina* (Cozens 1995, Brimmell et al. 1998). April–June Turkish *finschii* are c75% heavier than *cypriaca* (Cramp 1988). The low weight of *cypriaca* may be an adaptation to the insular climate and ecology of Cyprus, and to its latitude (Flint 1995, 2001), enabling it to better withstand the summer heat. Overwintering, first recorded 1978/9 (Flint & Stewart 1992), is becoming more frequent, with one or two birds in ten winters since 1993 (Colin Richardson pers comm).

**Habitat**

Cyprus Wheatear males require high song posts *eg* trees, bushes, boulders, higher ground, buildings, overhead wires (Flint & Stewart 1983, Oliver 1990). With that proviso it has an extremely wide habitat range (Plates 8–20), *eg* the only bird species (out of 34) found in every stage of vegetation from grassland to woodland (Massa & Catalisano 1987), and the only bird species (out of 33) encountered in all 40 transects in grassland, matorral, maquis, forest, arable land, orchards and vineyards (Pomeroy 2004). It is most common in the hills and mountains, especially on rough open ground with scattered trees, in open forest and in villages (Flint & Stewart 1992, Small 1994, Derek Pomeroy pers comm), but is scarce or absent in areas of dense bush/tree cover (Randler et al. 2010b). It also breeds in industrial and suburban areas, on boulder-strewn storm beaches, burnt and cleared previously forested areas, and rocky treeless ridges and hills with or without a few scattered low
shrubs in the central lowlands and badlands (Kuşkor 1999–2003). Some also breed on the open rocky slopes used by wintering finschii (Neophytou et al 1972, Flint 2000b, Alison McArthur pers comm). It is noteworthy that apparently similar wintering habitats of finschii in Jordan and Israel are occupied in summer by breeding melanoleuca (Andrews 1995, Shirihai 1996). Around coasts cypriaca is often common where the hills reach the sea and there are cliffs, or where it is rocky, but on coastal plains near Pafos and Kyrenia it is scarce or absent (Colin Richardson pers comm, PF pers obs).

These habitats of cypriaca apparently include those of breeding O. hispanica (Cramp 1988, Panov 2005), and those of melanoleuca in Greece, Turkey, Jordan and Israel (Handrinos & Akriotis 1997, Kirwan et al 2008, Andrews 1995, Shirihai 1996); and those in Turkey of oenanthe and finschii, and some of those of isabellina (Kirwan et al 2008, Roselaar 1995). Although the habitats appear similar the comparisons are based on subjective descriptions, and there are variations in latitude, climate and vegetation species composition between countries eg Cyprus has 128 endemic plants including the locally abundant Golden Oak Quercus alnifolia (Pantelas et al 1993). On Cyprus suitable habitats for breeding oenanthe are limited climatically, and those for isabellina and finschii very limited. Also, isabellina usually nests in the tunnels of burrowing rodents, which are important in determining its distribution (Panov 2005), and commonly does so in Turkey and Israel (Kirwan et al 2008, Shirihai 1996), and such mammals are absent from Cyprus (Kryštufek & Vohralík 2001).

Although Randler & Crabtree (2010) stated that cypriaca has different habitat preferences from melanoleuca, oenanthe and isabellina, the survey they cited (Randler et al 2010b) compared breeding cypriaca with migrant melanoleuca and oenanthe (it did not include isabellina); and found 40% overlap in habitat preferences between cypriaca and melanoleuca, and 25% between cypriaca and oenanthe. However, as is well known, migrants often occur in habitats in which they do not breed, eg in Israel, migrant melanoleuca occurs widely in open habitats with sparse low vegetation, but breeds in rocky hills/mountains within bushy wadis with scattered low trees (Shirihai 1996). On Cyprus migrants tend to concentrate near coasts where habitats may differ from those in the hills and mountains. Also, Randler et al (2010b) assessed cypriaca habitats within 100 m radius but those of migrants within 25 m, but Mediterranean habitats are often a fine mosaic, varying greatly over short distances in seemingly unlimited variations (Blondel & Aronson 1999, Rackham & Moody 1996), and this is the case on Cyprus (Flint 2000a); so using 100 m for migrants as well might have shown fewer differences.
The habitats occupied by a species often vary between the mainland and islands, and between islands, depending on which other species are present (Lack 1969). In Greece *oenanthe* breeds in open habitats with sparse low vegetation at medium and high altitudes, and is largely replaced by *melanoleuca* below 500 m. But on the eastern Aegean islands it breeds commonly down to sea level, and on Limnos (where *melanoleuca* is rare) it reaches a remarkably high density and also breeds in the villages and in the town, perching on buildings (Handrinos & Akriotis 1997). In this respect it appears similar to *cypriaca* on Cyprus.

**Food**

Wheatears exploit a wide variety and size range of prey, and even smaller wheatears are able to deal with large invertebrates (Panov 2005), in the case of *cypriaca*, praying mantises and large butterflies (Cant & Flint 2003) and even a small lizard (Flint & Stewart 1992). Thus despite the size differences, *cypriaca* would probably compete with the potential colonists for food, and especially so with *melanoleuca*, which is closest in size, morphology, foraging behaviour and habitat preference (Panov 2005, Randler *et al* 2010b). Also, male and female *cypriaca* differ in foraging behaviour: males more often use aerial sallies and pounce from higher perches while females more often forage on the ground (Randler *et al* 2010a); this may enable pairs to exploit their territories more thoroughly.

**Distance from the mainland and the numbers of colonists**

Islands closer to the mainland tend to have more species and those more distant fewer (MacArthur & Wilson 1967) and this seems to apply to the Mediterranean islands (Lo Valvo & Massa in Iapichino & Massa 1989). However, *oenanthe* breeds on the other large Mediterranean islands which are as distant from the mainland as Cyprus, as does *melanoleuca* on Crete (Hagemeijer & Blair 1997), so distance from the mainland alone can not explain their absence from Cyprus. Nevertheless, the distance of Cyprus from the mainland may be reducing their immigration rates and thus their chances of successfully colonising; *i.e.* were Cyprus very close to the mainland, birds from the mainland might often seek territories on the island, but with the mainland 72–110 km distant to the north and 105–180 km to the east this seems unlikely. In this respect, it is worthwhile to compare Cyprus with Lesvos, which is very close to the mainland, both to the north and to the east. Although only one sixth of the area of Cyprus it has three migrant breeding wheatears and...
one occasional breeder, as well as nine migrant breeding warblers (Brooks 1998) compared with three on Cyprus.

So it seems that on Cyprus potential colonists have to be recruited from migrants passing through in spring, but migrants arriving on an island where they do not breed are usually in a migratory state, programmed to continue their journeys (Newton 2003). This appears to be so on Cyprus, where although migrant wheatears occasionally sing, they generally do not show pre-breeding behaviour, tend to concentrate near the arrival and departure coasts and on the Karpas peninsula, rather than inland, and pass relatively quickly (Flint & Stewart 1992, PF pers obs). They may be considered transients, not potential colonists, and occasional birds which linger are apparently mostly lone laggard migrants. The potential breeding habitats of *melanoleuca* are also widespread, reducing the chances of migrants finding and reinforcing any existing small breeding population.

**Breeding success; population growth, fluctuations and ultimate size achievable**

There are no published studies of breeding success in *cypriaca*. The breeding records in the Cyprus bird reports mostly involve young at or near fledging or nests which are not followed up, but do show that, in addition to predation, nests may be lost to heavy rain and to human activity. The clutch sizes of *melanoleuca* in Turkey (Kirwan et al 2008) and of *cypriaca* (Flint & Stewart 1992) are similar. However, *melanoleuca* is usually single-brooded (Panov 2005), and is so in Israel (Shirihai 1996), and all records from Turkey refer to first broods (Kirwan et al 2008); whereas *cypriaca* is double-brooded (Bourne et al 1964) or may often be so (Sadler 1994, 1995, Cant & Flint 2003). Multiple broods of the latter are also indicated by its long breeding season: mainly April–June, but there are also records from lower altitudes of nestlings in July (Flint & Stewart 1992), of family parties late August (Richardson 2009) and nestlings once late September (Sanders 2000).

The range of population fluctuations will depend largely on other factors discussed here e.g. extremes of climate, and on losses on migration and in winter in Africa. The ultimate population size achievable for *melanoleuca* on Cyprus is probably potentially large, but for *oenanthe* would be limited by climate, habitat and altitude, and for *isabellina* and *finschii* very limited.

**Predators and parasites**

Mammalian nest predators on Cyprus include rats, foxes and hedgehogs, and feral dogs and cats, but not mustelids (Kryštufek & Vohralík 2001), which prey on wheatear nests.
Snakes and large lizards predate wheatear nests in warm climates (Panov 2005); both are extremely common on Cyprus where they are apparently significant nest predators (Took 1972, Bennett 1977, Flint & Stewart 1992). Nest parasites may cause losses of wheatear nestlings (Panov 2005), but I am not aware of any information from Cyprus. Ants may also cause losses of wheatear nestlings (Cramp 1988) and this has happened on Cyprus (Lucas 1974), where ants are extremely common (PF pers obs). Avian nest predators include the common Little Owl *Athene noctua* and five corvids, of which Magpie *Pica pica* and Hooded Crow *Corvus cornix* are common and widespread (Richardson 2010). Breeding *cypriaca* are exceptionally wary: Belcher (1929) described it as “a bird whose skill in outwitting the would-be examiner of its home is beyond belief until experienced”; Ashton-Johnson (1961) also found it extremely shy and suspicious and difficult to watch back to the nest, a comment he made about no other breeding species on Cyprus. Such behaviour suggests that *cypriaca* is under fairly intense pressure from nest predators. Even if a colonising wheatear was as wary it would presumably be liable to similar pressure, reducing its population growth rate and thus its chances of successfully colonising. On Cyprus, trapping of small birds is widespread, mainly in autumn but also in spring, and wheatears are vulnerable eg limed birds examined at Paralimni (c30–50% of the village catch) in spring 1968 included 477 *oenanthe*, 371 *cypriaca*, 181 *isabellina*, 96 *melanoleuca* and 8 *finschii* (Horner & Hubbard 1982).

**Competition**

The total number of breeding landbird species on an island is believed to be a dynamic balance between colonisations and extinctions. As the total increases the colonisation rate will decrease because of increased competition from the already established species and there will also be fewer potential colonist species. At the same time the extinction rate will increase because of a larger number of competitors and decreasing average population sizes, until equilibrium is reached. The total then remains approximately constant over time and is largely dependent on island area and distance from the mainland (MacArthur & Wilson 1967). Islands near but not yet at equilibrium are liable to be strongly influenced by the same qualities (Schoener 2010). Cyprus is a continental island, which can be expected to be at or near equilibrium most of the time (MacArthur & Wilson 1967) and, until recent anthropogenic and climate-change related increases, the species total had remained remarkably constant for nearly a century (Flint in prep). Also, on Mediterranean islands,
a c13 times increase in area doubles the species total (Flint & Stewart 1992) and species/area graphs indicate that for its area Cyprus might be expected to hold c70–80 breeding species (Iapichino & Massa 1989, Flint & Stewart 1992), which is close to the current total of 81 (BirdLife Cyprus 2011). For these reasons it seems probable that the island is at or near equilibrium, where competition from established species means almost no new colonists will succeed (MacArthur & Wilson 1967). This appears to be so on Cyprus, where at least 11 other small passerines have bred, or possibly/probably bred in the past, some of them several times, without colonising (Flint & Stewart 1992, BirdLife Cyprus 2011).

Nevertheless, since the 1990s, Blackbird Turdus merula and Sardinian Warbler Sylvia melanocephala have successfully colonised (Richardson 2010), as has the Greenfinch Carduelis chloris since the 1970s (Flint & Stewart 1992), and the latter two are now among the most numerous species on the island. All were previously short distance migrants and winter visitors and are now resident (Flint & Stewart 1992, Richardson 2010) and none was a trans-Saharan migrant like oenanthe, melanoleuca or isabellina. All have also spread in nearby countries (Flint in prep), a characteristic of successful island colonists (Newton 2003) and not shown by oenanthe, melanoleuca or isabellina. Climate change can affect equilibrium totals (Schoener 2010) and these successful colonisations are probably at least partly due to the rapid warming and drying of the island’s climate, which may be improving the survival of resident passerines in the now less cold and less wet winters, and which appears to be favouring resident over migrant breeders (Flint in prep).

Although Sardinian Warbler is believed to be not very closely related to the endemic and partly migratory Cyprus Warbler Sylvia melanothorax (Shirihai et al 2001, Flint 2001), it is noteworthy that the latter is declining where the former continues its spread (Pomeroy 2009). Circumstantial evidence suggests competition from Sardinian is a likely factor in the decline of Cyprus Warbler, though an extensive study (Jones 2006) found no evidence for a competitive mechanism.

Phylogenetic analysis indicates that Pied Wheatear O. pleschanka and Black-eared Wheatear O. hispanica appear to be conspecific, forming a superspecies with cypriaca with very low inter-specific divergence (Outlaw et al 2010). The boundary between O. pleschanka and O. hispanica may once have been further west than it is today (Flint 1995); O. hispanica is assumed to have spread eastwards from the west Mediterranean into southeast Europe and the Middle East (Panov 2005), but leaving Cyprus as a conspicuous gap in its east Mediterranean breeding range. Given their now complementary breeding
ranges (Porter & Aspinall 2010) and close taxonomic relationship, *cypriaca* appears to be the biogeographical counterpart of *melanoleuca* on Cyprus but adapted to the island’s environment, with its presence the main reason for the absence of *melanoleuca*.

Because of their taxonomic closeness, hybridisation between *cypriaca* and *melanoleuca* is a possibility (Randler & Crabtree 2010). But so far, apart from a male with a ‘black head’ (Richardson 2009), there are no records in the Cyprus literature and no recent reports (Colin Richardson pers comm) of unusual or aberrant plumage in *cypriaca*, nor of the plumage morphs (Panov 2005) which might be expected were hybridisation to occur, although they have been looked for.

**PRESENT AND POSSIBLE FUTURE CHANGES IN STATUS**

Since 2004 *cypriaca* numbers have declined by c60% in Pafos district; the decline apparently starting before the full effects of the 2004–2008 drought and continuing after it. The species is also no longer recorded in all transects there as it was previously, with the decline most apparent in arable habitats (Pomeroy 2009 and pers comm). It has also ceased to breed in some areas of the coastal strip north and northwest of Pafos (Alison McArthur pers comm). These declines suggest that *cypriaca* may be withdrawing from marginal habitats, at least in Pafos district. There are still good numbers in many areas though, eg Mavrokolymbos dam, Troodos, Pissouri bay and Lefkara (Colin Richardson pers comm), and population trends since 2006 for the whole island are not yet clear (Derek Pomeroy pers comm). There may also be a longer-term decline: Christensen (1974) found an extremely high density within the Kyrenia mountain range, with often 4 or 5 singing males heard from one point; but in those mountains in May 1999 and 2001, of 51 points in open forest, I recorded 4 birds at only 2 points and 5 birds at none, and of 45 points in open habitats: 4 birds at 5 points and 5 birds at only 1 (unpublished field data for Flint 2000a, 2003).

Hotter and drier breeding seasons may be reducing breeding success and the frequency of second broods. This may be exacerbated by the fact that the species is apparently not arriving earlier in response to the warming climate: the mean first arrival date per decade in the Cyprus bird reports 1970–2009 (excluding January–mid February possible overwintering birds) remaining unchanged at 5 March despite increasing observer coverage. Hotter breeding seasons may also have made reptiles active earlier, perhaps resulting in increased nest predation. Agricultural abandonment and intensification (Hellicar 2004) may also be factors. Cessation of grazing locally in the coastal strip north and northwest of Pafos has resulted in greater growth of grasses and other vegetation rendering the habitat less suitable, and in some such areas former *cypriaca* territories are now empty. The recent ploughing of open stony areas for cereals, again making the habitat less suitable, may also be a factor in local declines (Alison McArthur pers comm).

In recent decades several resident passerines, notably Sardinian Warbler and Greenfinch, which share some of the habitats of *cypriaca* have greatly increased; although they seem unlikely competitors they exploit some of the same food resources as *cypriaca* (Cramp 1988,
In autumn, departing *cypriaca* are very common along the south coast (Flint & Stewart 1992) where trapping has increased (Hellicar 2011). Also, *cypriaca* winters in southern Sudan and Ethiopia (Cramp 1988), where rising temperatures, increasingly unreliable rainfall, and rapid increases in human population and grazing animal numbers are causing severe habitat degradation, including deforestation, loss of wooded grassland and soil erosion (UNEP 2007, Oxfam International 2010). Trapping/hunting of small birds is common in north and east Africa and the Nile valley, and is almost certainly increasing (Contesso 2009). If there is a continuing decline in *cypriaca* this would reduce competition and improve the chances of other wheatears colonising, though factors adversely affecting *cypriaca* would probably affect them also.

**SUMMARY**

Given their complementary breeding ranges, and closeness in taxonomy, size, morphology, foraging behaviour and habitat preferences; competition from *cypriaca* which appears to be better adapted to the island’s habitats and climate, intensified by the effects of island biogeography, is probably the main reason for the failure of *melanoleuca* to colonise. Secondary reasons may be distance from the mainland/low numbers of colonists, extremes of climate, possible lower population growth rate than *cypriaca*, population fluctuations and predation. The reasons for *oenanthe* may be generally similar, though with less emphasis on competition and more on unsuitable climate and limited habitat. The main reason for the failure of *isabellina* and *finschii* to colonise Cyprus is probably very limited climatically suitable habitat, and for the former also shortage of nest sites.

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Sandgrouse 33 (2011) 161

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