Anthropogenic habitat change and assisted colonization are promoting range expansions of some widespread species with potential consequences for endemic fauna. The recent colonization of Cyprus by breeding Sardinian Warblers *Sylvia melanocephala* has raised concerns that it might be displacing the closely related and endemic Cyprus Warbler *Sylvia melanothorax*. Habitat associations of both species were examined using models of abundance within the 95% density kernel of the Sardinian Warbler’s range and also outside this range for Cyprus Warbler. Within the Sardinian Warbler’s range, the two species were associated with subtly different scrub habitats. Outside the Sardinian Warbler’s range, the Cyprus Warbler differed again in its habitat association, but this probably resulted from marked differences in habitat extent and availability in different parts of the island rather than from competitive displacement, as none of the habitat or land-use elements differentially associated with Cyprus Warblers was positively associated with Sardinian Warbler occurrence. This suggests that the Sardinian Warbler has exploited a different niche, rather than displacing the endemic species, and has perhaps benefited from changing land-use patterns, particularly recent fallows and abandoned agriculture, in contrast to the stronger association of Cyprus Warblers with semi-natural scrub.

**Keywords:** competitive displacement, habitat selection, Mediterranean shrublands, niche displacement.

Many species are undergoing range changes in response to changing climate and land-use (Parmesan & Yohe 2003), including many bird species (e.g. Thomas & Lennon 1999, Carrillo et al. 2007, Jetz et al. 2007). Colonization of new regions is often facilitated by human activity through deliberate or accidental introduction and through anthropogenic habitat change. For example, Australian species such as White-faced Heron *Egretta novaehollandiae* and Pacific Swallow *Hirundo tahitica* have colonized New Zealand naturally over the past century as a result of changes in land-use that created suitable conditions for their establishment (Clout & Lowe 2000). In Europe, the Black-shouldered Kite *Elanus caeruleus* is expanding its range through land-use change in the Iberian Peninsula (Balbontin et al. 2008). Such changing distributions alter local species composition and thus may have adverse consequences for species with restricted ranges through predation, spread of disease, niche displacement or interspecific competition (Mooney & Cleland 2001). Where range expansion results in novel contact between morphologically similar congeners that evolved in allopatry, there is the potential for competition through resource depletion, antagonistic interactions and interference, and/or territorial exclusion and displacement (Orians & Willson 1964, Cody 1969).

The Sardinian Warbler *Sylvia melanocephala* is the most widespread *Sylvia* warbler in the Mediterranean.
and has been expanding its range since the late 19th century (Fraissinet & Sultana 1997, Bulyuk & Leoke 2010). In 1994, it started to breed in Cyprus, the third largest island in the Mediterranean, having until then been just a winter visitor (Frost 1994). By 2001 its breeding range covered 600 km\(^2\) in the Pafos district in the west of the island (Pomeroy & Walsh 2002), but its recent extent of occurrence, particularly beyond the Pafos district, was poorly known prior to this study. Elsewhere in the Mediterranean, the Sardinian Warbler coexists with other Sylvia species through differential habitat use (Martin & Thibault 1996, Pons et al. 2008). Concern has been expressed that novel contact during the breeding season may cause decline of an endemic congener, the Cyprus Warbler Sylvia melanothorax, although no significant decline of this species has yet been recorded (Pomeroy & Walsh 2000, 2002, Jones 2006). The Cyprus Warbler is a Category 2 Species of European Conservation Concern (SPEC 2), is listed on Annex I of the EU Birds Directive and has the most restricted range of any species in its genus (Shirihai et al. 2001, Burfield & van Bommel 2004). It is widespread across Cyprus and is a partial migrant, with the majority of the population thought to overwinter in the Middle East and northeast Africa (Flint & Stewart 1992). In contrast, the Sardinian Warbler population on Cyprus appears to be sedentary and is perhaps augmented in winter by birds from elsewhere.

Shifts in migratory strategy in response to climate amelioration can give sedentary populations a competitive advantage over migrants through earlier territory settlement (Berthold 2001). Cyprus Warbler and Sardinian Warbler are both species associated with scrub (Shirihai et al. 2001) and there is overlap in the habitat types in which they have been recorded in the Pafos district, including semi-natural and agricultural habitats (Pomeroy & Walsh 2000). However, there is evidence to suggest the two species may be selecting subtly different habitat features. The Cyprus Warbler was found to be more numerous than the Sardinian Warbler in low-intensity farmland and in grazed thorny scrub habitats (Pomeroy & Walsh 2000), with no evidence of inter-specific territoriality and no indication that breeding success and nesting condition of one species was affected by the presence of the other (Jones 2006). Ecologically similar species that are competing with one another can coexist through adjustment of the niche of one species in response to the other (Mooney & Cleland 2001); reciprocal removal can demonstrate such niche displacement (e.g. Martin & Martin 2001). Alternatively, niches of possible competitors can be compared between areas where they occur in sympathy and in allopatry. The breeding distribution of Cyprus Warbler and Sardinian Warbler in Cyprus, with Cyprus Warbler found across the island and Sardinian Warbler restricted to the west, allowed us to adopt the latter approach.

This study had the following aims: (1) to quantify the current range and extent of overlap of the two species in the area of Cyprus that is under the direct control of the government of the Republic of Cyprus; (2) to establish the habitat associations of each species across a wide range of land-use and vegetation structures; (3) to compare the habitat associations of the two species to assess evidence of niche overlap; and (4) to assess evidence for niche shift in Cyprus Warbler in the area of sympathy with Sardinian Warbler consistent with the hypothesis of competitive displacement.

**METHODS**

**Site selection**

As part of a study of the effects of land-use change, bird surveys were undertaken along line transects at 202 localities, widely distributed across Cyprus (Fig. 1). Each locality received a single visit between 29 March and 30 June 2009 to record breeding individuals of both Sylvia species, although some migrant Sardinian Warblers may have been recorded in April (Cramp 1992, Flint & Stewart 1992, Shirihai et al. 2001). To avoid regional differences being confounded by seasonal effects, we returned to sample each administrative district on three or four occasions within the survey period. Sampling was stratified by district and within each of these, localities for survey were located across the range of land cover types available, including areas of scrub, forest, fallow land and all major cultivation types found on the island (olive, carob and citrus groves, cereals and viticulture). However, because of the difficulty of surveying the north part of the island where a population of Sardinian Warblers also exists (Pomeroy & Walsh 2002), surveys were conducted in the area controlled by the government of the Republic of Cyprus in the south of the island, with the exception of nine sites in the Mesaoria plain. This flat
region, which is predominantly under cereal cultivation, represents a landscape type not found elsewhere on the island. To survey a large number of localities in a season, site selection was constrained to those where vehicle access was possible to within 100 m of the survey start point. A network of farm roads and tracks extends throughout the countryside, providing access to all types of land-use. However, as no reliable maps of this network were available, locating survey start points pre-selected using GIS would have been prohibitively time consuming. Therefore, an element of opportunism was introduced, exploring the network of unmapped farm roads to locate examples of each major land-use type within each district.

The mean distance between nearest localities was 2.7 km (sd = 1.8 km) and no transects overlapped or intersected. In 21 cases (< 11%), survey localities were closer than 1 km from each other (mean distance to nearest locality = 0.68 km ± 0.19) but the shortest distance between these (480 m) was four to six times the length of a Sardinian or Cyprus Warbler territory (Jones 2006), so that survey localities could be considered discrete. The elevation of each locality was obtained from the Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM: Jarvis et al. 2008) and ranged from 10 to 1695 m, with 44% of survey localities at 249 m or lower, 34% between 250 and 499 m, 17% between 500 and 999 m, and 5% at 1000 m or higher.

**Bird and habitat surveys**

The fine-scale heterogeneity of land-uses in Cyprus precluded us from carrying out separate point samples within patches of discrete habitat, so line transects were used. At each survey locality, a 500-m line transect was walked cross-country in as straight a line as possible (unless terrain was impassable) oriented away from any roads and away from the early morning sun to facilitate visibility. The transect length of 500 m was chosen as an appropriate distance over which the fine-scale agricultural heterogeneity of the Cypriot landscape could be captured. Coordinates of transect start and end points were recorded using a handheld GPS receiver, and waypoints along the transect were recorded automatically at 20-m intervals.

Bird surveys were conducted from 30 min to 3 h after sunrise, recording all birds seen or heard and assigning them to perpendicular distance bands (< 25, 25–50, 50–100 and > 100 m), while walking the transect at a steady pace (mean survey duration = 28 min, sd = 15 min). All surveys were conducted by a single observer (C.I.), experienced in identifying the two species. Most birds were initially detected by auditory cues with the majority then confirmed visually, especially if there was any uncertainty in identification. Female Cyprus Warblers were identified by the presence of under-tail covert markings and absence of red orbital ring. Rüppell’s Warblers *Sylvia rueppelli* occur...
on passage but were scarce (only nine confirmed individuals) and could be identified reliably. Most individuals were detected within 50 m of the transect line (Cyprus Warbler: 81.5%; Sardinian Warbler: 85.5%). Nevertheless, vocalization and therefore detectability could potentially vary among habitats due to differences in predation risk, status (e.g. paired, unpaired) or visibility of the surveyor. This was examined by fitting models of detectability in DISTANCE software (Thomas et al. 2009); models for both species had better fit (Cyprus Warbler: ΔAICc = 35; Sardinian Warbler: ΔAICc = 9) when not stratified by land cover type (EU CORINE, Co-ordination of Information on the Environment, Land Cover classes: MANRE 2009). We were therefore confident that detectability did not differ between habitats and data were analysed in terms of the total number of registrations per transect without truncation by distance.

Land-use and habitat features (Table 1) were recorded at 11 points along the transect, at the start and end points and at 50-m intervals while retracing the route following completion of the bird survey. At each point, the presence of scrub vegetation, forest and agricultural land-uses was recorded within a radius of 30 m. Land-use was classified as: fallow (land cultivated not <1–2 years previously, characterized by annual grasses and a tall herb layer), tilled land, horticulture, cereal cultivation, tree groves and viticulture.

Tree groves were recorded as either (1) olive Olea europaea and/or carob Ceratonia siliqua, or (2) citrus. Olive and carob groves are structurally similar, traditionally forming open multipurpose agro-forestry plantations that include field crops and pasture (Delipetrou et al. 2008) and were therefore merged into a single category. In contrast, citrus groves are intensive monocultures, often irrigated and not usually multi-purpose. Almond groves were not analysed owing to their variable structure, ranging from boundary features lining terraces in vineyards to intensive irrigated plantations. Other fruit groves were scarce, being restricted to higher elevations, and were also not analysed.

Vineyards (viticulture) were divided into three categories: abandoned, unrotovated and rotovated. Most vineyards are rotovated in both winter and spring, to improve rainwater absorption and air circulation and for weed management. Rotovated viticulture was characterized by loose bare ground and fresh re-growth of weeds, whereas unrotovated viticulture had compact soil and a taller herb layer. Both differed from abandoned vineyards where there was mature regeneration of scrub vegetation among unproductive vine plants. The three individual categories of viticulture were significantly inter-correlated but all paired inter-correlations had \( r < 0.5 \), so the three categories were considered as independent predictor variables in the same models.

Density of trees (woody plants at least 3 m in height) at each point was estimated using the point-quarter method (Cottam & Curtis 1956), a commonly used and robust plotless density estimator. The presence of boundary features within 30 m of the point, including terraces, stone walls, herbaceous edges, fences, tree windbreaks and streams or gorges, was recorded.

Within a 10-m radius of each point, scrub composition was quantified by recording the presence of common indicator scrub species (Table 2) characteristic of (1) post-cultivation and field margin growth (six species); (2) semi-natural scrub (13 species); and (3) open woodland and forest edge

---

Table 1. Land-use and habitat variables, showing frequency range, mean and standard deviation of square-root-transformed frequency, and incidence (% non-zero frequencies).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Range</th>
<th>Mean</th>
<th>sd</th>
<th>Incidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horticulture (including potato)</td>
<td>0.305</td>
<td>0.709</td>
<td></td>
<td>17.8</td>
</tr>
<tr>
<td>Fallow land</td>
<td>1.771</td>
<td>1.134</td>
<td></td>
<td>76.2</td>
</tr>
<tr>
<td>Tilled land</td>
<td>1.128</td>
<td>1.100</td>
<td></td>
<td>56.9</td>
</tr>
<tr>
<td>Cereal (including harvested crop)</td>
<td>1.627</td>
<td>1.280</td>
<td></td>
<td>67.8</td>
</tr>
<tr>
<td>Olive and carob groves</td>
<td>1.496</td>
<td>1.353</td>
<td></td>
<td>59.9</td>
</tr>
<tr>
<td>Citrus groves</td>
<td>0.340</td>
<td>0.860</td>
<td></td>
<td>14.8</td>
</tr>
<tr>
<td>Viticulture</td>
<td>0.840</td>
<td>1.227</td>
<td></td>
<td>36.1</td>
</tr>
<tr>
<td>Rotovated</td>
<td>0.605</td>
<td>1.070</td>
<td></td>
<td>26.7</td>
</tr>
<tr>
<td>Unrotovated</td>
<td>0.244</td>
<td>0.564</td>
<td></td>
<td>17.3</td>
</tr>
<tr>
<td>Abandoned</td>
<td>0.317</td>
<td>0.694</td>
<td></td>
<td>19.3</td>
</tr>
<tr>
<td>Scrub</td>
<td>1.893</td>
<td>1.327</td>
<td></td>
<td>74.3</td>
</tr>
<tr>
<td>Post-cultivation growth</td>
<td>0–30</td>
<td>2.559</td>
<td>1.400</td>
<td>88.1</td>
</tr>
<tr>
<td>Semi-natural scrub</td>
<td>0–89</td>
<td>2.778</td>
<td>2.154</td>
<td>95.0</td>
</tr>
<tr>
<td>Open woodland shrub layer</td>
<td>0–28</td>
<td>1.119</td>
<td>1.316</td>
<td>52.0</td>
</tr>
<tr>
<td>Forest</td>
<td>0.773</td>
<td>1.098</td>
<td></td>
<td>40.1</td>
</tr>
<tr>
<td>Boundary features</td>
<td>2.442</td>
<td>1.178</td>
<td></td>
<td>84.2</td>
</tr>
<tr>
<td>Tree density (per ha)</td>
<td>0–8.69</td>
<td>0.698</td>
<td>1.158</td>
<td>100</td>
</tr>
<tr>
<td>Elevation (( \times 10^2 ) m)</td>
<td>0.10–16.95</td>
<td>3.53</td>
<td>3.20</td>
<td>100</td>
</tr>
</tbody>
</table>

All variables ranged from 0 to 11 prior to transformation, except tree density and elevation, which were not transformed, and scrub vegetation types.
shrub layer (three species), following Meikle (1977, 1985) and Davies et al. (2004). For analysis, species incidence was summed within each scrub category, at each sampling point (Table 1).

**Regional variation in land-use**

The west and southwest of the island are topographically heterogeneous and comprise a complex land-use mosaic, with natural vegetation interspersed with cultivated fields. Excluding the central Troodos mountain range, central and eastern Cyprus is less varied topographically, with cereal and vegetable cultivation dominating and with considerable areas of olive groves (MANRE 2009).

Although many of the land-uses and habitats recorded were widespread (e.g. cereal, tilled land, olive and carob groves, and scrub), a few were localized (Fig. 2). Horticulture, which requires fertile soil, mainly occurred at low elevations. Fallow land was widespread but was concentrated in the west of the island. Both citrus groves and viticulture were largely restricted to the Pafos and Lemesos districts in the west of the island. Forest was restricted to the Troodos mountain range and a few coastal sites.

Not surprisingly, many land-use and habitat variables were weakly to moderately inter-correlated ($r < 0.5$). These are nevertheless included in candidate models, as this is preferable to regression of residuals (Freckleton 2002). Strongly inter-correlated variables ($r > 0.5$) were not included simultaneously in the models. To aid interpretation, we considered it preferable to retain individual land-use and land cover variables rather than use data reduction techniques such as principal components analysis.

**Analysis**

We first quantified the breeding season range of the Sardinian Warbler and modelled habitat

---

**Table 2.** Scrub plant species used as indicators of differing anthropogenic or semi-natural Mediterranean scrubland habitats.

<table>
<thead>
<tr>
<th>Scrub species</th>
<th>Fallow and field margin</th>
<th>Phrygana</th>
<th>Garrigue</th>
<th>Maquis</th>
<th>Coniferous woodland and forest edge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Post-cultivation growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ziziphus lotus</td>
<td>x</td>
<td></td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Rhus coriaria</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rubus sanctus</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crataegus azarolus</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ferula communis</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asparagus acutifolius</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urginea maritima</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Semi-natural scrub</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cistus spp.</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Rhamnus oleoides</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pistacia lentiscus</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Pistacia terebinthus</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Calicotome villosa</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Genista sphaellata</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Ceratonia siliosa</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sarcopoterium spinosum</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Helichrysum stdachas</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Olea europaea</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lithodora hispidula</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thymus spp.</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asphodelus aestivus</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland shrub layer</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pinus brutia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Cupressus sempervirens</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Juniperus phoenicea</td>
<td></td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
</tr>
</tbody>
</table>

Classification based on Meikle (1977, 1985), and on European Nature Information System (EUNIS) habitat types (Davies et al. 2004). Phrygana consists of an open stand of sclerophyllous bushes up to 0.6 m in height, taller open stands (0.6–2 m) form garrigue, and thick stands around 2 m in height form maquis (Tomaselli 1977).
associations of both species within this range. Cyprus Warbler habitat association was then modelled separately outside the Sardinian Warbler’s breeding range to test for evidence of niche displacement. However, if there are differences in habitat composition and availability inside and outside the range of the Sardinian Warbler, these may affect detection of niche displacement, so that results must be interpreted with caution.

The Sardinian Warbler’s breeding range was estimated by calculating the 95% contour of the fixed bivariate normal kernel density estimate applied to the distribution of occupied localities where Sardinian Warbler was present, using least-squares cross-validation to select the smoothing parameter. While this may underestimate the full extent of occurrence of Sardinian Warbler, as non-surveyed landscapes were not classified, it serves to distinguish which survey localities potentially fall within the area of sympatry of the two species. The Sardinian Warbler’s breeding range included 123 survey localities, leaving 79 survey localities outside the range (Fig. 1). We assessed whether Cyprus Warbler abundance was related to Sardinian Warbler abundance within the latter’s breeding range, using Pearson’s correlation, r. We hypothesized that (1) if Sardinian and Cyprus Warbler strongly selected the same vegetation characteristics and inter-specific competition was negligible, then abundances should be positively correlated; (2) if Sardinian Warbler was displacing Cyprus Warbler, abundances should be negatively correlated; and (3) if the two species occupied different vegetation structures, abundances would not be related.

Abundance of Cyprus and Sardinian Warblers, in terms of the number of detections (of either sex) at each locality, was separately related to the land-use and habitat variables using generalized linear models (GLMs) with a log-link function and negative binomial error term. The latter error structure provided better fit, as judged by the second-order Akaike’s information criterion (AICc) and the ratio of deviance to degrees of freedom, than a Poisson error term. Minimal adequate models were developed using backward selection from the full model, which included all land-use and habitat variables, survey start time and day since start of the field season. Any habitat or land-use variable which on removal led to a substantial increase in the value of AICc (> 1:Burnham & Anderson 2002) was retained; time and day were retained as control variables in all models.

Frequencies (0–11) of each recorded land-use and habitat variable (Table 1) were considered as predictors, square-root transformed to reduce leverage effects of outlying scores, and then z-transformed to allow comparability among regression coefficients.

---

**Figure 2.** Habitat variables on each transect. Symbols are graduated according to the frequency values of the habitat variables along the transect (0–11), and zero frequencies are marked with points.
(Schielzeth 2010). All candidate variables used in modelling had high variance and were recorded on more than 10% of transects (Table 1). Owing to its low incidence (< 15%), horticulture was not included in the abundance models for either species within the Sardinian Warbler’s range, while the viticulture categories were pooled and citrus was not included in the Cyprus Warbler models outside the Sardinian Warbler’s range.

One set of models included scrub frequency, and a second set considered the frequency of the three separate types of scrub vegetation – post-cultivation growth, semi-natural scrub and woodland shrub layer – but excluded the strongly inter-correlated variables: forest (woodland shrub layer: \( r = 0.83, P < 0.001 \)), boundary features (post-cultivation growth and woodland shrub layer: \( r = 0.51 \) and \(-0.52\), respectively, \( P < 0.001 \)), and merged viticulture (post-cultivation growth: \( r = 0.54, P < 0.001 \)).

**RESULTS**

**Relative warbler range and abundance**

The 95% kernel of Sardinian Warbler breeding distribution covered a continuous area of 1859 km\(^2\), including 89% of Pafos district and 41% of Lemesos district, plus four disjunct areas further east in Lefkosa and Larnaka districts with a combined area of 200 km\(^2\) (Fig. 1). The Sardinian Warbler was found at 96 of the 123 survey localities within its estimated breeding range (including the two disjunct outlying areas), with a mean of 5.0 (sd = 4.7) detections at each locality. Cyprus Warblers were recorded at 43 localities within the Sardinian Warbler’s breeding range, and in 31 of 79 localities outside it (Fig. 1), with a mean of 1.0 (sd = 1.8) detections at each locality inside, significantly fewer than Sardinian Warbler \( t_{158} = 8.84, P < 0.001 \), and 1.4 (sd = 2.5) detections outside the range. The mean number of Cyprus Warblers recorded at sites where they were detected did not differ significantly inside (2.8 ± 0.3 se, \( n = 43 \)) and outside (3.6 ± 0.5 se, \( n = 31 \)) the breeding range of Sardinian Warbler \( t_{72} = 1.56, P = 0.124 \), but was significantly less than the number of Sardinian Warblers recorded at sites where the latter species was detected (6.4 ± 0.4 se, \( n = 96; t_{152} = 6.20, P < 0.001 \)). There was no correlation between the abundance of the two species \( r = -0.12, P = 0.200, n = 123 \) within the Sardinian Warbler’s range.

**Models of warbler abundance**

Within its range, the Sardinian Warbler was more abundant at sites with a greater frequency of fallow land, rotovated vines and scrub, and was less abundant at higher elevation. In models that considered scrub type, the Sardinian Warbler was more abundant at sites with a greater frequency of post-cultivation and semi-natural scrub vegetation and less abundant at sites with a greater frequency of citrus groves and at higher elevations (Fig. 3).

The most important predictor of Cyprus Warbler abundance within the range of the Sardinian Warbler in models that did not include scrub type was the frequency of scrub vegetation. In models that included scrub type, Cyprus Warbler abundance responded most strongly to the abundance of semi-natural scrub, with a weaker positive association with post-cultivation growth, as indicated by the relative changes in AICc on variable removal (Fig. 3). In both sets of models, within the area of breeding sympathy the Cyprus Warbler was less abundant at sites with greater tree density. In models that included scrub type, the Cyprus Warbler was less abundant at sites with a greater frequency of tilled land.

Although elevation did not differ \( t_{200} = 1.77, P = 0.078 \), land-use and habitat differed at survey points inside and outside the Sardinian Warbler’s range. Within that range there were more citrus fruit \( t_{197.0} = 2.83, P = 0.005 \), more viticulture \( t_{198.7} = 4.72, P < 0.001 \); rotovated vines: \( t_{197.1} = 5.23, P < 0.001 \); abandoned: \( t_{200.0} = 2.71, P = 0.007 \), more semi-natural scrub and post-cultivation growth \( t_{200}, t_{190.9} = 4.05 \) and 3.70, respectively, \( P < 0.001 \) and marginally higher tree density \( t_{198.8} = 1.89, P = 0.06 \).

Outside the Sardinian Warbler’s range, Cyprus Warbler abundance was strongly and positively associated with olive and carob groves and with scrub, and was also positively associated with boundary features, but negatively associated with cereal cultivation. In models that considered scrub type, Cyprus Warbler abundance was again strongly positively associated with greater frequency of semi-natural scrub and more weakly with post-cultivation growth (Fig. 3). Association of Cyprus Warbler abundance with olive and carob groves and boundary features differed inside and outside the Sardinian Warbler’s breeding range. However, these variables were not positively
associated with Sardinian Warbler abundance and therefore this could not be interpreted as evidence of competitive displacement.

**DISCUSSION**

The recently established Sardinian Warbler and the endemic Cyprus Warbler both occurred in greater abundance at sites with greater frequency of post-cultivation growth and semi-natural scrub, reflecting their use of scrub for both nesting and foraging (Jones 2006). However, the Sardinian Warbler was less strongly associated with scrub than its congener and responded positively to other habitat types, suggesting more generalist habitat associations, whereas the Cyprus Warbler showed a stronger selection for scrub. The abundance of the two species, where sympatric, was not correlated, but inside its breeding range the Sardinian Warbler was more abundant than the endemic congener, with five times as many registrations per transect. Contrasting patterns of Cyprus Warbler habitat association inside and outside the Sardinian Warbler’s range provided no evidence of competitive displacement, as the differing elements were not those selected by the latter species, suggesting that the two species have differing ecologies and requirements.

The habitat association models used in this study are correlative and do not necessarily reflect causation. With the exception of forest and natural scrub, the variables investigated represent different land-use practices that in themselves may not affect the abundance of the warblers but more...
likely act as proxies for the landscape or scrub associated with them. We interpret our results in light of this caveat by considering land-use in terms of related habitat structure.

Within the Sardinian Warbler’s range, both species were positively associated with greater frequency of post-cultivation growth and semi-natural scrub. However, the Cyprus Warbler was much more strongly associated with both types of scrub, as shown by the larger coefficients and ΔAICc values. In addition, it was less abundant at sites with greater tree density, indicating an association with more open habitats, avoiding dense groves and forest, and was also negatively associated with a greater frequency of tilled land, whether this occurred in arable fields or as grove understory. In contrast, tree density and tilled land were not retained as important predictors in models of Sardinian Warbler distribution. Unlike the Cyprus Warbler, the abundance of Sardinian Warblers was greater at lower elevations, as also found by Pomeroy and Walsh (2002).

The Sardinian Warbler was positively associated with greater frequencies of rotovated viticulture and fallow land. However, their importance was only evident when scrub type was not included in the models, suggesting that these habitat elements may have been proxies for regeneration of natural vegetation and associated scrub along terrace and vineyard margins. Active viticulture was also found to be important for Sardinian Warbler by Symes (2006), who recorded nearly twice as many Sardinian Warblers as Cyprus Warblers in managed vines and found that the Cyprus Warbler was positively associated with greater scrub cover within active vineyards but was more abundant in semi-natural scrub developed on vine terraces abandoned decades previously. In contrast to Sardinian Warbler, the Cyprus Warbler was not associated with fallow land or with viticulture in the current study. This suggests that the Cyprus Warbler is more of a scrub specialist than the Sardinian Warbler, which appears to be able to exploit recent disturbance and scrub regeneration in currently managed (rotovated viticulture and fallow land) agricultural landscapes.

Outside the Sardinian Warbler’s range, the Cyprus Warbler’s abundance was again greater at sites with a greater frequency of scrub vegetation. It was also positively associated with boundary feature frequency, most probably a proxy for remnants of scrub along terraces and field boundaries. Cyprus Warbler abundance was negatively associated with cereal cultivation; this may reflect a lack of semi-natural scrub vegetation in arable landscapes in this part of the island \( (r = -0.40, \ P < 0.001) \), as cereal cultivation was no longer retained when scrub type was included in the model. Although Pomeroy and Walsh (2002) found that the Cyprus Warbler was less numerous at lower elevations, we found no effect of elevation, perhaps because elevation is a proxy for the habitat variables which are the direct causes of variation in Cyprus Warbler abundance. The Cyprus Warbler was more abundant in transects with greater frequency of olive and carob groves outside, but not inside, the Sardinian Warbler’s range. There is more land under olive and carob groves in Lefkosia and Larnaka districts (outside the Sardinian Warbler breeding range) than in Pafos and Lemesos (Statistical Service 2005, MANRE 2009), so there may be more power to detect this effect outside the range. Previous work inside the sympatric breeding range found that the Cyprus Warbler was strongly positively associated with abandoned rather than managed groves (Symes 2006), reflecting the scrub vegetation that develops in such situations. In the current study, groves were associated with semi-natural scrub \( (r = 0.33, \ P < 0.001) \), particularly on shallow rendzina soils unsuitable for cultivation (C. Ieronymidou pers. obs.). That olive and carob groves were not retained in the model that included scrub type suggests that it is the scrub rather than the groves that are important to the Cyprus Warbler.

The differences between the models of Cyprus Warbler abundance inside and outside the Sardinian Warbler’s range show no evidence consistent with niche displacement by Sardinian Warbler, as the habitat elements differentially associated with Cyprus Warbler (olive and carob groves and boundary features) are not positively associated with Sardinian Warbler abundance. Instead, their differential selection is most probably due to differences among landscapes and habitats available for settlement in different parts of the island. While confirmation would require reciprocal removal experiments, the conclusion that active displacement is not occurring is supported by the lack of any relationship between the abundance of the two species within their sympatric range, and by the lack of inter-specific territoriality between the two species (Jones 2006).
This lack of evidence of niche displacement suggests that the perceived, although non-significant, decline in Cyprus Warbler in the areas where Sardinian Warbler has been expanding its range (Pomeroy & Walsh 2002, Jones 2006) is unlikely to be attributable to inter-specific competition. Sardinian Warbler expansion has probably been mediated through its more generalist habit, as reflected by its greater overall abundance in the area of shared range.

The abundance of both species will have been differentially affected by recent changes in land-use. Management of remaining areas of semi-natural sclerophyllous scrub habitat has changed greatly, with the loss of extensive goat grazing (Christodoulou 1959). Historically, free-ranging flocks of goats were grazed on semi-natural scrubland, but legislation in 1935 regulated goat distribution, causing a decline in goat numbers (by 33% between 1930 and 1957) and a shift in husbandry towards tethering (Christodoulou 1959). Data for the numbers of free-range goats are not available after 1960, but today most animals are tethered with a limited extent of grazing (Economides 1997, C. Triantafyllidou in litt. 2011). This decline in grazing intensity will have caused a structural and successional shift from compact, tightly grazed dwarf-shrub phrygana to taller, open-structured garrigue and maquis, as has occurred in Crete (Papanastasis & Kazaklis 1998). Change in scrub structure may have reduced habitat suitability for Cyprus Warbler, which appears to favour lower, more compact scrub structures (C. Ieronymidou and P.M. Dolman pers. obs.) that depend on regular browsing. The Cyprus Warbler has been found to be more numerous than the Sardinian Warbler in semi-natural scrub habitat and low-intensity agriculture, both of which were grazed (Pomeroy 1997, Pomeroy & Walsh 2002). In contrast, loss of extensive grazing could be an important driver for the expansion of the Sardinian Warbler, which breeds at higher densities in scrub plots with taller vegetation (Martin & Thibault 1996, Shirihai et al. 2001, Jones 2006). Notably, Preiss et al. (1997) found that the Sardinian Warbler was the only Mediterranean scrub bird species to increase following a 14-year period of grazing abandonment in southern France, whereas Sirami et al. (2007) found its population at the same locality was stable 11 years on, unlike most other scrub bird species. Ungrazed scrub offers taller and diffuse structures suitable for the Sardinian Warbler, whether this is in patches of semi-natural garrigue and maquis vegetation or along field margins of cultivated land-uses.

As elsewhere in Europe, low-intensity farmland in Cyprus faces the twin threats of intensification and regional homogenization in productive land, and abandonment of marginal lands. Between 1985 and 2003, irrigation has increased by 55% and agricultural machinery by 58%, whereas the extent of uncultivated farmland has increased by 36% (Department of Statistics and Research 1987, 1996; Statistical Service 2005). Overall, the area of land under agriculture declined by 42%, from 2000 km² in 1975 to 1160 km² in 2008 (FAOSTAT 2009) due to a combination of coastal and urban development and considerable abandonment of marginal land.

Loss of low-intensity farmland in Cyprus is likely also to affect a number of other priority (SPEC) species, such as European Roller Coracias garrulus, Black-headed Bunting Emberiza melanocephala and Eurasian Linnet Carduelis cannabina. While abandonment of marginal farmland may be beneficial to scrub-dwelling species such as the Cyprus Warbler (Symes 2006), uncultivated land is more likely to be built on.

Such changes in farmland management are likely to be exacerbated by the entry of Cyprus to the EU in 2004. For example, elements of the Common Agricultural Policy (CAP) offer subsidies for enhanced production and market competitiveness through Priority Axis I of the Rural Development Programme, whereas previous government policies to support marginal agriculture have been reduced (Department of Agriculture 2004). However, ongoing reform of the CAP, including decoupling of Pillar I payments from production, introduction of cross-compliance and the proposed ‘Greening’ scheme, along with extension of the Rural Development Programme (Pillar II) and further development of the Agri-Environment Programme, may offer mechanisms to sustain High Nature Value farming (Stoate et al. 2009, European Commission 2011). However, to achieve this will require careful targeting and development of appropriate prescriptions that, for example, incentivize preservation of scrub vegetation and boundary features on farmland and that support extensive grazing.

This study was funded by the A.G. Leventis Foundation and the University of East Anglia. We thank M.A. Hellicar and other staff at BirdLife Cyprus for their help and support and for
providing the vehicle used in fieldwork, and K. Bowgen, P. Cremona and S. Jones for assistance with data collection. We also thank V.R. Jones and an anonymous referee for their valuable comments on an earlier version of this paper.

REFERENCES


Received 10 June 2011; revision accepted 29 December 2011. Associate Editor: Stephen Browne.