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Research Paper

Habitat selection and interspecific competition between *Sylvia* warblers in Cyprus following the rapid expansion of a recent colonizer

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ABSTRACT. Many island endemics around the world have evolved from populations of colonists. Further colonizations may lead to interactions between older and newer colonists. Little is known, however, regarding the impact of more recent island colonizers on incumbent congeners, partly because of a dearth of examples of natural colonizations in the recent past. Sardinian Warbler (*Sylvia melanocephala*) recently colonized Cyprus and has rapidly expanded its breeding range. We examined the impact of the Sardinian Warbler colonization on the endemic Cyprus Warbler (*S. melanothorax*) and on another congener, the Spectacled Warbler (*S. conspicillata*). We performed 402 population surveys in 32 sample plots across the island, covering five different habitat types and variation across three seasons. Our results show that Cyprus Warbler has undergone a significant decline during the five years of the study, especially in disturbed habitats, while Sardinian and Spectacled Warbler populations have remained stable. Although the longer established Spectacled Warbler clearly segregated habitat with Cyprus Warbler, Sardinian Warbler numbers were negatively associated with Cyprus Warbler abundance, suggesting its presence may contribute to the endemic's decline. Maquis scrub was favored by both Cyprus Warbler and Sardinian Warbler, but the latter also occurred in high densities in disturbed habitats. The colonizer's prevalence in disturbed, mixed habitat, suggests it may replace the endemic in parts of its former range following anthropogenic perturbations. Natural colonizations may contribute to rapid population declines in island endemics in a similar way to introduced species, especially when combined with strong effects of habitat disturbance.

Sélection de l'habitat et compétition interspécifique entre les fauvettes des jardins à Chypre à la suite de l'expansion rapide d'une espèce colonisatrice récente

RÉSUMÉ. De nombreuses espèces endémiques des îles du monde entier ont évolué à partir de populations colonisatrices. De nouvelles colonisations peuvent ensuite donner lieu à des interactions entre les populations récentes et plus anciennes. On en sait peu, en revanche, au sujet de l'impact des colonisateurs les plus récents des îles sur leurs congénères déjà présents, en partie en raison de la rareté des exemples de colonisations naturelles dans un passé récent. La fauvette mélanocéphale (*Sylvia melanocephala*) a récemment colonisé Chypre et son territoire de reproduction s'est rapidement développé. Nous avons examiné l'impact de la colonisation de fauvettes mélanocéphales sur l'espèce endémique, la fauvette de Chypre (*S. melanothorax*) ainsi que sur un autre congénère, la fauvette à lunettes (*S. conspicillata*). Nous avons réalisé 402 enquêtes sur ces populations sur 32 territoires échantillons dans l'île, couvrant cinq types d'habitats et les variations au cours de trois saisons. Nos résultats indiquent que la fauvette de Chypre a connu un déclin important au cours des cinq dernières années de l'étude, en particulier dans les habitats perturbés, alors que les populations de fauvettes mélanocéphales et de fauvettes à lunettes sont restées stables. Même si la fauvette à lunettes, établie depuis plus longtemps, présente des habitats clairement séparés de ceux de la fauvette de Chypre, l'augmentation de la population de fauvettes mélanocéphales semble avoir coïncidé avec une baisse des nombres de fauvettes de Chypre, ce qui suggère que leur présence pourrait contribuer au déclin de l'espèce endémique. La fauvette de Chypre et la fauvette mélanocéphale semblent privilégier les broussailles et le maquis, mais cette dernière est également présente en forte densité dans les habitats perturbés. La prévalence des colonisateurs dans les habitats mixtes et perturbés suggère qu'ils pourraient remplacer l'espèce endémique dans certaines parties de son ancien territoire à la suite de perturbations anthropogéniques. Les colonisations naturelles pourraient contribuer au déclin rapide de certaines populations d'oiseaux endémiques des îles au même titre que les espèces introduites, en particulier lorsque ces phénomènes sont associés aux effets majeurs de la perturbation de l'habitat.

Key Words: *habitat selection; invasive species; interspecific competition; island endemics; Mediterranean islands; Sylvia warblers*

INTRODUCTION

Island endemism may result from populations colonizing islands that have adapted to the limited range of habitats found in their new environment, coupled with an absence of gene flow with mainland populations (Newton 2003). Additionally, a founder

effect might result in phenotypic differences in island populations compared with mainland counterparts (Spurgin et al. 2014). As a result of their smaller population size and reduced genetic diversity, insular species are more vulnerable to extinction, because they may be unable to adapt to the threats posed by new

colonizers (Ricklefs and Cox 1972) and habitat disturbance (Croonquist and Brooks 1993, Andr n 1994). Identifying the impact of new colonizers can be challenging because the timing of recent colonization events is seldom known. But, humans have often introduced species that have established populations in new regions around the world, and species introductions have been described as the second most frequent pressure on endemic species after habitat loss (Fahrig 2001, 2002, 2003, Bellard et al. 2016).

The impact of interactions with new colonizers is potentially greater on islands compared with continental regions (Blondel 2000), possibly because of the absence of coevolution between native insular species and potential competitors. Native insular species might be especially vulnerable to emerging competitive pressures. Such a negative impact of novel competitors is likely to be similar, regardless of if their origin is due to anthropogenic causes or natural colonization (Nackley et al. 2017). One factor that may contribute to the pressure on incumbent insular species is that islands rarely provide alternative habitats suitable for endemic species to shift their population ranges to in order to minimize competition with new colonizers (Jehl and Parkes 1983, Vil  and Hulme 2017).

A commonly cited example of such interspecific competition due to natural colonization of islands by mainland species is the case of *Sylvia* warblers in the Western Palearctic, where 17 *Sylvia* species regularly occur (Cramp and Brooks 1992). The outcomes of *Sylvia* warbler interactions vary, ranging from the displacement of native species by mainland colonizers to their coexistence (Cody and Walter 1976, Case and Cody 1987). Indeed, it has been argued that the ecological similarity of these *Sylvia* congeners has led to their segregation into different niches to reduce interspecific competition when they occur in sympatry (Cody 1978). On smaller islands, displacement of *Sylvia* warblers is hypothesized to have occurred, for example in Malta, where Spectacled Warbler *S. conspicillata* has declined over the last 30 years after a century of coexistence with the colonizing Sardinian Warbler (*S. melanocephala*; Shirihai et al. 2001). By contrast, eight *Sylvia* warbler species coexist along an ecological gradient in Catalonia (Guillaumet and Prodon 2011). The question of interspecific competition among *Sylvia* warblers thus remains controversial. Indeed, several studies have challenged the existence of competition among Mediterranean warblers proposed by Cody and Walter (1976), by arguing that warblers existing in the same habitat are segregated by their ecological preferences instead of by direct competition for space (Martin and Thibault 1996, Pons et al. 2008, Guillaumet and Prodon 2011).

In Cyprus, 11 *Sylvia* species regularly occur (Stylianou 2015). Of these, just three breed on the island: Cyprus Warbler (*S. melanothorax*), Sardinian Warbler, and Spectacled Warbler (Flint and Stewart 1992). These three species are phylogenetically related and belong to the Melizophilous sub-group, which includes *Sylvia* species confined to the Mediterranean region (Blondel et al. 1996, Voelker and Light 2011). The Cyprus Warbler is an endemic breeding species in Cyprus (Shirihai et al. 2001) whose population has strongly declined recently in western Cyprus, accompanied by a simultaneous increase in the breeding population of Sardinian Warbler (Pomeroy and Walsh 2000, 2002, Flint and McArthur 2014, Pomeroy et al. 2016). Previously a winter visitor, Sardinian Warbler established a breeding population in the early

1990s, on the Akamas Peninsula in the western part of the island (Frost 1994, Pomeroy and Walsh 2000).

Previous work in Cyprus has not found a direct causal explanation for the decrease of Cyprus Warbler numbers in areas colonized by Sardinian Warbler. Specifically, Jones (2006) found no evidence of competitive interactions during the breeding season in areas where the two species breed syntopically. Consistent with western Mediterranean *Sylvia* warbler communities (Martin and Thibault 1996), Cyprus and Sardinian Warblers appeared to establish home ranges independently of one another, with substantial home range overlap (Jones 2006). Also, Ieronymidou et al. (2012) argued against the case of competitive displacement of Cyprus warbler by Sardinian Warbler because, in areas where they coexisted, they exhibited subtly different preferences within similar habitat types. Ieronymidou et al. (2012) determined that both species' population trends are differentially affected by recent changes in land use, while Flint and McArthur (2014), in contrast, hypothesized that interspecific territoriality from Cyprus Warbler and interspecific aggression by Sardinian Warbler are two of the main factors driving the Cyprus Warbler decline. Subsequently, Hellicar and Kirschel (2021) found that both Cyprus warbler and Sardinian warbler occurred in lower numbers when the other occurred in high densities, preferring different goat and sheep grazing regimes. Spectacled Warbler favors the most arid parts of the island and has been described as resident on the island since at least the 19th century (Bucknill 1909). Despite it being one of the three *Sylvia* species breeding in Cyprus, its interactions with its two congeners, Cyprus and Sardinian warbler, have been overlooked by previous studies and its potential involvement in interspecific competition on the island is unknown.

In this study, our main objective was to unveil the possible impact of the recent establishment and expansion of a breeding population of Sardinian Warbler on the densities of its congeners, Cyprus and Spectacled Warblers, with much longer established breeding populations in Cyprus, in the light of previous work on competition and turnover of species on islands (Mayr 1965, Jehl and Parkes 1983, Dhondt 2012, Bellard et al. 2016, Hoffmann and Courchamp 2016, Wilson et al. 2016). Through this study we aimed to quantify population densities and dynamics in different areas, habitat types, and across seasons. In addition to the natural habitat types examined (pine forest, maquis, garrigue, and salt marsh) we included disturbed habitat mixtures, where severe anthropogenic disturbance has occurred (e.g., fragmentation, plantation of non-native plants, and agriculture) or wildlife severely disturbed the habitat, given that any of the study species might benefit from habitat disturbance (Cody and Walter 1976, Pomeroy and Walsh 2006, Ieronymidou et al. 2012, Hellicar and Kirschel 2021). Environmental factors that might affect species presence, such as altitude, temperature, and precipitation were also considered. Coexistence of congeners might result in strong interspecific interactions (Dhondt 2012, Grether et al. 2013), thus revealing how the presence of each species influences the densities of the other two species (Braz et al. 2020) and quantifying these effects was a major objective of the study.

METHODS

Study species

Cyprus Warbler is an endemic breeder in Cyprus and a partial migrant, with a significant part of its population wintering in

Israel, Jordan, and in the Sinai Peninsula (Shirihai et al. 2001), with a population size estimate of 70,000–140,000 pairs (BirdLife International 2017). It has the most restricted breeding range among all *Sylvia* species (Shirihai et al. 2001). The Cyprus Warbler is included in Annex I of the EU Birds Directive 2009/147/EC, suggesting that special conservation measures need to be taken to ensure species survival and reproduction (European Parliament 2009). In addition, it is classified as SPEC 2 in BirdLife International's *European birds of conservation concern* (BirdLife International 2017). Cyprus Warbler is widespread in Cyprus and breeds in a variety of habitats, even though it prefers tall maquis (highest densities during breeding season and in winter) and garrigue (preferably those dominated by *Cistus* spp.; Cramp and Brooks 1992). It avoids open areas including cultivations, dense forests, and dry areas with an average annual rainfall of less than 340 mm (Flint and McArthur 2014). It occurs commonly in semi-natural scrub habitats (Ieronymidou et al. 2012) and where there is a higher diversity of perennial plants (Hellicar and Kirschel 2021). Populations have been recorded from sea level up to an altitude of 1400 m a.s.l., becoming progressively less common in areas with altitudes greater than 1000 m a.s.l. (Flint and McArthur 2014).

Early records of the Sardinian Warbler in Cyprus dating back to the late 19th century suggested that it was then a winter visitor and passage migrant (Bucknill 1909). However, because of its increasing numbers in the summer, Sardinian Warbler was assumed to breed in Cyprus, even though evidence of its establishment was still lacking (Bannerman and Bannerman 1958). The first confirmed breeding record of the species in Cyprus was reported in 1992 in the northwest of the island (Frost 1994) followed by a breeding population identified in Pentadaktylos mountain range in the north of the island some years later (Pomeroy and Walsh 2000, Flint and McArthur 2014). Sardinian Warbler has since expanded its breeding range rapidly from the breeding population initially established in the west to now breed across most of Cyprus (Pomeroy and Walsh 2000, 2002, Jones 2006, Ieronymidou et al. 2012, Flint and McArthur 2014, Hellicar and Kirschel 2021). Based on recent reports, the total population of Sardinian Warbler in Cyprus is estimated between 60,000 and 110,000 breeding pairs (BirdLife International 2017), with their territories overlapping in several areas with those of Cyprus Warbler (Jones 2006, Ieronymidou et al. 2012). Yet, large numbers of Sardinian Warbler occur as migrants in Cyprus, either wintering on the island or as passage migrants (Shirihai et al. 2001, Flint and McArthur 2014). Across its range in Cyprus, Sardinian Warbler is more abundant at lower elevations, i.e., below 1000 m a.s.l., but breeding has been documented up to 1800 m, and it can occur even higher, to 2400 m, in its non-breeding range (Shirihai et al. 2001, Pomeroy and Walsh 2006, Ieronymidou et al. 2012). Sardinian Warbler exhibits a clear preference for dense shrub, tall and low maquis, sparse forests with bushy understory, olive groves, citrus crops, vineyards, suburban gardens and parks (Cody and Walter 1976). It is also a common colonizer of post-fire pioneer vegetation communities (Prodon 1988).

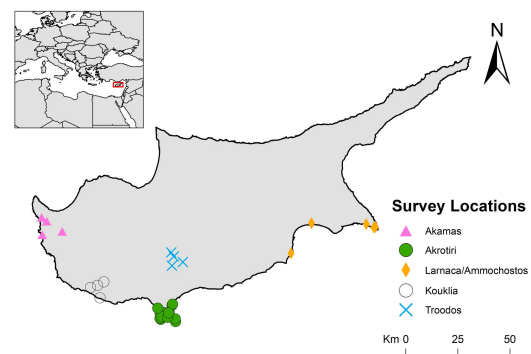
Spectacled Warbler is a resident species and partial migrant on the island of Cyprus (Shirihai et al. 2001, Flint and McArthur 2014). It exhibits a preference for areas with low mean annual rainfall (less than 450 mm / year), becoming absent from regions with annual precipitation over 450 mm (Flint and McArthur

2014). Where its range lies above the limit of 340 mm isohyet, it occasionally coexists with Cyprus Warbler (Flint and McArthur 2014). Across its range, Spectacled Warbler has been observed to breed syntopically with Sardinian Warbler (Cramp and Brooks 1992), such as on Kormakitis Peninsula in the northwest of the island (Flint and McArthur 2014). The species' population in Cyprus is estimated between 7,000 and 15,000 breeding pairs (BirdLife International 2017). Spectacled Warbler prefers habitats with low shrubs, low maquis areas with openings occupied by annual herbaceous vegetation, crop margins, and areas with halophytic vegetation (Shirihai et al. 2001).

Population surveys

Population surveys were carried out for the three *Sylvia* species breeding in Cyprus between 2013 and 2017 in 32 sample plots (Fig. 1). Plots were distributed in five regions of the island (Akamas, Kouklia, Akrotiri, Troodos, and Larnaka/Ammochostos), with much emphasis on the Akrotiri Peninsula in the south, where the expansion of Sardinian Warbler had been predicted (Flint and McArthur 2014). Akamas comprises the northwest tip of the island that is protected from anthropogenic development. Akamas is primarily covered by undisturbed garrigue and tall maquis as well as dense or open pine forests. Kouklia is in the southwest of the island. Its landscape comprises a mixture of habitats including fragmented tall maquis, garrigues, and patches of pine forests. Much disturbance is evident from agricultural activities. Akrotiri includes the southernmost tip of the island. The area comprises a mosaic of habitats varying from salt marsh to grasslands, garrigue, maquis, and pine forests. Human disturbance at Akrotiri is high, incorporating a military base with a well-developed road network throughout. Troodos is the primary mountainous area on the island, with its highest peak at 1952 m. Precipitation in the region is significantly higher compared to the other regions. Troodos retains dense pine forests and woody maquis. Larnaka/Ammochostos is a flat area in the east connected to the central plain. It is one of the most arid regions of the island. Cereal and potato cultivations are common there and dominate the landscape. Natural vegetation is sparse including low maquis, garrigue, and small patches of forests, mainly pine forests. Akrotiri and Larnaka/Ammochostos are the only regions with salt marsh.

Fig. 1. Survey plots were distributed across the island of Cyprus clustered in five areas: Akamas (triangles), Kouklia (open circles), Akrotiri (solid circles), Troodos (crosses), and Larnaka/Ammochostos (diamonds). Inset shows location of Cyprus in the Mediterranean Sea.



For each sample plot, surveys were performed during three seasons based on reports of their presence during those periods (Shirihai et al. 2001, Jones 2006): (a) pre-breeding season from mid-February to mid-March, (b) breeding season from mid-April to mid-June, and (c) wintering period from December to early January. Each plot was visited once in each season every year for the five years of this study, apart from in 2014 (year 2) when surveys were performed only during the wintering season because of unforeseen logistical reasons. Fieldwork targeted four natural habitat types where the three study species primarily occurred (Cramp and Brooks 1992, Shirihai et al. 2001, Jones 2006, Ieronymidou et al. 2012, Flint and McArthur 2014): (a) maquis (as defined in Davies et al. 2004) comprises evergreen sclerophyllous shrubs, with closed canopy structure and almost complete land cover. Trees are typically present as well as some annual plant species. Predominant species are *Genista fasselata*, *Calicotome villosa*, *Juniperus phoenicea*, *Pistacia lentiscus*, *Olea europaea*, and *Ceratonia siliqua*. (b) *Pinus brutia* forest comprises open woodland with *Pinus brutia* pines. (c) Garrigue (as defined in Davies et al. 2004), comprise low shrubland with extensive openings. Vernal species predominate and annual plants and geophytes are also abundant. Shrubs are found in patches with *Cistus* spp., *Thymus capitatus*, and *Sarcopoterium spinosum* the most common species. (d) salt marsh comprise perennial vegetation dominated by halophytes, mainly *Salicornia* spp. In addition, in this study we targeted anthropogenically disturbed, degraded habitats.

Sample plots were 2 ha rectangles (100 m × 200 m; Bibby et al. 2000, Sutherland et al. 2004). Uniform plots of each habitat type were identified in the field and delineated using a handheld GPS device. Because of the high habitat fragmentation along the target regions (Zomeni and Vogiatzakis 2014; P. Panayides 2006, *unpublished manuscript*), random selection of plots would have resulted in mixtures of habitats, thus we opted for study area selection through work in the field to ensure uniform plots were targeted. Surveys were undertaken by two observers, who during the preliminary stages worked together to standardize survey procedure (Sutherland et al. 2004). Observers walked in a loop along each plot surveying up to 25 m each side of the route taken, recording the number of individuals of all three target species seen or heard. Because distinguishing Cyprus and Sardinian Warblers vocally can be challenging (Cramp and Brooks 1992, Shirihai et al. 2001), we typically persisted until visual confirmation. Any individuals that were not unambiguously identified as an adult individual of one of the species were not included in the results. Target species exhibit a cryptic behavior apart from territorial males during pre-breeding and breeding seasons (Shirihai et al. 2001). Thus, to increase detectability, we used playback (Bibby et al. 2000, Sutherland et al. 2004). To that end, songs of territorial males of each of the three target species were recorded in the field within or near the study sites for use as playback stimuli. Each playback comprised at least two sequential full songs of each species with their natural silent intervals in-between. A handheld loudspeaker (Betron JRS40 Speaker, Benewy, CH.) was used to broadcast recorded songs of the three species in rotation with intervals in-between sessions. Loudspeaker volume was standardized at the same fixed level (Sutherland et al. 2004). Because of differences in detectability between habitat types across plots, survey duration varied according to vegetation and topography (see Sutherland et al.

2004), lasting between 20 and 45 minutes. Although double counts cannot be completely eliminated, especially with the skulking behavior of our target species, the amount of time spent in each plot allowed us to observe the movements of individuals helping to minimize the extent of double counting. Visits to the plots were randomly scheduled and performed between 6:00 am and 12:00 pm. Fieldwork was suspended during adverse weather conditions such as heavy rain and strong winds in accordance with other studies (Hostetler and Main 2001, Stagoll et al. 2010).

Data on monthly total rainfall and average temperature for the duration of the study were obtained from the nearest meteorological station for each plot (Department of Meteorology 2018). We used rainfall and temperature data of the two-month period that preceded surveys, because the combination of increased soil moisture and relatively high ambient temperature triggers a gradual invertebrate population increase over the following weeks (Janzen 1973, Speight et al. 2008, Ramya et al. 2017, Sugawara et al. 2017). The *Sylvia* warblers we studied feed mostly on invertebrates, and invertebrate population fluctuations determine the timing of establishment of home ranges and territories (Jones 2006). When the survey took place after the middle of any given month then the temperature and precipitation values of the survey month and the immediately preceding month were considered. On the other hand, when the survey was before the middle of each month then the temperature and precipitation values of the two immediately preceding months were used.

Statistical analysis

To test which factors affect the presence of the three *Sylvia* species breeding in Cyprus, we fitted Poisson Generalized Linear Mixed Models (GLMMs) implemented in lme4 in R (Bates et al. 2015, R Core Team 2020). Specifically, we fitted separate models using the numbers of each of the three target species as response and including as fixed factors the season (pre-breeding, breeding, and wintering), area (Akamas, Kouklia, Akrotiri, Larnaka/Ammochoostos, and Troodos), habitat type (maquis, garrigue, pine forest, salt marsh, and disturbed mixture), and year (as a continuous variable), as well as interaction terms between season and area and also between habitat and year. In each model, we also included as fixed factors the numbers of individuals of each of the other two species to test for potential interspecific competition, and observer, to account for potential observer bias. In addition, we set site code as a random factor to account for variation across sampling sites in the models. All numeric covariates were centered and standardized (Schielzeth 2010). Best fit models were selected based on the lowest corrected Akaike Information Criterion (AICc) with those within $\Delta AICc < 2$ of the lowest scoring model considered equivalent (see Table A1.1). Selected models were validated with the *testResiduals* function provided in the DHARMA R package (Harting 2019). Graphical representations of fitted coefficients were produced using the Effects package (Fox and Weisberg 2018) in R.

We also performed an analysis for the relative importance and partitioning of variation for the covariates. To implement such analysis, we used a linear modeling approach following Essl et al. (2019); first, we square root transformed our response variable and fitted linear mixed-effects models (LMMs) equivalent to our GLMMs. We then ran linear models using all fixed effects of the GLMMs as independent variables after deducting the contribution of the linear random effects from the response

values. We then calculated the relative importance of the predictors (Table A1.2) by performing R² partitioning by averaging over orders (Lindeman 1980) using the *calc.relimp* function from the *relaimpo* R package (Grömping 2007).

Playback stimuli were used during the surveys to aid bird detection. This approach can, however, lead to a detection bias according to which female individuals might be underestimated because they tend to adopt a more cryptic behavior, particularly during the breeding season. Therefore, we ran a series of further GLMMs but using the number of males detected as the response variable instead of total birds. Comparing results of models with and without females included would provide insight into the magnitude of detection-bias that could result from the use of playbacks in surveys.

RESULTS

We completed 402 surveys within the 32 sample plots across the three seasons between 2013 and 2017. We found a total of 1138 individuals of the three target *Sylvia* species (Table 1), with the most abundant being Cyprus Warbler (590 individuals) followed by Sardinian Warbler (387 individuals) and Spectacled Warbler, which was the least represented in our surveys (161 individuals).

Table 1. Survey results throughout the duration of this study from 2013 to 2017. Most abundant was Cyprus Warbler (*Sylvia melanothorax*), followed by Sardinian Warbler (*S. melanocephala*) and Spectacled Warbler (*S. conspicillata*). We detected more males (M) than females (F).

Area	Cyprus Warbler			Sardinian Warbler			Spectacled Warbler		
	M	F	Total	M	F	Total	M	F	Total
Akamas	43	3	46	74	9	83	0	0	0
Kouklia	100	21	121	52	6	58	0	0	0
Akrotiri	210	37	247	163	24	187	50	12	62
Troodos	92	26	118	11	0	11	0	0	0
Larnaka/ Ammochostos	45	13	58	41	7	48	82	17	99
Total	490	100	590	341	46	387	132	29	161

Model validation with DHARMA confirmed the reliability of our estimates for the models of the three species (Table A1.3). We show that Cyprus Warbler significantly declined over the five years of the study (Table 2, Fig. 2, Table A1.3). We found that Cyprus Warbler was highly affected by habitat, which explained ~60% of the variation in the model (Table A1.2). Specifically, it was present in significantly lower numbers in disturbed mixture, garrigue, pine forest, and salt marsh habitats than in maquis (Fig. 3), and a negative interaction of disturbed mixture with year (marginally non-significant when analyzing males only, Table A1.4a), and positive interaction of garrigue with year, indicated that Cyprus warbler declined significantly more over time in disturbed habitat (and less in garrigue) than in maquis. Cyprus Warbler was also negatively associated with both Spectacled Warbler and Sardinian Warbler abundances. We found no differences between areas in Cyprus Warbler nor in the interaction of area with season (Fig. 4). The best supported model for Cyprus Warbler, however, included area and its interaction with season (Table A1.3), but an equivalent model ($\Delta AICc = 0.75$), excluding

those 12 non-significant areas and its interaction with season effects, revealed significantly lower numbers of Cyprus Warbler in winter compared to the breeding season (Table 2).

Table 2. Generalized Linear Mixed Model (GLMM) output for the effect of season, area, habitat type, year, and congener abundance, as well as the interactions of year with habitat, and season with area, on numbers of adult individuals of each *Sylvia* species that breeds in Cyprus, across 402 surveys. Significant results are presented in bold font.

(a) Cyprus warbler (<i>Sylvia melanothorax</i>)				
Random effects:	Variance	Std. dev		
Site code	0.706	0.840		
Fixed effects:	Estimate	Std. Error	z	p
Intercept	1.165	0.330	3.530	<0.001
Breeding	-0.007	0.091	-0.080	0.936
Wintering	-0.829	0.118	-7.008	<0.001
Disturbed mixture	-1.251	0.479	-2.612	0.009
Garrigue	-1.396	0.481	-2.900	0.003
Pine Forest	-1.197	0.473	-2.530	0.011
Salt marsh	-4.699	1.094	-4.294	<0.001
Year	-0.331	0.061	-5.354	<0.001
Spectacled warbler	-0.339	0.161	-2.467	0.013
Sardinian warbler	-0.160	0.055	-2.894	0.003
Disturbed mixture × year	-0.236	0.113	-2.092	0.036
Garrigue × year	0.269	0.117	2.283	0.022
Pine forest × year	0.183	0.109	1.682	0.092
Salt marsh × year	0.993	0.945	1.051	0.293
(b) Sardinian warbler (<i>S. melanocephala</i>)				
Random effects:	Variance	Std. dev		
Site code	0.094	0.307		
Fixed effects:	Estimate	Std. Error	z	p
Intercept	1.092	0.268	4.072	<0.001
Breeding	-0.735	0.278	-2.639	0.008
Wintering	-0.688	0.256	-2.683	0.007
Akrotiri	-0.708	0.279	-2.535	0.011
Cape Greko	-1.691	0.467	-3.618	<0.001
Kouklia	-1.213	0.427	-2.839	0.004
Troodos	-2.540	0.641	-3.959	<0.001
Disturbed mixture	0.035	0.221	0.159	0.873
Garrigue	-1.103	0.255	-4.324	<0.001
Pine Forest	-0.881	0.240	-3.662	<0.001
Salt marsh	-4.095	0.908	-4.510	<0.001
Year	-0.216	0.120	-1.794	0.072
Cyprus warbler	-0.159	0.069	-2.310	0.020
Observer 2	0.485	0.193	2.513	0.011
Breeding: Akrotiri	0.314	0.347	0.900	0.365
Wintering: Akrotiri	0.973	0.307	3.163	0.001
Breeding: Cape Greko	0.325	0.645	0.505	0.613
Wintering: Cape Greko	2.112	0.485	4.354	<0.001
Breeding: Kouklia	0.993	0.497	1.996	0.045
Wintering: Kouklia	1.513	0.443	3.415	<0.001
Breeding: Troodos	0.416	0.951	0.437	0.662
Wintering: Troodos	1.169	0.749	1.562	0.118
Disturbed mixture × year	0.161	0.119	1.354	0.175
Garrigue × year	0.309	0.162	1.907	0.056
Pine forest × year	0.420	0.154	2.718	0.006
Salt marsh × year	1.048	0.851	1.232	0.218
(c) Spectacled warbler (<i>S. conspicillata</i>)				
Random effects:	Variance	Std. dev		
Site code	20.140	4.488		
Fixed effects:	Estimate	Std. Error	z	p
Intercept	-7.772	2.323	-3.345	<0.001
Breeding	0.440	0.208	2.115	0.034
Wintering	0.357	0.205	1.744	0.081
Disturbed mixture	-0.236	2.566	-0.092	0.926
Garrigue	1.186	2.514	0.472	0.636
Pine Forest	-0.473	2.594	-0.182	0.855
Salt marsh	7.330	3.228	2.270	0.023
Observer 2	0.947	0.154	5.945	<0.001

Fig. 2. Plots illustrating fitted coefficients (black line) and 95% confidence intervals (shaded gray) of the best supported Generalized Linear Mixed Model (GLMM) for each species including year as a fixed factor in the model. Cyprus Warbler, *Sylvia melanothorax* (a) declined significantly over the period, while numbers of (b) Sardinian Warbler, *S. melanocephala* and (c) Spectacled Warbler, *S. conspicillata* were stable. Y axis is on a log scale.

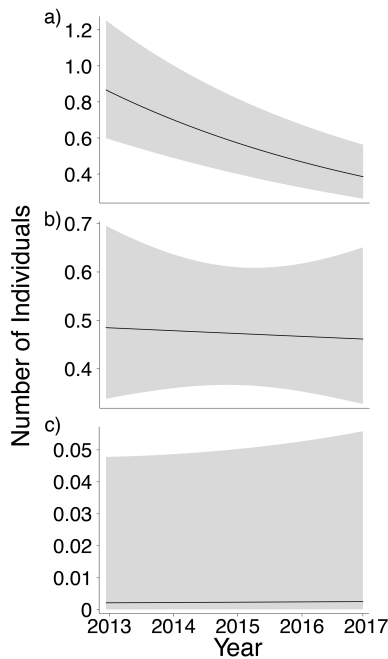


Fig. 3. Mean number of individuals (\pm SE) of each species per survey by habitat. Cyprus Warbler (*S. melanothorax*; dark gray) occurs in significantly greater numbers in maquis than in other habitats, while Sardinian Warbler (*S. melanocephala*; mid gray) occurs in similar numbers in disturbed habitats as in maquis. Spectacled Warbler (*S. conspicillata*; light gray) occurs mostly in salt marsh.

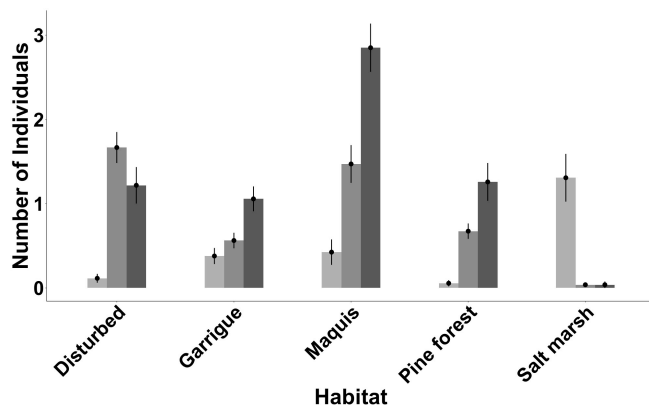
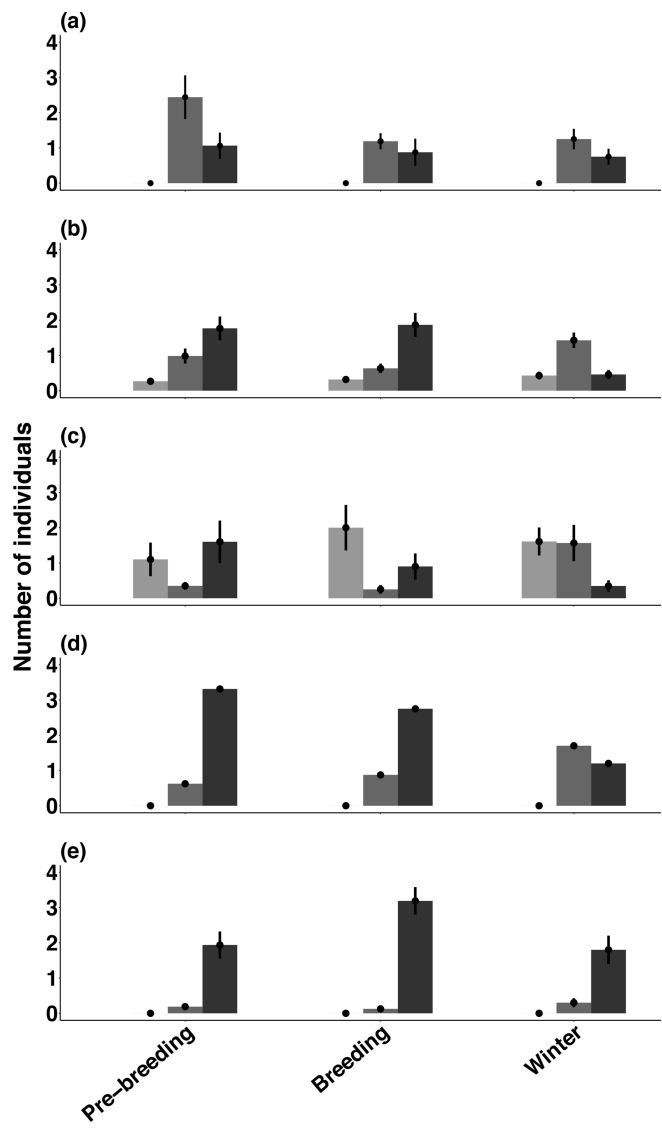


Fig. 4. Mean abundances of each species (\pm SE) across areas: (a) Akamas, (b) Akrotiri, (c) Larnaca/Ammochostos, (d) Koukليا, (e) Troodos, and between seasons. Sardinian Warbler (*Sylvia melanocephala*; mid gray) varies most by area and season of the three species, occurring in higher numbers in the pre-breeding season, and higher numbers overall in Akamas, but relatively lower numbers there in winter compared to Koukليا and Larnaca/Ammochostos compared to their relative abundances among those areas in the pre-breeding season. Cyprus Warbler (*S. melanothorax*; dark gray) differs in abundances only in Akrotiri, where it occurs in lower numbers in winter compared to its relative abundance between seasons in Akamas. Spectacled Warbler (*S. conspicillata*; light gray) was absent from surveys in three areas but occurred in most numbers in Larnaca/Ammochostos and was also present in Akrotiri, with numbers stable across seasons.



Sardinian Warbler occurred in significantly lower numbers during the breeding and wintering season compared to the pre-breeding season (Table 2, Fig. 4) and in all other areas compared to Akamas (Fig. 4). Our results also suggest that Sardinian Warbler occurred in relatively higher numbers during winter in Akrotiri and Larnaka/Ammochostos, and during winter and the breeding season (non-significant for males only) in Kouklia, than in Akamas, when compared with their relative abundances in the pre-breeding season. Habitat revealed to be the most influential variable in the best supported model for Sardinian Warbler, explaining approximately 50% of the variation (Table A1.2). However, in contrast to Cyprus Warbler, Sardinian Warbler occurred in lower numbers in garrigue, pine forest, and salt marsh compared to maquis; we did not find significant differences between their numbers in maquis and disturbed, mixed habitats (Fig. 3). But Sardinian Warbler also occurred in lower numbers where Cyprus Warbler occurred in higher abundances, and although there was no overall effect of year, it did occur in relatively higher numbers in pine forest than in maquis over time. In addition, there was an effect of observer, with observer 2 detecting relatively higher numbers of Sardinian Warbler compared to observer 1.

Spectacled Warbler was found in higher numbers in the breeding season compared to pre-breeding (non-significant for males only) and exhibited a highly significant preference for salt marsh habitat (with habitat explaining more than 90% of the variation in the model, see Table A1.2) over maquis (Table 2), while observer 2 again observed more Spectacled Warblers compared to observer 1.

Our results also show that the models with only male individuals of the three *Sylvia* species as response variable produced similar results to the models that included both males and females (Table A1.5). The only differences were those that might represent Type II errors resulting from smaller sample sizes, suggesting that the use of playback is unlikely to have significantly biased bird detection among the sexes during our surveys.

DISCUSSION

The present study is the first to comparatively assess the populations of all three *Sylvia* species breeding in Cyprus. Our results demonstrated a significant overall decline in the populations of Cyprus Warbler from 2013 to 2017, in line with and continuing on from the findings of previous studies in Cyprus (Pomeroy and Walsh 2000, Flint and McArthur 2014, Pomeroy et al. 2016, Hellicar and Kirschel 2021). On the other hand, Sardinian and Spectacled Warbler maintained stable populations throughout the study period.

The expected association of Cyprus Warbler with undisturbed maquis habitats (Cramp and Brooks 1992, Shirihai et al. 2001) represents a potential explanation for its decline. Indeed, across Cyprus, maquis as well as other natural habitats are negatively impacted by urbanization, wildfires and fragmentation (Vogiatzakis et al. 2008). These factors increase the pressure on Cyprus Warbler, which has to cope with smaller scattered patches of preferred habitat (Opdam 1991). Small fragmented habitats can increase the risk of local population decline (Fahrig 2002). Even in years with high breeding success when Cyprus Warbler can potentially exhibit local increases (Jones 2006), part of the

population is forced to disperse into the nearby fragmented habitat patches thus might be exposed to increased predation and decreased foraging success (Fahrig 2003). The decline we found in disturbed habitat is especially concerning, coupled with our results that suggest it occurs in lower numbers where Sardinian warbler is abundant, indicative of competition. By contrast, Cyprus Warbler may benefit from low intensity grazing within scrub habitat (Hellicar and Kirschel 2021), and high nature value farming practices (Hellicar et al. 2019).

Sardinian Warbler might take advantage of habitat fragmentation and expansion of disturbed mixtures, something that has been found to benefit some species (Fahrig 2003). Indeed, Sardinian Warbler was found in lower densities in natural habitats compared to Cyprus Warbler but occurred relatively more frequently in disturbed mixtures (Fig. 3), where the endemic may have declined more dramatically because of the combined effects of disturbance and competition. These differences in species densities might indicate that the decline of the Cyprus Warbler is not solely attributed to higher abundances of a newly established congener (Opdam and Wascher 2004), Sardinian Warbler, whose population at sites included in the study was stable from 2013 to 2017. But the presence of Sardinian Warbler alone might still negatively affect Cyprus Warbler populations, either through direct aggressive interactions or indirect effects such as disease spread (Jones 2006), or apparent competition (see Holt and Bonsall 2017).

Spectacled Warbler's preference for salt marsh habitat over maquis, and the avoidance of salt marsh by Cyprus Warbler, suggests that their different evolutionary histories constrained them from using similar habitats. As a result, they have historically coexisted in Cyprus (Cramp and Brooks 1992, Shirihai et al. 2001, Flint and McArthur 2014), independently of one another with Spectacled Warbler breeding in the most arid areas of the island (Flint and McArthur 2014), whereas Cyprus Warbler's distribution is confined by the 340 mm isohyet, thus avoiding the most arid regions.

Variation in species abundance among areas was really only evident in the recent colonist. The significantly lower abundance of Sardinian Warbler in all other areas compared to Akamas is indicative of its initial colonization and breeding population establishment there (Frost 1994, Shirihai et al. 2001, Flint and McArthur 2014, Pomeroy et al. 2016). Twenty-five years after its initial colonization of Cyprus in the early 1990s (Pomeroy and Walsh 2000), Sardinian Warbler has established a large breeding population on the island (Stylianou 2015) and is currently in an advanced colonization stage (Ricciardi et al. 2013). Its population stronghold remains in the west, but following dispersal southwards along the coast, it has progressively colonized areas to the east (Flint and McArthur 2014) where it is now a common breeder (Stylianou 2015). Sardinian Warbler is also a common wintering species in Cyprus (Shirihai et al. 2001, Flint and McArthur 2014), yet we found it is most abundant during the pre-breeding season in Akamas than in the breeding and wintering seasons. Cyprus resides on one of the main Afro-Palaearctic migration routes for many species (Hahn et al. 2009), including *Sylvia* warblers such as the Sardinian Warbler (Shirihai et al. 2001, Doswald et al. 2009). Sardinian Warblers migrate from Africa and fly over Cyprus (Shirihai et al. 2001), when they possibly use the

island as a stopover site, joining resident and late wintering birds, thus increasing local abundances. The migrating birds funnel through the Akamas Peninsula during spring where extensive maquis habitat might temporarily sustain the locally increased warbler populations. Sardinian warbler might also exhibit some local wintering movements, moving away from the northern Akamas site further south to Kouklia, Akrotiri, and Larnaca/Ammochostos. Nevertheless, our results indicate a lower abundance of Sardinian Warbler at higher elevations, consistent with it preferring lower elevations (Pomeroy and Walsh 2002, Ieronymidou et al. 2012).

There has been much debate regarding whether interspecific competition plays an important role in governing *Sylvia* warbler populations and their distributions (Cody and Walter 1976, Martin and Thibault 1996). Previous studies have suggested the presence of other breeding congeners in Cyprus might significantly affect population dynamics of the endemic Cyprus Warbler (Pomeroy and Walsh 2000, Pomeroy et al. 2016). In addition to differences in abundances attributed to habitats, seasons, and areas, we found a negative relationship between Sardinian Warbler and Cyprus Warbler abundances. Both Cyprus and Sardinian Warblers exhibited a preference for maquis habitat, yet consistent with Hellicar and Kirschel (2021) focusing on grazed natural scrub, we found that relative numbers of Cyprus and Sardinian Warbler were negatively associated with one another's density. Previous studies found no evidence of resource competition between Cyprus and Sardinian warbler in Cyprus (Jones 2006, Ieronymidou et al. 2012), but our results suggest there might be competition, though its effect appears to be comparatively much smaller on Cyprus Warbler numbers than that of habitat disturbance. A relative increase in Cyprus Warbler over time in garrigue might even represent displacement from maquis and recently disturbed mixtures.

Thus far no study has found evidence of direct interference competition between breeding *Sylvia* warblers in Cyprus, though this is something that needs further study. Based on the phenotypic similarity in plumage and song between Cyprus and Sardinian Warbler, direct interference competition might occur between the species, which studies in other phenotypically similar and closely related species of birds have shown can result in character displacement or competitive exclusion (e.g., Kirschel et al. 2009, 2019, 2020). Indeed, Cyprus Warbler has been shown to be attracted by playback of Sardinian Warbler song in Cyprus (Sebastianelli et al. 2020). Further work is thus needed to explore the possible effects of direct interactions between these *Sylvia* warbler species and how they might influence their coexistence and population dynamics. Our study does suggest however that habitat disturbance may be having a profound effect on Cyprus warbler numbers, with Sardinian warbler potentially benefiting as a result. The impact of habitat degradation on birds has long been established, and the insular endemic Cyprus warbler appears to be yet another species vulnerable to ongoing disturbance of natural habitats, compounding any possible competition with its recent colonizer.

Natural colonization events explain many of the present distributions of species, and ensuing interactions can lead to local changes in habitat use and might even lead to extinction, but the time scales of such taxon cycles are seldom known. Much research

has focused on the effect on insular endemics of species introduced to islands, with endemic species often disappearing within decades (Freed and Cann 2009). The influence of natural colonizations on insular endemics could be similar, but our study suggests that habitat disturbance may play a greater role than competition from a natural colonization on insular species range contraction and decline, though together these factors may provide added pressure on island endemics.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/1937>

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Table A 1.1. Model selection table based on corrected Akaike Information Criterion (AICc), in which the best three models with different combinations of predictors are compared for each response variable. Selected models for each response variable are indicated in bold. AICc, delta AICc, AICc weight, log-likelihood (LL) of each model, number of estimated parameters (K) as well as marginal and conditional R² are presented.

Model Description	AICc	Delta AICc	AIC weights	LL	K	Mar. R2	Con. R2
<i>S. melanothorax</i> ~ season*area + habitat * year + Spectacled warbler + Sardinian warbler + (1 site)	1054.16	0	0.49	-498.06	27	0.728	0.889
<i>S. melanothorax</i> ~ season + habitat * year + Spectacled warbler + Sardinian warbler + (1 site)	1054.91	0.75	0.34	-511.84	15	0.692	0.886
<i>S. melanothorax</i> ~ season + habitat * year + Spectacled warbler + Sardinian warbler + observer + (1 site)	1056.77	2.61	0.13	-511.68	16	0.692	0.887
<i>S. melanocephala</i> ~ season * area + habitat * year + Cyprus warbler + observer + (1 site)	917.63	0	0.54	-429.79	27	0.738	0.771
<i>S. melanocephala</i> ~ season * area + habitat * year + Cyprus warbler + Spectacled warbler + observer + (1 site)	918.35	0.71	0.38	-429	28	0.736	0.772
<i>S. melanocephala</i> ~ season * area + habitat * year + Cyprus warbler + Spectacled warbler + (1 site)	921.44	3.81	0.08	-431.7	27	0.736	0.772
<i>S. conspicillata</i> ~ season + observer + (1 site)	408.72	0	0.55	-199.28	8	0.003	1
<i>S. conspicillata</i> ~ season + habitat + observer + (1 site)	409.56	0.85	0.36	-195.55	9	0.240	1

<i>S. conspicillata</i> ~ season + habitat*year + observer + (1 site)	412.6	3.88	0.08	-191.76	14	0.240	1
Males <i>S. melanothorax</i> ~ season + habitat * year + Spectacled warbler + Sardinian warbler + (1 site)	945.3	0	0.44	-457.03	15	0.672	0.831
Males <i>S. melanothorax</i> ~ season * area + habitat * year + Spectacled warbler + Sardinian warbler + (1 site)	945.76	0.46	0.35	-443.86	27	0.710	0.870
Males <i>S. melanothorax</i> ~ season + habitat * year + Spectacled warbler + Sardinian warbler + Observer + (1 site)	947.26	1.96	0.17	-456.92	16	0.671	0.864
Males <i>S. melanocephala</i> ~ season * area + habitat * year + Cyprus warbler + observer + (1 site)	853.36	0	0.67	-397.66	27	0.707	0.738
Males <i>S. melanocephala</i> ~ season * area + habitat * year + Cyprus warbler + Spectacled warbler + observer + (1 site)	855	1.63	0.3	-397.32	28	0.705	0.739
Males <i>S. melanocephala</i> ~ season * area + habitat * year + Cyprus warbler + Spectacled warbler + (1 site)	859.69	6.33	0.03	-400.82	27	0.704	0.740
Males <i>S. conspicillata</i> ~ season + habitat + observer + (1 site)	364.95	0	0.77	-173.25	9	0.249	1
Males <i>S. conspicillata</i> ~ season + habitat * year + observer + (1 site)	367.77	2.82	0.19	-169.34	14	0.256	1
Males <i>S. conspicillata</i> ~ season + habitat * year + Cyprus warbler + Spectacled warbler + observer + (1 site)	371.16	6.21	0.03	-168.87	16	0.276	1

Table A 1.2. The table shows relative importance proportions (lmg metrics) for the covariates of the linear models having all individuals of a) Cyprus, b) Sardinian and c) Spectacled warbler and their respective males (d, e, f) as response variables. All response variables have been square root transformed.

a) Cyprus warbler	lmg
Fixed effects:	
Season	0.157
Habitat	0.604
Year	0.040
Spectacled warbler	0.115
Sardinian warbler	0.038
Habitat × year	0.043
b) Sardinian warbler	
Fixed effects:	
Season	0.108
Area	0.218
Habitat	0.492
Year	0.018
Cyprus warbler	0.014
Observer	0.011
Season × area	0.092
Habitat × year	0.042
c) Spectacled warbler	
Fixed effects:	
Season	0.027
Habitat	0.941
Observer	0.030
d) Cyprus warbler males	
Fixed effects:	
Season	0.164
Habitat	0.589
Year	0.047
Spectacled warbler	0.111
Sardinian warbler	0.038
Habitat × year	0.048

e) Sardinian warbler males

Fixed effects:

Season	0.119
Area	0.211
Habitat	0.490
Year	0.018
Cyprus warbler	0.018
Observer	0.015
Season × area	0.085
Habitat × year	0.040

f) Spectacled warbler males

Fixed effects:

Season	0.017
Habitat	0.956
Observer	0.025

Table A 1.3. Output of validation tests performed with DHARMA. The table shows results for one-sample Kolmogorov-Smirnov (KS) test, non-parametric dispersion test and bootstrapped outlier test for the models of the three *Sylvia* species.

Cyprus Warbler:

KS test	D = 0.042	$p = 0.453$	
Dispersion test	Disp. = 0.398	$p = 0.4$	
Outlier test	Freq. = 0.002	$p = 1$	Exp. Freq = 0.004

Sardinian Warbler:

KS test	D = 0.031	$p = 0.824$	
Dispersion test	Disp. = 1.024	$p = 0.776$	
Outlier test	Freq. = 0	$p = 0.6$	Exp. Freq = 0.003

Spectacled Warbler:

KS test	D = 0.065	$p = 0.065$	
Dispersion test	Disp. = <0.001	$p = 0.08$	
Outlier test	Freq. = 0	$p = 1$	Exp. Freq = 0.007

Table A 1.4. Best fit model for effect of season, area, habitat type, year and other *Sylvia* species abundance, as well as the interactions of year with habitat and season with area, on the number of adult individuals of *Sylvia melanothorax* Cyprus, across 402 surveys. Significant results are presented in bold font.

Random effects:	Variance	Std. dev		
Site code	0.605	0.778		
Fixed effects:	Estimate	Std. Error	z	p
Intercept	0.609	0.545	1.117	0.263
Breeding	-0.303	0.364	-0.835	0.403
Wintering	-0.464	0.356	-1.303	0.192
Akrotiri	0.512	0.544	0.941	0.346
Cape Greko	0.683	0.657	1.040	0.298
Kouklia	1.062	0.641	1.657	0.097
Troodos	0.683	0.650	1.052	0.292
Disturbed mixture	-1.265	0.449	-2.818	0.004
Garrigue	-1.369	0.450	-3.037	0.002
Pine Forest	-1.161	0.442	-2.626	0.008
Saltmarsh	-4.530	1.073	-4.220	<0.001
Year	-0.334	0.061	-5.405	<0.001
Sardinian warbler	-0.117	0.056	-2.076	0.037
Spectacled warbler	-0.344	0.147	-2.343	0.019
Breeding × Akrotiri	0.340	0.387	0.878	0.380
Wintering × Akrotiri	-0.791	0.419	-1.888	0.058
Breeding × Cape Greko	-0.269	0.469	-0.573	0.566
Wintering × Cape Greko	-0.951	0.536	-1.774	0.076
Breeding × Kouklia	0.169	0.420	0.404	0.686
Wintering × Kouklia	-0.474	0.440	-1.075	0.282
Breeding × Troodos	0.796	0.429	1.855	0.063
Wintering × Troodos	0.365	0.433	0.844	0.398
Disturbed mixture × year	-0.232	0.113	-2.055	0.039
Garrigue × year	0.275	0.118	2.332	0.019
Pine forest × year	0.168	0.108	1.544	0.122
Saltmarsh × year	0.972	0.936	1.038	0.299

Table A 1.5. GLMM results of the best supported models (based on lowest AICc score), for the effect of season, area, habitat type, year and other *Sylvia* species abundance, as well as the interactions of season with area, on the number of male individuals of each *Sylvia* species that breeds in Cyprus. Significant results are presented in bold font.

a) Cyprus warbler males

Random effects:	Variance	Std. dev		
Site code	0.675	0.821		
Fixed effects:	Estimate	Std. Error	z	p
Intercept	1.042	0.325	3.205	0.001
Breeding	-0.049	0.100	-0.491	0.623
Winter	-0.898	0.130	-6.875	<0.001
Disturbed mixture	-1.327	0.475	-2.789	0.005
Garrigue	-1.480	0.480	-3.080	0.002
Pine Forest	-1.150	0.466	-2.466	0.013
Saltmarsh	-4.547	1.086	-4.186	<0.001
Year	-0.378	0.067	-5.632	<0.001
Spectacled warbler	-0.365	0.165	-2.207	0.027
Sardinian warbler	-0.171	0.059	-2.896	0.003
Disturbed mixture × year	-0.244	0.127	-1.915	0.055
Garrigue × year	0.298	0.130	2.296	0.021
Pine forest × year	0.197	0.118	1.669	0.095
Saltmarsh × year	1.032	0.941	1.097	0.272

b) Sardinian warbler males

Random effects:	Variance	Std. dev		
Site code	0.093	0.305		
Fixed effects:	Estimate	Std. Error	z	p
Intercept	0.913	0.271	3.358	<0.001
Breeding	-0.801	0.300	-2.667	0.007
Wintering	-0.668	0.269	-2.482	0.013
Akrotiri	-0.731	0.285	-2.558	0.010
Cape Greko	-1.547	0.466	-3.319	<0.001
Kouklia	-1.046	0.426	-2.453	0.014
Troodos	-2.396	0.641	-3.738	<0.001
Disturbed mixture	0.053	0.222	0.239	0.810
Garrigue	-1.088	0.258	-4.208	<0.001
Pine Forest	-0.815	0.242	-3.369	0.001
Saltmarsh	-3.946	0.905	-4.359	<0.001

Year	-0.215	0.129	-1.662	0.096
Cyprus warbler	-0.193	0.074	-2.598	0.009
Observer 2	0.569	0.205	2.768	0.005
Breeding: Akrotiri	0.346	0.377	0.918	0.358
Wintering: Akrotiri	1.003	0.324	3.092	0.001
Breeding: Cape Greko	0.160	0.692	0.232	0.816
Wintering: Cape Greko	1.901	0.497	3.824	<0.001
Breeding: Kouklia	0.898	0.521	1.721	0.085
Wintering: Kouklia	1.347	0.454	2.965	0.003
Breeding: Troodos	0.501	0.959	0.523	0.601
Wintering: Troodos	1.155	0.753	1.532	0.125
Disturbed mixture × year	0.197	0.127	1.551	0.120
Garrigue × year	0.325	0.174	1.867	0.061
Pine forest × year	0.433	0.161	2.684	0.007
Saltmarsh × year	1.068	0.846	1.263	0.206

c) Spectacled warbler males

Random effects:	Variance	Std. dev		
Site code	16.57	4.071		

Fixed effects:	Estimate	Std. Error	z	p
Intercept	-7.275	2.292	-3.174	0.001
Breeding	0.294	0.223	1.320	0.186
Wintering	0.190	0.220	0.861	0.383
Disturbed mixture	-0.274	2.444	-0.112	0.910
Garrigue	1.200	2.401	0.500	0.617
Pine Forest	-0.595	2.495	-0.239	0.811
Saltmarsh	6.744	3.064	2.201	0.027
Observer 2	0.898	0.176	5.089	<0.001
