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Changes in Population Densities of Two White-Eye Species (Passeriformes: Zosteropidae) Along an Altitudinal Gradient in Sri Lanka

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ABSTRACT

Understanding relationships between population density and habitat quality are crucial in bird conservation attempts. The present study was conducted to document the densities of Sri Lanka White-Eye (*Zosterops ceylonensis*) (SLWE) and Oriental White-Eye (*Z. palpebrosus*) (OWE) in solitary and co-existence situations. Censuses of the two white-eye species were conducted in their allopatric and sympatric zones, between September 2017 and June 2019. The allopatric ranges of both species acted as 'controls' for this experiment. Analysis of covariance was used to capture the changes in densities in zones of allopatry whereas, correlation test was done to analyze density changes in sympatric zone. Results showed that there was a marked decline in density of OWE from the end of its allopatric zone to the beginning of sympatric zone. SLWE showed no such change. One-way ANOVA showed that the changes in densities with elevation were significant ($P<0.01$), which was supported by the analysis of covariance ($P<0.01$). A significant negative correlation ($P<0.01$) of density in sympatry with increasing elevation was observed for OWE while SLWE showed no significant correlation between density and elevation, and no negative correlation of densities in sympatry. Association of density of OWE with changes in habitat with elevation was suggested as one possibility since forest structure alone does not limit the distribution of OWE according to its pattern on distribution in India where OWE is the sole white-eye species. Previous studies have also shown that at least one of these species show some character displacement in the sympatric zone. Thus, it can be inferred that SLWE has evolved with sufficient differences for ecological isolation from OWE. This has resulted in ecological release to certain extent where OWE must have been replaced with changes in vegetation structure together with competition from its congeneric species.

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INTRODUCTION

The occurrence of a given species at a given habitat depends on specific environmental conditions (Lisboa and Freire, 2012). Therefore, comparing densities among habitats are essential in understanding ecological patterns and processes. Applied research directed at bird conservation regularly attempts to understand habitat preferences, and the relationships between population density and habitat quality or area (Sutherland *et al.*, 2004). Some authors have traced sharp discontinuities in distributions of bird species with respect to habitat structure by using presence/absence data alone (MacNally, 1990) confirming that this approach appears to be sensitive to sampling of habitat types.

Competition theory predicts that populations of a species that occur in areas or habitats lacking one or more competing species, that exploit some of the same resources, should exhibit ecological release relative to populations occupying similar situations where the competing species are present (MacArthur *et al.*, 1972; Wright, 1980; Pianka, 1981; Wiens, 1989). Population densities may thus be high in the absence of competitors (Wiens, 1989) leading to density compensation (MacArthur *et al.*, 1972; Wright, 1980) where niche breadth of the population can increase with habitat, elevation, foraging or diet. Morphology of these populations may shift in the direction of the missing species, through character displacement (Grant, 1972).

Density compensation can also occur in some guilds within a community (Wiens, 1989). Cody (1983) found that numbers of South African afromontane forest bird species declined along a gradient of increasingly smaller and more isolated habitat-islands where. vegetation structure varied considerably across the gradient. For the Cape white-eye (*Zosterops pallidus*), density decreased from 2.5 pairs/ha where it occurred alone and with a single additional species, down to one third of this level where it coexisted with four additional species (Grant, 1972).

A strong correlation between the total vegetation volume and breeding bird density has been recorded previously for some bird communities in Arizona and New Mexico in the United States (Mills *et al.*, 1991). Swift *et al.* (1984) showed that significant variation in total breeding bird density and abundance in some feeding guilds could be explained by habitat variables. Another study by Andrén (1992) showed that, in Sweden, the density of corvids increased as forest became fragmented and intermixed with agricultural land. Similarly, a number of other studies have shown correlations of bird density and diversity with vegetation (Hooper *et al.*, 1973; Cody, 1981; James and Wamer, 1982; Kutt, 1996; Kinley and Newhouse, 1997; Moreira, 1999; Fondell and Ball, 2004; Winter *et al.*, 2005; Fischer *et al.*, 2012).

In the present study, two closely related white-eye species found in Sri Lanka were used as a model system to investigate species replacement through local adaptation as a result of competition. The two species were Sri Lanka White-Eye (SLWE); *Zosterops ceylonensis*, which is endemic to Sri Lanka, and Oriental White-Eye (OWE); *Z. palpebrosus*, which is a native species in Sri Lanka, also found in other countries. The former is slightly larger in size, has a stronger bill, and darker olive and lesser yellow back side (Ali and Ripley, 2001). The SLWE inhabits exclusively the high elevations.

SLWE is usually found in pairs during the breeding season. Outside the breeding season, it may be found in large scattered flocks (Ali and Ripley, 2001). It appears to be more sociable than the OWE which is found in forests, groves, gardens, orchards, and also in mangroves (Ali and Ripley, 2001). OWE usually goes in pairs or small flocks, frequently in company with small babblers or other insectivorous bird species (Henry, 1971; Ali and Ripley, 2001). It is an entirely arboreal species, only descending to ground level to bathe.

According to the preliminary studies it was observed that there is a marked decline in the density of OWE from the end of its allopatric zone to the beginning of the sympatric zone, whereas the SLWE does not show such a change between allopatric and sympatric zones. The density of the OWE decreased from the lower end of the zone of sympatry to the upper end of the zone of sympatry indicating that there is gradual replacement of the OWE in the upper elevations. This gradual replacement may partly be due to certain morphological differences (Wijesundara and Freed, 2018). Thus, the objective of the present study was to assess the variations of densities of the two white-eye species where they co-exist and exist separately.

MATERIALS AND METHODS

Censuses of the two white-eye species were conducted in areas of allopatry and sympatry of the species, between September 2017 and June 2019 (Table 1). Censuses were conducted between sunrise and sunset of each census day, with peak counting hours between 0630 h and 1000 h and 1530 h and 1830 h. The peak counting hours represented the time period of the day when birds were most active (Mulwa *et al.*, 2007). All field observations were carried out by the first author.

Birds were counted using a line transect integrated point count method along lines located using a systematic random procedure according to the Distance Sampling Protocol (Buckland *et al.*, 1993; Buckland *et al.*, 2001; Thomas *et al.*, 2002; Thomas *et al.*, 2010a). When using line transects integrated with point counts, some important features of Distance Sampling are that radial distance should be measured from the observer to the animal's original location, movement of animals after detection is not a problem as long as the original location can be established accurately and the appropriate distance was measured. It is of concern if an animal is detected more than once along the same transect, and the program fully allows for the fact that many animals not on the point count station will remain undetected (Buckland *et al.*, 1993; Buckland *et al.*, 2001).

Birds were censured in a total of 47 point transects covering all habitats in the zones of allopatry and sympatry of both species (Figure 1), with at least two replicates per elevation. The number and length of transects were determined by the total area of the habitat available. Whenever possible, existing trails were uased to avoid cutting of vegetation. When using point counts, this layout was permissible (Buckland *et al.*, 1993, Buckland *et al.*, 2001).

Table 1: Sampling areas in the allopatric and sympatric areas of the two white-eye species for density estimation (OWE=Oriental White-Eye; SLWE=Sri Lanka White-Eye; NP=National Park; SNR=Strict Natural Reserve; VRR=Victoria-Randenigala-Rantambe).

Area	Species
Hantana	OWE allopatric
Dekinda	OWE allopatric
Alagalla	OWE allopatric
Naranga	OWE allopatric
Kaluwagala	OWE allopatric
VRR Sanctuary	OWE allopatric
Ramboda	OWE allopatric
Bambarakele	OWE/SLWE sympatric
Bomuralla	OWE/SLWE sympatric
Galway's Land NP	OWE/SLWE sympatric
Hakgala SNR	OWE/SLWE sympatric
Ambewela	OWE/SLWE sympatric
Pattipola	SLWE allopatric
Horton Plains NP	SLWE allopatric

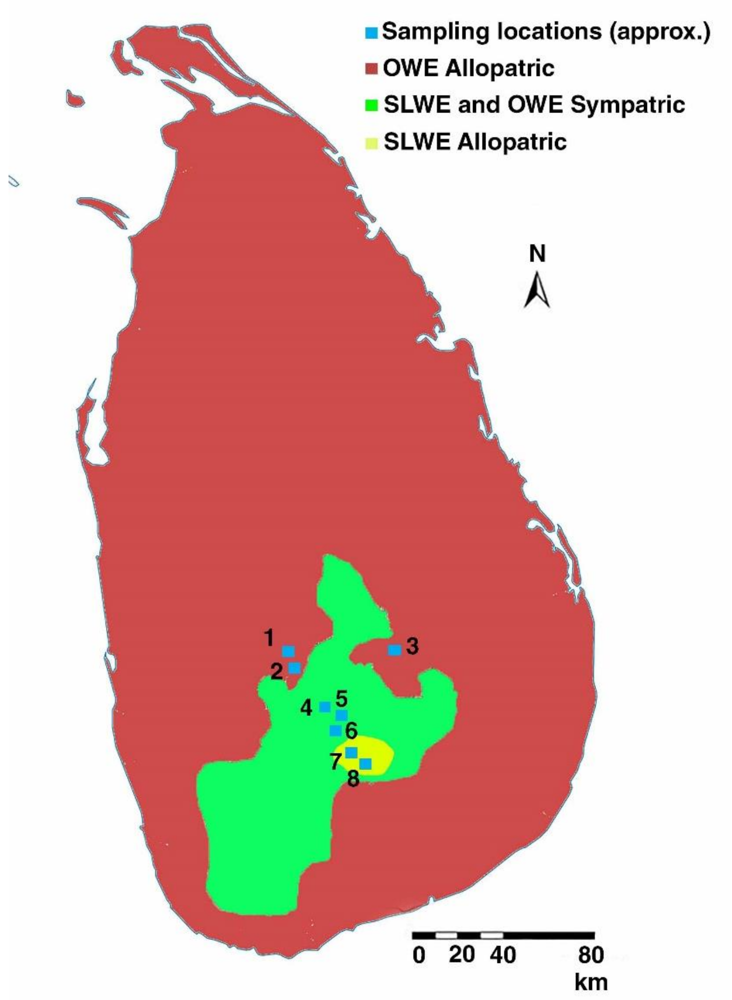

Figure 1: Distribution of Sri Lanka white-eye (SLWE) and Oriental white-eye (OWE). Sampling locations in the present study are shown as blue squares each of which had six sampling sites except location 4, which had only five (Modified from Wijesundara and Freed, 2018).

The allopatric ranges of both species considered as controls for the study. About 10-15 minutes were spent at each point count station. Once an individual or a group of individuals (flock) was seen or heard, the original locations were noted down and the distance was estimated using a range-finder (Bushnell Yardage Pro Compact 800, Bushnell Corporation, Kansas, U.S.A.), and the number of individuals (in the case of flocks) were counted. For observing birds and counting individuals in each flock, 8 × 40 and 10 × 42 standard birding binoculars (Nikon 8 × 40 Action Extreme; Nikon Monarch 10 × 42) were used. In places where dense canopy made it impossible to count individuals because of low visibility, counting was done when the birds moved from one tree to another, following the method employed by Mulwa *et al.* (2007). To minimize time-of-day bias, each point count station was given an equal chance of visitation during different times of day. By dividing the day into different census sessions (e.g. 0630-1000 h and 1530-1800 h), it was possible to spend approximately equal amount of sampling in each session during the study period. On each visit, the radial distance to the individual or flock from the point count station was estimated and the flock size was noted. DISTANCE version 6.2 (Thomas *et al.*, 2010b) was used to analyse the data.

Analysis of covariance was done to analyse the changes in densities in the zones of allopatry. The model included density from beginning of zone with species as a factor. Correlation test was carried out to analyze the changes in densities in the zone of sympatry. Results were considered significant at $\alpha = 0.05$. Both tests were carried out using Minitab 16 statistical software (Minitab, Inc., 2010).

RESULTS AND DISCUSSION

Comparing densities is important given the size of the zone of sympatry, which is greater than those described in most previous studies of species replacement (Haffe,r 1969; Terborgh, 1971; Diamond, 1973; Haffer, 1974; Terborgh, 1977; Mallet-Rodrigues *et al.*, 2010). Table 2 shows the densities of the two white-eye species in the study areas in sympatric and allopatric zones. Changes of density of two species of white-eyes along an altitudinal gradient (Figure 2) showed that there was a marked decline in the density of the OWE from the end of its allopatric zone to the beginning of its sympatric zone, and in general, it showed a trend of decreasing density with increasing altitude. The SLWE showed no such change from its sympatric to allopatric zones. The highest density of OWE was recorded at an elevation of 550 m a.s.l., and the lowest at Ambewela (1842 m a.s.l.). This species was not found beyond that elevation. Density of SLWE also showed a slight decreasing trend but was not as sharp as that of the OWE. In general, the density of the SLWE was more or less the same throughout its range, from 1745 m to 2165 m. Within the zone of sympatry, the OWE showed a decreasing trend in its density from the edge of its allopatric range to the edge of the allopatric range of the SLWE.

Both one-way ANOVA and analysis of covariance confirmed that densities of SLWE changed significantly ($P < 0.01$) with elevation. According to the Pearson correlation test for sympatric area there was a significant negative correlation of density with increasing elevation for the OWE ($P < 0.01$) while SLWE showed no significant correlation.

Even though it was expected that there could be a negative correlation of densities in the overlapping range, it was not shown by SLWE, suggesting that only OWE density is associated with habitat in the zone of sympatry. During the present study, it was observed that the habitat changed with elevation. The nature of tree species changed with elevation, from the beginning to the end of the zone of sympatry. In general, the trees became shorter in height from the edge of its allopatric range to the edge of the allopatric range of the SLWE. At the highest elevations, the forest becomes a 'pygmy forest', and this is where the SLWE was observed in allopatry. In this zone, it was noted that the structure of the trees was different where trees were often gnarled, with rough bark, and they rarely exceeded 20 m in height. This has also been observed previously by Perera (1975).

In India, where only the OWE is found, the vegetation structure changes with elevation (Blasco *et al.*, 1996; Ali and Ripley, 2001). However, OWE in India is found from the sea level up to the summits of high mountains. Therefore, the forest structure alone does not seem to limit the distribution of OWE. In Sri Lanka, the gradual replacement of OWE by SLWE starts approximately at an elevation of 1700 m a.s.l., and the former species is completely replaced by the latter species at an elevation of about 1900 m a.s.l. The vegetation type in this zone is montane rainforests. Thus, the vegetation structure alone is not the cause of this replacement. In fact, in the present study, it was found that SLWE did not change its density significantly from the allopatric to the sympatric zones. However, the SLWE was found in its maximum density in the sympatric zone (Bomuralla site, 24.2 birds/ha). This has previously been reported for birds in New Guinea (Diamond, 1973) where two species of warblers, *Crateroscelis murina* and *C. robusta*, which differ ecologically in their altitudinal range, replaced each other at a certain elevation in which they had their maximum abundance. Accordingly, with increasing elevation *C. murina* became increasingly abundant, and at 1643 m, which is not far from its altitude of maximum abundance, it suddenly disappeared while *C. robusta* suddenly appeared near its maximum abundance.

Table 2: White-eye densities (birds per ha) in surveyed areas in sympatry and allopatry. [OWE=Oriental White-Eye; SLWE=Sri Lanka White-Eye; ALLO=Allopatric; SYM=Sympatric; NP=National Park; SNR=Strict Natural Reserve; VRR=Victoria-Randenigala-Rantambe]

Species-Allopatic/Sympatric-Area	Elevation (m a.s.l.)	Density Estimate of OWE (± SE)	Density Estimate of SLWE (± SE)
OWE-Allo-Hantana	540	14.61 ± 3.88	
OWE-Allo-Dekinda	490	15.67 ± 3.03	
OWE-Allo-Alagalla	609	17.31 ± 8.01	
OWE-Allo-Naranga	544	22.05 ± 12.2	
OWE-Allo-Kaluwagala	559	18.06 ± 7.38	
OWE-Allo-VRR Sanctuary	201	16.32 ± 5.89	
OWE-Allo-Ramboda	964	14.16 ± 7.49	
OWE-SLWE Sym-Bambarakele	1910	2.74 ± 2.10	23.93 ± 11.69
OWE-SLWE Sym-Bomuralla	1805	4.91 ± 4.02	24.22 ± 5.48
OWE-SLWE Sym-Galway's Land NP	1935	1.62 ± 1.48	19.55 ± 8.26
OWE-SLWE Sym-Hakgala SNR	1891	2.59 ± 1.43	18.73 ± 7.24
OWE-SLWE Sym-Ambewela	1846	1.44 ± 1.11	20.73 ± 15.06
SLWE-Allo-Pattipola	1972		22.57 ± 22.91
SLWE-Allo-Horton Plains NP	2111		20.66 ± 18.87

In the present study, the OWE showed its maximum density in its allopatric zone, while its density was drastically reduced (from 14.16 birds/ha to 2.58 birds/ha) in the sympatric zone (Figure 2). In general, the vegetation structure did not change drastically in this area, but there was a marked decline in the OWE in the presence of the SLWE. Furthermore, the average density for this species in the allopatric zone was 16.87 birds/ha whereas the average density in the sympatric zone was 2.66 birds/ha. The SLWE did not show a significant change in its average density in allopatric and sympatric zones (i.e. 21.61 and 21.43 birds/ha respectively). A previous study has shown that the density of the Cape White-Eye (*Zosterops pallidus*) decreased from 2.5 pairs/ha where it occurred alone and with a single additional species, down to one third this level where it coexisted with four additional species (Cody 1983). This trend of declining density in higher-diversity systems was not shown by any of the other species in Cody's study system. The summed density of the two white-eye species was more or less constant in the sympatric zone (Figure 2). This observation is consistent with observations of Cody (1983) for South African Afromontane forest birds.

It has previously been reported that SLWE had some of its morphological measurements diverged in the sympatric zone (Wijesundara and Freed, 2018). As shown in their study, SLWE in the sympatric zone had a significantly different bill length and width from those in the allopatric zone, suggesting that SLWE has evolved sufficient differences to be ecologically isolated from its congeneric species, the OWE. This has resulted in ecological release (lack of competition) to a certain extent. Together with changes in vegetation structure and the competition from its congeneric species, the OWE must have been replaced.

Competition is evident in the changes of some morphological characters, especially those related feeding. The OWE is generally observed at high foraging levels (heights) in its allopatric range. The SLWE is observed to be equally at home both at high and low foraging levels. These observations are consistent with the observations of previous workers (Legge, 1880; Wait, 1922; Wait, 1925; Henry, 1971; Henry, 1998; Ali and Ripley, 2001). The shortening of vegetation structure explains part of the reason for lowered densities of the OWE starting from the lower end of the sympatric zone to the higher end of the sympatric zone.

OWE has been observed to breed in India at 3000 m altitude in the Himalayas (Ripley, 1982), where in the summer, the mean annual temperatures range from 15 to 18 ˚C. However, in Sri Lanka, the highest point OWE was found was 2484 m a.s.l., and only the SLWE could be observed beyond this elevation. The mean annual temperature at these elevations, where the SLWE breeds, is below 15 ˚C. On average, the sympatric zone of the two species has a mean annual temperature in the range of 15 to 17 ˚C, whereas the allopatric zone of OWE has a mean annual temperature of above 22 ˚C. Therefore, it seems that temperature does not limit the distribution of the OWE.

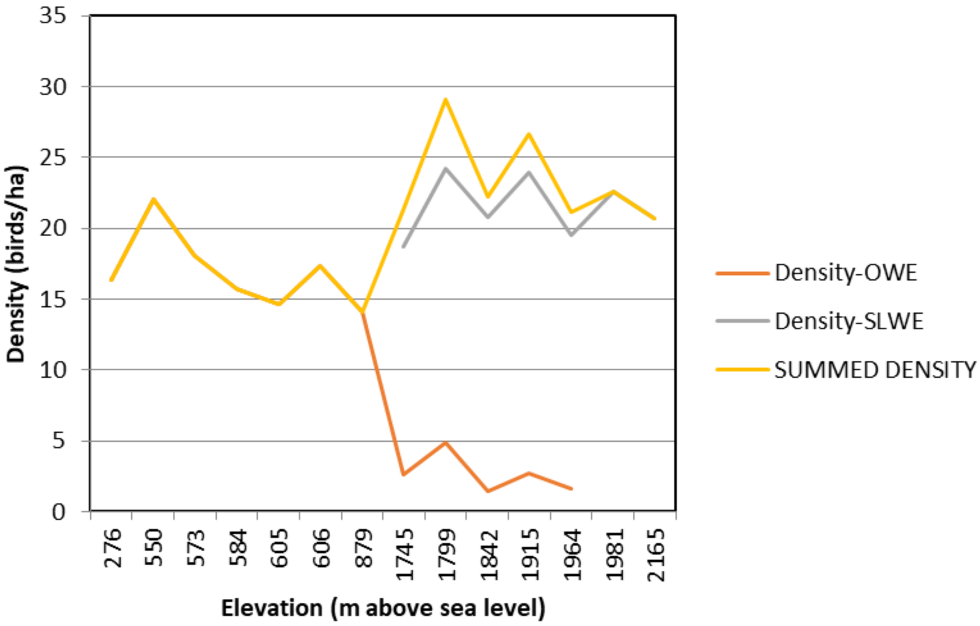

Figure 2: Density of the Oriental White-Eye (OWE) and Sri Lanka White-Eye (SLWE) on an altitudinal gradient.

CONCLUSIONS

According to the results obtained by the present study, the reasons for replacement of the OWE with the SLWE may partly be related to changes in vegetation structure along with competition from its congeneric species. The SLWE was found in its maximum density in the sympatric zone. The coexistence of the two congeneric species has resulted in divergence of foraging heights and morphological characters in the sympatric zone.

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