Winter Ecology of Three Species of *Phylloscopus* Warblers

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By

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CERTIFICATE

This is to certify that *Ms. Mousumi Ghosh* of the Wildlife Institute of India, Dehradun has carried out original research work titled **'Winter ecology of three species of *Phylloscopus* warblers'** towards the partial fulfillment of the M. Sc (Wildlife Science) degree from Saurashtra University, Rajkot, India. The study was conducted under our supervision from November, 2006 to June, 2007. I also certify that this research work has not been submitted for the award of any other degree to any University.

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Contents

1.1 Review of literature

3. Study area

4. Methods

4.3 Behaviour

4.5 Analysis

5. Results

5.5 Behaviour

6. Discussion

6.1 Patterns of species occupancy rates

6.2 Segregation by foraging behaviour

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

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Summary

This study focussed on three species of *Phylloscopus* warblers, *P. humei*, *P. xanthoschistos*, and *P. chloronotus* which overwinter sympatrically in the foothills of western Himalayas. The patterns of habitat occupancy, foraging behaviour, and foraging microhabitat of three species of warblers were examined to determine the nature of ecological complementarity facilitating their co-existence in the non-breeding season. Moreover, investigating the morphology-ecology associations among congeners also becomes critical since recent divergence may hinder our understanding of the mechanisms of their ecological segregation, as is the case with these species. Hence, morphology-ecology associations were also examined. A total of 91 points were sampled for bird detections five times each between December 2006 and March 2007. Prey abundances across habitat types were quantified. Behavioural data was also collected. The three species were found to differ in the occupancy of the sampled area. However, the bird occupancy did not correlate with differences in prey abundances across habitat types. The warbler species showed clear segregation in the use of foraging behaviour, foraging microhabitat, and proportion of large prey intake. The movement pattern was also found to vary across the three species. Morphology-ecology associations revealed the close interaction of morphology and ecology in shaping the ecological segregation of the three species in the non-breeding season. One major finding was that *P. xanthoschistos* is able to meet its demand for large arthropods in this northern site (31.5 % large prey intake) previously believed to be low in large arthropod abundance. Finally, the study demonstrated that the ecology of *P. xanthoschistos* (previously *Seicercus*) is very similar to other members of the genus *Phylloscopus*.

1. INTRODUCTION

The genus *Phylloscopus* comprises of the Old World leaf warblers most of which breed in the temperate areas of Europe and Asia, and overwinter in Africa, Southern Europe, India, and Southeast Asia. Including 15 species (six in Africa, eight in Southeast Asia and one in Canary Island) which are known to be non-migratory (Price et al. 1997), forty-nine species of the genus have been described (Monroe & Sibley 1993, Alstrom et al. 1992, Olsson et al. 1993, Alstrom & Olsson 1995). The recent generic shift of *Seicercus xanthoschistos* into *Phylloscopus xanthoschistos* (Olsson et al. 2004, Alstrom et al. 2006) has added another species to the genus and revealed that the genus was not monophyletic as previously held (Price et al. 1997). This genus has been the subject of some notable ecological studies owing to the remarkable species diversity, close relatedness among species, and very similar morphology and ecology (Gaston 1974, Price 1991, Price et al. 1997, Forstmeier et al. 2001). In addition, the phylogeny of most of the species is well worked out based on mtDNA sequences (cytochrome b), which allows better understanding of ecological relationships by controlling for phylogeny (Price et al. 1997).

The present study looks at the factors permitting the co-existence of three species of *Phylloscopus* warblers, Lemon-rumped Warbler *Phylloscopus chloronotus*, Hume's Warbler *Phylloscopus humei,* and Grey-hooded Warbler *Phylloscopus xanthoschistos* in their winter quarters in the Shiwalik hills of Himachal Pradesh. In the breeding season, *P. humei* ranges in mixed fir and birch forests in the hills and mountains of southern-central Asia, from western Himalayas north to Sayan and Altai Mountains (Baker 1997, Kazmeirczak 2000). In winter, the species is widespread in the deciduous forests and scrubs in the northern part of the Indian subcontinent (between approximately 32°N and 15°N), and Southeast Asia (Ali & Ripley 1983, Gross & Price 2000). The breeding range of *P. chloronotus* extends mostly in the tall conifer forests with dense shrub undergrowth, from the mountains of Safed Koh in eastern Afghanistan, towards northwestern Himalayas and east to northern Burma, and further northwards to the mountains of western China (Ali & Ripley 1983). It winters in the lower elevation woods and bush-covered hillsides, and is known to sometimes flock with other itinerant parties of small passerines (Baker 1997). *P. xanthoschistos* is a common resident in the western Himalayas from northwestern Pakistan, Kohat and Kashmir, and the distribution extends along the Himalayas to Arunachal Pradesh in northeastern India (Ali & Ripley 1983). It is subject to summer-winter vertical movements. In the breeding season, it typically inhabits open coniferous, evergreen or deciduous hill forests; in winter participates in mixed species flocks keeping mostly to middle and lower storey and upper strata of shrubs (Baker 1997).

This study looked at the non-breeding patterns of coexistence of the three species of warblers in terms of their occupancy, foraging behaviour and microhabitat, movements, and morphology-ecology associations. Another objective of the study was to assess the ecology of *P. xanthoschistos* following its inclusion into the genus based on phylogenetic evidences. Also, the overwintering of *Phylloscopus xanthoschistos* in the northern latitudes contradicts the negative correlation of body size with non-breeding latitude as demonstrated among over-wintering warblers of the genus *Phylloscopus* in response to decline in large prey abundance towards northern latitudes (Katti & Price 2003, Trevor Price *pers. commun.*). Hence, another objective of the study was to examine the manner in which the species optimizes the intake of the required size-class of prey in proportion to its body size in its wintering quarters.

1.1 REVIEW OF LITERATURE

1.1.1 Co-existence of congeners

Detailed investigation of the mechanisms facilitating the co-existence of closely related species in an area is essential for understanding their population dynamics, role of species interactions in community organization (MacArthur 1958, Cody 1974), and congruence between ecology and phylogeny (Forstmeier et al. 2001). Two hypotheses are often invoked to explain the coexistence of congeners in the same habitat. The first one involves 'interference competition' for space, sometimes resulting in interspecific territoriality (Cody & Walter 1976, Cody 1978, Bourski & Forstmeier 2000); and the second one emphasizes the importance of subtle differences in morphology leading to differential patterns of habitat use and foraging behaviour which together act as mechanisms of ecological segregation (Lack 1971, Weins 1989, Latta & Wunderle 1998). However, these two hypotheses may not be mutually exclusive and both the mechanisms may sometimes be complementary to each other (Martin & Thibault 1996).

In an analysis of ecological isolation in birds, Lack (1971) identified three important means (range, habitat, feeding or food) by which closely-related species may achieve ecological segregation to reduce competition. If two ecologically similar species occupy disjunct geographical ranges with no overlap, they are not expected to show any evolutionary response to competition (Lack 1971). But species showing high degree of sympatry often show morphological and behavioural adaptations that enable them to exist together and exploit resources in an efficient manner. Non-overlapping patterns of vertical and horizontal segregation of coexisting species along the vegetation structure are well-known examples of such ecological isolation (MacArthur 1958, Crome 1978, Salewski et al. 2002).

Mechanisms of ecological segregation are theoretically most challenging when closely related species use the same resource at the same time in the same habitat. In such cases, competition theory predicts that the species should differ in food types, or foraging strategies, or should show divergence in major morphological features (Lack 1971, Tilman 1982, Morrison et al.1990). Any study aimed at assessing the nature of ecological segregation among closely related species should reflect the hierarchical framework of these mechanisms (Loyn 2002). This approach is essential for understanding the relationships between the mechanisms of ecological isolation acting at different scales of habitat selection, resource use and morphology-ecology relationships, and also the manner in which these shape the resulting patterns of co-existence among closely related species (Rees et al. 1996).

Birds are known to respond to various cues in a complex, scale-dependent manner to ascertain the suitability of their wintering habitat (Hutto 1985). Within the hierarchical framework of habitat selection, the distribution and abundance of food resources figure as the most prominent cues used by birds to select foraging sites at both the between-habitat, and within-habitat scales. In fact, food often emerges as the most important limiting factor for populations of passerines in the non-breeding season (Hutto 1985, Schluter & Repasky 1991, Katti & Price 1996). It then follows that the distribution and abundance of arthropods may largely determine the resource use patterns of insectivorous birds at different temporal and spatial scales (Keane & Morrison 1999).

Although food may play a crucial role, many other attributes such as vegetation structure and composition are also critical in determining habitat suitability for a particular bird species (Table 1). Identifying such variables, which determine the occupancy of a particular habitat type by a species, is critical to underline the mechanism of segregation operating among closely related species at this scale. However, where species-specific habitat preferences are not so pronounced, other aspects of their ecology such as feeding zone within the vegetation, and foraging strategies should be examined to explain the existing patterns of co-existence (Cody 1978, Robinson & Holmes 1982).

Table 1. Key segregating mechanisms facilitating the coexistence of congeners in similar habitats.

Bird taxa	**Habitat**	**Key variables explaining co-existence**	**References**
Dendroica warblers	Pine forests in North America	Foliage height diversity & horizontal stratification	MacArthur & MacArthur 1961
Parus Chikadees	Foothills of Rocky Mountain	Foraging preference for conifers and dead trees	Hill & Lein 1989
Sylvia warblers	Matorral	Choice of plant species for foraging, the height of the plant, the portion of the plant volume used and the plant structure explored, foraging behaviour	Martin & Thiboult 1996
Acanthiza Thornbills	Open wood land and chenopod shrublands in Australia	Density of trees & shrubs	Loyn 2002
Phoenicurus Redstarts	Mosaic urban habitat in Czech Republic	Proportion of trees and buildings, frequency of foraging techniques, intake of taxonomically different prey	Sedláček et al. 2004

1.1.2 Ecological studies on Phylloscopus communities

Price (1991) and Forstmeier et al. (2001) studied habitat choice in symaptrically breeding *Phylloscopus* warblers in Kashmir and Siberia respectively to understand the ecological and evolutionary aspects of habitat choice in these birds. These two studies produced very contrasting findings. Price (1991) inferred that apart from morphology which explained the ecological variation among the breeding warblers to a large extent, interspecific competition also played a major role in determining the distribution patterns of the warblers. However, the intensity of interspecific competition was found to be relatively low in the Siberian community of *Phylloscopus* warblers with closely related species occupying similar habitats.

Price (1991) looked at the ecology and morphology of eight species of breeding *Phylloscopus* warblers, and the warbler-like Goldcrest *Regulus regulus* along an altitudinal gradient. The study recognized the fact that morphology-ecology associations play a critical role in elucidating the nature of ecological segregation among closely related species where recent divergence makes it difficult to understand the underlying mechanisms. Some striking correlations emerged between morphology and ecology of these closely related species. While body size was found to be correlated with prey size, a measure relating beak size to tarsus length was correlated to the habitat and mean elevation occupied. Additionally, feeding method was found to be correlated to a measure of beak width relative to its length. However, interspecific differences in feeding method, prey size and habitat choice were found to be largely uncorrelated to each other. Forstmeier et al. (2001) found that while the productive habitats were occupied by larger species, smaller species were more prevalent in habitats characterized by poor soil. In the same study the development of larger feet among some species, specialized for hopping and climbing, was attributed to foraging in microhabitats where flying is constrained by extremely dense vegetation. On the other hand, it was found that the species foraging in more open vegetation and preying on larger insects possess smaller perching feet, but have long pointed wings and larger beaks. These findings agree with other similar studies on *Phylloscopus* warblers (Gaston 1974, Marchetti et al. 1995, Forstmeier & Keßler 2001).

Studies of similar nature in the non-breeding season are lacking, although a comprehensive review looking at the relationship of winter ecology of the species to their breeding season ecology was presented by Price & Gross (2005). They concluded that most ecological aspects such as parallel divergence between species in terms of morphology, locomotory and feeding behaviour, and plumage patterns seem to have been initially driven by adaptations to the breeding season. Additionally, although the breeding and non-breeding range sizes were found to be correlated, the relative roles of the two seasons seem unclear.

1.1.3 Ecology of the study species

Of the three species studied here, *P. chloronotus, P. humei,* and *P. xanthoschistos,* the former two have been subjected to detailed investigation in the breeding season (Price 1991), and were also reviewed by Price & Gross (2005) with respect to their non-breeding ecology. In addition, Gross & Price (2000) undertook a study to understand the factors determining the wintering range limits of *P. humei* in India. The study looked at some sites in Himachal Pradesh as the northern limit and Mahabaleshwar in the Western Ghats as the southern limit. In Naina Devi, limited investigation of non-breeding ecology of *P. chloronotus* and *P. xanthoschistos* was also undertaken as they are the closest competitors of *P. humei* in this northern site

(Table 2). Naina Devi lies in the Shiwaliks like Simbalbara Wildlife Sanctuary where this study was carried out. The forests of Naina Devi are deciduous and semi-evergreen in nature (Gross & Price 2000). However, *P. xanthoschistos* did not receive much importance in most of these studies as it was still classified as *Seicercus*. Hence, relatively limited information about the ecology of this species is available.

Table 2. Summary of results from previous studies focusing on the three study species.

Species	Weight (gm)	Foraging height (metres)	Hops*	Standpicks (%)	Large Prey (%)
P. chloronotus	5.1	2.8	3.6	26	3
P. humei	6	6.8	7.2	45	1
P. xanthoschistos	6.8#	3.5	--	72	13

References: * per ten movements from Price & Gross (2005), % standpick and % large prey from Gross & Price (2000), weights from Price (1991), #Price (unpublished data).

Plate I

Picture 1. Grey-hooded Warbler *Phylloscopus xanthoschistos* (previously *Seicercus)*.

Picture 2. Whistler's Warbler *Seicercus whistleri.*

2. OBJECTIVES

The main objectives of the study were:

a. To estimate occupancy rates of three sympatric species of *Phylloscopus* warblers in the non-breeding season.

b. To investigate patterns of co-existence and niche partitioning among the three species of *Phylloscopus* warblers in terms of resource use and foraging strategies.

c. To examine the ecology of *P. xanthoschistos* in relation to other *Phylloscopus* warblers.

d. To assess the wintering of *P. xanthoschistos* in the Shiwaliks with respect to the availability of large prey.

The above objectives aim to answer the following research questions:

- Do the occupancy rates of the three species differ over the sampled area during the non-breeding season?
- Do the occurrences of the three species of warblers across habitat types correspond to prey abundances?
- Do they show differential use of horizontal and vertical strata of vegetation?
- If they overlap in vegetation strata, do they differ in their choice of the insect prey size?
- Do the warblers differ in their foraging and locomotory behaviour?
- What are the relationships among ecology, behaviour, and morphology?

The field work was carried out from November 2006 to March 2007, which corresponded to the non-breeding season of the three species of warblers.

3. STUDY AREA

The study on the wintering *Phylloscopus* warblers was carried out in Simbalbara Wildlife Sanctuary (SWLS) and adjoining Reserve Forests in the Poanta Forest Division (Fig. 1). This area is a representative of the lower Shiwalik. The flora, fauna and physical features show affinities to Western Himalaya, Punjab Plains and Upper Gangetic plains. It occurs in the biogeographic province 4A (Rodgers & Panwar 1988). The Sanctuary was notified as a Game Sanctuary for the first time on 8 February, 1958, under the Indian Forest Act 1927, the Punjab Wild Birds and Wild Animal Protection Act 1933, and other relevant acts. Prior to its notification, Simbalbara was a hunting preserve of the former Maharajah of Sirmaur (Singh et al. 1990). A revised notification was issued in 1972, and the Sanctuary was renotified on 27 March, 1974.

3.1 Physical features

SWLS (30°24’21’’-30°28’13’’N and 77°18”-77°31’26”E) is located in the Poanta Valley and covers an area of 19.03 sq. km. The altitudinal range is from 400 m to 660 m above msl (Singh et al. 1990). The hills are composed of unconsolidated sandstone and conglomerate that are extremely prone to erosion.

3.2 Climate

The temperature ranges from 10°C to 46°C with a mean annual rainfall of 1260 mm (Singh et al. 1990). Most of the precipitation in this area occurs during southwest monsoon. Additionally, occasional winter rains also occur due to the western disturbance. Frost sometimes occurs during December and January.

3.3 Vegetation

These forests are considered the western limit of Sal (*Shorea robusta*) in India. The forests of SWLS can be described as Moist Sal-bearing forests (3C/C2) according to Champion & Seth (1968). The common species in the Sal-dominated forest include *Mallotus phillipinensis, Terminalia alata, Ougenia dalbergoides, Cordia dichotoma, Ehretia laevis, Grewia tilifolia,* and *Bauhinia vahlii.* On the ridges, species such as *Anogeissus latifolia, Buchanania lanzan, Diospyros melanoxylon,* and *Boswellia serrata* are commonly found. The Sanctuary has some pockets of *Acacia catechu* and bamboo. Along the streams, species such a *Syzigium cumini,* and *Ficus spp.*, are prevalent. Plantations were undertaken in the past with the objective of improving wildlife habitat and cover an area of over 4 hectares. The introduced species planted include poplar (1983-84), bamboo (1966-68) and *Eucalyptus*. Some plantations of fodder species have been also carried out from 1983-84.

3.4 Fauna

The important faunal species inhabiting these forests include Leopard *Panthera pardus*, Leopard Cat *Prionailurus bengalensis,* Goral *Nemorhaedus goral*, Sambar *Cervus unicolor*, Chital *Axis axis*, Barking Deer *Muntiacus muntjak,* Jackal *Canis aureus*, Wild pig *Sus scrofa*, Rhesus macaque *Macaca mulatta*, Common Langur *Semnopithecus entellus,* Black-naped Hare *Lepus nigricollis nigricollis,* and Indian Pangolin *Manis crassicaudata.* A breeding programme for Chital, Hog Deer and Barking Deer was initiated in 1978, with plans of reintroducing Chital. However, the facility is no longer functional.

Tiger *Panthera tigris* pugmarks were seen in the Sanctuary and in adjoining Kalesar National Park in Haryana in the year 2003. Elephants *Elephas maximus* from

Rajaji National Park occasionally cross the Yamuna and have been recorded in the Sanctuary. One twenty six species of birds were recorded in the study area between December 2006 and March 2007, which included many winter migrants. Many species of butterflies such as Peacock Pansy *Junonia almana,* Lemon Pansy *Junonia lemonias*, Common Mime *Chilasa clytia,* Indian Fritillary *Argynnis hyperbius,* Common Map *Cyrestis thyodamas,* Common Lascar *Neptis hordonia,* Common Sailor *Neptis hylas,* and more were encountered during the study period.

3.5 Land use and human disturbance

There are no villages inside the Sanctuary area. However, the surrounding area has 35 villages, many of which are inhabited by *Gujjars* with large cattle holdings (Singh et al. 1990). Consequently, the forest faces a constant pressure due to fuelwood extraction, fodder collection, lopping, grazing by buffaloes and cattle, and also grazing by sheep and goats owned by nomadic *Gaddis* in winter. A road passing through the sanctuary is used by *Gujjars*, and other nomadic graziers. Visiting rights in relation to Kaludeo temple exist (Singh *et al.* 1990). Pilgrims visit this temple and also the Dargah near the rest house. Hence, entry into the sanctuary is not regulated. The part of the Sanctuary adjoining Kalesar forest of Haryana is reported to be prone to poaching from across the border. In addition, occasional cases of illegal felling and smuggling of *Acacia catechu* are also reported.

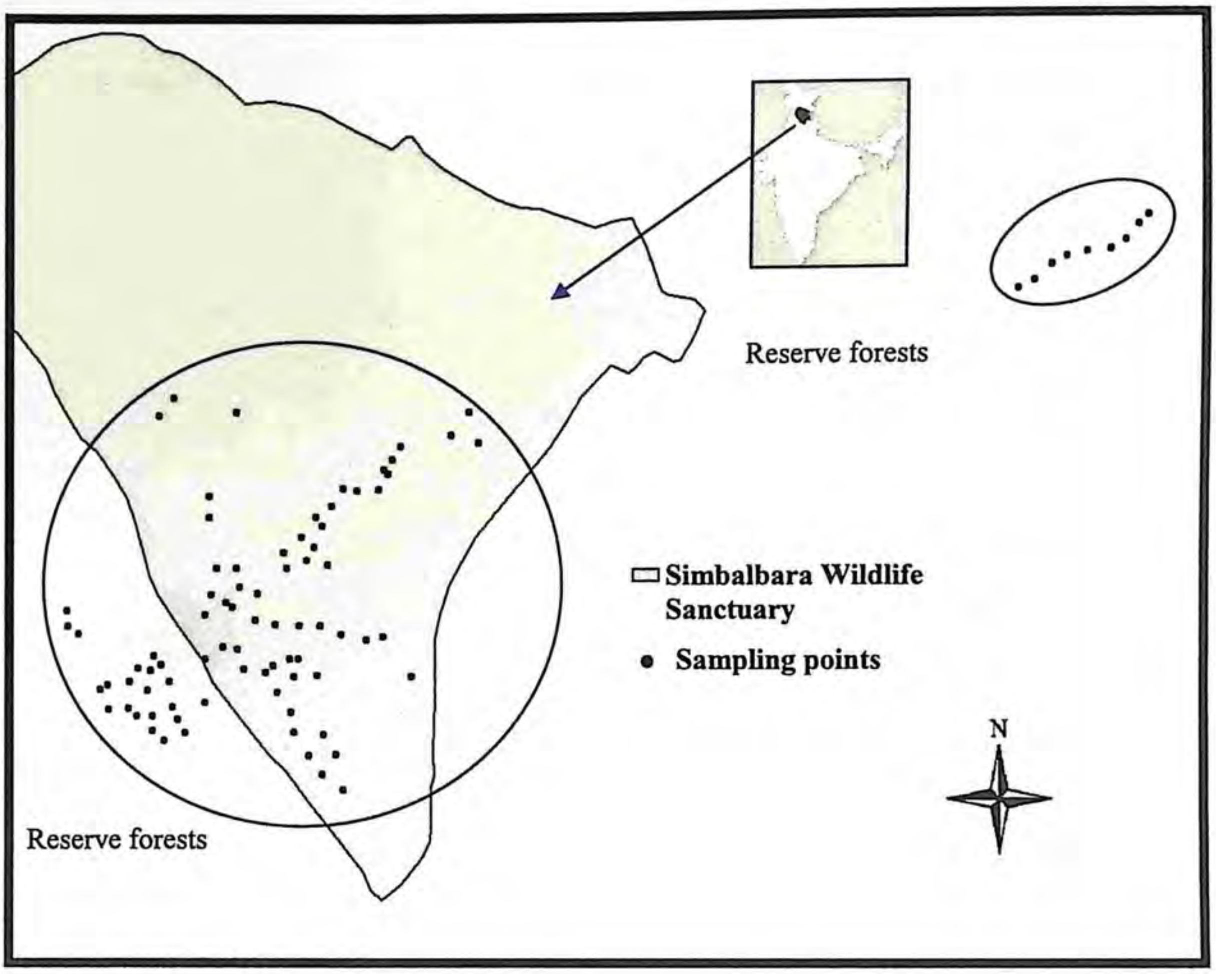

Figure 1. Map of Simbalbara Wildlife Sanctuary and adjoining reserve forests in Poanta Forest Division showing the location of sampling points. The intensive study area has been shown in blue circle.

4. METHODS

4.1 Birds

Point-count sampling was employed to estimate the occupancy of the three target species of warblers, *P. chloronotus, P. humei,* and *P. xanthoschistos*. A total of 91 point-count stations (sites) were established along existing forest trails maintaining a minimum of 110 meters intervals between any two stations (Fig. 1). The trails were stratified among three distinct vegetation cover types: *Eucalyptus* plantation, Sal-dominated forest, and Ridge slopes. Point counts were carried out early in the morning (07: 00 hrs to 10: 30 hrs). During each sample count, which was carried out for a duration of five minutes after reaching a point, the following data were collected: species, number of individuals of each species, and distance from observer to each individual when first detected. In addition, the horizontal position of the bird in the vegetation (outer, middle, or inner canopy) was recorded. For each bird record, detection cue (visual or vocal) was also noted down. Each point was sampled five times between December 2006 and March 2007.

4.2 Arthropods

Since all the three species are essentially foliage gleaning insectivores, sampling of arthropods was done following the bagging-method of Morse (1976) and Katti & Price (1996). This method primarily assesses the availability of the foliage-dwelling arthropods. Nearly 99 % of the arthropods are known to be extracted by this method when the branches are placed in the sampling bag (Morse 1976). The only limitation of this technique is that it tends to underestimate the abundance of strongly-flying insects. But the fact that *Phylloscopus* warblers are primarily foliage-gleaners

Plate II

Picture 3. *Eucalyptus* plantation.

Picture 4. Ridge slopes.

Picture 5. Sal-dominated forests

with negligible intake of these strongly-flying insects makes this method appropriate for the study (Morse 1973, 1976).

The sampling was done in each of the vegetation types and was stratified with respect to the dominant plant species in the given habitat type. The vegetation was classified into trees and shrubs (greater or less than 2m) (Smith et al. 2001) and 45 samples of live branches from each class were collected to assess the availability of prey from each vegetation cover type. From each class of plants a small branch was chosen based on feasibility (branches higher than 10 m could not be reached) and enclosed within a large plastic bag and then broken off. The arthropods were anaesthetized within the bag using a piece of cotton soaked in chloroform and were sorted into two size classes (viz., large and small) based on whether the total body length of the insect was greater or less than 4mm (Gross & Price 2000). The foliage from each branch was collected and weighed, and was also investigated for insects concealed inside. Since the study was designed to assess the diets based only on feeding observations of birds and was not supplemented by faecal and regurgitation samples from the birds, identification of prey beyond these two size classes during behavioral sampling was not possible (Gross & Price 2000). Hence, the arthropods were classified into 'large' and 'small' for the study.

4.3 Behaviour

4.3.1 Foraging

Sampling for foraging behaviour was done through point observation method (Wagner 1981, Morrison 1984). Point observations permit accumulation of large number of independent samples over a short period of time (Gross & Price 2000). Individuals of the target species were searched opportunistically. An individual bird was followed till it performed a prey capture (Gross & Price 2000), and each individual constituted one independent sample. If the bird was lost from view before completion of prey capture, the individual was abandoned. Subsequently a new individual was located after walking for about 100 m to avoid sampling the same individual and the process was repeated.

The capture method was categorized into standpick (capture of a resting arthropod without involving flight), flightpick (capture of resting arthropod where the bird searches for the prey while in flight, includes 'flypick and 'hoverpick' of Price (1991)), and flycatch (capture of a flying insect by flying). The parameters recorded during these observations were: type of foraging method (flightpick, standpick, flycatch) used, foraging substrate (e.g. foliage, twig, branch, and trunk) used, tree species, foraging height, foliage density around the bird (see below), and the size of the prey taken. The prey was categorized as large if it was seen in the bill and required mandibulation or small if the prey was not visible in the bill. This classification is known to correspond to the size classification (> or < 4 mm) of arthropods used for arthropod sampling (Gross & Price 2000). Foraging height was measured for each observation.

To measure the foliage density around the foraging bird, an imaginary 1 m radius sphere was visualized around the bird and the amount of light passing through it was visually estimated in percentages to the nearest multiple of five (e.g. 5 %, 10 %, 25 %, etc.). Accordingly, the foliage density was placed in four classes following the quantitative scale given by Remsen & Robinson (1990): 'very low' (95-100% light passes through), 'low' (75-95% of light passes), 'moderate' (45-75% 0f all light passes through the sphere), and 'high' foliage density (only 0-45% of light passes).

4.3.2 Movements

Additionally, in a separate series of observations, individuals of all three species were followed for ten movements and each movement performed was recorded as a hop, hover, or fly (Price & Gross 2005). If the individual was lost from view before completion of a series of ten consecutive movements, the observation was discarded.

4.4 Morphology-ecology associations

Published morphological measurements of two species, *P. chloronotus and P. humei*, were used from Price (1991). For *P. xanthoschistos*, measurements taken from ringed birds in the non-breeding season (January 1994) in Naina Devi were used (Price unpublished data). The data has been summarized in Table 3. To correct for body-size differences, original linear measurements were divided by cubic root of body mass (Leisler & Winkler 1985). For further analysis, only the corrected values were used.

Table 3. Original morphological measurements of the three species.

Species	Wing length (mm)	Weight (g)	Tarsus length (mm)	Beak length (mm)	Beak width (mm)
P. chloronotus	51.2	5.1	16.5	4.7	2.4
P. humei	55.9	6	17.5	5.1	2.2
P. xanthoschistos	54.6	6.8	18.2	6	2.7

4.5 Analysis

4.5.1 Proportion of area occupied (PAO) estimation

Distance analysis based on detection distances to estimate densities (Buckland et al. 1993, 2001) could not be not performed on the bird dataset due to inadequate number of detections for all the three species. The site-occupancy model described by Mackenzie et al. (2002) has been used to obtain occupancy of the three species of *Phylloscopus* warblers during the non-breeding season. This model is a likelihood-based method of estimating the proportion of sites occupied by a species when the detection probability of the species is less than 1 ($p < 1$). The technique is an extension of the traditional closed-population capture-recapture theory. It assumes that (1) the community of species is closed (no emigration, immigration, colonization or extinctions), during the study, (2) the species are correctly identified, and (3) the detection probability of a species at any one site is independent of the probability of detecting the species in all other sites. The parameters estimated by using the detection/non-detection data obtained by repeated sampling (at least twice) of the sites include

Ψ_i = probability that a species is present at a site i,

p_{it} = conditional probability that a species is detected at the site i at time t.

Ninety-one sites were visited five times each during the study. Counts were obtained for each species from each site on every sampling occasion. The best-fit model for each species based on lowest Akaike Information Criteria (AIC) (Akaike 1973, Burnham and Anderson 1998) was chosen from seven models offered by PRESENCE 2.0 (Hines 2006), i.e. (1) 1 group, constant *p*, (2) 1 group, survey-specific p, (3) 2 groups, constant p, (4) 2 groups, survey-specific p, (4) 3 groups, constant p, (6) 3 groups, survey-specific p, and (7) Abundance induced Heterogeneity (Royle/Nicols Het) model. In these models, groups refer to the number of groups in the population of sites occupied with different detection probabilities. In the first six models, estimates of p (conditional detection probability) and ψ for the three warbler species were based on single season occupancy models of PRESENCE 2.0 (Hines 2006). The last model also gives an estimate of population density of the species (λ) (Royle & Nichols 2003). In order to test for community closure, estimates of ψ and p using single group, survey specific p models were compared, as these species are known to be migratory. In another set of analyses, the model assuming constant species occupancy and detection probabilities across surveys and sampling points, ψ (.) p (.), was employed using the detections for each species stratified across the habitat types (*Eucalyptus* plantation, Sal-dominated forests, and Ridge slope forests). This model was used with the purpose of examining the association between the unconditional detection probability ($\hat{p}$, given by ψ x p; Royle & Nichols (2003)) in each habitat type with prey abundances in each of these habitat types. However, it must be noted that the models used in the above two analyses may not be the best representation of the data obtained for the study species.

4.5.2 Arthropods

For trees and shrubs, the mean number of small (< 4mm), large (≥ 4mm) as well as total number of arthropods per branch were calculated with standard errors for each vegetation type, i.e. *Eucalyptus* plantation, Sal-dominated forest, and Ridge slopes. One-way ANOVA, followed by post-hoc Tukey's test was performed to test for differences in means for large and small arthropods per branch across the three vegetation cover types. Similar parameters were also calculated, after combining the samples across vegetation types, for December 2006-January 2007 (early winter) and February 2007-March 2007 (late winter) separately. This was done with the objective of comparing the study site, with respect to prey availability, to other sites where similar sampling techniques were employed (Table 6). To check for differences in arthropod abundances between these two periods independent sample t-test was carried out. All the tests were performed by using the statistical software SPSS 14.0 (Norusis 2005).

4.5.3 Foraging height and horizontal position in vegetation

The mean foraging height for all three species was calculated along with associated standard errors. To test for differences in the means, one-way ANOVA was performed using SPSS 14.0 (Norusis 2005) after the data was found to conform to normality of distribution and homogeneity of variances. Since, data for use of horizontal position in the vegetation was categorical in nature, proportion of detections in 'outer', 'middle' and 'inner' positions were calculated for each species. Standard errors were placed on proportions following Zar (2005). Chi-square test for multiple proportions was performed to test for differences in use of each position across species.

4.5.4 Foraging behaviour

The proportions of 'standpick', 'flightpick' and 'flycatch' were calculated for each species with standard errors. To test for differences in use of a particular foraging method across species, Chi-square test for multiple proportions was performed. Similar calculations were carried out to test for differences in intake of large prey by the three species. Additionally, to look at the influence of foliage density on the foraging method being used, data was combined across the three species since data for any one species was insufficient for the purpose. A total of 261 prey captures were ranked in four classes of foliage density (described in section 4.3.1), and the proportion of each foraging method used within each class was calculated.

4.5.5 Movements

The mean numbers of hop, hovers, and fly per ten movements for each species were calculated with associated standard errors. Differences across species in use of these locomotory methods were tested by using one-way ANOVA, following tests showing compliance of the dataset to normality of distribution and homogeneity of variances.

4.5.6 Morphology-ecology associations

The proportions of hops were plotted against the tarsus lengths (corrected for body size differences) for all the three species, while a ratio of beak width to beak length was plotted against the proportions of standpicks observed for each species. The association between wing length (corrected for body size differences) and proportion of flightpicks was also plotted. The objective here was to assess the patterns in morphology-ecology associations shown by these species in relation to previous findings (see section 1.1.2).

5. RESULTS

5.1 Occupancy estimates

A total of 455 (91 points, 5 repeats) point counts were carried out which yielded 291 detections of the three target species. Seven models were tested for each of the three species of warblers (Table 4) and based on the model with the lowest AIC value, estimates of p and ψ were obtained. The 2 groups, constant p model performed best for *P. chloronotus* with estimated $\psi = 0.676$ (±0.133*)*. The probability of group membership (2) for group 1 and 2 were 0.016 (± 0.016) and 0.984 respectively. The estimated detection probability *(p)* for group 1 was 1 (± 0.00), while the estimated p was 0.165 (± 0.038) for group 2. For *P. humei,* Abundance Induced Heterogeneity (Royle/Nichols Het) model was chosen based on lowest AIC (Table 4). The estimated detection probability *(r)* was (0.139 ± 0.047), while the average abundance per site *(λ)* was estimated to be (3.34 ± 1.13). Based on these estimated parameters, ψ was found to be (0.96 ± 0.04). Using λ, the population abundance was found to be 304.09 (±103.07). The '1 group survey-specific p' model was found to represent the data of *P. xanthoschistos* counts better than other competing models. While ψ was estimated to be 0.66 (± 0.107), the estimates of p differed across the sampling occasions (Fig. 3). Based on the best-fit models, the overall estimate of occupancy was found to be much higher for *P. humei* as compared to *P. chloronotus* and *P. xanthoschistos*, which showed almost similar occupancy estimates (Fig. 2)

Table 4. Competing models for the three species ranked by AIC, ΔAIC, *w* (Akaike weight), from best to worst.

Species	N	n	Model	AIC	ΔAIC	*w*	K	-2L
P. chloronotus	55	123	2 groups, Constant P	329.71	0.00	0.515	4	321.711
			Abundance Induced Heterogeneity(Royle/Nichols Het) model	330.87	1.16	0.289	2	326.873
			1 group, Constant P	332.63	2.92	0.120	2	328.634
			3 groups, Constant P	333.71	4.00	0.070	6	321.711
			1 group, Survey-specific P	338.57	8.86	0.006	6	326.567
			2 groups, Survey-specific P	343.72	14.01	0.001	12	319.719
			3 groups, Survey-specific P	347.91	18.20	0.000	18	311.906
			Repeated Count Data(Royle Biometrics)	674.31	344.60	0.000	2	670.314
P. humei	175	175	Abundance Induced Heterogeneity(Royle/Nichols Het) model	593.63	0.00	0.713	2	589.630
			2 groups, Constant P	596.43	2.80	0.176	4	588.430
			1 group, Constant P	598.19	4.56	0.073	2	594.190
			3 groups, Constant P	600.43	6.80	0.024	6	588.430
			2 groups, Survey-specific P	602.26	8.63	0.010	12	578.260
			1 group, Survey-specific P	603.63	10.00	0.005	6	591.628
			3 groups, Survey-specific P	608.85	15.22	0.000	18	572.852
P. xanthoschistos	60	151	1 group, Survey-specific P	339.60	0.00	0.899	6	327.604
			2 groups, Survey-specific P	344.02	4.42	0.099	12	320.018
			Abundance Induced Heterogeneity(Royle/Nichols Het) model	353.69	14.09	0.001	2	349.694
			3 groups, Survey-specific P	354.00	14.40	0.001	18	317.996
			1 group, Constant P	354.50	14.90	0.001	2	350.498
			2 groups, Constant P	357.40	17.80	0.000	4	349.397
			3 groups, Constant P	361.40	21.80	0.000	6	349.397

N = no. of detections, n = no. of individuals, K= No. of parameters, L= loglikelihood.

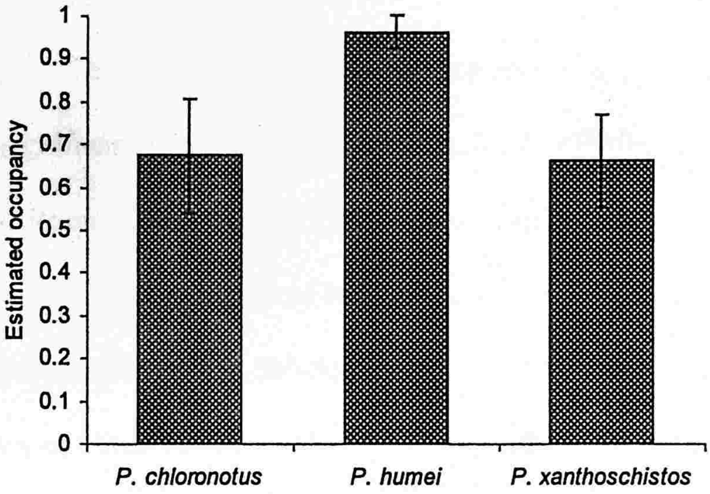

Figure 2. Estimated occupancy ψ (± 1 SE) for the three species based on the best-fit models.

Using the '1 group, survey-specific p' model, it was found that while *P. chloronotus* and *P. humei* did not show much variation in detection probabilities across the five sampling occasions and thereby did not seem to violate the assumption of community closure, *P. xanthoschistos* showed a marked decline in detection probability in the fifth survey (Fig. 3).

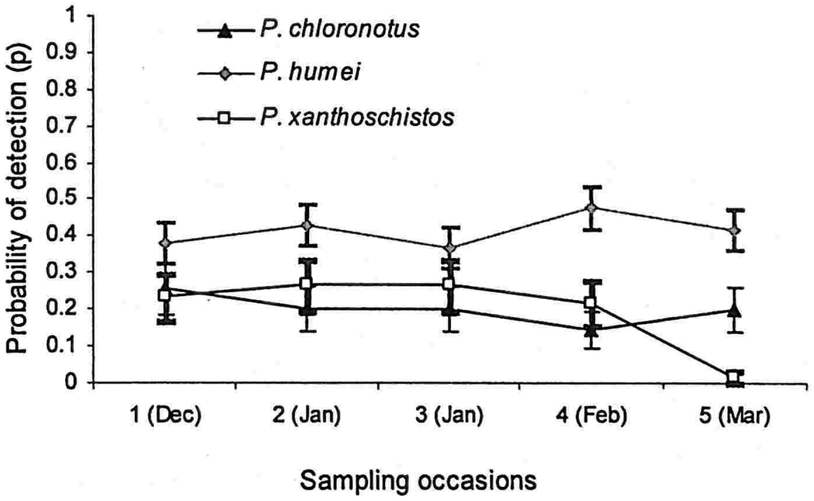

Figure 3. Survey-specific estimates of probability of detection (p) (± 1 SE) for the three species, *P. chloronotus, P. humei,* and *P. xanthoschistos.*

5.2 Prey abundances

The abundance of large arthropods (here it refers to abundance per bag) for trees is significantly higher in Sal-dominated forests when compared to *Eucalyptus* plantations and Ridge slopes (Table 5). However, shrubs across the three vegetation types harbour almost similar numbers of large arthropods. The abundance of small arthropods is again remarkably higher in Sal-dominated forest, for both trees and shrubs. Notably, although trees on ridge slopes yielded 4 (±0.86) arthropods per branch, the yield by shrubs in the same habitat is much lower at 1.93 (±0.29).

Table 5. Arthropod abundances across different habitat vegetation types.

	Arthropod class	***Eucalyptus* plantation**	**Sal-dominated forest**	**Ridge slopes**	**df**	**F**	**Sig.**
Trees	Large	0.36 (±0.12)	0.84 (±0.16)	0.16 (±0.06)	2	6.19	0.003
	Small	3.0 (±0.46)	7.67 (±0.64)	4 (±0.86)	2	13.90	0
	N	45	90	45			
Shrubs	Large	0.6 (±0.19)	0.78 (±0.14)	0.31 (±0.08)	2	2.39	0.094
	Small	3.78 (±0.31)	7.04 (±0.62)	1.93 (±0.29)	2	22.22	0
	N	45	90	45			

N= No. of bags inspected

The arthropod abundance in Simbalbara during December-January (early winter) is comparable to Naina Devi (Gross & Price 2000). There is a marked decline in total arthropod abundance from December-January (early winter) to February-March (late winter) in both shrubs ($t=4.049$, $N=180$ bags, $p < 0.0001$) and trees ($t=4.305$, $N=180$ bags, $p < 0.0001$). This decline is associated with a simultaneous decline in foliage biomass per branch for shrubs ($t=6.632$, $N=180$ bags, $p<.0001$) and trees ($t=9.051$, $N=180$ bags, $p< 0.0001$). The correlation between total arthropod abundance and foliage biomass per branch for shrubs ($r=0.423$, $p < 0.01$), and trees ($r=380$, $p < 0.01$) is significant.

Comparing across sites, in late-winter arthropod abundance is higher (4.52 ± 0.33 for shrubs and 4.53 ± 0.54 for trees) than Naina Devi where it had declined to 2.58 (± 0.34) in February. Expectedly, the total arthropods (per bag) are much lower than Mahabaleshwar (35.5 ± 6.89) in the Western Ghats, which is far warmer and receives very high rainfall (Gross and Price 2000). The abundance of large arthropods looks similar across sites (Table 6).

Table 6. Arthropod abundances in winter in study site and other locations from Gross & Price (2000).

Location	**Altitude (m)**	**Latitude**	**Longitude**	**Census dates**	**Arthropods/ branch**				
					Total	SE	Proportion of large (> 4mm)	SE	N
Simbalbara shrubs(Dec-Jan)	580	30°25’ N	77°29’ E	16/12/06-19/1/07	7.95	1.04	0.13	0.05	55
Simbalbara shrubs(Feb-March)	580	30°25’ N	77°29’ E	9/2/07-15/3/07	4.52	0.33	0.10	0.03	125
Simbalbara trees(Dec-Jan)	580	30°25’ N	77°29’ E	16/12/06-19/1/07	8.45	0.77	0.08	0.03	74
Simbalbara trees(Feb-March)	580	30°25’ N	77°29’ E	9/2/07-15/3/07	4.53	0.54	0.10	0.03	106
Naina Devi (Dec)	680	31°15’ N	76°20’ E	19/12/98-30/12/98	7.67	0.71	0.08	0.04	45
Naina Devi (Feb)	680 m	31°15’ N	76°20’ E	1/2/98-13/2/98	2.58	0.34	0.02	0.02	50
Mahabaleshwar	850 m	17°56’ N	73°40’ E	19/1/98-28/1/98	35.5	6.89	0.06	0.03	50

5.3 Prey abundances and detection probabilities

The unconditional detection probability ($\hat{p}$) for all three species was plotted against the various categories of arthropods averaged across each habitat type to examine if prey abundances influence $\hat{p}$.

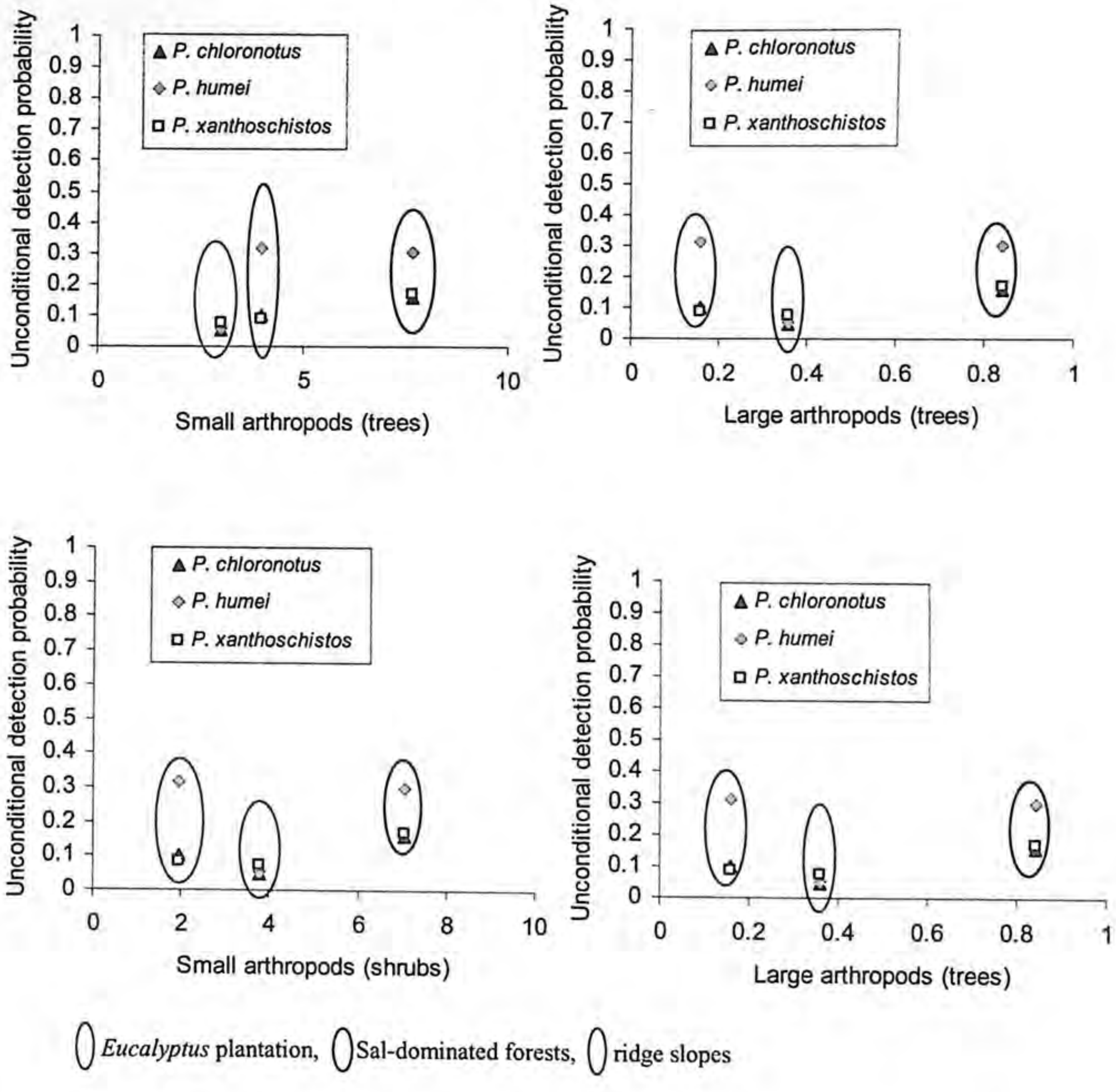

Figure 4. Scatter plot of unconditional detection probability ($\hat{p}$) against various categories of prey in different habitat types.

For all the three species, there was no clear pattern showing influence of prey abundances on unconditional detection probability $\hat{p}$ (Fig. 4). Only $\hat{p}$ for *P. xanthoschistos* showed a strong but insignificant correlation ($r = 0.995$, but $p > 0.05$) with small prey abundance in trees.

5.4 Foraging height and horizontal position in vegetation

The present study shows clear segregation of *P. humei* from *P. xanthoschistos* and *P. chloronotus* by foraging height ($F=21.34$, $df=2$, $p < 0.01$), thereby supporting previous findings by Gross & Price (2000) in Naina Devi. In general, *P. humei* occupies the higher tree canopy, whereas both *P. chloronotus* and *P. xanthoschistos* forage mostly in the lower canopy and shrubs (Tukey's multiple comparisons, *P. humei* > *P. xanthoschistos* ≥ *P. chloronotus,* $p < 0.05$) (Fig. 5). The data from the present study also demonstrates that while the larger-bodied species, *P. humei* and *P. xanthoschistos* forage in the interiors of the tree and shrub volume, the smaller-bodied *P. chloronotus* shows significantly greater use of the outer parts of the vegetation ($\chi^2= 31.93$, $df=2$, $p < 0.001$) (Fig. 6). The use of middle parts of vegetation is higher among *P. humei* and *P. xanthoschistos,* but varies significantly across the species ($\chi^2=20.64$, $df=2$, $p < 0.001$). They did not show any significant difference in the use of the inner positions in vegetation ($\chi^2=5.35$, $df=2$, $p > 0.05$).

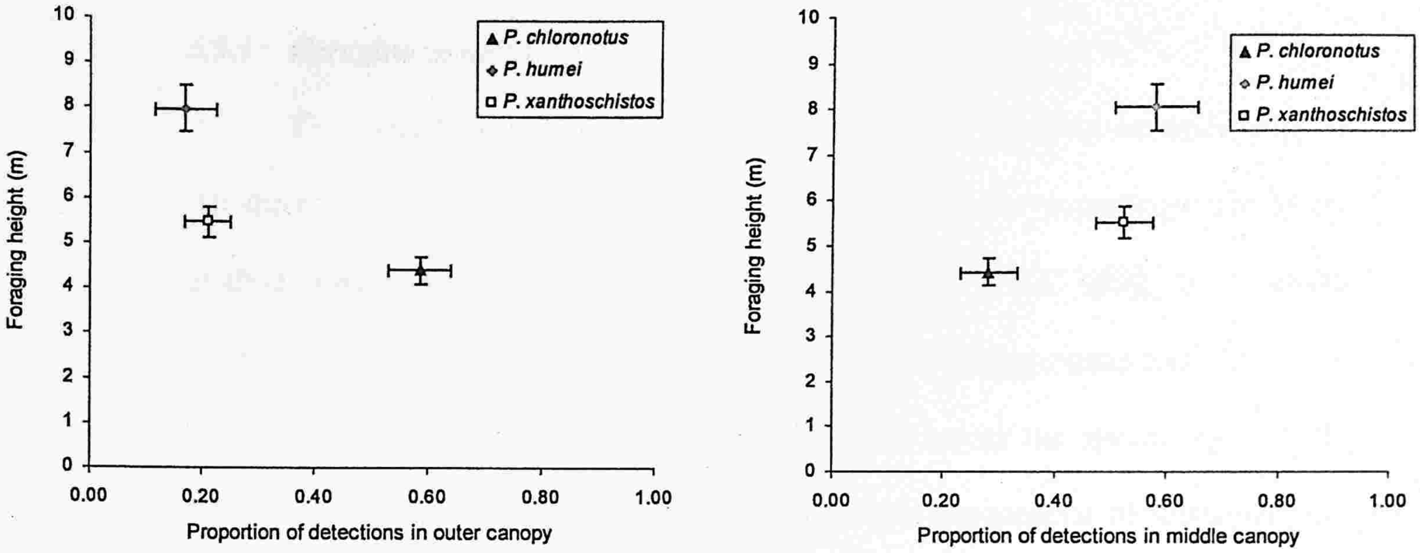

Figure 5. Scatter plot of foraging heights (± 1 SE) and proportion of detections in the outer and middle canopy (± 1 SE) of the three species. The sample sizes for foraging height: *P. chloronotus (81), P. humei (84)* and *P. xanthoschistos (81).* For detections in outer and middle canopy sample sizes are *P. chloronotus (82), P. humei (47)* and *P. xanthoschistos (100).*

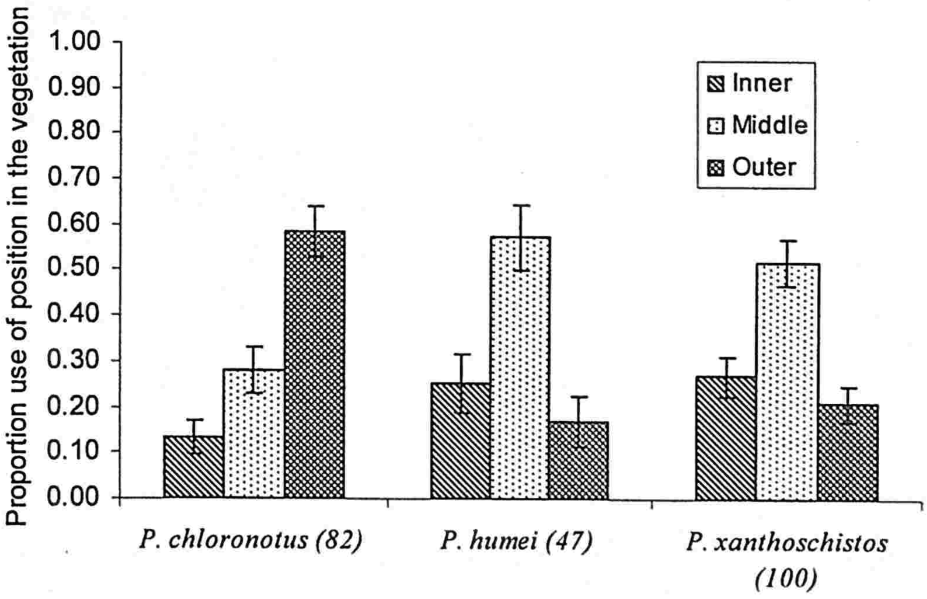

Figure 6. Scatter plot of proportions of detections in the three horizontal strata of vegetation. Standard errors on proportions were placed following Zar (2005).

5.5 Behaviour

5.5.1 Foraging maneuvers

The species also differ significantly in the use of foraging methods (Fig. 7). All three species primarily forage by standpicking, but the percentage use of the method varies significantly across the species (χ^2=10.42, df=2, $p < 0.01$). Flightpicking was the second most frequently used foraging maneuver. However, significant differences exist in the use of flightpick across the species (χ^2= 17.49, df=2, $p < 0.001$). *P. chloronotus* uses almost equal proportions of standpick and flightpick for prey capture. The frequency of use of flycatch as a feeding method is lower across the three species, and the species use this method with almost identical frequencies (χ^2= 1.26, df=2, $p > 0.05$).

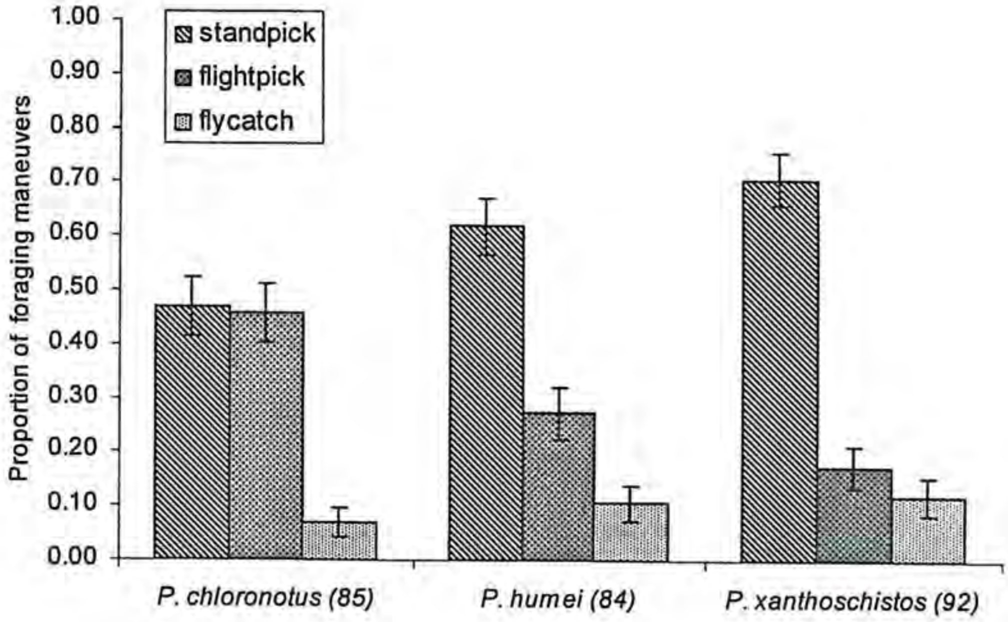

Figure 7. Proportions (±1 SE) of foraging methods used by each species. Sample sizes are shown in parentheses.

Notably, the very high use of standpicking by *P. xanthoschistos* for foraging furnishes good evidence that it is not a flycatcher warbler as previously held. Also, the proportion of standpick is much higher for both *P. humei* (0.62 ± 0.05) and *P. chloronotus* (0.47 ± 0.05) than previously recorded values (Table 2).

5.5.2 Substrate and foliage density

All three species use foliage most frequently (Table 7). Comparison across species, however, showed significant differences in the percentage use of foliage as a substrate (χ^2=16.40, df=2, $p < 0.001$). The percentage use of branch also varied across the species (χ^2=6.49, df=2, $p < 0.05$), with no observation of *P. chloronotus* foraging from a branch. Although, the warblers were seen foraging more in the twigs than the branches, the percentage use is almost similar in case of twigs across the species (χ^2=5.84, df=2, $p > 0.05$). No significant differences were seen in the percentage use of twig, trunk and air between the species ($p > 0.05$). Additionally, all the species foraged in almost similar density of foliage cover (Kruskal-Wallis Test: χ^2 =2.61, df=2, $p > 0.05$).

Table 7. Percentages of prey captures from different substrates.

Species	Twig	Branches	Trunk	Foliage	Air	Total
P. chloronotus	8.24	0.00	0.00	85.88	5.88	85
P. humei	13.10	4.76	2.38	70.24	9.52	84
P. xanthoschistos	21.98	6.59	4.40	58.24	8.79	91

5.6 Prey Size

The proportion of large prey captures was much higher for *P. xanthoschistos* (0.315±0.049) as compared to either *P. humei* (χ^2=8.49, df=1, $p < 0.01$), or *P. chloronotus* (χ^2=20.95, df=1, $p < 0.001$) (Fig. 8). The proportions of large prey captures by *P. humei* and *P. chloronotus* do not vary significantly from each other (χ^2=3.68, df=1, $p > 0.05$). However, these proportions are higher than previously recorded values for both the species (Table 2).

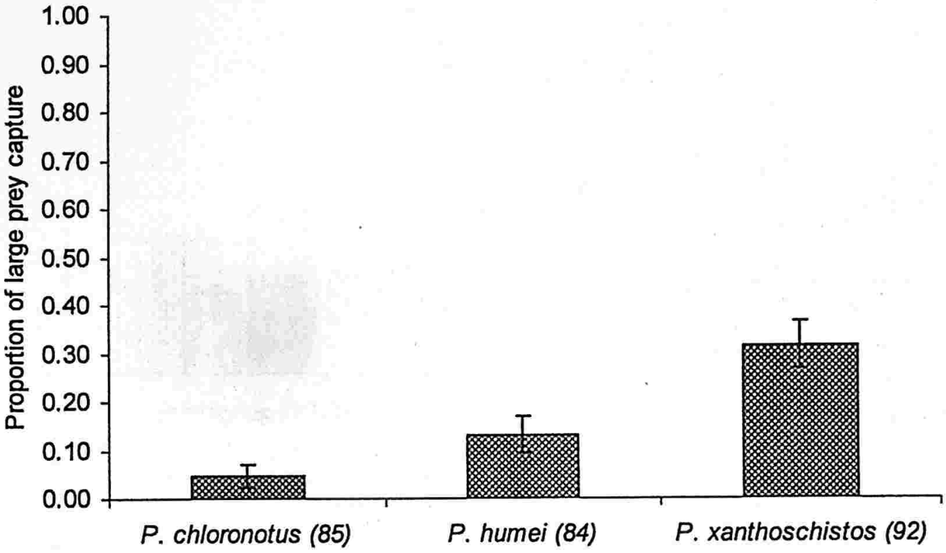

Figure 8. Proportions (± 1 SE) of large prey captures. Sample sizes are shown in parentheses.

5.7 Movements

The three species differ significantly from each other in the number of hops, hovers, and flights per ten movements (Fig. 9). Among the three species, *P. xanthoschistos* shows the most frequent use of hopping for locomotion per ten movements, followed by *P. humei* and *P. chloronotus* (F=45.23, df=2, $p < 0.0001$). The mean number of hops per ten movements for *P. chloronotus* reported here are much higher than the previously published value of 3.1 (±0.03) (Table 2). The frequency of hover (F= 23.79, df=2, $p < 0.0001$) and fly also vary significantly across the three species (F= 16.06, df= 2, $p < 0.0001$).

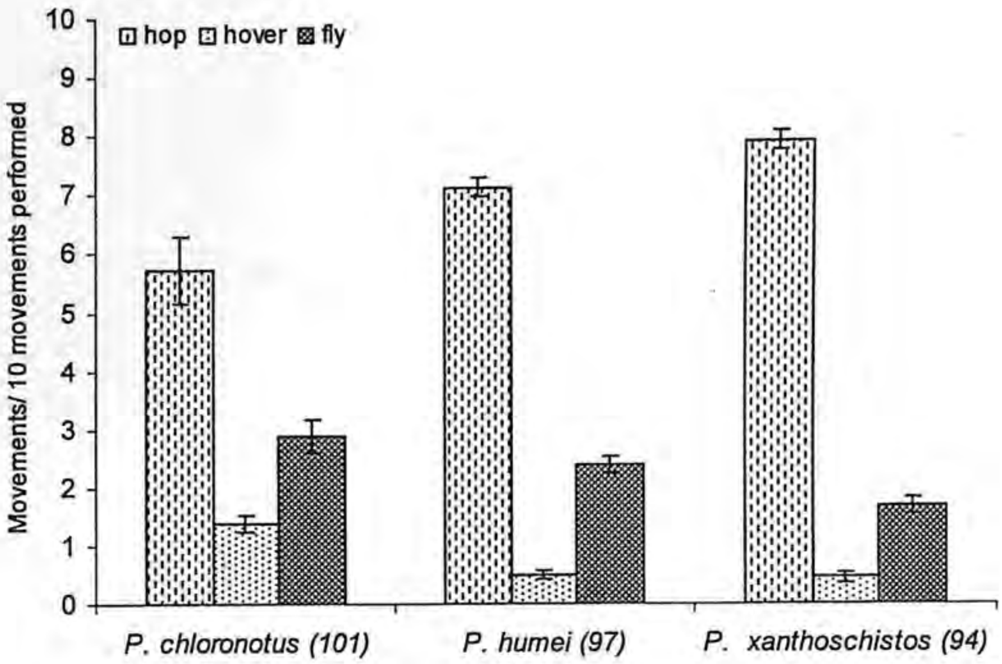

Figure 9. Mean numbers (± 1 SE) of hop, hover and fly (per ten movements) for the species. Sample sizes are indicated in parentheses.

5.8 Morphology-ecology associations

The use of foraging maneuvers involving flight (flightpicks) is more in species of lower body mass with *P. chloronotus* using wings more often than *P. humei* and *P. xanthoschistos* for capturing prey (Fig. 10). Foraging behaviour seems to be equally related to wing length (corrected for body-size differences) with decline in use of standpick across the species as wing length increases (Fig. 11). However, the association between frequencies of standpicks and bill shapes (beak width/ beak length ratio) is not so clear. *P. xanthoschistos* shows greater use of standpick than *P. humei*, although the latter possesses a more slender bill (Fig. 12). Interestingly, the use of hops seems to decrease with increase in corrected tarsus length (Fig. 13).

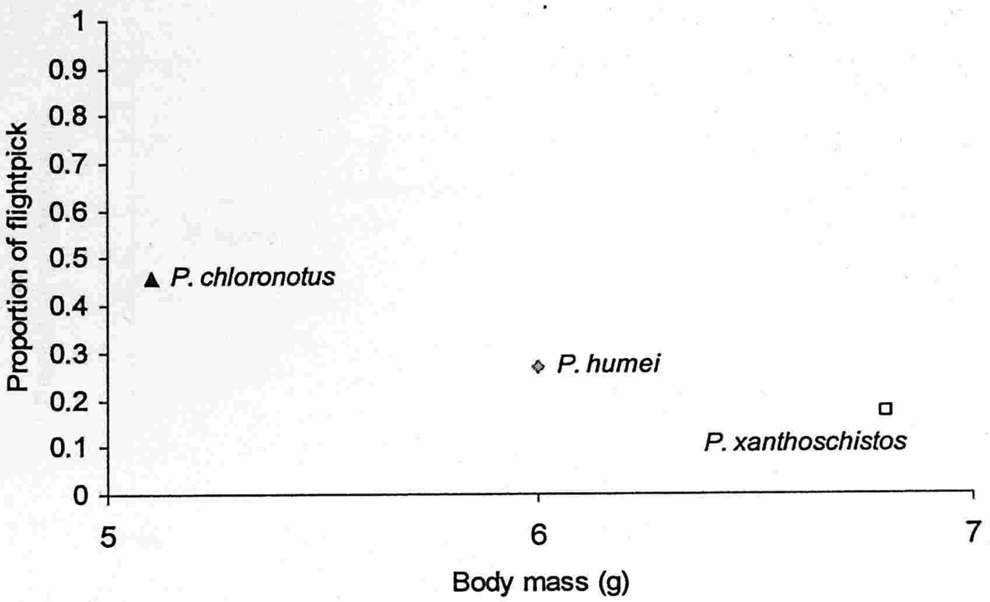

Figure 10. Scatter plot of proportion of flightpicks and body mass (in grams).

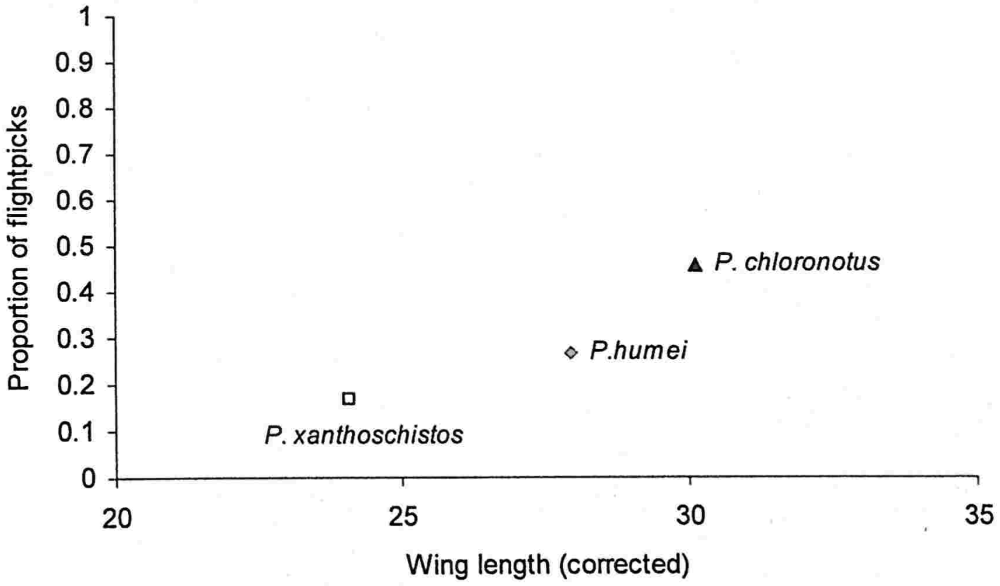

Figure 11. Scatter plot of proportion of use of flightpicks and wing length (corrected).

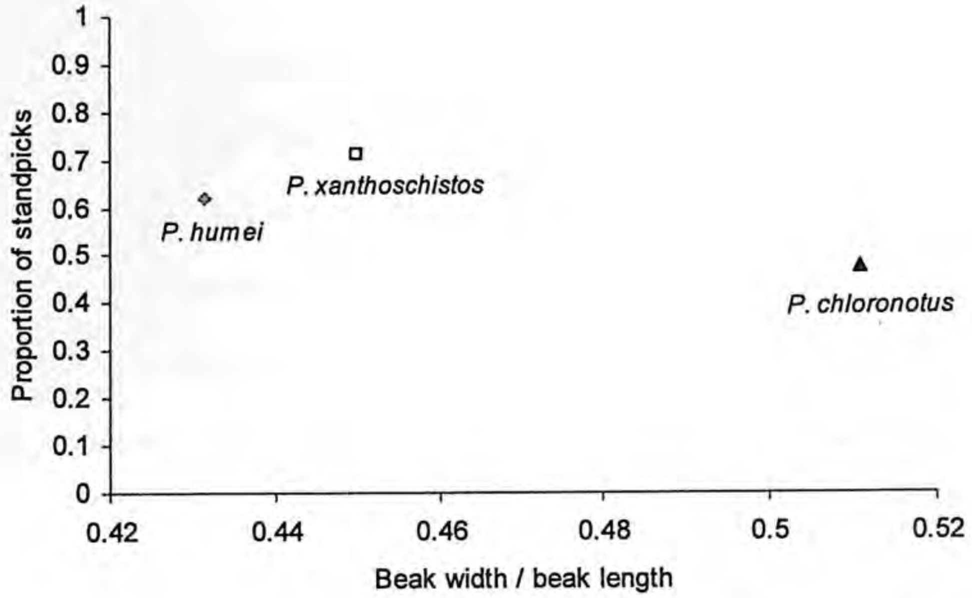

Figure 12. Scatter plot of proportion of standpicks and beak width / beak length ratio.

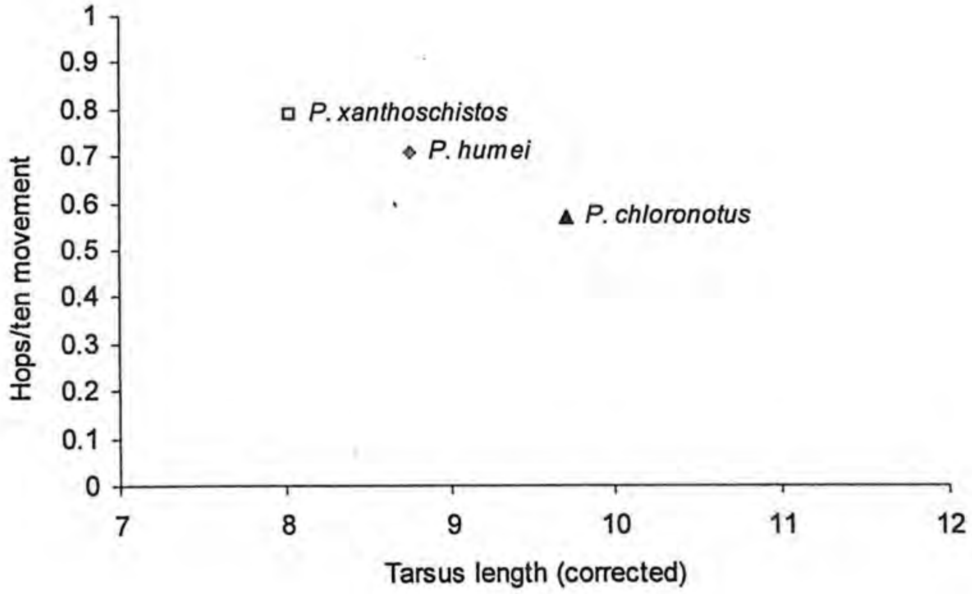

Figure 13. Scatter plot of hops per ten movements and tarsus length (corrected).

6. DISCUSSION

The study reveals some clear patterns regarding the ecological segregation of the three species of warblers in their winter quarters. The three species differ with respect to their overall occupancy rates in the sampled area. Prey abundances also differ across the habitat types, but do not seem to influence the warbler detection probabilities in these habitat types. The three species segregate by means of foraging height, substrate used for foraging, relative use of horizontal position in the vegetation, use of foraging maneuver, percent large prey intake, and locomotory behaviour. Morphology explains the differences in behaviour to a large extent.

6.1 Patterns of species occupancy rates

6.1.1 Occupancy estimates

The assumption of closure of the community is not violated by *P. chloronotus* and *P. humei* during the sampling duration. However, the detection probability *(p)* of *P. xanthoschistos* shows a sharp decline towards the fifth sampling occasion (mid-March). This decline is consistent with the expected reduction in detection probability towards the end of non-breeding season as a result of earlier departure of the species from the wintering grounds towards their breeding areas in this region (George 1957). Accordingly, the most suitable representation of the detections of the species is obtained from the '1 group, survey-specific *p*' model which reflects the early return migration of the species. Sites occupied by *P. chloronotus* were found to form two groups; while the first group had very few sites with high estimated detection probability, the second group comprised of many sites that showed very low detection probability. This is an indication of differential occupancy of the habitat and needs further investigation. The Royle/ Nichols (2003) model of abundance based heterogeneity emerged as the best-fit model for *P. humei*. Finally, the occupancy rates of *P. humei* exceeded those of *P. chloronotus* and *P. xanthoschistos*, which showed almost identical occupancy. Based on the best-fit models, it may be concluded that the three species show high degree of overlap in the estimated proportion of sites occupied in the sampled area in the non-breeding season.

6.1.2 Prey abundances

Across the habitat types, it was found that all three species of warblers did not respond to the differences in prey abundances in terms of their unconditional detection probabilities ($\hat{p}$). Only *P. xanthoschistos* followed the small prey abundance in trees although the correlation was not significant. Notably, $\hat{p}$ was found to be much lower in *Eucalyptus* plantations than in the natural habitats (Sal-dominated forests and Ridge slope forests) for all three species, thereby indicating lower use of this habitat dominated by the exotic species although overall prey abundances in the habitat are higher than ridge slope habitat. The absence of any significant correlation between prey abundances and $\hat{p}$ across different habitat types could possibly be attributed to the implication of other habitat factors (e.g. vegetation composition and structure) which have not been investigated in this case.

6.2 Segregation by foraging behaviour

6.2.1 Microhabitat

The three warbler species show clear segregation by means of their mean foraging heights and relative use of horizontal positions in the vegetation. *P. humei* forages much higher in the canopy as compared to *P. chloronotus* and *P.*

xanthoschistos, which do not differ significantly in their foraging heights. However, in the lower canopy and shrubs, *P. chloronotus* segregates from *P. xanthoschistos* by restricting its foraging activities mostly to the outer parts of vegetation, whereas the latter uses the middle parts of the vegetation more frequently. In general smaller species are seen to forage higher in the vegetation than their larger relatives (Alatola & Moreno 1987, Forstmeier & Keßler 2001). However, the three species studied here do not follow the trend. In this case, *P. humei* occupies tree crowns, while *P. xanthoschistos* and *P. chloronotus* tend to restrict themselves to the subcanopy and upper shrub layers. This can be explained as follows. Price & Gross (2005) have shown that high-altitude breeding habitats selected for adaptations similar to those selected for canopy foraging in the non-breeding season. This resulted in species breeding in higher elevations *(P. humei)* foraging higher up in the tree crowns in winter, while those breeding at lower altitudes (*P. chloronotus* and *P. xanthoschistos)* occupying the subcanopy and bushes in their winter habitats.

Notably, here the smaller-bodied species (*P. chloronotus)* uses the peripheral parts of vegetation, while the heavier ones use the interiors. Many previous studies, focusing mainly on coexisting species of European tits (*Parus spp*.) and New World warblers have also shown that heavier species tend to forage in the inner parts of vegetation whereas the smaller species restrict their foraging activities to the peripheral foliage (Norberg 1977, Alatola & Moreno 1987, Sodhi & Paszkowski 1995). Two contending hypotheses have been invoked to explain this pattern. According to the first hypothesis, foraging efficiency may be related to body size in a manner which makes heavier species more efficient at exploiting inner canopy while the reverse may be true for the smaller species. The findings of Norberg (1977) and Moreno et al. (1997) support this hypothesis. In these studies it was found that the smaller species (or smaller individuals within the same species) use the more energy-consuming search methods (such as hanging in case of tits), and occupy the outer parts of vegetation where such methods are required for searching for prey. In support of a second hypothesis, Alatola & Moreno (1987) reported that body-size influences interspecific social dominance relations and affect foraging site selection by tits. Among the species studied here, the species showing the most frequent use of outer parts of vegetation *(P. chloronotus),* also shows the highest proportion of hovering while foraging which is energetically more expensive than standpicking. The greater use of hovering by smaller *Phylloscopus* warblers is well-established (Price 1991, Marchetti et al. 1995). However, body size adaptations to each microhabitat may be simultaneously complicated by the influence of social dominance. Hence, it is not easy to specify the mechanisms determining the foraging site selection among these warblers.

The three warbler species are essentially foliage-gleaners and forage in similar densities of vegetation. However, they differ in the relative use of foliage and branches for foraging. This can be explained, to a great extent, by the tendency of *P. chloronotus* to forage greatly in the outer parts of vegetation, which excludes use of inner parts such as branches and trunk.

6.2.2 Foraging maneuvers

Standpick dominates the foraging maneuvers of all the three study species, although the extent varies significantly. The species also differ in the use of flightpick, with *P. chloronotus* using it almost as often as standpick, while the frequency is much lower among *P. humei* and *P. xanthoschistos.* The results clearly show that *P. xanthoschistos* is definitely not a flycatcher-warbler. The greater use of inner parts of vegetation by *P. xanthoschistos* and *P. humei* makes standpick a more efficient way of capturing prey for these species as compared to *P. chloronotus* which flightpicks towards the periphery. Flycatch is expectedly not very frequently used by these essentially foliage-gleaning birds. The frequency of standpicking is, however, much higher for *P. humei* and *P. chloronotus* as compared to previously reported values from Naina Devi (Price & Gross 2005). This may be possibly explained by the influence of foliage density and vegetation structure on the foraging strategies being used. The influence of foliage density on the foraging method being used is confirmed by the findings of Forstmeier and Keßler (2001). They found a positive correlation between the density of vegetation the warblers forage in and the frequency of gleaning (defined as a combination of 'picking' and 'reaching' which is same as standpick in this study) for prey capture. In this case, as the foliage density increases there is a pattern, though not significant, of the relative use of both standpick and hoverpick to increase for the warblers (Fig. 14).

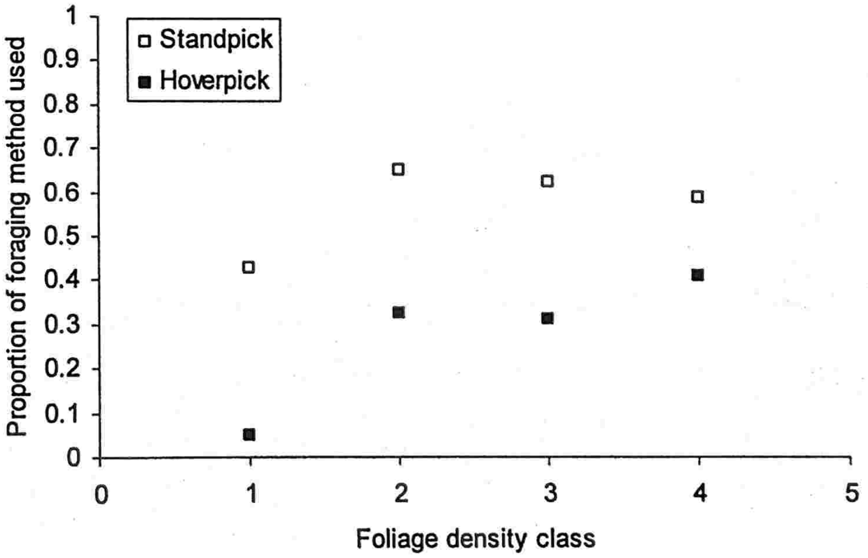

Figure 14. Scatter plot of proportion of use of foraging maneuvers against foliage density classes with increasing foliage density. This analysis was performed by combining the foraging observations across the three species (section 4.5.4).

However, to confirm the role of vegetation attributes in influencing the more frequent use of gleaning among warblers in Simbalbara in comparison to Naina Devi, the vegetation structure of these two sites needs to be assessed for differences with comparable data.

6.3 Prey size

The proportion of large prey capture differs significantly across the three species of warblers. The relative amount of large prey items observed captured by *P. xanthoschistos* is the highest, followed by *P. humei* and *P. chloronotus*. It is worth noting that the overwintering of *P. xanthoschistos* in the northern latitudes contradicts the negative correlation of body size with non-breeding latitude as demonstrated among over-wintering warblers of the genus *Phylloscopus* (Katti & Price 2003, Trevor Price *pers. commun.*). This has been explained in terms of lack of adequate large prey in northern latitudes. However, the proportion of large prey capture by *P. xanthoschistos* in this study is comparable to the winter large prey intake of *P. trochiloides* (32 %) *in* its winter quarters in southern India (Price & Gross 2005). This suggests that there is enough prey available to sustain a large-bodied species like *P. xanthoschistos* in this northern site through winter. Furthermore, although the total arthropod abundance (in terms of arthropods per bag) in Simbalbara is much lower than that recorded in southern sites previously (Table 6), the proportion of large arthropods does not seem to be significantly different. However, the relative numbers of large arthropods seem to be higher than the previously reported proportions obtained in Naina Devi. This may also explain the fact that the large prey intake of the other two smaller species, *P. humei* and *P. chloronotus,* exceeds previously recorded figures (Table 2).

6.4 Movements

The species show considerable difference in their locomotory behaviour. While *P. xanthoschistos* and *P. humei* traverse through the vegetation primarily by hopping, the use of hover and fly match the frequency of hops in the locomotory behaviour of *P. chloronotus.* In their review of correlated evolution of ecological differences among *Phylloscopus* warblers in breeding and non-breeding seasons, Price & Gross (2005) hypothesized that the variation in vegetation density on tree crowns and subcanopy is responsible for this difference. Hopping is assumed to be a more efficient way of navigating through the relatively more homogeneous foliage matrix offered by tree crowns. Alternatively, the base species negotiate through the relatively sparse subcanopy mainly by flying. Even when they land on a high-density microhabitat, such as a shrub, they mostly use the surface instead of the volume of the same by means of hovering. This may explain the preponderance of flying and hovering in the locomotory repertoire of *P. chloronotus.* On the other hand, *P. xanthoschistos* is a hopping specialist although it also forages in the subcanopy and shrubs like *P. chloronotus*. However, unlike *P. chloronotus,* this species explores the interiors of the vegetation by hopping. These findings seem to support the hypothesis of Price & Gross (2005). To confirm the same, however, there is need to undertake further quantitative assessment of the differences in the vegetation profiles of shrub and canopy microhabitat. Apart from the influence of microhabitat, morphology may be a crucial determinant of movement pattern of a species. The role of morphology in influencing the ecology and behaviour of these warblers has been discussed in the following section.

6.5 Morphology-ecology associations

The morphology-ecology associations for the three species show the interactions between non-breeding foraging behaviour and morphology. For instance, the use of foraging maneuvers involving flights shows an increase as the body size decreases and corrected wing lengths increase which agree with previous findings (Marchetti et al. 1995, Forstmeier & Keβler 2001). This has been explained in terms of constraints imposed by larger body size on the use of such energy-expending techniques. Foraging behaviour is also influenced to a large extent by ecological variables like foliage density and vegetation structure as discussed in previous section (6.2.2).

Contrary to previous findings where species with longer tarsi were seen to hop more often (Price & Gross 2005), there is a decrease in proportion of hops with increase in tarsus length (corrected) for these three warbler species. It is worth noting that while Price & Gross (2005) found this association by plotting a principal factor (PC2 interpreted as 'a morphological measure largely influenced by tarsus length') against the number of hops per ten movements for five species of *Phylloscopus* warblers, here the corrected tarsus length (by dividing it by cubic root of body mass, Winkler & Leisler (1985) to correct for body-size differences) has been used for the three species studied. In this case, it seems that the movement pattern of these species may be influenced more by their microhabitat than morphology as has been discussed in section 6.4.

Price (1991) found that species with wider beaks tend to standpick less often and instead use maneuvers involving flight (flightpicks) with greater frequency. However, among the three species of warblers, *P. xanthoschistos* tends to standpick more than *P. humei* which has a relatively more slender bill. In general, the lesser use of foraging maneuvers involving flights by *P. xanthoschistos* and *P. humei* has been explained in terms of greater use of middle and inner portions of the vegetation volume where standpick serves as a more efficient method of prey capture (section 6.2.2). However, unlike *P. humei*, *P. xanthoschistos* was found to be restricted from using the peripheral parts of the vegetation and thereby showed reduced use of aerial foraging maneuvers (more efficient maneuver in outer parts of vegetation) due to the presence of *P. chloronotus* in this foraging zone. This may explain the higher proportion of standpicks than is expected from its bill shape.

Therefore, it may be concluded that the interactions between morphological adaptations and non-breeding microhabitat selection plays a critical role in determining the foraging behaviour. The adaptive significance of these interactions, however, requires further investigation aimed at understanding the relative roles of breeding and non-breeding seasons in limiting the abundance and distribution of these species.

6.6 *P. xanthoschistos:* A *Phylloscopus (Seicercus)* Warbler

P. xanthoschistos has been recently placed in the genus *Phylloscopus* following assessment of its phylogeny based on cytochrome b sequence of mt DNA (Olsson et al. 2004, Alstrom et al. 2006). This study provided the opportunity to examine the ecology of a species, which though recognized as being very similar to *Phylloscopus* warblers, had been previously classified as a flycatcher-warbler (believed to make greater use of wings for capturing prey) under the genus *Seicercus* (Ali & Ripley 1983, Baker 1997). The species was assigned to the genus *Seicercus* primarily due to its strikingly colourful plumage as compared to other *Phylloscopus* warblers (Sibley & Monroe 1990, Grimmett et al. 1998, Baker 1997). In this context, it is interesting to note that the species is nested within a clade of *Phylloscopus* species characterized by very high morphological divergence in spite of the fact that they show relatively low divergence of cytochrome b (6.8 %) within the clade (Olsson et al. 2005).

With respect to its ecology, the study found conclusive evidence showing that *P. xanthoschistos* is certainly not a flycatcher warbler since it used a very high proportion of standpicks for prey captures. The species was also found to capture a proportion of large prey comparable to that of *P. trochiloides* in its winter quarters in southern India. Comparable data is not available to examine the large prey intake of the species in relation to other *Seicercus* warblers. However, based on these observations, it can be concluded that the ecology of *P. xanthoschistos* supports its inclusion into the genus *Phylloscopus.*

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