FORAGING BEHAVIOUR OF TWO TAILORBIRDS IN SINGAPORE: HABITAT, MORPHOLOGICAL AND TEMPORAL COMPARISONS

Malcolm C. K. Soh

Department of Biological Sciences, National University of Singapore, Blk S2 Science Drive 4, Singapore 117543.

ABSTRACT. – I compared the morphological traits or differences in habitat characteristics to study their effects on the foraging behaviour of the Dark-necked Tailorbird (Orthotomus atrogularis) and the Ashy Tailorbird (O. ruficeps). I also made seasonal comparisons for the former. The results show that despite differences in the wing length between these two tailorbird species, their frequency use of different foraging maneuvers did not differ. The differences in height of the vegetation between the habitat types (mangrove versus rainforest) probably contributed to the differences in tailorbird foraging heights. However, the foraging maneuvers and substrate used by the Dark-necked Tailorbird were significantly different when compared between different periods (May - September 1997 and December 1997 - March 1998). Therefore, my findings suggest that the foraging behaviour of these tailorbirds may be affected by variables such as season and certain habitat variables.

KEY WORDS. - Tailorbird, Orthotomus, foraging behaviour, seasonal variation, morphology.

INTRODUCTION

The morphology of a bird is considered as an important factor in restricting the range of foraging maneuvers it can perform (Martin & Karr, 1990). Moermond (1990) suggested that any subtle differences in morphological traits, such as the length of the wing, tarsus and toes of birds could result in different foraging maneuvers. However, there are also other ornithologists who claim that the habitat of the bird can be instrumental in influencing other related foraging behaviours such as the height at which it forages and the substrate from which it obtains its prey (Maurer & Whitmore, 1981; Robinson & Holmes, 1982; Holmes & Schultz, 1988). Habitat characteristics such as vegetation height and prey abundance could affect foraging behaviour (Robinson & Holmes, 1982; Holmes & Schultz, 1988). The foraging methods of even similar species of birds can differ between areas with different vegetation structures (Maurer & Whitmore, 1981). Apart from vegetation structure and diversity, seasonal variation can play a major influence on the foraging behaviour of birds (Hejl & Verner, 1990; Miles, 1990; Sakai & Noon, 1990; Keane & Morrison, 1999).

The objective for this study was to explore the relative importance of morphological traits, spatial and temporal variation in habitat characteristics in influencing the foraging behaviour of two closely related species of birds (see beyond). Three predictions were made from this study. The first prediction was that differences in the morphological traits of the two species of birds would result in differences in foraging maneuvers. The second prediction was that the different habitat types of the birds would result in differences in the bird foraging heights and the substrates from which the prey was taken. The third prediction was that the bird foraging behaviour would vary temporally within the same locality.

My study focused on two species of tailorbirds Sylviid warblers, namely the family representing the Old World warblers (Baker, 1997). Tailorbirds are small insectivorous birds with long bills and rufous caps. Four species of tailorbirds are found in Singapore (Hails & Jarvis, 1987). They are the Common Tailorbird (*Orthotomus sutorius*), the Dark-necked Tailorbird (*O. atrogularis*), the Rufous-tailed Tailorbird (*O. sericeus*) and the Ashy Tailorbird (*O. ruficeps*). Only the Dark-necked Tailorbird and the Ashy Tailorbird were studied. The Dark-necked Tailorbird is found predominantly in rainforests while the Ashy Tailorbird occurs chiefly in mangroves (Hails & Jarvis, 1987).

The need to study their foraging behaviour and habitat use is critical in light of the diminishing native habitat. The mangrove habitats in South East Asia are under serious threat (Sodhi et al., 1997). Rapid economic development such as fish or prawn farming, port, housing and industrial development is responsible for the immense loss of native mangal habitats (Chou et al., 1997). An estimate of 1% of the mangroves including coastal mudflats is all that is left in Singapore (Chou et al., 1997). As for the rainforest habitats in Singapore, only 5% of native rainforest remain (Turner et al., 1994).

STUDY SITES AND METHODS

Morphological Measurements

Measurements for exposed portions of the beak, wing (unflattened) and tarsus lengths were taken for both sexes of the tailorbirds using electronic vernier calipers (± 0.1 mm). The specimens were obtained from the Raffles Museum of Biodiversity Research (RMBR) in the National University of Singapore. Nine subspecies of Dark-necked Tailorbird and eight subspecies of Ashy Tailorbird are recognised (Baker, 1997). Only the subspecies, O. a. altrogularis and O. r. cineraceus both found in the Malay Peninsula and Singapore, were measured.

Study Site Description

Observations took place in four study sites. The mangrove sites were located at Sungei Mandai (1°28'N, 103°46'E) and Pasir Ris Park (1°23'N, 103°57'E) (Lim, 1992; Sodhi et al., 1997) The rainforest sites included Nee Soon and MacRitchie forest (1°22'N, 103°43'E, both occuring in the Central Catchment Area).

The Mandai mangal is an isolated patch of 10 ha located on the Northwest of Singapore (Sodhi et al., 1997). Railway construction in the early 1900s caused extensive habitat destruction, but it has since recovered well (Murphy & Sigurdsson, 1990). Mandai mangal is likely to be cleared soon for reclamation (Sodhi et al., 1997).

In contrast to Mandai mangal, the 5 ha mangrove forest at Pasir Ris was set aside as a nature area (Chou et al., 1997). An underground channel supplies the mangal with a source of freshwater from a river nearby. A rivulet allows periodic inundation of saltwater to the patch. Such measures along with the replanting of native mangrove plants have encouraged the mangrove vegetation to flourish. A boardwalk cutting across the mangal allows visitors to enter and view the mangal interior.

The MacRitchie is a forest fragment of some 530 ha within the Central Catchment Area (Loh, 1997). The site is a mix of secondary and small patches of primary rainforest (Corlett, 1991). Surrounding this fragment is a main road, a golf course and a reservoir. A jogging track, heavily utilised especially during the weekends, cuts through this forest.

The Nee Soon forest is also part of the Central Catchment

Area, covering an area of about 1100 ha (Loh, 1997). Much of this site is represented secondary rainforest (Turner, 1994) with a small patch of swamp forest which still has a rich diversity of flora and flora (Ng & Lim, 1992). Nee Soon forest is sometimes used as an army training ground.

Observations of the Dark-necked Tailorbirds were made in Nee Soon and MacRitchie forests, while the observations of the Ashy Tailorbirds were observed in Mandai and Pasir Ris mangroves. Most of my field observations of the Ashy Tailorbirds were made on the landward side of the mangroves where the species is most likely to occur. All observations were made between 0700 h and 1200 h on fair weather days. Because weather can affect foraging behaviour (Morse, 1989), I did not make any observations on rainy days.

Foraging Observations

Four foraging maneuvers were observed and recorded for the tailorbirds: glean (bird picks up prey from substrate while perched), snatch (bird obtains prey by short flight or hop from perch), hover (bird picks up prey from substrate while hovering) and hawk (bird chases prey in mid-air). The recorded substrates from which tailorbirds obtained their prey were leaf, twig (part which connects to leaf or leaves), branch (part which separates from trunk and connects to twig or twigs), trunk, air (which includes spider webs) and ground.

The height of the bird foraging activity on tree or shrub and the height of the tree and shrub on which the foraging took place were estimated visually. Any significant changes (> 1 m) in bird foraging height were also recorded during a foraging sequence. A "foraging sequence" was defined here as all foraging observations recorded 10 seconds after the moment the bird was first seen until it departs. Only alternative foraging sequences were recorded for an individual to reduce statistical dependence and pseudoreplication. Each sequence was timed using a stopwatch.

The foraging activities of both sexes of tailorbirds were recorded. Although it is possible that the foraging patterns between sexes could be different (Morton et al., 1993; Sodhi & Paszkowski, 1995), I pooled observations for both sexes for a given species to gain a wider variety of foraging behaviours and to obtain a larger sample size for comparisons between species.

Three sets of observations for the Dark-necked Tailorbird were carried out between May and June 1997, between July and September 1997 and between December 1997 and March 1998. Observations for the Ashy Tailorbird were made between January to March 1998. There were a total of 45 sequences were recorded in MacRitchie, 43 in Nee Soon, 22 in Mandai and 21 in Pasir Ris. The total observation time for the sequences for the Dark-necked Tailorbird and Ashy Tailorbird were approximately 73 minutes and 51 minutes respectively.

Data were analyzed using SAS, version 6.12. Significant differences for all the statistical tests were set at a = 0.05.

THE RAFFLES BULLETIN OF ZOOLOGY 2001

Table 1. Mean measured traits of specimens of the Dark-necked Tailorbirds and Ashy Tailorbirds. ± represents standard error. Sample sizes are in parenthesis.

Morphological Trait	Sex	Dark-necked Tailorbird	Ashy Tailorbird
Mean Beak Length	Male	13.93 ± 0.72 (13)	14.64 ± 0.76 (9)
Mean Beak Length	Female	$13.23 \pm 0.68 (11)$	13.88 ± 0.06 (3)
Mean Wing Length	Both	45.50 ± 3.25 (24)	$47.68 \pm 3.17 (14)$
Mean Tarsus Length	Both	16.65 ± 1.06 (24)	$17.33 \pm 0.93 (14)$

Table 2. Results of Mann-Whitney test to compare the measured traits of the Dark-necked Tailorbirds and Ashy Tailorbirds. The first and second figures represent the Z and P values respectively. The figures in bold indicate significant differences. Refer to Table 1 for sample sizes.

	Dark-necked males and females	Ashy males and females	Dark-necked and Ashy	
Beak	-2.00, 0.045	-2.02, 0.043	1.71, 0.09 for males	
			1.48, 0.14 for females	
Tarsus	-0.40, 0.69	-0.94, 0.35	1.90, 0.06	
Wing	-1.87, 0.06	-1.25, 0.21	2.00, 0.046	

Data for foraging maneuvers and substrates were analysed using Chi-squared test for independence. I had to pool certain variables for a specific comparison to satisfy requirements of the Chi-squared test. Mann-Whitney *U*-tests were used to compare the vegetation and bird foraging heights and measured data from RMBR specimens. It should be noted that vegetation and bird foraging heights from July to September 1997 were not recorded.

RESULTS

Bird Morphology

Only beak lengths showed significant differences between sexes for the Dark-necked Tailorbird and Ashy Tailorbird (Tables 1 & 2). The wing lengths between sexes of the two species were not significantly different. The tarsus length too was not significantly different. Measurements for wing length and tarsus length for both sexes were thus pooled. There were significant differences in wing length between species. The Dark-necked Tailorbird on average had a shorter wing length than the Ashy Tailorbird. There were no significant differences in tarsus length between species. The beak lengths were compared between species but the sexes were compared separately. No significant differences in beak length between species were found in males and females.

Foraging Maneuvers

The data for foraging maneuvers from May - June 1997 were pooled with data from July - September 1997 to obtain a larger sample size for comparison with data from December 1997 - March 1998. The foraging maneuvers used by the Dark-necked Tailorbird at Nee Soon between May - September 1997 and December 1997 - March 1998 were significantly different (Table 3). The Dark-necked Tailorbird gleaned more on average in May - September 1997 than in December 1997 - March 1998 (Fig. 1). Also, gleaning seemed to be the only foraging maneuver used during May - September 1997, but from December 1997 - March 1998,

other than gleaning, there were also nine snatches and one hover recorded.

The foraging maneuvers used by the Dark-necked Tailorbird at MacRitchie between May - September 1997 and December 1997 - March 1998 were also significantly different (Table 3). As with Nee Soon, the Dark-necked Tailorbird glean on average more from May - September 1997 than from December 1997 - March 1998 (Fig. 2). Also, apart from gleaning, four snatches and hovers and one hawk were observed from December 1997 - March 1998 compared to May - September 1997 where the tailorbirds were only observed to glean. Thus, the foraging maneuver observations of the Dark-necked Tailorbird from May - September 1997 were not used for subsequent comparisons between the two species since observations for the Ashy Tailorbird were only recorded from January - March 1998.

The foraging maneuvers of the Dark-necked Tailorbird from December 1997 - March 1998 did not differ significantly between Nee Soon and MacRitchie (Table 4), the data were pooled. The foraging maneuvers of the Ashy Tailorbird from January - March 1998 did not differ significantly between Mandai and Pasir Ris (Table 4), the data were pooled.

Finally, I compared the maneuvers used by the Dark-necked Tailorbird occupying the forest habitat and the maneuvers used by Ashy Tailorbird occupying the mangrove habitat (Fig. 3). There were no significant differences in foraging maneuvers between species in their respective habitats (Table 4).

Table 3. Results of the Chi-square test to compare the frequency of foraging maneuvers and substrate used by the Dark-necked Tailorbirds between May - September 1997 and December 1997 - March 1998. The figures represent the χ^2 , df and P value respectively. The figures in bold indicate significant differences.

	Maneuvers	Substrate	
Nee Soon	10.5, 2, 0.005	43.09, 2, 0.001	
MacRitchie	13.64 , 3 , 0.003	9.07, 3, 0.03	

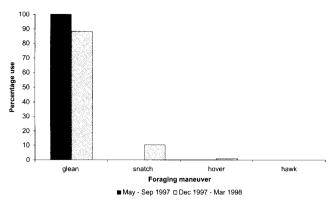


Fig. 1. Seasonal comparison of the foraging maneuvers used by Dark-necked Tailorbird in Nee Soon forest. Total number of sequences recorded from May to September 1997 and December 1997 to March 1998 were 17 and 26, respectively.

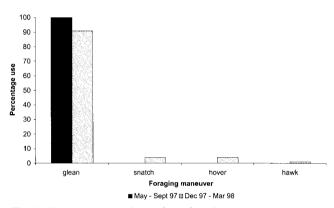


Fig. 2. Seasonal comparison of the foraging maneuvers used by Dark-necked Tailorbird in MacRitchie forest. Total number of sequences recorded from May to September 1997 and December 1997 to March 1998 were 14 and 31, respectively.

Foraging Substrates

I also pooled the foraging substrate data from May - June 1997 with data from July - September 1997. The foraging substrates used by the Dark-necked Tailorbird at Nee Soon were significantly different between May - September 1997 and December 1997 - March 1998 (Table 3). The Dark-necked Tailorbird used more twigs and branches in Nee Soon from May - Sept 1997 but more leaves were used from December - March 1998 (Fig. 4). The foraging substrates used by the Dark-necked Tailorbird at MacRitchie were also significantly different between those periods (Table 3). More twigs than leaves were used during the May - September 1997 period and vice versa for December 1997 - March 1998 (Fig. 5). The observations for foraging substrate from May - September 1997 were not used for further analysis.

The foraging substrates of the Dark-necked Tailorbird from December 1997 - March 1998 differed significantly between Nee Soon and MacRitchie (Table 4). More leaves and less twigs were used by the Dark-necked Tailorbird in Nee Soon than in MacRitchie (Fig. 6). Since the foraging substrates used by the Ashy Tailorbird from January - March 1998 did not show any significant differences between Mandai and Pasir Ris (Table 4), the data were thus pooled.

Last, I compared the substrates used by the Dark-necked

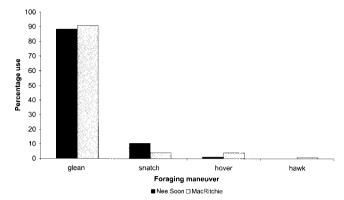


Fig. 3. Foraging maneuvers used by Dark-necked Tailorbird in Nee Soon and MacRitchie forest from December 1997 to March 1998. Total number of sequences recorded for Nee Soon and MacRitchie were 26 and 31, respectively.

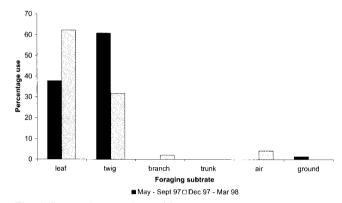


Fig. 4. Seasonal comparison of foraging substrates used by Darknecked Tailorbird in Nee Soon forest. Total number of sequences recorded from May to September 1997 and December 1997 to March 1998 were 17 and 26, respectively.

Table 4. Results of the Chi-square test to compare the frequency of foraging maneuvers and substrate used by both tailorbirds between sites and habitat types. The figures represent the c^2 , df and P value respectively. The figures in bold indicate significant differences.

	Maneuvers	Substrate
Nee Soon & MacRitchie	5.02, 3, 0.17	9.07, 3, 0.03
Mandai & Pasir Ris	1.39, 2, 0.5	4.24, 4, 0.38
Forest & mangrove	1.71, 3, 0.64	
MacRitchie & mangrove		8.19, 4, 0.09
Nee Soon & mangrove		1.56, 4, 0.816

Tailorbird occupying the different forest study sites (MacRitchie and Nee Soon) and the substrates used by Ashy Tailorbird occupying the mangrove habitat (Fig. 6). There were no significant differences in foraging substrate used between MacRitchie and mangrove habitat (Table 4). There were also no significant differences in the foraging substrate used between Nee Soon and mangrove habitat (Table 4).

Vegetation Heights and Bird Foraging Heights

No vegetation and bird foraging heights were recorded from May - June 1997 and July - September 1997. Bird foraging heights and the vegetation heights used by Dark-necked Tailorbird to carry out foraging (Table 5) recorded from

Table 5. Results of Mann-Whitney test to compare the bird foraging and vegetation heights of both tailorbirds. The figures represent the Z, df and P values respectively. The figures in bold indicate significant differences.

	Bird foraging height	Vegetation height	
Nee Soon & MacRitchie	-0.26, 31, 26, 0.80	0.15, 31, 26, 0.88	
Mandai & Pasir Ris	0.04, 22, 21, 0.97	1.58, 22, 21, 0.11	
Forest & mangrove	-4.83, 57, 43, 0.0001	-4.28, 57, 43, 0.0001	

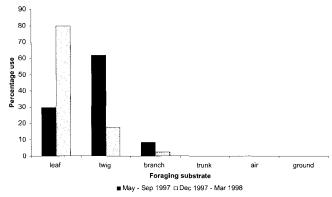


Fig. 5. Seasonal comparison of foraging substrates used by Dark-necked Tailorbird in MacRitchie forest. Total number of sequences recorded from May to September 1997 and December 1997 to March 1998 were 14 and 31, respectively.

December 1997 - March 1998 showed no significant differences between Nee Soon and MacRitchie. These two data sets were pooled for subsequent analysis. Bird foraging heights and the height of vegetation used by the Ashy Tailorbird to carry out foraging (Table 5) did not differ significantly between Sungei Mandai and Pasir Ris. These two data sets were thus pooled.

Lastly, the bird foraging and vegetation heights were compared between the two species of tailorbirds, the Darknecked Tailorbird occupying the forest habitat and the Ashy Tailorbird occupying the mangrove habitat (Figs. 7 & 8). Bird foraging heights and the vegetation heights (Table 5) showed significant differences between forest and mangrove habitat. The vegetation in the forest habitat were on average higher (Mean = 6.93 ± 0.59 m) than the mangrove habitat (Mean = 3.31 ± 0.27 m). Similarly, the Dark-necked Tailorbird foraged on average higher (Mean = 5.11 ± 0.49 m) than the Ashy Tailorbird (Mean = 1.81 ± 0.20 m).

DISCUSSION

Foraging Maneuvers

Closely related species that share similar morphological traits are likely to show similar foraging maneuvers (Robinson & Holmes, 1982). The measurements of the two species of tailorbirds taken for beak, wing and tarsus length reveal that they were only morphologically different in wing length between species (P = 0.046). It should be noted that although the tarsus lengths were not significantly different the P value was very close to significant level (P = 0.06). Unfortunately, a more accurate assessment of the wing measurements cannot

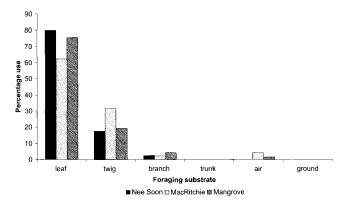


Fig. 6. Foraging substrates used by Dark-necked Tailorbird in Nee Soon and MacRitchie forest and Ashy Tailorbird in mangrove habitat from December 1997 to March 1998. Total number of sequences recorded for Nee Soon, MacRitchie and mangrove habitat were 26, 31 and 43, respectively.

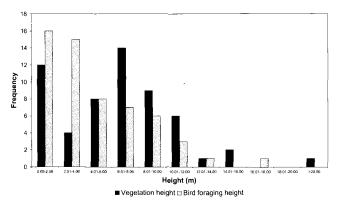


Fig. 7. Vegetation heights and the foraging heights of Dark-necked Tailorbird in the forest (both Nee Soon and MacRitchie). The sample size for vegetation height (number of trees or shrubs) and bird height (number of foraging sequences) is 57..

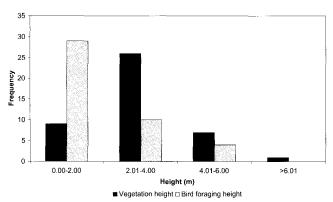


Fig. 8. Vegetation heights and the foraging heights of Ashy Tailorbird in the mangrove (both Mandai and Pasir Ris). The sample size for vegetation height (number of trees or shrubs) and bird height (number of foraging sequences) is 43.

be made due to the small collection of tailorbirds available at the RMBR. Although there were differences in morphology between the two species in wing length and possibly tarsus length, there were no corresponding differences in the foraging maneuvers between species. This result is contrary to the first prediction that differences in the morphological traits of the two species of birds would result in differences in foraging maneuvers. Therefore, we can probably conclude that slight differences in wing length between these tailorbirds do not influence the methods used to capture prey.

Perhaps another measure of morphology for these birds such as wing length to bird weight ratio would make a better comparison. This is based on the assumption that the tailorbirds forage in a manner that maximises the net energy gained per unit time (Morse, 1989). If the wing length to weight ratio for a particular bird is high, it could afford to use more energetically expensive maneuvers such as hovering or snatching to capture certain prey. Unfortunately, this ratio cannot be applied my study since the weight was not given for from the museum specimens in the RMBR.

Although morphology has an important influence on foraging behaviour, other factors could play a greater role (Robinson & Holmes, 1982; Gustafsson, 1988; Martin & Karr, 1990; Vanderwerf, 1994; Whelan, 2001). One such factor is seasonal variation. Seasonal variation in foraging behaviour can occur at three levels: within season (Hejl & Verner, 1990; Miles, 1990; Sakai & Noon, 1990; Keane & Morrison, 1999), between seasons (Cale, 1994; Wiedenfeld, 1989) and yearly variation (Hejl & Verner, 1990; Miles, 1990; Keane & Morrison, 1999). Since our sample sizes were not sufficient to test if the validity of within or yearly variations in foraging behaviour, "seasonal variation" as defined in this study is the change in the foraging behaviour (either in foraging maneuvers or substrates used) between two different periods spanning a few months. Comparing the foraging maneuvers between different periods (May - September 1997 and December 1997 - March 1998) for the Dark-necked Tailorbird, significant differences were apparent. For both forest habitats (Nee Soon and MacRitchie) the Dark-necked Tailorbirds were observed only to glean from May -September 1997 whereas from December 1997 - March 1998 the birds not only gleaned less but a greater variety of maneuvers were used (snatching, hovering and hawking).

I can only speculate why the Dark-necked Tailorbirds adopt a more varied approach to foraging for the latter period. One possibility could be due to seasonal fluctuations in their preferred prey. Suppose the Dark-necked Tailorbird's preferred prey experienced a population decline from December 1997 - March 1998, it is probable that they could turn their attention to feeding on alternative food sources which may require such energetically expensive maneuvers to capture prey. However, to test such a hypothesis, we must first establish that tailorbirds show a preference to a particular group of insects or food source.

Foraging Substrates

Seasonal variations also seem to affect the types of substrates used by foraging birds. This could account for the significant differences in substrate used by the Dark-necked Tailorbird in both Nee Soon and MacRitchie between May - September 1997 and December 1997 - March 1998. It may be that during the rainy season especially during the months of November and December (Chia & Foong, 1991), the proportion of leafeating insects, predominantly Lepidopteran larvae would increase (Holmes & Schultz, 1988). This could be the reason for leaves used as the preferred foraging substrate to twigs, branches and other parts of a tree during the December 1997 - March 1998 (Figs. 4, 5). However, this is based on the assumption that caterpillars or other leaf-eating insects are the preferred prey of tailorbirds.

The seasonal variations could also be attributed to the migratory season. The period of observations for the Darknecked Tailorbirds started in December 1997 - March 1998, which coincides with the period in which most Palaeartic migrants appear in Singapore (Hails & Jarvis, 1987). Observations taken from May - September 1997 mark the period when the migrants would be absent. Migrants like the Inornate Warbler (Phylloscopus inornatus), Easterncrowned Warbler (P. coronatus) and the Arctic Warbler (P. borealis) (Strange, 1993; Hails & Jarvis, 1987) could compete with the resident tailorbirds for same food resources. Noske (1995) discovered that the Arctic Warbler and the Ashy Tailorbird were very similar in foraging behaviour with a mean overlap of 70% in substrates used for foraging. Interspecific competition between Dark-necked Tailorbird and insectivores of similar size like the migratory warblers as mentioned may affect its foraging behaviour (could also apply for foraging maneuvers).

There was also interspecific variation in substrates used by Dark-necked Tailorbird between sites. From December 1997 - March 1998, the Dark-necked Tailorbirds used significantly more leaves and less twigs in Nee Soon than in MacRitchie (Fig. 5). Although both sites are mostly composed of secondary forest, they may, however, be different in terms the degree of human intrusion or modification. For instance, Vanderwerf (1994) observed that the Elepaio in more altered habitats (Chasiempis sandwichensis) used more leaves and less twigs more often than the birds in undisturbed habitats. Other than habitat modification, the variation in substrate use could also be attributed to microhabitat differences such as the vegetation physiognomy (Whelan, 2001). To test this hypothesis, we would need data on the types of vegetation used by the Dark-necked Tailorbirds in different localities to determine if there are indeed differences in foliage structure between them. If so, such distinct foraging microhabitats could account for the difference in substrates used by Dark-necked Tailorbirds between Nee Soon and MacRitchie.

Bird Foraging Heights

The significant differences in bird foraging heights between the two species is likely to be attributed to corresponding differences in the vegetation heights. Generally, mangrove trees are shorter than trees found in a rainforest due to the unstable nature of the mangrove soil and the constant exposure to winds and waves (Hutchings & Saenger, 1987). This result is consistent with the second prediction that different habitat structures would probably result in differences in bird foraging heights.

Contrary to observations on the Dark-necked Tailorbird being confined to mostly dense undergrowth (Hails & Jarvis, 1987), several observations in this project revealed that foraging activity of this species could occur fairly frequently in the tree canopy (Fig. 7). This could be due to competition with other insectivorous birds that typically forage in the shrubs such as the very common Striped Tit-Babbler (Macronous gularis) and Chestnut-winged Babbler (Stachyris erythroptera) (Hails & Jarvis, 1987). Thus, the scarcity of available food in the undergrowth due to a higher proportion of undergrowth feeders may encourage the Darknecked tailorbird to forage higher than usual.

Many of the birds seen in gardens and parks in Singapore possibly originated from mangroves (Hails & Jarvis, 1987; Noske, 1995) including the Common Iora (Aegithina tiphia), Glossy Starling (Aplonis panayensis) and Olive-backed Sunbird (Nectarinia jugularis) (Hails & Jarvis, 1987). These mangrove birds are thought to be more plastic than forest birds in their foraging (Noske, 1995). This plasticity could be due to the adaptation to fluctuating levels of food attributed to tidal changes and/or physiological tolerance of high light intensity and temperature (Noske, 1995) or the amount of exposure to edge. Because the Ashy Tailorbird is essentially a mangrove bird, it is likely to be plastic in foraging. If given the opportunity to occupy an adjacent rainforest habitat, it might, like the Dark-necked Tailorbird, forage higher in the vegetation. It would be interesting to compare the foraging heights of the Ashy Tailorbird occurring in the rainforest with those occurring in the mangrove to test this little researched hypothesis. However, Ashy Tailorbirds are rarely encountered away from mangroves and could be dependent largely on such habitats for its continued existence (Hails & Jarvis, 1987).

Conclusions

The findings in this study show that the morphological differences in wing length between the two species of tailorbirds probably did not result in any significant differences in foraging maneuvers. A wing length to bird weight ratio is perhaps more likely to reflect of corresponding changes in foraging maneuvers. However, the differences between the mangrove and forest habitats of the birds probably resulted in significant differences in the foraging height possibly due to differences in vegetation heights. The foraging maneuvers and substrate used by the Dark-necked Tailorbird were significantly different when

compared between different periods (May - September 1997 and December 1997 - March 1998). Prey abundance, the type of prey available, competition with migrant birds vary seasonally and these in turn may affect the foraging behaviour of the Dark-necked Tailorbird. In short, this study shows that seasonal variations are a important consideration in foraging studies.

ACKNOWLEDGEMENTS

The author wishes to thank Navjot Sodhi for sharing his creative ideas and reading the manuscript critically. Thanks are also due to Yang Chang Man and Kelvin Lim from the RMBR for assisting in providing the specimens for measurement. I am also grateful to Hugh Ford and an anonymous referee for reviewing the manuscript and offering insightful suggestions. The study was partially supported by a research grant from the National University of Singapore (RP960416).

LITERATURE CITED

- Baker, K., 1997. Warblers of Europe, Asia and North Africa. Princeton University Press. Pp. 400.
- Cale, P., 1994. Temporal changes in the foraging behaviour of insectivorous birds in a sclerophyll forest in Tasmania. *Emu*, 94: 116-126.
- Chia, L. S. & S. F. Foong, 1991. Climate and Weather. In: Chia, L. S., A. Rahman & D. B. H. Tay (eds.), *The Biophysical Environment of Singapore*. Singapore University Press. Pp. 13-50.
- Chou, L. M., B. P. L. Goh & T. J. Lam, 1997. Workshop on Environmental Issues and Regional Needs. Sarawak, Malaysia. Pp. 1-12.
- Corlett, R. T., 1991. Vegetation. In: Chia, L. S., A. Rahman & D. B. H. Tay (eds.), *The Biophysical Environment of Singapore*. Singapore University Press. Pp. 134-154.
- Gustafsson, L., 1988. Foraging behaviour of individual coal tits, *Parus ater*, in relation to their age, sex and morphology. *Anim. Behav.*, **36**: 696-704.
- Hails, C. J. & F. Jarvis, 1987. Birds of Singapore. Times Edition. Singapore. 168 pp.
- Heij, S. J. & J. Verner, 1990. Within-season and yearly variations in avian foraging locations. *Stud. In Avian Biol.*, **13**: 202-209.
- Holmes, R. T. & J. C. Schultz, 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Can. J. Zool., 66: 720-728.
- Hutchings, P. & P. Saenger, 1987. Ecology of Mangroves. University of Queensland Press. Queensland, Australia. 388 pp..
- Keane, J. J. & M. L. Morrison, 1999. Temporal variation in resource use by Black-throated Gray Warblers. *The Condor*, **101**: 67-75.
- Lim, K. S., 1992. *Vanishing Birds of Singapore*. The Nature Society (Singapore), Singapore. 103 pp.
- Loh, W. Z., 1997. The effects of habitat fragmentation on two bird communities in Singapore. Hons. thesis, National University of Singapore, Singapore. 95 pp.

- Martin, T. E. & J. R. Karr, 1990. Behavioural plasticity of foraging maneuvers of migratory warblers: multiple selection periods for niches? In: Morrison, M. L., C. J. Ralph, J. Verner & J. R. Jehl Jr. (eds.), *Studies in Avian Biology No. 13*. Cooper Ornithological Society. Pp. 353-359.
- Maurer, B. A. & R. C. Whitmore, 1981. Foraging of five bird species in two forests with different vegetation structure. Wilson Bull., 93(4): 478-490.
- Miles, D. B., 1990. The importance and consequences of temporal variation in avian foraging behavior. In: Morrison, M. L., C.
 J. Ralph, J. Verner & J. R. Jehl Jr. (eds.), *Studies in Avian Biology No. 13*. Cooper Ornithological Society. Pp. 210-217.
- Moermond, T. C., 1990. A functional approach to foraging: morphology, behaviour and the capacity to exploit. In: Morrison, M. L., C. J. Ralph, J. Verner & J. R. Jehl Jr. (eds.), Studies in Avian Biology No. 13. Cooper Ornithological Society. Pp. 427-430.
- Morse, D. H., 1989. *American Warblers: An Ecological and Behavioral Perspective*. Harvard University Press, Cambridge. 406 pp..
- Morton, E. S., M. V. D. Voort & R. Greenberg, 1993. How a warbler chooses its habitat: field support for laboratory experiments. *Anim. Behav.*, **43**: 47-53.
- Murphy, D. H. & J. B. Sigurdsson, 1990. Birds, mangrove and man: Prospects and promise of a new Sungei Buloh Bird Reserve. In: Chou, L. M. & P. K. L. Ng (eds.), Essays in Zoology. National University of Singapore, Singapore. Pp. 233-243.
- Ng, P. K. L. & K. K. P Lim, 1992. The conservation status of the Nee Soon freshwater swamp forest of Singapore. Aquatic Conservation: Marine and Freshwater Ecosystems 2: 255-266.
- Noske, R. A., 1995. The ecology of mangrove forest birds in Peninsula Malaysia. *Ibis*, **137**: 250-263.
- Robinson, S. K. & R. T. Holmes, 1982. Foraging behaviour of forest birds: the relationship among search tactics, diet and habitat structure. *Ecology*, **63**: 1918-1931.

- Sakai, H. F. & Noon, B. R., 1990. Variation in the foraging behaviors of two flycatchers: associations with stage of the breeding cycle. In: Morrison, M. L., C. J. Ralph, J. Verner & J. R. Jehl Jr. (eds.), *Studies in Avian Biology No. 13*. Cooper Ornithological Society. 237-244 pp.
- Sodhi, N. S. & C. A Paszkowski, 1995. Habitat use and foraging behaviour of four parulid warblers in a second-growth forest. *J. Field Ornithol.*, **66**: 277-288.
- Sodhi, N. S., J. P. S. Choo, B. P. Y.-H. Lee, K. C. Quek & A. U. Kara, 1997. Ecology of a mangrove forest bird community in Singapore. *Raffles Bull. Zool.*, 45(1): 1-13.
- Strange, M. & A. Jeyarajasingam, 1993. *Birds: A Photographic Guide to the Birds of Peninsula Malaysia and Singapore*. Sun Tree Publishing Ltd, Singapore. 258 pp.
- Turner, I. M., 1994. Primary and Secondary Forest. In: Wee, Y.
 C. & P. K. L. Ng (eds.), A First Look at Biodiversity: Lessons for the Conservation of Tropical Biodiversity in Singapore.
 Pp. 11-21. National Council of the Environment. Singapore
- Turner, I. M., H. T. W. Tan, Y. C. Wee, A. B. Ibrahim, P. T. Choo & R. T. Corlett, 1994. A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. *Conserv. Biol.*, **8**: 705-712.
- Vanderwerf, E. A., 1994. Intraspecific variation in Elepaio foraging behaviour in Hawaiian forests of different structure. *The Auk*, 111(4): 917-932.
- Whelan, C. J., 2001. Foliage Structure influences foraging of insectivorous forest birds: an experimental study. *Ecology*, 82(1): 219-231.
- Wiedenfeld, D. A., 1989. Foraging in temperate and tropical-breeding and wintering male Yellow Warblers. In: Hagan III, J. M. & D. W. Johnston (eds.), Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press. Washington and London. Pp. 321-328.