Ecological segregation of woodcreepers (Dendrocolaptidae) in the state of Rio de Janeiro, Brasil

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The 48 Neotropical woodcreepers feed in a variety of ways, such as among *Mauritia* palm fronds (e.g., Cinnamon-throated Woodcreeper *Dendrexetastes rufigula*), as obligate ant followers (e.g., White-chinned Woodcreeper *Dendrocincla merula*) or by probing the ground (e.g., Scimitar-billed Woodcreeper *Drymornis bridgesii*). However the typical foraging method of a member of this group, which lacks obvious ecological counterparts in the rainforests of South-East Asia and Africa (Pearson 1977, G. H. Orians, pers. comm.), is to glean bark-living arthropods while ascending a tree trunk, rather in the manner of a *Certhia* treecreeper. The bird then crosses, often by a descending glide, to begin the ascent of another trunk. Determinants of a species' preferred feeding station are thus likely to include height above ground and trunk diameter, both of which are readily measured, and bark characteristics. The woodcreepers are therefore potentially admirable (and hitherto unused) subjects for quantitative studies of niche overlap. I report here on the overlap of the woodcreepers of the rainforests of South-East Brasil.

STUDY AREA AND SPECIES SEEN

Observations were made during 1980 and 1981 in the months October to December, the breeding season. Four study sites were visited in the state of Rio de Janeiro.

(1) Poco d'Anta National Biological Reserve. Secondary forest of various stages of maturity, and also areas of scrub and marsh. Altitude 0–300 m.
(2) Serra do Tingua. Mature secondary forest (lower elevations) or primary forest (higher elevations). Altitude 150–1400 m.
(3) Serra dos Orgaos National Park. Secondary forest (300–1000 m) and moist primary forest (1000–1700 m).
(4) Serra da Siberia, Novo Friburgo. Moist mature secondary forest at 1100 m.

The eight species observed are listed in Table 1, together with their measurements and the weights of mist-netted individuals. Observations were however concentrated on three species, Olivaceous, White-throated and Lesser Woodcreepers (see Table 1 for scientific names), for the following reasons. Plain Brown Woodcreepers often feed on the ground while following ants (Willis 1972, pers. obs.) and so their foraging was not well documented by the methods to be described. The three large species all occurred at Tingua but Planalto and Buff-throated Woodcreepers were observed too infrequently for their niches to be measured. However Buff-throated Woodcreepers were not observed above 800 m (see also De Schauensee & Phelps 1978) and are at least partly separated from White-throated Woodcreepers, seen up to 1600 m in the Serra dos Orgaos, by altitude. Lesser and Scaled Woodcreepers have partly non-overlapping distributions (De Schauensee 1970). At the sites where Scaled Woodcreepers were observed they were too scarce to permit comparison with the Lesser Woodcreeper. With its long curved bill the Black-billed Scythebill probes, for example, fallen dead trunks and in dense

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TABLE 1

The mean measurements (±s.d.) of the woodcreepers of Rio de Janeiro state, Brasil. Linear measurements (mm) were taken from specimens of the appropriate race in the British Museum (N.H.), weights (g) from live specimens mist-netted during this study. Sample sizes in parentheses. Scarce implies less than 0·1 birds seen per man-day

	Wing	Bill	Tarsus	Tail	Weight	Area(s) seen during this study	Notes
Plain Brown Woodcreeper *Dendrocincla fuliginosa*	104·7±4·55 (10)	23·7±1·18 (9)	25·0±0·76 (10)	88·3±4·03 (10)	38·5±3·16 (5)	1, 2, 3	Not seen above 900 m
Olivaceous Woodcreeper *Sittasomus griseicapillus*	74·0±3·97 (10)	11·9±0·75 (10)	18·5±1·09 (9)	74·5±5·32 (9)	13·9±1·27 (6)	2, 3, 4	
White-throated Woodcreeper *Xiphocolaptes albicollis*	131·8±3·97 (10)	45·8±2·80 (10)	32·2±1·27 (10)	119·7±7·63 (10)	118 (1)	2, 3, 4	
Planalto Woodcreeper *Dendrocolaptes platyrostris*	120·6±2·55 (10)	32·4±1·51 (10)	28·3±1·27 (9)	120·0±4·36 (10)	—	2, 3	Scarce
Buff-throated Woodcreeper *Xiphorhynchus guttatus*	117·8±3·60 (6)	36·4±1·08 (6)	25·4±1·07 (6)	102·9±5·06 (6)	—	2	Scarce: not seen above 800 m
Scaled Woodcreeper *Lepidocolaptes squamatus*	100·8±2·93 (6)	27·9±0·54 (7)	20·2±1·15 (3)	84·8±1·99 (6)	—	2, 3, 4	Scarce
Lesser Woodcreeper *L. fuscus*	78·5±3·72 (10)	24·2±1·20 (10)	19·9±0·55 (9)	72·4±3·53 (10)	21·8±1·36 (20)	1, 2, 3, 4	
Black-billed Scythebill *Camphyloramphus falcularius*	102·2±2·59 (9)	68·7±2·36 (9)	23·1±0·84 (9)	101·8±3·23 (9)	46·3±5·13 (3)	2, 3, 4	

undergrowth, using foraging methods different to those characteristic of woodcreepers. As a result of these several factors observations were concentrated on White-throated, Lesser and Olivaceous Woodcreepers. The majority of observations were made in the higher level primary forest of the Serra dos Orgaos, lesser numbers at the other three sites. In the Serra dos Orgaos there were no significant altitudinal differences in the distribution of these three species whose bill measurements (Table 1) are in the ratio 3·85 : 2·00 : 1 (cf. Hutchinson 1959).

METHODS

I walked slowly through the forest until encountering a woodcreeper. It was then watched when foraging until it had traversed up to four trunks or branches. The heights between which it moved on each trunk were recorded and the diameter of the trunk was estimated, using diameter at 1·3 m as a reference, at 0·3 m intervals on the ascent. Thus each woodcreeper sighted provided a succession of points on a two-dimensional matrix of height versus trunk (or branch) diameter (May 1975). The girth of each tree utilized was measured at 1·3 m, as were the girths of the two nearest trees whose girths exceeded 10 cm. The bark of each tree was simply categorized as smooth or rough. I also noted whether the foraging was on a trunk or a branch and whether the bird was solitary or part of a mixed flock. No attempt was made to identify tree species utilized since I suggest a woodcreeper may select a trunk on which to land on the basis of its diameter, height and bark structure, features which are not constant for any one tree species. Because observations were concentrated in a National Park, birds were not collected to determine their diets. Thus it must be emphasized that the overlap measures given below refer only to foraging station.

Hawking for insects is an extremely infrequent foraging method, observed once in Olivaceous Woodcreepers but never in the other two species.

RESULTS AND DISCUSSION

There was considerable overlap between species in their selection of foraging heights (Fig. 1), although Lesser Woodcreepers generally foraged lower than the other two. Most woodcreeper foraging was concentrated between about 3 and 10 m at which level foliage density is generally low in tropical rainforests (Pearson 1977, Terborgh 1980). The concentration was most marked in the White-throated Woodcreepers (Fig. 1). Possibly the woodcreepers, especially the larger species, prefer to feed on trunks where their progress is least impeded by leaves.

On each trunk Lesser Woodcreepers ascended, on average, 1·05 ± s.d. 0·935 m ($n = 41$), less than Olivaceous Woodcreepers (1·96 ± 1·20 m : $n = 52$) and significantly less ($t = 4·52$, 71 df, $P < 0·001$) than White-throated Woodcreepers (2·51 ± 1·79 m: $n = 32$).

The mean trunk (or branch) diameter at the point of foraging was 17·4 ± s.d. 8·53 cm ($n = 329$) for White-throated Woodcreepers, 13·9 ± 6·82 cm ($n = 273$) for Lesser Woodcreepers and 13·0 ± 9·13 cm ($n = 418$) for Olivaceous Woodcreepers, the larger species generally foraging where the diameter was higher. This might arise because large woodcreepers, with more widely separated feet, find difficulty in perching on small trunks or because large species, searching for more widely dispersed large food items (Elton 1935), can scan a larger area when ascending a wide trunk. Niche overlap in the two dimensions (May 1975), height and diameter, was: White-throated *v.* Olivaceous 0·368; White-throated *v.* Lesser 0·619; Lesser *v.* Olivaceous 0·526. The two higher figures, which concern the two species pairs most similar in body size, are close to figures for limiting similarity discussed by Cody (1974), although it should be remembered that the woodcreeper figures would be decreased

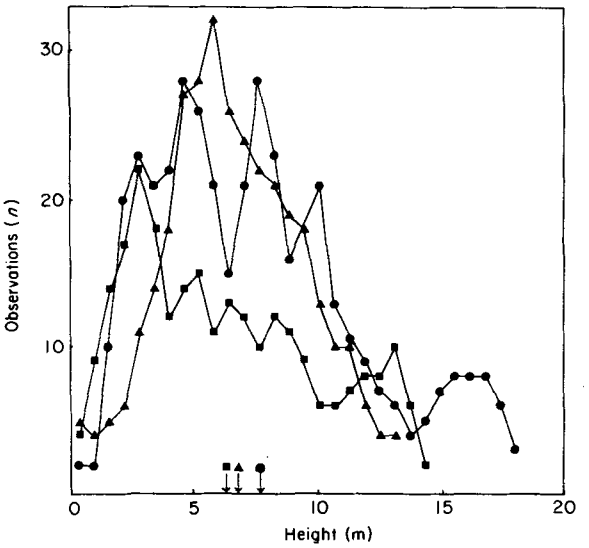

FIGURE 1. The number of observations, at different heights above the ground, of three woodcreeper species, Olivaceous(●), White-throated (▲) and Lesser (■), in the state of Rio de Janeiro, Brasil. When a woodcreeper ascended from, say, 6 to 9 m, it is considered to have provided observations at 6·0, 6·3 . . . 8·7 and 9·0 m. The number of birds watched is given in Table 2. Mean heights for each species are indicated by an arrow beside the abscissa. Overlap values calculated using Horn's (1966) index are: White-throated *v.* Olivaceous 0·870; White-throated *v.* Lesser 0·841; Lesser *v.* Olivaceous 0·861.

if differences in the food items taken, to be anticipated on the basis of bill size differences (Kear 1962), were included in the overlap measure.

The species showed no significant differences ($\chi^2_2 = 1{\cdot}07$, NS) in the use of different bark types, the proportion of observations on rough bark being 44·4% ($n = 45$) for White-throated, 36·0% ($n = 75$) for Olivaceous and 35·7% ($n = 70$) for Lesser Woodcreepers. There were however differences in the proportion of observations of foraging on branches as opposed to trunks (Olivaceous 29·2% ($n = 89$), White-throated 14·0% ($n = 57$), Lesser 7·6% ($n = 79$)) and these significant differences ($\chi^2_2 = 14{\cdot}1$, $P < 0{\cdot}001$) parallel the differences in foraging height. The higher the species foraged the more likely it was to be observed on a branch, at least partly because the lower parts of trees tended to be devoid of branches.

The girths at 1·3 m of the trees on which the three woodcreeper species foraged are shown in Figure 2. Lesser Woodcreepers used significantly smaller trees than the other two species and this species was recorded in the immature secondary forest of Poco d'Anta. The variance of the girths of trees used by Olivaceous Woodcreepers was significantly greater ($P < 0{\cdot}001$) than of those used by White-throated Woodcreepers, and this would presumably allow the former to occur in a greater variety of forest types. Also shown, for the Serra dos Orgaos, is the distribution of girths of the two trees with girths exceeding 10 cm nearest to the trees used for foraging. This latter distribution, a precipitous decline of frequency with size characteristic of tropical rainforest (Dawkins 1958), showed no significant difference between species, suggesting that the species were not using structurally different areas of forest. All species showed a tendency to use trees larger than those randomly available, possibly because larger trees (girth $\geqslant 60$ cm) were more likely ($\chi^2_1 = 8{\cdot}93$, $P < 0{\cdot}01$) to have rough bark (51·2% of trees: $n = 66$) than smaller trees (girth < 60

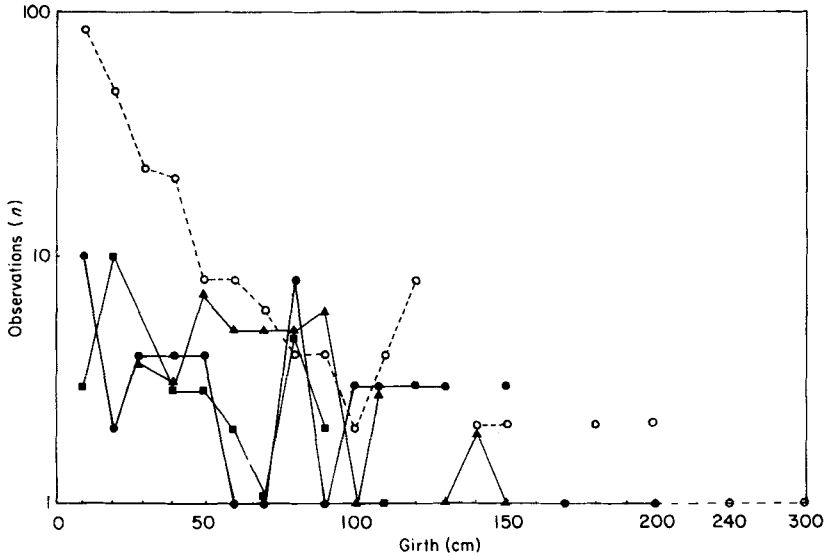

FIGURE 2. The girths at 1·3 m of the trees on which three woodcreeper species (specific symbols as Fig. 1) foraged in the Serra dos Orgaos, Brasil. Girth 10 = 10–19 cm, etc. Also shown (○ – – – ○), summed for the three bird species, is the distribution of girths of the two trees nearest to the trees used for foraging.

	Mean girth	s.d.	*n*	*t*	*P*
White-throated	78·6	29·5	43	4·60	<0.001
Lesser	48·3	28·1	35	2·96	<0·01
Olivaceous	75·3	48·8	52		

cm: 21·8% with rough bark: $n = 64$). Rough bark may yield more insect food. The tendency to use larger trees was most marked in White-throated Woodcreepers, which would presumably be the last of the three species to recolonize regenerating secondary forest.

There were differences in the proportion of occasions the species were observed in mixed flocks (Table 2). Such differences may be related to the mean girths of the trees utilized by the species. Lesser Woodcreepers, using the smallest most numerous trees and climbing, on average, 1·05 m on each, may be able to maintain most readily the pace of a feeding flock whereas White-throated Woodcreepers, moving from one large tree to another and climbing a greater amount (2·51 m) on each, may not. It is

TABLE 2

The number of occasions on which three woodcreeper species were observed foraging either solitarily or in mixed flocks

	Solitary	Mixed flock
Olivaceous	20	8
White-throated	15	1
Lesser	12	14

$\chi^2_2 = 10{\cdot}56$, $P < 0{\cdot}01$.

also possible that two furnariids frequently found in mixed flocks in the Serra dos Orgaos could exclude White-throated and Olivaceous Woodcreepers from such flocks, either by behavioural dominance or resource depression. The Sharp-billed Treehunter *Heliobletus contaminatus* commonly forages like a woodcreeper on the smaller branches, possibly excluding Olivaceous Woodcreepers, while the Pale-browed Treehunter *Chiclocolaptes leucophrys* feeds predominantly in bromeliads where White-throated Woodcreepers also search.

In summary, three of the woodcreepers that employ similar feeding methods in Rio de Janeiro rainforests are separated by foraging height and tree size. The tree size differences can be related to the species' occurrence in different types of forest. However the trunk-gleaning woodcreeper niche is not one that allows great diversification of foraging method. Coexistence of species may then depend particularly on differences in the size of prey taken and this could be responsible for the substantial size differences (Table 1) of the three sympatric species closely studied.

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The relationships between breeding experience, egg volume and reproductive success of the kittiwake *Rissa tridactyla*

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Several aspects of the breeding performance of seabirds have been shown to improve with age (or experience) (e.g., Coulson & White 1958, Coulson 1966, Mills 1973, Davis 1975, Ryder 1975, Coulson & Horobin 1976, Haymes & Blokpoel 1980,

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