

Sexual differences in the foraging behaviour of the frill-necked flycatcher *Arses telescopthalmus* in New Guinea

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Abstract

The foraging behaviour of male and female *Arses telescopthalmus* was studied at Brown River, Papua New Guinea. Significant differences exist between the sexes. The male mainly frequents the lower understorey and forages substantially on bare substrates, particularly vertical ones such as trunks and hanging vines. The female occurs mainly higher in the subcanopy, sallies frequently after aerial insects and forages mainly off leafy substrates. Both male and female show morphological adaptations to their specialized roles. Sexual differences in a species' foraging behaviour usually occur in depauperate avifaunas but the study area is rich in potential competitors of *Arses*. It is suggested that past environmental fluctuations may have initiated differentiation of male, female or both.

Introduction

Sexual differences in the foraging behaviour of certain species of birds have long been known. Probably the most-quoted examples are the striking dimorphism in the beak of the New Zealand Huia *Neornorpha acutirostris* (Van Tyne & Berger 1976) and the greatly-differing foraging behaviour of the sexes of some species of raptors (e.g. Cade 1960). Two strategies appear to be followed, one where males and females of similar morphology forage in different parts of the same area (e.g. Morse 1968) and the other where strongly dimorphic males and females use the same area but employ different foraging techniques (e.g. Selander

1972). The suggested advantage is that, by having different niches, males and females reduce intraspecific competition for food (Rand 1952).

Arses telescopthalmus is a small (length 150–162 mm) insectivorous bird found in all lowland New Guinea, some of its satellite islands and Cape York Peninsula. All forms of *Arses*, except *A. telescopthalmus insularis* of northern New Guinea, have males that are boldly marked black and white. In *A. t. insularis* the white of the throat and breast is replaced by rufous. Females of *A. telescopthalmus* are mainly rufous with a black cap and white abdomen, the exception being *A. t. loralis* of Cape York in which the female is black and white. Thus *Arses telescopthalmus* has one subspecies in which both sexes are brightly coloured, one where both are dull and the rest including that at my study area where the male is bright and the female dull.

The only published ecological data on *Arses telescopthalmus* are by Croxall (1977). In a visit to nine localities in New Guinea, including my study area, Croxall provided information on the foraging ecology of 50 species of passerines.

Study area and methods

Data were obtained during a study of the bird community of lowland rainforest near Brown River, (9° 16' S 147° 05' E) Central Province, Papua New Guinea, from December 1975 to November 1977 (Bell 1977).

The study area was in lowland tropical rainforest, conforming to the structure described by Richards (1952) of a main canopy (c. 25–35 m high), with a few taller emergents, a sparse subcanopy (c. 8–25 m) and a dense understorey (c. 8 m). The area is fully described by Mabbott *et al.* (1965). Mean annual rainfall is

2010 mm (data from Port Moresby Provincial Forestry Office), with a distinct wet season, usually from December to May (ca 80% of the total). During the study there was a harsh dry season from June to October 1976 and a less harsh, but more prolonged one, from May 1977 until the end of the study.

Data on foraging height were taken in 725 h of quantified observation, evenly divided between hours of the day (0600–1800 h) and months of the year, at Three Mile Experimental Plot 4.5 km north of Brown River bridge. The author traversed the study plot (*c.* 2.5 ha) once every 2–3 h and recorded the numbers and sex of all birds seen, the height above ground where each bird was first seen, and the composition of any mixed-species flocks encountered. Subsequent heights to which a bird moved were not noted, so each observation of height represents different birds, or the same birds seen on separate occasions. Height was classified as 0 m, 0–1 m, 1–2 m, 2–4 m, 4–6 m, 6–8 m, subcanopy (*c.* 8–25 m), lower half of the main canopy (*c.* 25–30 m), upper half of the main canopy (*c.* 30–35 m) and emergents (> 35 m). Estimation of height was practised and accuracy of $\pm 10\%$ was found to be possible, up to a height of 10 m. Above 10 m it was necessary to record the vegetation layer rather than the height. Only birds seen foraging were counted. The criterion for whether one sex was alone was that by observation, the two sexes were out of sight of each other. Limited mistnetting was simultaneously carried out and birds caught were marked with CSIRO (Australia) numbered bands, plus colourbands.

Data on foraging activity were taken opportunistically during the study and also in additional visits to Brown River Forestry Station and Mount Lawes National Forest, both near the study plot. Data taken were, for each foraging move (i.e. from one perch to another), the method of foraging and the substrate foraged upon. Other information (e.g. nests, young etc.) was recorded incidentally. Morphological data were taken from specimens held by CSIRO Division of Wildlife Research, Canberra.

Indices of ecological overlap, for height, foraging method and substrate, were calculated using Schoener's (1968) equation:

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^n |P_{x_i} - P_{y_i}|$$

where α = overlap and P_{x_i} and P_{y_i} = frequencies of observations of sexes (or species) x and y in category i of n categories. For each pair of sexes or species the three indices of overlap were combined into a single index of overlap. Because the three indices are not completely independent an arithmetical mean was used. These means probably overstate the degree of overlap. Where data for individual foraging moves did include all three variables, the actual overlap was much lower than that derived from an arithmetical mean (see Appendix 1).

Results

Social organization

More males were seen than females (363 vs 240) but the author believes this to result from the conspicuous plumage of the male and his frequenting the lower levels of vegetation. Intraspecific flocks were not seen and the only occasions on which more than one adult bird of either sex were seen all involved aggression. Even though the sexes usually foraged at different heights, when a female was seen in the canopy, a male was usually heard or seen nearby in the understorey.

Retrap data, spot-mapping and observations of colour-banded birds indicated that a territory is about 2 ha in area, and is vigorously defended against intruders year round. Males may react to intruding males, females to females and a pair together may confront an intruding pair.

Foraging height

Figure 1 shows the distribution, by vegetation layers, of males alone, females alone and both sexes together. Data from areas of secondary growth are not included because in such situations species of the main canopy will often descend to lower levels, i.e. to the canopy of the secondary growth. Table 1 shows frequency of occurrence by sexes alone and both sexes together, compared with breeding records.

The difference in vertical distribution of each sex, when alone, is significantly different from

TABLE 1. Average sightings per day of individuals and pairs of *Arses telescopthalmus* at Brown River, 1975-77, compared to known nesting records

	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.
Nest records*												
Sightings of lone individuals/12 h	9	10	8	6	10	9	9	13	7	10	11	11
Sightings of pairs/12 h	0.7	0.7	0.7	1.4	1.8	1.1	0.4	0.7	0.2	1.6	1.0	1.7

*One record = one occupied nest; month is that in which the first egg is laid.

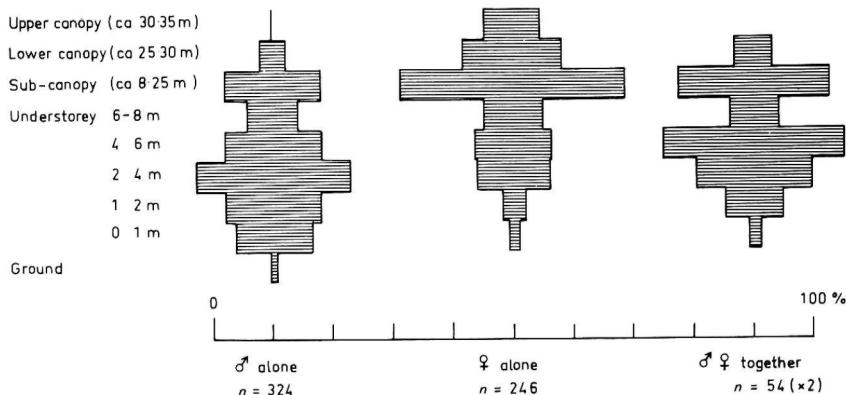


FIG. 1. Percentage distribution, by vegetation layers, of male, female and pairs of *Artes telescophthalmus* at Brown River, 1974-77.

that expected from the combined data for all occurrences. The male occurs significantly more than expected at levels below 6 m ($\chi^2_4 = 21.49, P < 0.001$) and the female occurs significantly more than expected at levels above 6 m ($\chi^2_3 = 42.16, P < 0.001$). Thus males forage mainly in the understorey (79.8%) and mostly in the lower half of it (55.5%). Conversely females forage mainly above the understorey (60.5%). However, when together the sexes

occur at heights significantly different to that when alone. When together males forage significantly more at levels above 4 m than when alone ($\chi^2_5 = 38.89, P < 0.001$). Females forage significantly more at levels below 8 m than when alone ($\chi^2_3 = 38.24, P < 0.001$). When together the sexes forage roughly evenly between the subcanopy, upper understorey and lower understorey.

At Brown River some species showed sea-

TABLE 2. Comparison of foraging methods and substrate of male and female *Artes telescophthalmus*

Substrate	Method	n^*	σ (%)	n^*	σ (%)
Air	Sallying	8	(2.5)	20	(20.0)
Trunks	Snatching	25	(7.8)		
	Hovering	7	(2.2)		
Bare vines	Gleaning	63	(19.6)	3	(3.0)
	Snatching	1	(0.3)		
	Hovering	1	(0.3)		
Branches	Gleaning	34	(10.6)	3	(3.0)
	Snatching	16	(5.0)	7	(7.0)
	Hovering	1	(0.3)		
Leaves	Gleaning	41	(12.7)	14	(14.0)
	Snatching	15	(4.7)	9	(9.0)
	Hovering	9	(2.8)	3	(3.0)
Leaf debris	Gleaning	87	(27.0)	35	(35.0)
Palm fronds	Gleaning	3	(0.9)	5	(5.0)
Ground	Gleaning	4	(1.2)	1	(1.0)
Total		322	(100.0)	100	(100.0)
No. of individuals		81		32	
% overlap ♂/♀	Foraging method	0.825	Foraging method/substrate		
	Substrate	0.629	combined	0.626	

* n = no. of foraging moves, i.e. from one perch to another.

sonal differences in foraging height but *Arses* showed none nor were there differences in the frequency of both sexes together during the breeding season (Table 1). At Brown River small insectivores showed diel differences, shifting down to the understorey at midday, where temperatures may be 6°C cooler than in the canopy (Bell 1977). For diel difference the male, already frequenting lower levels of vegetation, would not be expected to change. The female, however, appears to be affected as there were no records for the upper part of the main canopy (> 30 m) between 1100 and 1600 h.

Foraging methods

I consider here four foraging methods, 'sallying', 'snatching', 'hovering' and 'gleaning'. Sallying (sometimes called hawking or flycatching) is where the bird flies out to seize a flying insect. Snatching is where a flying bird takes a perched insect. Hovering is a version of snatching, where a bird hovers and takes a perched prey. Gleaning is where both bird and prey are perched.

Table 2 shows the distribution of foraging methods and foraging substrate of male and female *Arses telescopthalmus*. There is significant difference between male and female, in that the female sallies much more than expected ($\chi^2_3 = 26.40$, $P < 0.001$).

Foraging substrate

As shown in Table 2 there are significant differences between the sexes in the substrate upon which they forage. As previously demonstrated the female spends more time sallying after aerial prey. Even deleting this 'substrate', i.e. the air, the female spends significantly less time than the male in foraging upon bare substrates such as trunks, large vines and branches ($\chi^2_3 = 22.04$, $P < 0.001$). Moreover 41% of male foraging is on vertical bare surfaces (trunks or vines), compared to 6% for the female. Table 2 shows that the female forages more off leaves than does the male, 53% (67% if aerial feeding is excluded) compared to 37%.

Only the male was seen on the ground, although the sample was small (seven moves by

three birds). Ground-feeding does not appear to be reported for the species. Given the extreme difficulty in observing ground feeding birds in rainforests actually foraging (e.g. Pearson 1971) the occurrences of male *Arses* at ground levels may be more than the data suggest.

Foraging associations with mixed-species flocks

Mixed-species feeding flocks of small insectivorous birds are a regular occurrence in New Guinea as they are in rainforests elsewhere (e.g. Asia, McClure 1966; Africa, Greig-Smith 1977; the neotropics, Buskirk 1976). At Brown River 13 species regularly associate and during 1975–77 144 flocks were recorded in which *Arses* occurred 57 times (41 males alone, 13 females alone and three pairs). 13.3% of all lone males, 6.6% of all females and 5.7% of the 54 pairs seen were in flocks.

Both males and females associated with all other species. Although the sample for the female is small the degree of association appears to differ between the sexes. Only 9% of male participation was with the monarch *Monarcha chrysomela* but one third of female participation was. This is not surprising because *Monarcha chrysomela* is found mainly at higher levels (Bell 1977).

It is known that some bird species, when associated in mixed-species flocks, forage at heights different to those frequented when alone (e.g. Morse 1970; Pearson 1971). This is so for almost all species so participating at Brown River (Bell 1977). Table 3 shows that

TABLE 3. Frequency of occurrence, by vegetation layers, of male *Arses telescopthalmus* alone and in mixed-species feeding flocks

Vegetation layer	σ alone		σ in flocks	
	n	(%)	n	(%)
Upper canopy (30–35 m)	1	(0.3)		
Lower canopy (25–30 m)	14	(4.3)	2	(4.9)
Subcanopy (8–25 m)	49	(15.2)	13	(31.7)
Understorey (6–8 m)	22	(6.8)	7	(17.1)
(4–6 m)	62	(19.3)	5	(12.2)
(2–4 m)	86	(26.8)	4	(9.8)
(1–2 m)	46	(14.3)	9	(21.9)
(0–1 m)	40	(12.4)	1	(2.4)
Ground	2	(0.6)		
Total	322	(100.0)	41	(100.0)

male *Arses* forage significantly differently ($\chi^2_8 = 18.35$, $P < 0.05$) when in mixed-flocks than when foraging alone, the trend being away from the lower understorey and towards the sub canopy. The sample for the female is too small for analysis.

Morphological differences

Seventeen male and 20 female skins were examined. Twenty-four skins were of the sub species found at Brown River, *A. t. henkei*, but as no significant difference was found between them and the remaining specimens (*A. t. insularis*) all were used. Unfortunately many of the data required (e.g. surface area of wings), could not be obtained without damage to the skins so measurements were confined to the following: wing length, of folded right wing from shoulder to extremity of primaries; tail length, from insertion of two central rectrices to tip of the longest one; beak length, from tip of upper beak to base of the most distal feathers; beak width, at base at point where beak length measured and at anterior of nares; rictal bristles, distance from most forward tip of bristles to line at right angles to tip of beak; front claw length, direct line from tip to top of base of right middle claw; rear claw length, as for front claw; curvature of rear claw, vertical line from top of inner curve to line from tip of claw direct to base of underside of claw. In addition weights were taken of eight males and six females netted at Brown River.

The measurements are shown in Table 4. While there is no significant difference in wing-length, the female has a significantly longer tail, the wing:tail ratio being 91% compared to 84% for the male. Beaks are of similar length but that of the female is significantly wider at the anterior nares, i.e. towards the front of the beak. Rictal bristles are significantly larger in the female. The male has a significantly longer front claw and a more curved rear claw. There is no significant difference in weights.

Discussion

My data are completely at variance with those of Croxall (1977). He records no birds in the understorey whereas from my records ca 80% were for males; he records only 6% of foraging moves as gleaning whereas I recorded 70%; he mentions that the male 'occasionally' clings to trunks whereas its bias towards trunk-feeding has long been known (e.g. Rand 1942). Croxall's data is based on 147 foraging moves (Croxall pers. comm.) by an unstated number of individuals; mine are based on 603 individuals for height, and 422 moves by 113 individuals for foraging method and substrate. I believe the discrepancies arise from Croxall's sample being small and split between at least two localities and forest types.

TABLE 4. Morphological data of specimens of *Arses telescopthalmus* in collection at CSIRO Division of Wildlife

Measurements (mm)	Values and s.d. (mm)		Difference	Significance by <i>t</i> -test
	♂	♀		
Wing length	78.88 ± 2.88	76.04 ± 2.40		n.s.
Tail length	66.47 ± 4.71	69.28 ± 2.94	♀ longer	$P < 0.05$
Beak length	11.15 ± 0.63	11.60 ± 0.67		n.s.
Beak width at base	5.54 ± 0.45	5.32 ± 1.02		n.s.
at anterior nares	2.67 ± 0.25	3.04 ± 0.42	♀ wider	$P < 0.05$
Rictal bristles gap from tip of beak to tip of longest bristle	5.54 ± 1.01	3.97 ± 0.97	♀ smaller	$P < 0.01$
Front claw-length	4.61 ± 0.59	3.98 ± 0.36	♂ larger	$P < 0.05$
Rear claw length	5.79 ± 0.43	5.51 ± 0.52		n.s.
Curvature of rear claw	1.82 ± 0.18	1.61 ± 0.31	♂ deeper	$P < 0.05$
<i>n</i>	17	20		
Weight (g)	16.75 ± 1.58	15.33 ± 1.75		n.s.
<i>n</i>	8	6		

Social organization

Year-round defence of territory, often by both sexes combined, supports existing evidence that the species is monogamous and has a strong pair bond. Both sexes equally share building of nests, incubation, brooding and feeding of young (Rand 1942; Bell 1967).

Foraging height

The trend, towards the middle layers of the forest, when both sexes are together, could be expected during the breeding season. The nest is invariably built on a bare vine 3–12 m from the ground, with the mean of 12 nests (Rand 1942 (4); Watson *et al.* 1962 (2); Bell 1967 (2); personal observation (4)) at $5.5 \text{ m} \pm 2.6 \text{ sd}$. However, sightings of both sexes together do not correlate with breeding records, as shown in Table 1.

Foraging methods

The pursuit of flying prey by the female accords with her partiality for the mid-levels of the forest, where the less dense foliage and higher light intensity would make sallying more practicable than in the understorey. Of the four other major salliers in the bird community, three (*Machaerirhynchus flaviventer*, *Microeca flavovirescens* and *Peltops blainvilli*) rarely occur in the understorey.

Foraging substrate

The preferences for leafy substrates by the female and bare ones by the male are independent of foraging height. Leaf density is least in the middle layer (Bell 1977) frequented by the female, as it appears to be in tropical forests everywhere (Pearson 1977). Leaf density is very high in the understorey, frequented by the male. Bare surfaces such as trunks, lianes and large branches, favoured by the male, occur in all layers frequented by both sexes but appear to be most available in the middle layers.

Foraging associations with mixed-species flocks

The move upwards by the male when in mixed-species flocks may be connected to the movements of the 'nucleus' species of such

flocks, *Gerygone chrysogaster*. A 'nucleus' species is a species (usually gregarious) which attracts others into a flock (Morse 1970). *Gerygone chrysogaster* was the only intraspecifically gregarious member of the flocks, was found more often than not in them, was the species most associated with by all the other member species, and showed little change in foraging height when in mixed-flocks (Bell 1977). It foraged mainly in the subcanopy and understorey above 6 m (ca 75% of 456 occurrences) so the trend upwards by male *Arses* is not surprising.

Morphological differences

The morphological data show adaptations, by each sex, to its differing niche. The male appears significantly adapted to his role of feeding on bare, usually vertical, substrates such as trunks and vines. Norberg (1979) showed that longer toes and curved claws increased a bird's ability to climb and illustrated this for titmice *Parus* spp. and creepers *Certhia* sp. Male *Arses* exhibits such features, despite the difficulty in accurate measurement of claws, which are subject to much wear and warping (Richardson 1942). The male also has a more slender beak, suited to probing into fissures of bark (e.g. Partridge 1976).

The female seems less strongly adapted to her specialized role of aerial feeding but the author stresses that the very important data on wing-loading was unobtainable from the specimens examined. Among related forms longer wings usually indicate a bias towards aerial feeding (Dilger 1956) or feeding in less dense vegetation (Hamilton 1961), but the difference in wing-lengths of the two sexes of *Arses* is not significant. Female *Arses* has a longer tail, which can assist in manoeuvring (Hartman 1961), an advantage for an aerial insectivore. Cameron (1975) showed that, with three species of fantails *Rhipidura* spp., the one with the highest tail/wing ratio was predominantly an aerial feeder. The wider beak of the female accords with a well-known trend among aerial insectivores of widely unrelated families e.g. swifts and tyrannid flycatchers (Van Tyne & Berger 1976). Long rictal bristles, as possessed by female *Arses*, are regarded as aids to aerial feeding (e.g. Van Tyne & Berger 1976). Leder-

er (1972) produced evidence, in one family, that rictal bristles were not used in the capture of prey but Stettenheim (1973) suggested that they may assist in retaining prey already held in the beak or that they may protect the eyes during flight. Cameron (1975) established a strong link between length of rictal bristles and the extent of aerial feeding, among *Rhipidura* spp.

The conspicuous colouring of male *Arses telescopthalmus* appears unrelated to differences in foraging ecology. Baker & Parker (1979) in an analysis of the entire European avifauna, arrived at certain attributes related to conspicuous coloration in males. With species possessing bright coloration on any or all of the head, back, front or belly, the trend was for small size, polygamy and incubation and care of young by the female. Apart from size *Arses* fits none of these attributes. Baker & Parker (1979) concluded that bright coloration evolved almost entirely as a response to predator-based selection pressure, and not for reasons of sexual attraction or male/male competition. Certainly, pair-bonds and territorial defence seem as strong among the monomorphic flycatcher species at Brown River as it is among the dimorphic ones.

General

Clearly the sexes of *Arses telescopthalmus* forage as differently as do separate species. At Brown River there are, in primary rainforest, 11 other species of obligate insectivores in the size-range 12–20 g, and which could be considered potential competitors of *Arses*. Table 5 shows the overlap between the sexes of *Arses*, and the overlap between each sex and those

other species with which overlap is greater than that for the opposite sex. With both male and female there are three other species whose foraging overlap is closer to the male or female than to that of the opposite sex. In addition four other species have an overlap value close to one sex of *Arses*, one with the male (*Poecilodryas hypoleuca*) and three with the female (*Rhipidura rufiventris*, *Monarcha chrysomela* and *M. melanopsis*). The remaining potential competitor, the fantail *Rhipidura threnothorax*, is a feeble-flying ground-feeder, a most aberrant flycatcher and shows little overlap with any other species (Bell 1977).

Morse (1968) in a study of nearctic warblers, Parulidae, considered that the preference shown by male warblers for feeding stations higher in the forest was related to the need for singing perches to overlook the territory and for surveillance of the next-site, usually among lower dense vegetation. The male *Arses* at his usual feeding station in the understorey, can neither overlook his territory nor guard the next-site. The female can do so but showed less aggression against intruders than did the male (six vs 18 occurrences). Thus, the behavioural and morphological divergence of sexes of *Arses telescopthalmus* is more likely related to a reduction of intersexual competition for food.

If competition between sexes for food is greater than between each sex and other species, in some circumstances individuals which differ ecologically from the opposite sex may be favoured, leading to divergence. Such sexual differences, and related morphological ones, occur most strikingly with insular forms, to a degree that it cannot be mere coincidence (Selander 1966; Ligon 1968). The suggestion is that given the depauperate faunas of islands

TABLE 5. Foraging overlap between male and female *Arses telescopthalmus* and other insectivore species of similar size

	Height (n)	Foraging method (n)	Substrate (n)	Average
♂ <i>Arses</i> /♀ <i>Arses</i>	0.579 (363 ♂) (240 ♀)	0.825 (322 ♂) (100 ♀)	0.629 (322 ♂) (100 ♀)	0.678
♂ <i>Arses/Rhipidura hyperythra</i>	0.870 (148)	0.888 (100)	0.455 (100)	0.738
♂ <i>Arses/Rhipidura rufidorsa</i>	0.851 (76)	0.747 (73)	0.543 (73)	0.714
♂ <i>Arses/Monarcha guttula</i>	0.910 (295)	0.867 (63)	0.607 (63)	0.794
♀ <i>Arses/Microeca flavovirens</i>	0.922 (150)	0.506 (69)	0.728 (96)	0.719
♀ <i>Arses/Machaerirhynchus flaviventer</i>	0.862 (50)	0.673 (47)	0.584 (46)	0.706
♀ <i>Arses/Pachycephala griseiceps</i>	0.931 (350)	0.813 (124)	0.750 (124)	0.831

n = for height, individual birds; for foraging method and substrate, individual moves from one perch to another.

generally and resultant speciation to fill vacant niches (MacArthur & Wilson 1967), sexes of a species could likewise differentiate. Selander (1972) showed that among woodpeckers, sexual differentiation in ecology and morphology was greatest among insular forms, including species found on both mainland and islands. But *Arses telescopthalmus* is not in a depauperate bird community. At the study plot of 2.5 ha, there were about 100 species of breeding birds. These included congeneric groups, eight of two species each, three of three, three of four, one of five and one of eight. Thus it could be presumed that niches are tightly packed, as postulated by Mayr (1969) for tropical rain forests generally.

How, then, were the sexes of *Arses* able to differentiate into subniches? Pearson (1977) drew attention to the paucity of trunk-feeding species in New Guinea, which lacks the specialized trunk-feeding families found throughout the world e.g. woodpeckers Picidae, creepers Certhiidae, nuthatches Sittidae, woodcreepers Dendrocolaptidae, treecreepers Climacteridae and sittellas Neosittidae. Treecreepers and sittellas are Australian and still occur in cool montane forests of New Guinea. The strong affinities between the avifaunas of montane New Guinea and cool temperate Australia (Schodde & Calaby 1972) imply a replacement, in New Guinean lowlands, by forms adapted to hot tropical forests following upon climatic change (Nix & Kalma 1972). The lowland forests have, to some extent, been occupied by forms derived from Asia, but no woodpecker or nuthatch, families which come close to the Australian region, has reached New Guinea. Therefore, male *Arses* may have differentiated to fill a depauperate niche, that of trunk-feeding, as did the honeyeater *Melithreptus validirostris* in Tasmania (Keast 1968). The related *Arses kaupi* in Queensland (also a trunk-feeder) does overlap slightly with tree creepers but is not common in the area of overlap (Bravery 1970; Gill 1970).

The female *Arses'* specialized habit of aerial feeding may be the ‘newer’ role of the species. In general, the warmer the climate year round, the more aerial-feeding species coexist (Lein 1972). If New Guinean lowland forests were once cooler, a warming of the climate may have increased opportunities for aerial-feeders;

however, there seem as many montane aerial-feeders in New Guinea as lowland ones.

A third suggestion is that the ancestor of present-day *Arses* may have evolved in a really depauperate environment. Nix & Kalma (1972) postulate that c. 16 000 BP drier conditions permitted savanna to occupy much of the present lowland areas of New Guinea now covered in rainforest. During that period lowland rainforest may have been fragmented into ‘islands’ and the usual extinctions following such isolation would have occurred (MacArthur & Wilson 1967). Certainly the present distribution of lowland species in New Guinea suggests that the ‘mix’ of species varied between areas and was richest, as expected, in the likely refugia comprising the largest areas of rainforest, i.e. in present Irian Jaya.

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Appendix 1. Actual overlap between foraging of male and female *Arses telescopthalmus* for moves in which all variables were recorded

	Male n	Male (%)	Female n	Female (%)
1. Main canopy				
Sallying			3	(3.9)
Leaves				
snatching	2	(0.9)		
gleaning	7	(3.2)		
Branches				
snatching			1	(1.3)
gleaning	6	(2.7)		
2. Sub-canopy				
Sallying			4	(5.3)
Leaves				
snatching			4	(5.3)
hovering			2	(2.6)
gleaning			5	(6.6)
Branches				
gleaning			3	(3.9)
Trunks				
hovering			2	(2.6)
gleaning	6	(2.7)	1	(1.3)
Vines				
gleaning			1	(1.3)
Debris				
gleaning				(2.6)
3. Upper understorey (4–8 m)				
Sallying			5	(6.6)

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