

Coexistence and competition between overwintering Willow Warblers *Phylloscopus trochilus* and local warblers at Lake Naivasha, Kenya

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Huge numbers of Willow Warblers winter in East Africa, and at Lake Naivasha the Willow Warbler becomes the most abundant species in its guild; in some habitats half the individuals in the guild are Willow Warblers, and most likely such numbers influence the ecology and behaviour of the local species in the guild. In a four-month study restrictions/displacements in the presence, and releases in the absence, of Willow Warblers were observed in several of the local species. In the course of the autumn the Willow Warblers also changed their habitat distribution from groves to woodland, presumably because of interference from the numerous local birds in the grove-habitat. Shortly after arrival the habitat and microhabitat distributions (and foraging behaviour) of the Willow Warblers were almost identical to those of local species such as the Black-bellied Apalis. However, in the course of the autumn and winter clear divergences occurred between the two groups in several ecological and behavioural parameters.

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Introduction

Every winter billions of migrant Palaearctic passerines visit Africa south of the Sahara. Most species winter in the savanna, and this includes about one billion Willow Warblers *Phylloscopus trochilus* (Moreau 1972, Curry-Lindahl 1981). These huge numbers of winter visitors should influence the ecology and behaviour of the local African species (e.g. McArthur 1972, Cody 1974, Diamond 1975). During the winter, increased competition for food and space should occur, and restrictions in the food and habitat distributions of the local species are to be expected. However, detailed field observations are needed to test this hypothesis.

A main problem is to find an appropriate bird community for study. The following criteria should be fulfilled: (1) At least one winter visitor should be very nu-

merous, comprising at least 20–25% of the individuals in the guild. The winter visitor(s) should have some negative behavioural effect on the local species. During interspecific encounters the winter visitor must be dominant over, or “irritating” to, the local species. (2) Food should – at least sometimes – be in short supply compared with the total demand of the individuals in the guild. (3) The habitat structure should be heterogeneous. Otherwise significant habitat shifts are not possible. Furthermore, the shifts should be detectable for the observer, which means that an open structure like a savanna is preferable as a study area to a dense structure like a mountain forest.

During February and March 1980 I made some preliminary observations in the *Acacia*-savanna at Lake Naivasha, and found an appropriate bird community for the study: A Willow Warbler guild. Part of the guild is

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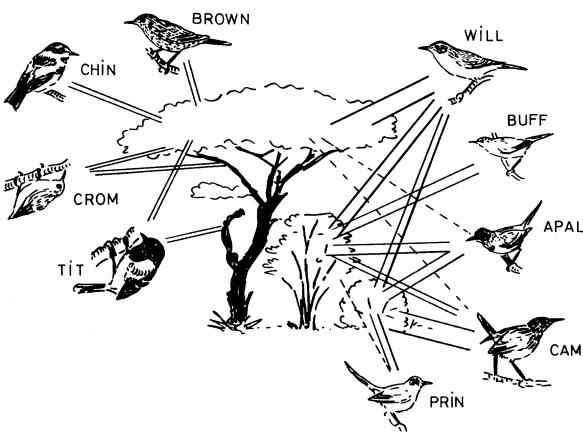


Fig. 1. Part of the Willow Warbler guild in the *Acacia* savanna at Lake Naivasha in Feb./March 1980. The thickness of the bands are measures of each species' relative abundance in the crowns of the higher trees, the lower trees, and the bushes, respectively. The Willow Warbler was by far the most numerous warbler in the tops of the high acacias, and was thought to depress the within-habitat distribution of the four species shown to the right. Tab. 2 should be consulted for the abbreviations of the species names.

shown in Fig. 1, which in a sketchy way shows the micro-habitat distribution and relative abundance of nine species. The vertical distribution of the four local warblers to the right may have been lowered because of numerous Willow Warblers in the tops of the high trees.

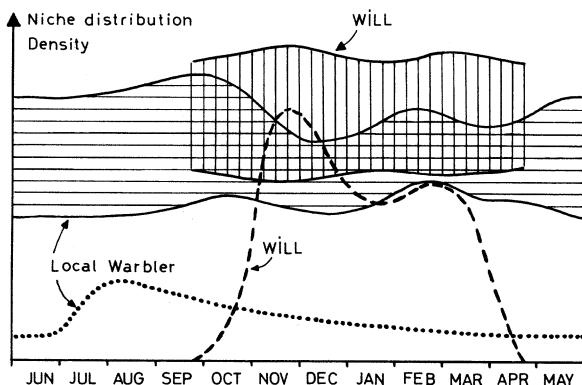


Fig. 2. The expected niche shift in a local competitor in the absence/presence of Willow Warbler (WILL) in the guild. The densities of the Willow Warbler and the local competitor in the course of the year are denoted by hatched and dotted lines. The niche breadths are also shown; that of the Willow Warbler is supposed to be almost constant, only widening slightly when the Willow Warbler is most numerous, whereas the niche breadth and position of the local warbler change in the course of the year. When the density of the Willow Warbler is high, the niche of the local warbler narrows and moves "down"; this may be termed a niche displacement. When the Willow Warbler is absent or scarce, the niche of the local warbler expands and moves "upwards"; this may be termed a niche release. The niche is envisaged mostly as a vertical, within-habitat distribution but may also be regarded as a horizontal within- or between-habitat distribution, or as a food/prey distribution.

In order to investigate the possible influence of the Willow Warbler I spent four months in Kenya from 18 August to 17 December, 1981. The time of my arrival was planned to be well ahead (1–1.5 month) of the arrival of the Willow Warbler to enable me to study the micro-habitat distribution of the local species in the absence of Willow Warblers. After the arrival of the Willow Warblers any micro-habitat restrictions and/or shifts could then be observed (Fig. 2). Likely micro-habitat releases/extensions after their departure (Fig. 2) were not, however, investigated in the present study.

The habitats studied

The investigation was carried out on the western side of Lake Naivasha, about 100 km NW of Nairobi (Fig. 3). The study area is situated about 2000 m above sea level. The vegetation type is savanna: Bushes, scrub, groves on grass-land, and woodland. The area supports quite a lot of cattle – and also much wildlife, including impala, giraffe, eland, bushbuck and leopard.

Eight stations were established and numbered as follows (number of visits per station and dates of study in parentheses): 1. *Long*: (5; 11 and 18 Sep, 31 Oct, 22 Nov, 3 Dec). 2. *Campsite*: (4; 24 Sep, 1 Oct, 6 Nov, 11 Dec). 3. *Airfield*: (27). 3a. *Riding Ground*: (4; 24 Aug, 11 Oct, 14 and 24 Nov). 4. *Kinja II*: (15). 5. *Kinja I*: (17). 6. *Mennell*: (11). 7. *Hudson*: (10).

Stn 3 and Stns 4–7 were visited at regular intervals throughout the period. The stations may be ranked on a vegetational scale from simple grass/bush to high *Acacia*-woodland (Fig. 4).

Ninety-nine % of all trees in the area are yellow fever-trees *Acacia xanthophloë*. At the escarpments of Stn 6 Euphorbia-trees are common, and *Jacaranda*-trees are scattered at Stns 5, 6 and 7. Whistling-thorn acacias *Acacia drepanolobium* are widespread at Stn 1.

The bush and scrub vegetation is more diverse: Ole-

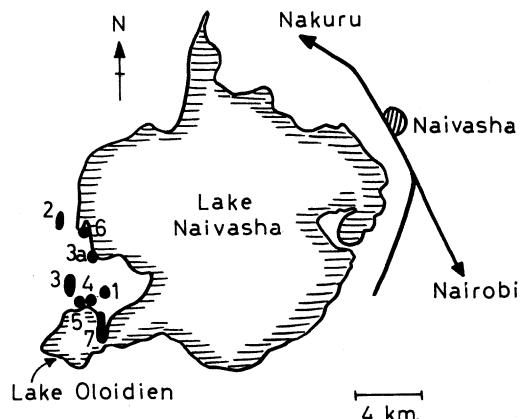


Fig. 3. The study area on the western shore of Lake Naivasha. The numbers denote the stations where observations were carried out.

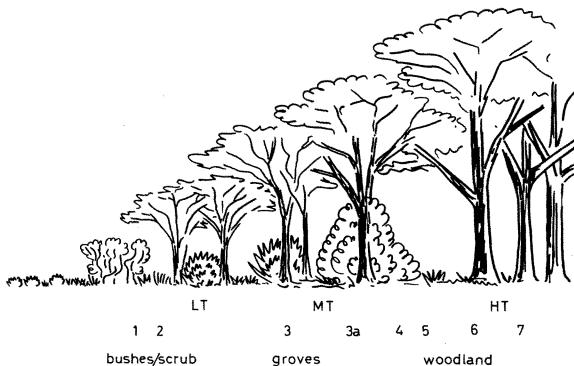


Fig. 4. The vegetational gradient from grass with low *Psiadia* bushes to *Acacia* woodland. Three different size groups of *Acacia* trees were distinguished: LT (low trees), MT (medium-sized trees) and HT (high trees). The greatest vegetational diversity/heterogeneity is not at the extreme right but occurs in the MT shrub habitat at Stn 3a and in some parts of Stns 4 and 5. The approximate position of the stations on the gradient is denoted below.

leswe (Compositae: *Tarchonanthus camphoratus*) is an up to 4–5 m high bush/tree. It is the dominant species at Stn 2, and is also very common at Stn 1. Oleleswe resembles a hybrid between elder *Sambucus* and willow *Salix*. Other important bushes are *Lycium europaeum*, *Rhus natalensis/vulgaris* and *Teclea simplicifolia*. The former is very similar in appearance to the European species *Lycium hamilifolium* – but it is more open and slender. *Rhus* resembles a privet *Ligustrum vulgare* and *Teclea* a dense pear tree/bush *Pyrus communis*. *Lycium*, *Rhus* and *Teclea* are particularly common at Stns 1, 3, 3a and 4. *Cassia* trees or bushes are fairly common at Stn 5, where *Citrus*-plantations and gardens are found nearby. In some areas – especially at Stns 1 and 3 – *Aloë* is widespread, and the sunbird-flower *Leonotis* is especially common at Stns 1, 2 and 4. *Psiadia punctulata* is a very common, dominant, low and open bush in the grassy areas, especially at Stn 3. *Senecio petitianus* is a common epiphyte and may cover much of the lower and inner parts of the *Acacia*-trees. It is especially common at Stns 3 and 3a, forming a significant part of the vegetation there. Among the weeds the prickling *Achyranthes aspera* is common at Stns 4 and 5, and *Nepeta azurea* at Stn 1.

Three different sizes of *Acacia xanthophloë* were distinguished (Fig. 4): HT (high tree), MT (medium-sized tree) and LT (low tree). HT is a single-stood tree with a thick trunk, normally at least 15 m high and without many twigs and leaves in the lower and inner parts. An MT is between 5 and 15 m in height, normally with many twigs and leaves also in the lower and inner parts (including the epiphytic *Senecio*). It often grows in closely packed groups of trees. LT is less than 5 m in height and occurs singly or as a group of small trees.

It is possible to distinguish between three major habitat types (Fig. 4): (1) Bushes/scrub (Stns 1 and 2). (2)

Groves/bushes on grassland (Stn 3). (3) Woodland, i.e. high and scattered trees on grassland with some bushes/scrub mostly on the fringes (Stns 4, 5, 6 and 7). The bushes/scrub habitat was found on the dry hills and escarpments, while the woodlands occurred as “islands” in the grove habitat. The latter was woodland in the past but because of tree-felling (for charcoal burning), cattle browsing and erosion it is now both a degraded habitat and a succession on its way back towards a woodland state. What is called the woodland habitat is also somewhat artificial, as most undergrowth is being removed in order to create productive grass (which is even sometimes irrigated) for the cattle.

In the bushes/scrub habitat (Stns 1 and 2) the scattered *Acacia* trees were mostly MT, and HT were absent. The dominant bushes were *Oleleswe*, *Aloë*, *Psiadia*, *Rhus* and *Teclea*.

In the grove habitat at Stn 3 about 75% of the trees were MT. HT constituted about 10% and LT 15%. This habitat was also characterized by dense undergrowth of bushes and scrub of *Psiadia*, *Senecio*, *Solanum*, *Aloë*, *Lycium*, and also small acacias. Stn 3a could be described as a dense version of Stn 3: A gallery wood/scrub down to Lake Naivasha. As it was visited only four times, and is difficult to rank on the habitat-scale, this station is omitted from most considerations.

The woodland habitat was dominated by HT (75–90% of all trees at Stns 5, 6 and 7). MT constituted between 5 and 20%, and LT about 5% at the same three stations. Stn 4 is a woodland habitat but transitional to Stn 3, and the tree composition was 45% HT, 45% MT and 10% LT. Except at Stn 5 the bushes and small scrub areas are outside or on the fringes of the woodland, and especially Stns 6 and 7 are very parklike in appearance.

Material and methods

Every morning I walked through the area of one of the stations, stopping frequently to observe the foraging birds. The time spent per station varied between 1 and 3.5 h depending on the area covered. The walking speed and the area covered per hour, however, showed no consistent variation from station to station or in the course of the season. The birds were observed with 10 × 50 binoculars, and normally each individual was followed for at least 10 s.

The total number of observation hours was 176.7 including station 3a. Tab. 1 shows the number of observation hours in the three different habitats during four periods: (I) from 18 Aug to 20 Sep, (II) from 21 Sep to 25 Oct, (III) from 26 Oct to 20 Nov, and (IV) from 21 Nov to 14 Dec. These periods were chosen for the following reasons: Period I: No Willow Warblers present, except for three in the grove habitat first observed on 19 Sep. Period II: Few Willow Warblers present, except for the grove-habitat. Period III: High numbers of Willow Warblers. Period IV: Many Willow Warblers present, but probably decreasing numbers compared with period III.

Tab. 1. The number of observation hours in the three habitats during four periods of the autumn and winter. Observations at Stn 3a not included.

	18 Aug– 20 Sep I	21 Sep– 25 Oct II	26 Oct– 20 Nov III	21 Nov– 14 Dec IV
Bushes/shrub	3.67	6.75	5.42	6.42
Groves	18.67	9.58	10.92	6.42
Woodland	28.92	26.33	25.83	19.08
Total	51.25	42.67	42.17	31.92

For every observed member of the Willow Warbler-guild (Tab. 2) – and also for many other related species – the following notes were taken: The feeding position in the vegetation, foraging and feeding movements, prey taken, aggressive and submissive behaviour, and calls or songs. Often the discovery of the individual was mediated by the call or song. I always tried to find and observe such birds, but especially for the more skulking species – such as the Grey-backed Camaroptera *Camaroptera brevicaudata* – most of the records consisted of birds recorded only by their call or song.

As many species were observed in mixed-species parties of 5 to 30 individuals, each single bird was normally watched for only 10–30 s as many short observations were considered better than a few detailed ones, at least at this preliminary stage of the study. All individuals seen or heard were recorded in order to assess the number of birds per species per hour (Tabs 2 and 3).

For any given tree, the bird's foraging positions were recorded as follows (Fig. 5). H, M and L mean high, medium and low and I and E interior (stem, branches, inner twigs) and exterior (outer twigs and leaves) parts,

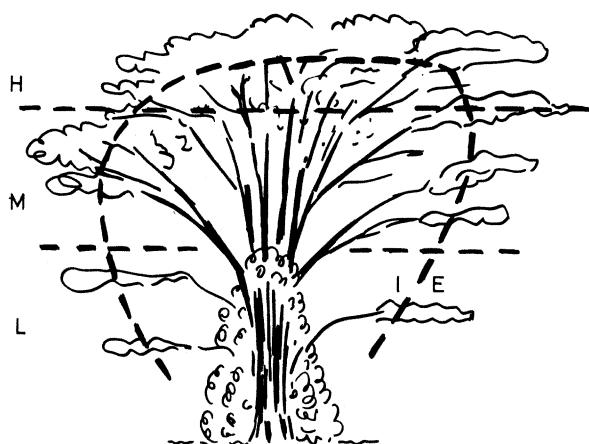


Fig. 5. A small group MT *Acacia* trees. Three different height zones may be distinguished: H (high), M (medium) and L (low). Furthermore an interior (I) and exterior (E) zone are recognized. The latter comprises (most of) the twigs and leaves, and the former the stem, branches and the *Senecio* epiphyte.

Tab. 2. The bird species in the WILL guild at Lake Naivasha. As WILL was not observed prior to 19 Sep the "true" number of WILL per hour (comparable with the densities of the local species) was about 15. During late autumn and winter WILL thus constituted more than 20% of all individuals in the guild (cf. Tab. 3). Abbreviations for Palearctic migrants in italics.

Species	Inds h ⁻¹
WILL	Willow Warbler <i>Phylloscopus trochilus</i>
CAM	Grey-backed Camaroptera <i>Camaroptera brevicaudata</i>
APAL	Black-breasted Apalis <i>Apalis flavida</i>
MASK	Masked Weaver <i>Ploceus intermedius</i>
RATT	Rattling Cisticola <i>Cisticola chiniana</i>
VAR	Variable Sunbird <i>Nectarinia venusta</i>
DRON	Drongo <i>Dicrurus adsimilis</i>
BOU	Tropical Boubou <i>Laniarius ferrugineus</i>
BUL	Yellow-vented Bulbul <i>Pycnonotus barbatus</i>
PRIN	Tawny-flanked Prinia <i>Prinia subflava</i>
REICH	Reichenow's Weaver <i>Ploceus baglafecht reichenowi</i>
CUC	Black Cuckoo Shrike <i>Campethera sulphurata</i>
ORI	Black-headed Oriole <i>Oriolus larvatus</i>
YELL	Yellow Whiteeye <i>Zosterops senegalensis</i> ..
SLAT	White-eyed Slaty Flycatcher <i>Dioptrornis fischeri</i>
CHIN	Chin-spot Flycatcher <i>Batis molitor</i>
SPEC	Spectacled Weaver <i>Ploceus ocularis</i>
TIT	White-breasted Tit <i>Parus albiventris</i>
SCAR	Scarlet-chested Sunbird <i>Nectarinia senegalensis</i>
BUFF	Buffbellied Warbler <i>Phyllolais pulchella</i> ..
PAR	Paradise Flycatcher <i>Tersiphone viridis</i>
CROM	Redfaced Crombec <i>Sylvietta whyti</i>
BRIM	Brimstone Canary <i>Serinus sulphuratus</i>
ROB	White-browed Robin Chat <i>Cossypha heuglini</i>
BUSH	Brownheaded Tchagra <i>Tchagra australis</i> ..
BROWN	Brown Tit-warbler <i>Parisoma lugens</i>
CAP	Grey-capped Warbler <i>Eminea lepida</i>
HON	Lesser Honeyguide <i>Indicator minor</i>
SPOT	Spotted Flycatcher <i>Muscicapa striata</i>
EORI	European Oriole <i>Oriolus oriolus</i>
BRON	Bronze Sunbird <i>Nectarinia kilimensis</i>
SPEK	Spekes Weaver <i>Ploceus spekei</i>
DUSK	Dusky Flycatcher <i>Alseonax adustus</i>
BLACK	Blackcap <i>Sylvia atricapilla</i>
WAHL	Wahlberg's Honeyguide <i>Prodontiscus regulus</i>
KLAAS	Klaas' Cuckoo <i>Chrysococcyx klaas</i>
BRU	Northern Brubru <i>Nilaus afer</i>
GOLD	Golden-winged Sunbird <i>Nectariniareichenowi</i>
Total	+ 23 species less than 0.10 ind h ⁻¹ , total .
	68.51

respectively. The number of different combinations (called micro-habitats) in the trees thus becomes $3 \times 3 \times 2 = 18$ (e.g. HT, M, E means that the bird was in a high tree, at medium height, and in the exterior parts of the tree).

Species names of the birds were abbreviated as shown in Tab. 2, and these abbreviations will from now on be used in the text. The most frequently used abbreviations

Tab. 3. Number of birds h^{-1} of the species in the "narrow" WILL-guild in the three habitats during the four periods (see text). The mean values should be noted. Some species like WILL and MASK clearly increase in the course of the autumn. APAL and BUFF also show tendencies to increase, whereas PAR and CUC decrease.

		I	II	III	IV	Mean		I	II	III	IV	Mean	
CHIN	Bushes/scrub	0.0	1.6	0.9	0.6	0.8	TIT	Bushes/scrub	0.0	0.0	0.2	0.0	0.1
	Groves	1.3	1.9	1.7	2.0	1.7		Groves	0.1	0.4	0.5	0.2	0.3
	Woodland	0.8	0.6	0.7	1.2	0.8		Woodland	1.7	2.1	1.2	1.4	1.6
	Mean	0.7	1.4	1.1	1.3			Mean	0.6	0.8	0.6	0.5	
PAR	Bushes/scrub	0.0	0.3	0.0	0.0	0.1	YELL	Bushes/scrub	0.0	0.4	0.0	0.2	0.2
	Groves	0.4	0.2	0.0	0.5	0.3		Groves	3.4	0.7	0.2	0.3	1.2
	Woodland	1.5	0.9	1.1	0.4	1.0		Woodland	0.6	0.0	0.6	3.2	1.1
	Mean	0.6	0.5	0.4	0.3			Mean	1.3	0.4	0.3	1.2	
CAM	Bushes/scrub	3.3	6.1	6.8	6.2	5.6	REICH	Bushes/scrub	0.3	1.2	0.2	0.2	0.5
	Groves	8.7	11.3	10.7	11.1	10.5		Groves	0.8	0.4	0.5	0.0	0.4
	Woodland	4.3	7.3	6.9	7.1	6.4		Woodland	2.1	2.2	3.1	4.2	2.9
	Mean	5.4	8.2	8.1	8.1			Mean	1.1	1.3	1.3	1.5	
APAL	Bushes/scrub	3.0	8.3	9.2	5.8	6.6	SPEC	Bushes/scrub	0.0	0.1	0.0	0.0	0.0
	Groves	8.1	12.6	18.6	17.9	14.3		Groves	1.2	0.4	1.2	0.3	0.8
	Woodland	1.8	3.3	4.1	4.8	3.5		Woodland	1.5	1.4	1.1	1.2	1.3
	Mean	4.3	8.1	10.6	9.5			Mean	0.9	0.6	0.8	0.5	
WILL	Bushes/scrub	0.0	3.9	15.0	13.7	8.2	MASK	Bushes/scrub	0.0	0.0	1.7	1.6	0.8
	Groves	0.1	7.5	10.6	9.4	6.9		Groves	5.0	2.4	2.3	1.2	2.7
	Woodland	0.0	5.8	25.3	23.3	13.6		Woodland	1.6	5.0	23.9	9.7	10.1
	Mean	0.0	5.7	17.0	15.5			Mean	2.2	2.5	9.3	4.2	
BUFF	Bushes/scrub	0.0	0.1	0.6	0.4	0.3	CUC	Bushes/scrub	0.0	0.9	0.4	0.0	0.3
	Groves	1.9	1.0	1.5	4.5	2.2		Groves	2.6	1.8	1.8	0.3	1.6
	Woodland	0.3	0.4	0.4	0.5	0.4		Woodland	2.8	2.1	1.3	0.6	1.7
	Mean	0.7	0.5	0.8	1.8			Mean	1.8	1.6	1.2	0.3	
RATT	Bushes/scrub	4.6	1.5	5.5	6.9	4.6	All 16 species	Bushes/scrub	20.7	38.0	51.9	46.0	39.1
	Groves	11.2	18.1	13.7	13.7	14.2		Groves	53.4	70.9	73.1	69.6	66.8
	Woodland	1.7	2.1	2.7	1.7	2.1		Woodland	24.6	36.2	77.0	62.7	50.1
	Mean	5.8	7.2	7.3	7.4			Mean	32.9	48.4	67.3	59.4	
CROM	Bushes/scrub	0.5	0.4	0.7	0.5	0.5	All 16 species ex WILL	Bushes/scrub	20.7	34.1	36.9	32.3	31.0
	Groves	0.8	2.4	1.6	1.7	1.6		Groves	53.3	63.4	62.5	60.2	59.9
	Woodland	0.2	0.3	0.5	0.8	0.5		Woodland	24.6	30.4	51.7	39.4	36.5
	Mean	0.5	1.0	0.9	1.0			Mean	32.9	42.6	50.4	44.0	
PRIN	Bushes/scrub	1.4	3.9	2.4	3.1	2.7	All 16 species ex WILL and MASK	Bushes/scrub	20.7	34.1	35.2	31.7	30.4
	Groves	4.6	5.4	5.7	3.1	4.7		Groves	48.3	61.0	60.2	59.0	57.1
	Woodland	0.9	0.4	0.4	0.7	0.6		Woodland	23.0	31.2	27.8	29.7	27.2
	Mean	2.3	3.2	2.8	2.3			Mean	30.7	42.1	41.1	40.1	
VAR	Bushes/scrub	7.6	9.3	8.3	6.7	8.0	WILL %	Bushes/scrub	0.0	10.3	28.9	29.8	17.3
	Groves	3.2	4.4	3.7	3.4	3.7		Groves	0.0	10.6	14.5	13.5	9.7
	Woodland	2.8	2.3	3.7	1.9	2.7		Woodland	0.0	16.0	32.9	37.2	21.5
	Mean	4.5	5.3	5.2	4.0			Mean	0.0	12.3	25.4	26.8	

are WILL (Willow Warbler), APAL (Black-breasted Apalis *Apalis flavida*) and CAM (Grey-backed Camptoptera).

For WILL and APAL (presumed to be the most important competitor to WILL) I focused particularly on their foraging behaviour. Different types of behaviour were distinguished: *JU*, *FL*, *HO*, *SFE* and *FE*. This order denotes a general increase in use of the wings and the length and duration of the foraging movement. The method used is highly correlated with the kind of prey taken. *JU*-foraging mostly means the taking of small and/or relatively immobile prey (caterpillars, spiders, aphids), whereas *SFE* and *FE* are directed towards fast-moving and often fairly large prey such as flies or

moths. The distribution of foraging movements – and seasonal shifts in their distribution – may thus be a good measure of the kind of prey taken.

JU signifies jumping along a branch or twig, from one branch or twig to another. The wings are kept close to the body, which is held in an extended posture. The movement is mostly in the vertical plane – a zigzagging up- or downwards. The bird weaves rather slowly through the vegetation, and is on the move almost all the time.

FL means fluttering and is often observed in combination with, or as an alternative to *JU*. *FL* is a faster movement. The single step is longer, and the movement more erratic and more in the horizontal plane than *JU*.

HO means hovering and is a movement from the outside into or onto the vegetation, usually leaves or flowers.

FE means a flight of at least 1–2 m towards prey in the air or prey on a solid surface such as a branch, a leaf, or a flower. A shorter *FE* is called a *SFE*.

The feeding movement was also sometimes noted: A gentle *PICK*, a faster *SNAP*, a vigorous *PECK*, or a “wide” *SMACK*. These movements are correlated with the foraging movements and the kind of prey taken. *PICK* often terminates *JU* and *HO*, and *SMACK* or *SNAP FE*. *PICK* is used when feeding on slow and/or immobile prey, whereas *SNAP* and *SMACK* are directed towards a potentially fast or flying prey.

Some observations were also made of the food eaten: Birds were trapped in mistnets in the grove habitat (Stn 3) in the following periods: 26–30 Aug, 8–10 Sep, 2–3 Oct, 3–5 Nov, and 16–17 Nov. The stomach and intestine contents were sucked out using the method of Moody (1970) and Laursen (1978). More than 100 birds were examined, including 7 WILL, 31 APAL, 32 CAM and 13 PRIN.

The food abundance and distribution were investigated directly by sampling as follows: (1) Once every week or ten days a total length of about 10 m of *Acacia* twigs with leaves were cut off and immediately placed in a large plastic bag containing ethyl acetate, which killed all arthropods in less than one hour. The arthropods were then sorted into groups: lepidopterous larvae, spiders, beetles, flies, hymenopterans etc. The length of each individual was measured to the nearest half mm. Normally spiders were the most abundant animals, while lepidopterous larvae contributed most to biomass. Throughout the autumn 14 samples were taken at Stn 5

and 15 samples at Stn 3, always around noon. (2) On the same occasions sweep-net samples were taken in the herbs and lower bushes beneath *Acacia* trees at the same two stations. Twenty sweeps were made per sample.

These two sampling procedures were intended to give a crude estimate of the abundance and distribution of the prey available to insectivorous birds in the woodland (Stn 5) and grove habitats (Stn 3).

The dry weights of the various prey groups were not measured but instead the following three measures were used as expressions of the relative amount of food available: (1) The number of individuals; (2) the summed lengths of all the individuals; and (3) the sum of the squared lengths. These variables are highly and positively intercorrelated; the correlation coefficient between any two of them is usually in the range 0.80 to 0.95.

Results

Vegetation and food

In the course of a four-month study the vegetation and the abundance and distribution of food change to a greater or lesser degree.

In mid-August most acacias were almost devoid of leaves and in the initial state of producing new ones. Many trees were flowering. The leaf-mass was at a maximum in late October or early November, decreasing by mid-December to about half or a third of the maximum. Most of this decrease seemed to be caused by shrinking or withering, since no rain fell during November–December. Defoliation by herbivores seemed

Tab. 4. The woodland habitat. Numbers of WILL, APAL, CAM, and MASK in four micro-habitats during the two periods (I + II) and (III + IV). HT (high tree), MT (medium tree), and LT (low tree) denote tree-size, H (high), M (medium) and L (low) height in tree, I and E is number of birds in interior and exterior layers, respectively, and T and B denote numbers in trees (HT + MT + LT) and bushes, respectively. The mean rank values are given. (*), *, ** and *** correspond to $P < 0.10$, $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively (χ^2 -tests of within-species coincidence of (I + II) and (III + IV)).

	WILL		APAL		CAM		MASK	
	I+II	III+IV	I+II	III+IV	I+II	III+IV	I+II	III+IV
HT 3	80	537	56	21	47	10	133	527
MT 2	48	229	24	30	23	14	31	236
LT 1	1	44	13	12	17	6	15	26
Mean	2.61	2.61*	2.46	2.14**	2.34	2.13(*)	2.66	2.63***
H 3	81	406	45	19	22	2	132	510
M 2	39	312	36	29	44	12	29	237
L 1	9	92	12	15	21	16	18	42
Mean	2.56	2.39*	2.35	2.06*	2.01	1.53**	2.64	2.59***
I 0	39	153	11	15	54	18	16	52
E 1	90	657	82	48	33	12	163	737
Mean	0.70	0.81**	0.88	0.76(*)	0.38	0.40	0.91	0.93
T 1	129	810	93	63	87	30	179	789
B 0	13	41	16	26	168	66	3	3
Mean	0.91	0.95(*)	0.85	0.71*	0.34	0.31	0.98	1.00

Tab. 5. The grove habitat. Numbers of WILL, APAL, CAM, PRIN, BUFF, RATT, and MASK in the four micro-habitats during the periods (I+II) and (III+IV). See Tab. 4 for further explanations.

	WILL		APAL		CAM		PRIN		BUFF		RATT		MASK	
	I+II	III+IV	I+II	III+IV										
HT 3	26	29	62	39	38	9	24	6	4	4	23	5	30	5
MT 2	29	80	110	109	81	20	61	23	15	25	93	18	75	21
LT 1	3	24	51	41	42	12	39	19	23	10	97	44	9	3
Mean	2.40	2.04**	2.05	1.99	1.98	1.93	1.88	1.73	1.55	1.85*	1.65	1.42*	2.18	2.07
H 3	16	74	68	49	10	3	37	9	23	19	30	6	51	10
M 2	36	48	102	94	72	14	47	19	16	20	46	16	61	16
L 1	6	11	53	46	79	24	40	20	3	0	118	26	2	3
Mean	2.17	2.47**	2.07	2.02	1.57	1.49	1.98	1.77	2.48	2.49	1.55	1.58	2.43	2.24(*)
I 0	13	18	47	42	88	32	20	9	2	0	64	16	31	6
E 1	45	115	176	147	73	9	104	39	40	39	130	32	83	23
Mean	0.78	0.86	0.79	0.78	0.45	0.22*	0.84	0.81	0.95	1.00	0.67	0.67	0.73	0.79
T 1	58	133	223	189	161	41	124	48	42	39	213	67	114	29
B 0	3	5	32	29	72	19	54	30	1	0	205	93	1	0
Mean	0.95	0.96	0.87	0.87	0.69	0.68	0.70	0.62	0.98	1.00	0.51	0.42(*)	0.99	1.00

to be less important. In fact, the leaves of the *Acacia* trees seemed less gnawed than the leaves in a Danish wood.

The changes in leaf-mass and degree of flowering have two important consequences: (1) The vegetational structure and complexity change, and this in itself may influence the habitat and micro-habitat distribution of the birds. (2) The pool of prey available to the insectivorous birds is not constant; this may also influence the habitat and micro-habitat distribution of the birds. There may well be a positive correlation between leaf-mass and prey abundance, at least in the initial phases of leafing (Laursen 1976, 1981).

The results of the prey sampling are given in Tabs 9–12. I regard the *Acacia* samples as the most reliable estimate of the relative amounts of food available to the birds in the course of the autumn, since most species (especially WILL, APAL, BUFF and MASK) foraged almost exclusively in the *Acacia* trees. However, fast-moving or flying prey are heavily under-represented in the *Acacia* samples, and may in fact constitute an important part of the food taken by the birds. Therefore, sweepnet-sampling in the ground-vegetation was also considered important (it is not possible to use a sweepnet in the thorny *Acacia* trees).

There is a generally decreasing trend in the number of arthropods in the *Acacia* samples in the course of the autumn; most correlation coefficients in Tabs 9 and 10 are negative.

For the sweepnet samples the picture is more varied, but most correlation coefficients of Tabs 11 and 12 are positive. In all categories considered, the amount of arthropods was less at Stn 3 (groves) than at Stn 5 (woodland).

A few groups, especially spiders (Araneae) and beetles (Coleoptera), were numerous in both kinds of samples. Comparisons are shown in Tab. 13. Obviously the

relative decrease in the course of the autumn is more pronounced in the *Acacia* samples.

If the sweepnet-samples are taken as a sort of control, reflecting the arthropod pool not influenced by bird predation, these results may be interpreted as showing that predation by birds is depleting the amount of arthropod food in the *Acacia* trees in the course of the autumn.

In order to assess the relative amount of prey available in the course of the autumn, a weighted product of leaf-mass and the abundance of arthropods in the *Acacia* samples should be calculated; this is because twigs with leaves were selected for sampling, where arthropods were presumably more abundant than on twigs without leaves or with only a few leaves. Fig. 6 is such an estimate, which also shows the presumed relative

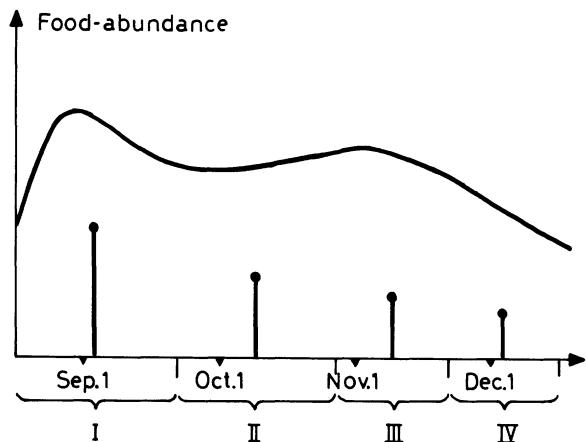


Fig. 6. The estimated relative abundance of food (arthropod prey) in the course of the autumn. The four columns in the middle of the periods I to IV show the relative amount of food per individual bird (cf. the densities in Tab. 3).

amount of arthropod prey per predator in periods I, II, III and IV (Tab. 1)

As a supplement to the samplings the following field-notes are considered important:

20 Sep: "At the start, the general impression was of few Lepidoptera-larvae and many spiders – at both stations. Lepidoptera-larvae were not considered an important part of the diet of the insectivorous birds. Now the number of Lepidoptera-larvae has increased and the larvae are also larger. This trend has occurred in parallel with the increase in the amount of leaves. All bird species – also BOU, ORI and WATT – are now preying among the twigs and leaves on Lepidoptera-larvae of a size of about 2 cm."

10 Oct: "Many flies in the flowering acacias – but only few birds seem to prey upon the flies". This observation gives rise to the following remark: "A specialized flycatcher-role seems not to be profitable in the community. In order to be profitable one of the following conditions has to be fulfilled: Either the flying prey should be large and abundant (as in Denmark during late spring), or the total amount of food should be low and in deficit compared with the demand (then every food-item becomes profitable). The latter situation is normal on the island of Christiansø during early spring where all passerine species try to catch the sparse and tiny chironomids".

18 Nov: "Many flies are now taken in the air by WILL indicating scarcity of large stationary prey like Lepidoptera-larvae."

Bird densities

Tab. 2 shows the overall mean densities (birds h^{-1}) for the whole season at all stations for the 38 (61) species in the WILL guild and Tab. 3 presents the number of birds per hour of the 16 most closely associated species in the same guild. The mean values of the four columns and

the three rows give the seasonal density-trend and habitat-preference, respectively.

The last four sub-tables of Tab. 3 should be noticed. When WILL – and especially WILL and MASK – are excluded, the combined density of the remaining 14 species is fairly constant throughout the season. The high percentage of WILL, especially in woodland and in the periods III and IV, is noteworthy.

The mean density of all 16 species is clearly higher in the grove habitat than in the woodland and, especially, the bushes/shrub habitat. However, the differences are levelled out if species outside the "narrow" WILL guild are considered. In the woodland habitat high numbers of Blue-eared Glossy Starling *Lamprotornis chalybaeus*, Superb Starling *Spreo superbus*, Wattled Starling *Creatophora cinerea*, DRON, BOU and ORI were found, all of which feed to some degree on Lepidoptera-larvae in the trees (except DRON which is a big sallying flycatcher). In the bushes/shrub habitat, such groups as finches, waxbills and sunbirds were more numerous than in the two other habitat types.

Figs 7–10 give additional information on the densities of the three most important species, WILL, APAL and CAM. All three species show a general increase in the course of the autumn. CAM increases until about 1 Oct. This increase may be due to juvenile-production solely, as the general impression of CAM is one of a stationary species. The increase of APAL is too large to be ascribed to juvenile-production alone; on any single day the percentage of juveniles never exceeded 30. Certainly there must have been a significant influx of APAL

Tab. 6. Comparisons of the micro-habitat utilization of WILL and APAL. The numbers are the mean rank numbers of Tabs 4 and 5. Differences tested by χ^2 . Significance levels as in Tab. 4.

Woodland				Groves				
I+II		III+IV		I+II		III+IV		
WILL	APAL	WILL	APAL	WILL	APAL	WILL	APAL	
HT/MT/LT	2.61	2.46***	2.61	2.14***	2.40	2.05**	2.04	1.99
H/M/L	2.56	2.35(*)	2.39	2.06**	2.17	2.07*	2.47	2.02***
I/E	0.70	0.88**	0.81	0.76	0.78	0.79	0.86	0.78(*)
T/B	0.91	0.85	0.85	0.71***	0.95	0.87	0.96	0.87**

Tab. 7. Niche breadths of WILL and APAL in the woodland and the grove habitat, respectively, in the periods (I+II) and (III+IV). The numbers are Simpson's index of diversity, D, as a measure of micro-habitat variance in the two periods. The calculations are based on Tabs 4 and 5.

Woodland				Groves				
WILL		APAL		WILL		APAL		
I+II	III+IV	I+II	III+IV	I+II	III+IV	I+II	III+IV	
HT/MT/LT	0.48	0.48	0.55	0.63	0.55	0.56	0.63	0.58
HT/MT/LT/B	0.56	0.52	0.65	0.73	0.59	0.59	0.70	0.66
H/M/L	0.51	0.59	0.60	0.64	0.53	0.55	0.64	0.63

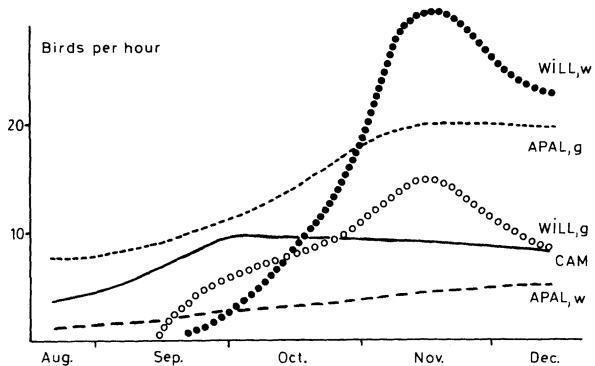


Fig. 7. Number of birds h^{-1} of WILL, APAL and CAM. The first two species are shown in the woodland (w) and grove (g) habitats separately. The smoothed curves are based on Tab. 3 and Fig. 8.

into the Naivasha area, and maybe half of the November/December birds were migrants or winter visitors. WILL peaked about 10–15 Nov., and then showed a slight decrease. This was also the general impression in the field. However, a Mann-Whitney U-test comparing the numbers per hour in the four woodland stations in the periods 5–20 Nov ($n = 9$) and 1–14 Dec ($n = 7$) failed to show any significant difference between the two samples ($P = 0.13$, one-tailed).

Fig. 8 shows the density trend of WILL on the habitat gradient (Fig. 4) in the course of the autumn. Early in the season WILL was most numerous in the grove habitat (Stn 3), but later on the density became higher in the bushes/shrub habitat (Stns 1 and 2) and especially in the woodland (Stns 4 to 7).

Figs 9 and 10 show the densities of WILL, APAL and CAM in the woodland and grove habitats. The four periods are combined into two: I+II (few WILL) and III+IV (many WILL), and two types of density are indicated: (1) Total density, and (2) density of birds observed by eye in trees. The ratio of (2) to (1) decreases from period I+II to period III+IV in all species and habitats. In the woodland the ratios were 0.84 and 0.74 (WILL), 0.67 and 0.32 (APAL), and 0.28 and 0.09

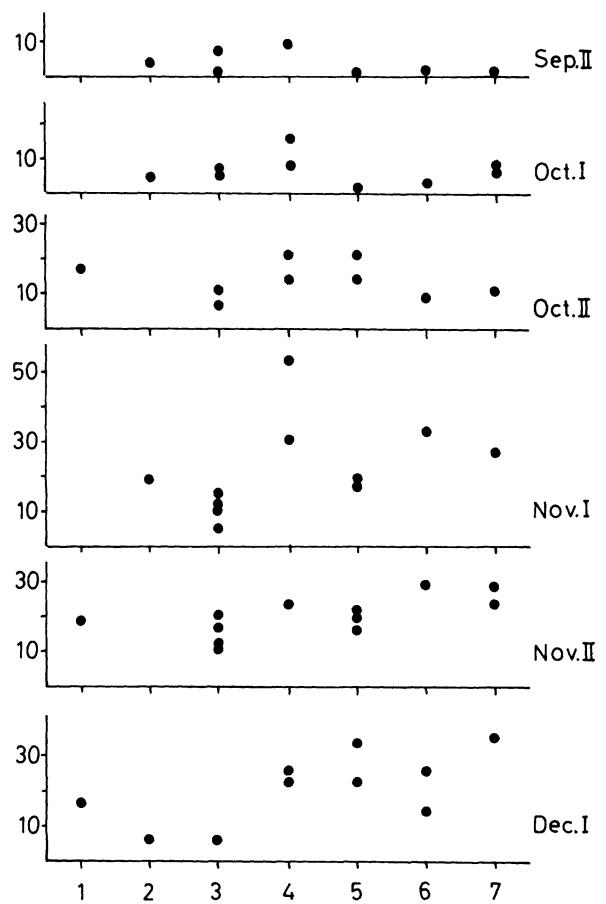


Fig. 8. Observed numbers of WILL h^{-1} at the 7 stations arranged on the habitat scale of Fig. 4. Each month is divided in a first and a second half, and by moving downwards the seasonal trend in habitat distribution may be observed.

(CAM). In the grove habitat the ratios were 0.78 and 0.69 (WILL), 0.82 and 0.54 (APAL), and 0.60 and 0.20 (CAM).

The significant decreases in these ratios may have several causes, and may influence the estimation of the true

Tab. 8. Numbers of WILL and APAL displaying different kinds of foraging behaviour (ranked from 0–4) in the periods (I+II) and (III+IV). The asterisks (see Tab. 4) show the probability of within-species coincidence in the two periods. Foraging methods (abbreviations) explained in the text.

Foraging method (rank)	Woodland				Groves			
	WILL		APAL		WILL		APAL	
	I+II	III+IV	I+II	III+IV	I+II	III+IV	I+II	III+IV
JU (0)	82	379	21	39	30	58	35	107
FL (1)	49	345	11	3	25	53	9	16
HO (2)	11	66	3	1	7	24	2	7
SFE (3)	4	71			2	18	1	2
FE (4)		11				4		
Mean rank	0.57	0.84**	0.49	0.12***	0.70	1.09(*)	0.34	0.27

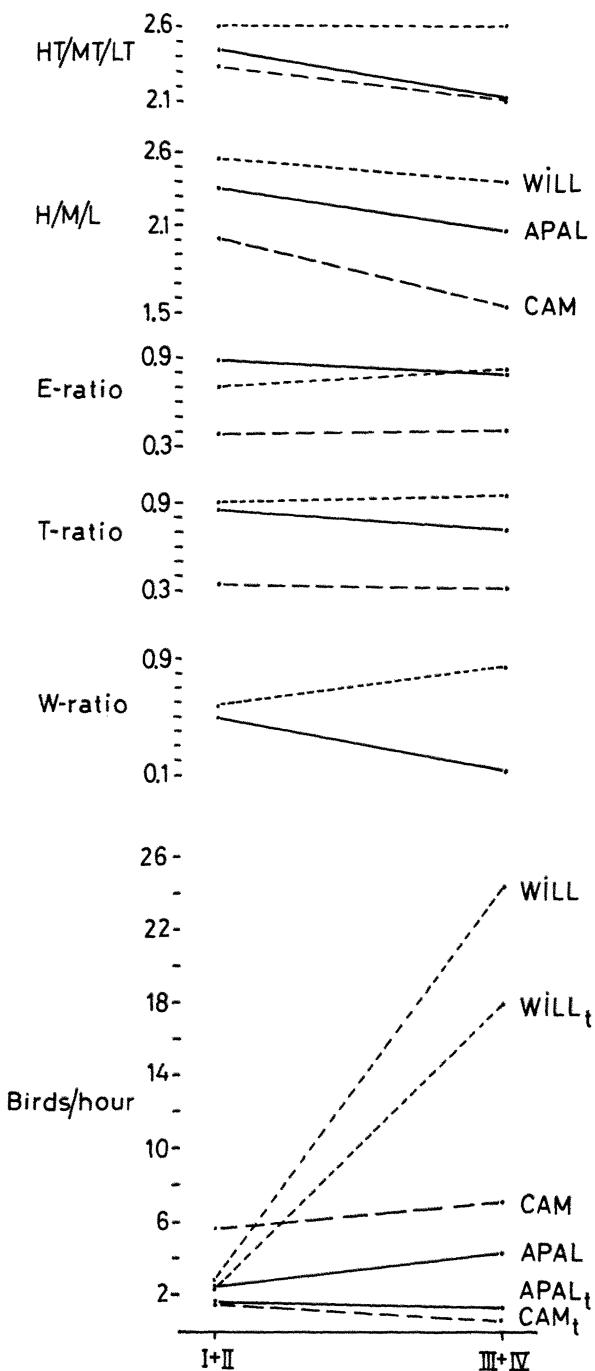


Fig. 9. Woodland. The lower section shows the number of birds h^{-1} of WILL, APAL and CAM in the periods I+II and III+IV. The index t with the species abbreviation refers to the numbers recorded by eye in trees, while abbreviations without an index refer to the numbers seen or heard in trees and bushes. The upper five sections are graphical presentations of the "mean values" of Tabs 4 and 5 and "woodland" of Tab. 8. The expectation is a general divergence of the "mean values" from early (I+II) to late (III+IV) autumn. This divergence should arise mostly through a shift in the scarcer species APAL and CAM as WILL becomes numerous in the late period. To some extent this expectation is met.

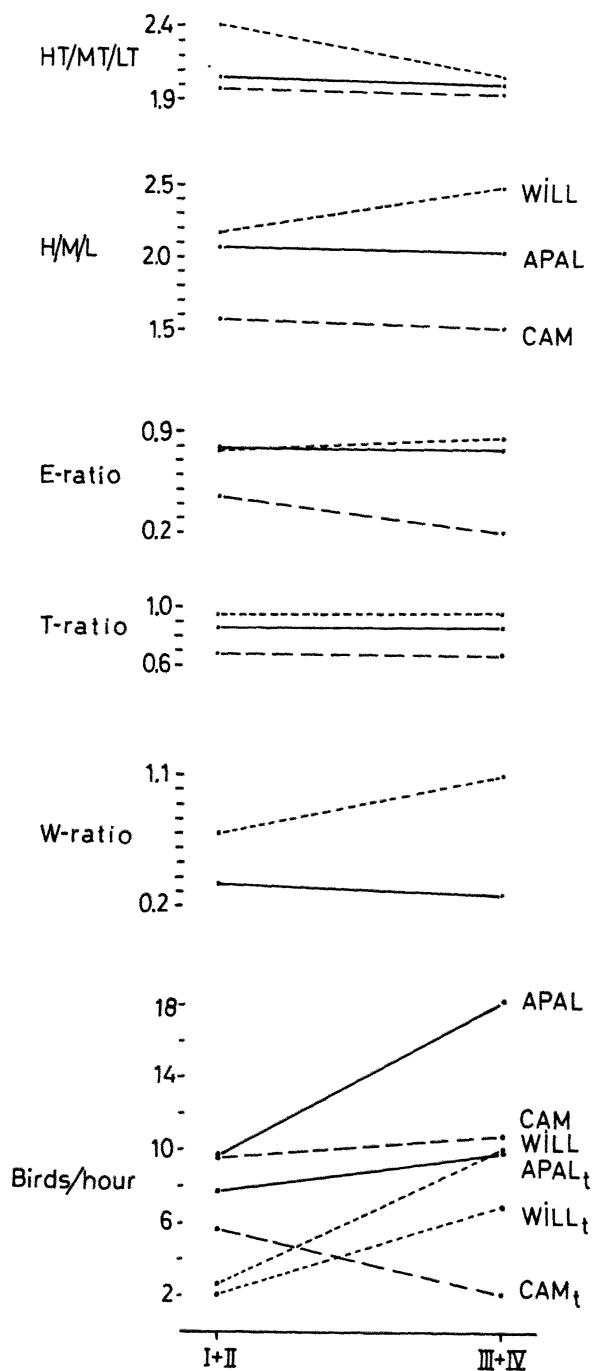


Fig. 10. Groves. Otherwise legend as to Fig. 9. In this case WILL is the scarce species which is expected to shift most extensively. Certainly this seems to be the case.

densities in different ways. APAL and especially CAM may become more skulking in the course of the autumn, i.e. relatively fewer birds are observed by eye. Probably this holds true for CAM, where the decreasing ratio may also express a tendency to move out of the trees and into the bushes, or moving to the more interior and

Tab. 9. Numbers and sizes of arthropods per m *Acacia* twig with leaves at Stn 3 (grove habitat). n denotes the mean number of individuals, Σmm the summed lengths of all individuals, and $\Sigma(mm)^2$ the summed squared lengths of all individuals. Mean denotes the sample mean value (mean of the means) and the bottom row the sample mean value of Stn 3 divided by the corresponding sample mean value of Stn 5 (Tab. 10). r is the correlation coefficient between the rank number of the dates and the amounts of arthropods. r = 0.51, 0.64 and 0.74 correspond to P = 0.05, 0.01 and 0.001 (two-tailed test, n = 15).

Date	Lepidoptera-larvae			Araneae			All species		
	n	Σmm	$\Sigma(mm)^2$	n	Σmm	$\Sigma(mm)^2$	n	Σmm	$\Sigma(mm)^2$
23 Aug	2.48	16.97	310.31	1.38	3.72	12.34	6.34	28.48	355.17
27 Aug	1.55	16.90	197.18	1.13	3.66	14.30	2.96	21.62	215.46
8 Sep	2.18	27.39	363.03	0.34	0.67	1.34	2.86	29.24	369.83
17 Sep	2.71	31.88	426.47	1.35	3.15	7.59	6.40	47.81	538.42
29 Sep	0.73	7.88	89.05	1.61	3.36	7.74	4.97	21.46	177.96
8 Oct	0.34	2.61	21.48	1.59	3.86	10.63	2.95	9.60	124.86
14 Oct	1.16	13.44	167.51	0.74	1.96	6.11	3.06	19.90	195.02
24 Oct	0.43	5.04	74.26	1.30	3.65	11.30	4.16	21.34	256.93
1 Nov	0.44	5.75	84.69	1.07	2.65	10.11	2.13	10.35	101.53
9 Nov	0.33	1.69	10.41	2.19	6.01	29.07	15.85	51.17	253.17
13 Nov	0.77	5.40	50.02	0.98	1.92	4.17	7.29	20.89	99.33
21 Nov	0.62	6.46	73.28	1.23	2.87	7.38	3.49	16.20	127.89
27 Nov	0.48	3.73	31.03	1.27	3.21	8.71	3.26	12.61	65.32
9 Dec	0.27	3.38	43.93	0.82	1.96	5.32	3.74	14.47	86.09
15 Dec	0.58	4.59	38.67	0.87	1.93	4.93	3.67	10.24	103.33
Mean	1.00	10.21	132.09	1.19	2.97	9.40	4.88	22.36	204.69
r	-0.74**	-0.70**	-0.73**	-0.06	-0.14	-0.10	0.04	-0.39	-0.69**
Stn3/Stn 5	0.58	0.67	0.75	0.20	0.19	0.18	0.38	0.47	0.67

Tab. 10. Numbers and sizes of arthropods per m *Acacia* twig with leaves at Stn 5 (woodland habitat). r = 0.53, 0.66 and 0.78 correspond to P = 0.05, 0.01 and 0.001 (n = 14). See Tab. 9 for further explanation.

Date	Lepidoptera-larvae			Araneae			All species		
	n	Σmm	$\Sigma(mm)^2$	n	Σmm	$\Sigma(mm)^2$	n	Σmm	$\Sigma(mm)^2$
24 Aug	1.14	13.92	173.32	4.55	13.07	44.49	9.10	39.32	270.30
1 Sep	1.63	16.37	220.11	8.44	19.93	62.93	20.88	68.08	401.37
12 Sep	2.16	24.86	341.15	9.46	27.23	90.64	16.89	75.87	559.63
24 Sep	1.63	15.04	197.76	7.48	21.22	78.82	19.19	65.61	367.03
5 Oct	1.18	10.83	123.34	4.14	11.78	40.62	8.16	34.27	227.01
13 Oct	1.50	13.72	151.60	4.79	14.04	52.77	11.29	48.03	301.95
24 Oct	1.10	9.25	84.53	4.80	14.40	52.30	8.50	35.45	206.73
31 Oct	1.89	13.78	109.86	5.68	15.81	60.61	12.62	46.26	238.35
7 Nov	3.52	28.85	279.15	4.62	12.31	41.95	11.33	50.56	358.98
16 Nov	1.47	10.40	77.97	8.02	16.21	40.59	16.38	45.37	180.09
22 Nov	2.01	11.37	180.38	3.64	10.62	35.96	9.67	33.90	262.54
29 Nov	0.74	6.71	76.61	5.56	13.89	42.40	8.24	28.85	247.10
10 Dec	2.00	19.88	252.59	5.53	14.76	48.32	12.71	48.88	357.62
16 Dec	1.91	17.64	194.27	5.51	12.81	34.83	13.71	49.66	310.06
Mean	1.71	15.19	175.90	5.87	15.58	51.95	12.76	47.87	306.41
r	0.17	-0.08	-0.20	-0.32	-0.49	-0.59*	-0.29	-0.43	-0.33

lower parts of the trees where CAM is less easily spotted. A second explanation of the decreasing ratio is that the birds become more noisy (aggressive/territorial) in the course of the autumn, leading to an increased fraction of birds being recorded only by ear. This is probably the major explanation in APAL. A third factor, less attention on the part of the observer to calling and singing CAM and APAL during the first two weeks of

observation, is also thought to have made a minor contribution.

Within-habitat distribution

The potential number of competitors of WILL in the Naivasha area is very high (Tab. 2), and the amount of diffuse competition (McArthur 1972) is probably signifi-

Tab. 11. Numbers and sizes of arthropods per 20 sweeps with a net at Stn 3 (grove habitat). See Tab. 9 for explanation and significance of r.

Date	Diptera (Brachycera) and Hymenoptera			Coleoptera, Homoptera and Heteroptera		
	n	Σmm	$\Sigma(mm)^2$	n	Σmm	$\Sigma(mm)^2$
23 Aug	85	253	879.5	18	66	285.5
27 Aug	28	95.5	423.75	27	93	382
8 Sep	9	30.5	116.75	25	75.5	253.75
17 Sep	19	55.5	456.75	14	52	217.5
29 Sep	33	113	452	21	80.5	327.25
8 Oct	41	100.5	278.75	23	70	229.5
14 Oct	18	55.5	197.75	26	107	530.5
24 Oct	20	62.5	212.25	61	185.5	629.75
1 Nov	45	126	414.5	69	195	616
9 Nov	17	77	397.5	12	38	127.5
13 Nov	55	171	660	47	156	644.25
21 Nov	13	52	230.5	23	98	498.5
27 Nov	27	68	178.5	47	171.5	772.75
9 Dec	48	159.5	597.25	38	137	560.75
15 Dec	21	58.5	194	84	266.5	962.5
Mean	31.93	98.53	378.65	35.67	119.43	469.20
r	-0.17	-0.16	-0.25	0.57*	0.64*	0.70**
Stn 3/Stn 5	0.42	0.50	0.57	0.66	0.59	0.45

Tab. 12. Numbers and sizes of arthropods per 20 sweeps with a net at Stn 5 (woodland habitat). See Tab. 9 for explanation and Tab. 10 for significance of r.

Date	Diptera (Brachycera) and Hymenoptera			Coleoptera, Homoptera and Heteroptera		
	n	Σmm	$\Sigma(mm)^2$	n	Σmm	$\Sigma(mm)^2$
22 Aug	24	70	272	22	104	611.75
1 Sep	74	226	1057	48	187	926.5
12 Sep	91	240.5	736.25	46	203.5	1194.75
24 Sep	76	196.5	883.5	63	274	1703
5 Oct	51	144	521.5	46	149	645
13 Oct	40	122	588	36	151	743
24 Oct	38	100.5	307.25	56	246	1499
31 Oct	38	113.5	528.25	51	213.5	1098.5
7 Nov	43	104	295	86	314	1530
16 Nov	71	191	567.5	65	202.5	844.25
22 Nov	51	135	433.5	27	138	975.5
29 Nov	182	391	952.5	83	237	961
10 Dec	76	209.5	682.25	51	182.5	815.75
16 Dec	208	534.5	1524.75	73	232	947.5
Mean	75.86	198.43	667.80	53.79	202.43	1035.39
r	0.54*	0.51	0.28	0.49	0.27	-0.03

cant. However, diffuse competition is impossible to measure in the data collected, and therefore special attention has been paid to a few species, especially APAL and CAM, which closely resemble WILL in micro-habitat distribution and foraging behaviour (i.e. large overlap in diet is to be expected). Furthermore, these species are numerous, which implies that the competitors may have observable effects on WILL, and that the effects of WILL on APAL and CAM should be observable despite the noise arising from stochastic variation.

For the sake of clarity and to damp the stochastic variations, the material has been combined into two periods as was done above.

Before presenting the results a few expectations should be pointed out. The naive expectation, if competitive displacements occur, is a large and significant shift in the "mean" or center of gravity of the scarce species and no change, or only a slight shift, in the abundant species.

Besides displacements in the "mean", changes in the

variance of the micro-habitat distributions may also be expected in connection with changes in the intra- and interspecific densities. In the present context with few classes (3–4) the variance is presumably most appropriately described by an index of diversity, e.g. Simpson's $D = \Sigma 1 - p^2$. Within a given species, D may be assumed to increase when the density of birds increases; the marginal or less preferred "places" or micro-habitats are taken into use (e.g. Svärdson 1949). This may be tested in the case of WILL (and MASK) in woodland, and APAL in the grove habitat.

In general, interspecific influences on the microhabitat utilization of the scarcer competitor(s) are more difficult to predict. In the case of APAL in woodland one could predict either an increasing or a decreasing index of diversity from period I+II to period III+IV as WILL comes in from "above" (HT and H).

Tabs 4 and 5 show the micro-habitat distribution of four and six species in the woodland and grove habitats. They also show mean rank-values. For instance, the mean tree-size rank-value for WILL in period I+II (Tab. 4) is 2.61, calculated as the mean of 80 birds in HT(3), 48 birds in MT(2) and 1 bird in LT(1). Of course such a procedure is dubious or even bad mathematics, but for superficial comparisons the mean rank-values are practical. Figs 9 and 10 give graphical comparisons based on them. The differences within species (periods I+II and III+IV compared) and between species (WILL/APAL) were tested using χ^2 tests. Of course, with this test a significant difference between two distributions may arise because of differences in both "mean" and variance.

The intraspecific seasonal trends, with special attention to changes in the "mean", in WILL, APAL and CAM were as follows:

Woodland habitat

WILL: More even distribution with regard to tree-size (same "mean", increased variance, $P < 0.02$); lower position in trees ($P < 0.05$); more exterior position in trees ($P < 0.01$); tendency to forage more in trees and less in bushes ($P < 0.10$).

APAL: In lower trees ($P < 0.01$); lower position in trees ($P < 0.05$); tendency to more interior position in trees ($P < 0.10$); more in bushes and less in trees ($P < 0.05$).

CAM: Tendency to use lower trees ($P < 0.10$); lower position in trees ($P < 0.01$); unaltered interior/exterior position in trees ($P > 0.80$); unaltered tree/bush-distribution ($P > 0.50$).

Grove-habitat

WILL: In lower trees ($P < 0.01$); higher position in trees ($P < 0.01$); weak tendency to use more exterior positions in trees ($P < 0.30$); unaltered tree/bush-distribution ($P > 0.50$).

APAL: Tendency to use lower trees ($P < 0.20$); unaltered height in trees ($P > 0.50$); unaltered interior/exterior position in trees ($P > 0.70$); unaltered tree/bush-distribution ($P = 0.80$).

CAM: Unaltered tree-size distribution ($P > 0.30$); unaltered height in trees ($P > 0.70$); more interior position in trees ($P < 0.01$); unaltered tree/bush distribution ($P > 0.90$).

Interspecific seasonal trends and comparisons between WILL and APAL are summarized in Tab. 6. The general tendency in an increased difference from period I+II to period III+IV.

If the four woodland habitats are considered individually the same overall trends are obvious, except in the E-ratio of APAL. At Stn 5 and especially at Stn 6 APAL foraged more in the outer parts of trees than WILL throughout the autumn, whereas the opposite was found at the other stations, and also at Stn 3 (grove habitat). Interpretations of the combined woodland data for this ratio should therefore be made cautiously. The situation at Stn 6, with a pure woodland stand in the center of the area and separate areas of bushes or shrub on the fringes, is particularly clearcut. When WILL becomes abundant in periods III and IV, APAL and CAM move out of the woodland-stand (decreasing T-ratio), and APAL also moves into lower trees and to lower positions in the trees in the course of the autumn. The same tendency could not be investigated in CAM as almost no birds were observed in the trees during III+IV.

D-values are shown in Tab. 7 with special reference to the breadth of the micro-habitat distributions. Most of the expectations mentioned above are met, but the decreases in APAL in the grove-habitat are "mysterious", though may of course be explained as specialization because of increased density in the whole guild. The increased range of MASK in the woodland habitat (Tab. 4) both with regard to the size of trees used and the height within trees should also be noticed.

Foraging behaviour

Table 8 shows the five types of foraging movements. The probability of coincidence between WILL and

Tab. 13. Correlation coefficients, r , between the three variables: Number of individuals per m *Acacia* twig with leaves, number of individuals per 20 sweeps, and season (rank numbers).

	Station 3		Station 5	
	Araneae	Coleoptera	Araneae	Coleoptera
Acacia/sweepnet	-0.37	-0.11	0.05	0.22
Acacia/season	-0.06	0.15	-0.32	-0.44
Sweepnet/season	0.38	0.63	0.11	-0.17

APAL in the grove habitat is $P < 0.05$ (I+II) and $P < 0.001$ (III+IV). In the woodland habitat the probabilities are $P > 0.70$ (I+II) and $P < 0.001$ (III+IV). Again the expectation of a large shift in the scarce species is reasonably well met. Mean-rank foraging movements (W-ratio) are also shown in Figs 9 and 10.

Stomach/intestine contents

Unfortunately the stomach/intestine contents of only six WILL could be examined. All were trapped between 3 and 17 Nov. Remains of beetles were found in all, whereas remains of Lepidoptera-larvae, spiders, flies and bugs (Heteroptera) were only found in single birds.

Five birds in a total of 31 APAL had either no stomach/intestine contents, or only prey fragments which I could not identify. Remains of spiders, Lepidoptera-larvae and beetles were found in 15, 12 and 16 birds, respectively. A few birds had also eaten flies (6), bugs (3) and hymenopterans (1). A peculiar – and perhaps significant – observation was that the number of APAL with remains of Lepidoptera-larvae and beetles, respectively, was 8 and 2 until 3 Oct (16 birds), whereas the corresponding figures were 3 and 14 from 3 Nov and onwards (15 birds). This looks like a predator switch where the less profitable prey (i.e. beetles) is taken when the more profitable prey (Lepidoptera-larvae) becomes scarce. As shown in Tab. 9, Lepidoptera-larvae decreased strongly in the course of the autumn (because of predation?), whereas the amount of beetles showed no clear seasonal trend – at least not on the *Acacia* twigs at Stn 3 (Tab. 13). Therefore, the higher proportion of beetles in the diet during late autumn cannot be explained by beetles being more abundant then.

Eight birds in a total of 32 CAM had either no stomach/intestine contents or only prey fragments which I could not identify. Remains of spiders, Lepidoptera-larvae and beetles were found in 13, 9 and 15 birds, respectively. A few birds had also eaten flies (4), bugs (1) and hymenopterans (7). No seasonal trend was observed in the food composition of CAM. Compared with APAL it seems that CAM eats more hymenopterans and fewer Lepidoptera-larvae. Only three CAM contained two or more Lepidoptera-larvae, whereas in APAL the same was true of 10 birds.

The conclusion is that there are some differences between APAL and CAM, but also much overlap in the prey distributions. It is not possible to demonstrate any influence of WILL on the prey distributions of APAL and CAM. The switch from Lepidoptera-larvae to beetles in APAL occurs about the time when WILL becomes numerous. However, WILL never becomes a dominant species in the grove habitat (where all the trapping was carried out), and only a single WILL stomach contained the remains of a Lepidoptera-larvae.

Discussion

The simple expectation was micro-habitat displacement and/or restriction of one or several local species when the numerous WILL entered the community. The data (Tabs 4–8, Figs 9 and 10 and the Appendix) support this expectation: APAL and CAM decreased their use of the preferred tree size and the preferred height in trees, and APAL also shifted towards a lower T-ratio. CAM and PRIN moved out of the *Acacia* trees in woodland, and CAM also moved more to the interior of the trees. WILL and APAL clearly diverged from each other in foraging behaviour.

In addition to the expectation, WILL also showed a clear habitat shift from groves to woodland in the course of the autumn (Tab. 3, Fig. 8).

The question now is whether competition is a factor behind these observed niche shifts. I believe so. When I arrived in August 1981 I was surprised by the “many” APAL, CAM, PRIN and RATT up in the *Acacia* trees in the woodland. Certainly their densities were rather low (and the habitat seemed unsaturated), but I remembered the woodland as being almost “free” of these species during February and March 1980. In the course of the autumn 1981 the situation changed towards the winter 1980 state. This is an indication (albeit weak) that the situation in autumn 1981 was not atypical.

A necessary condition for the occurrence of exploitation competition is that the supply of food should be less than the demand. There were several indications of food scarcity during late autumn: (1) The quantity of arthropods, especially Lepidoptera-larvae, decreased. (2) The quantity of Lepidoptera-larvae in the diet of APAL decreased (and the quantity of beetles increased). (3) The level of aggression between guild members increased. (4) The degree of FL/SFE foraging increased in WILL.

Interference leading to (micro-)habitat shifts may also operate under conditions without lack of food. Territorial behaviour, aggression, pursuit, avoidance etc. are the evolutionary outcomes of scarcity of food or space. Of course, scarcity of food reinforces interference behaviour, but one should always expect a certain level of interference. The composition of the guild and the abundance of different species may be considered important parts of the “universe” of a species and to be influential in deciding whether to stay or to leave the area or habitat (cf. Maurer 1984).

My tentative conclusion is that the micro-habitat shifts of the local warblers probably arose because of WILL interference, whereas the habitat shift of WILL was the result both of interference from the local birds and of a low food level in the groves, because of heavy exploitation during late autumn when the density, particularly of APAL, was high.

In principle my results resemble those of Alatalo (1981, 1982) and Alerstam et al. (1974) on tits Paridae: micro-habitat restrictions or displacements in the pres-

ence of (especially, socially dominant) competitors, and release in the absence of the competitor(s).

Many other investigations claim (micro-)habitat shifts of various bird species in the presence/absence of a competitor (e.g. McArthur 1972, Cody 1974, Diamond 1978, Pontin 1982, Fjeldså 1983). However, the great majority of these are based on natural "experiments" mostly on islands where the number and combination of species vary from one island to the next, or on comparisons between islands and the mainland. The problem with all such observations is that the "resource state" (Abbott 1980) is not the same in the different areas compared, making it exceedingly difficult to determine the influence, or lack, of interspecific competition (e.g. Boag and Grant 1984, Rabøl, in press). At least in birds, experimental evidence of (micro-)habitat shifts caused by removals/introductions of a competing species is almost lacking. Connell (1980, 1983) and Schoener (1983) have recently reviewed the field, and only three cases of competitively induced (micro-)habitat shifts were reported (Mewaldt 1964, Davis 1973, Williams and Batzli 1979).

Returning to the WILL-guild in Kenya the next question should be whether the seasonal arrival of WILL is anticipated by the local birds, i.e. whether some information is laid down in the genes of these birds influencing e.g. breeding period, (micro-)habitat preference etc. Does a circannual clock exist, driving a cycle of (micro-)habitat preferences also in the hypothetical absence of WILL? This might be so, and in fact CAM showed micro-habitat shifts slightly before WILL arrived.

The small numbers of warblers in the treetops of the *Acacia* woodland outside the WILL season also suggest a genetically based "avoidance" of this (micro-)habitat by the local warblers. As the woodland habitat is more or less artificial, WILL may also be regarded as an opportunist exploiting a "niche" which the local warblers are not well adapted to – and which is probably unsuitable as a breeding habitat. The arrival and presence of WILL seem at least to be one of several factors that shift the "centre of gravity" and change the breadth of the niche space of the local warblers.

When moving around in Kenya one is struck by how locally the winter visitors are distributed. Over just a few hundred kilometres the bird community, of both residents and winter visitors, changes dramatically. Over the same distance in Europe the species composition changes much less.

WILL is extremely common in the Naivasha/Nakuru area, but none are observed in the savannas of Mara, Amboseli and Samburu. In contrast, the Olivaceous Warbler *Hippolais pallida* is very common in the *Acacia* trees of Samburu but almost absent in the Naivasha area. Both WILL and the Olivaceous Warbler are common in Tsavo. Many other examples could be mentioned.

It is tempting to consider WILL and other migrants

wintering in Africa as African birds specialized for breeding in other, much more extensive areas with super-abundant food resources and relaxed competition during the short summer time. But, of course, the migrants are something else and more than just other African species. Their morphology, physiology and behaviour are tuned to meet the demands of the long migratory journey and the variety of environments visited. When considering competition and coexistence in the WILL guild at Lake Naivasha, however, it seems important not to consider WILL as a foreign, temporary element, but as a full member of the local community which is absent for some time just like many others of the "local" species seem to "migrate". WILL is not a foreign intruder, it is a well adapted species returning to its home.

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Appendix – notes and comments on the species in the “narrow” WILL guild

The following notes, comments and sketches should be regarded as a supplement to the quantitative presentation in Tabs 4–8. Figs 13–15 summarize the seasonal (micro)-habitat distribution of WILL, APAL and CAM.

WILL

Song and call. Many WILL were singing, but the numbers singing clearly diminished in the course of the autumn. The call, however, was uttered more frequently late in the autumn, especially by solitary birds. The percentages of singing birds were 33, 18 and 8 in periods II, III and IV ($n = 249, 763$ and 505, respectively), whereas the percentages of birds calling were 8, 10 and 21 in the same periods.

The songs and calls of the Willow Warbler are probably mainly an intra-specific “business” without much effect on the local warblers. The presumed nearest competitors all sing and call very differently. The similarly structured songs of BUFF, PRIN, APAL and CAM which may possibly have inter-specific effects, can be arranged on a rank scale: BUFF sings a very thin preeeet, PRIN sings preet-preet-preet, APAL drewt-drewt-drewt and CAM tjoung-tjoung-tjoung (reminiscent of a weak Thrush Nightingale *Luscinia luscinia*).

On 9 Oct I write: “Songs and calls of WILL, APAL and CAM seem to excite the birds intra- and inter-specifically. If one bird or a couple are scolding, other birds will follow”.

Greenish Warblers *Phylloscopus trochiloides* wintering in India also sing (Price 1981), mostly during the early part of the autumn. These birds are sedentary and strongly territorial towards conspecifics. The call is also used as a territory marker. However, WILL at Lake Naivasha is much less sedentary and territorial, and moves around in loose “flocks” with the local species, as is another wintering leaf warbler, *Phylloscopus occipitalis*, said to do (Price 1981).

Interference. In several cases WILL was observed pursuing or annoying other species in the guild. It seems that WILL is an active species, more commonly pursuing other species than vice versa. However, vigorous attacks directed towards the supposed more important competitors (APAL, CAM and PRIN) were few. In general these species react to the presence of WILL (or other species) by being alert and restless and by snarling and raising head and tail feathers. In APAL and CAM, and also to a lesser extent in PRIN, pursuits are often seen, but almost always between conspecifics. Very often WILL seems more curious than aggressive when pursuing other species, but in any case disturbance arises. However, in the course of the autumn WILL becomes more aggressive as indicated by the following notes: 29 Sep: “No aggression between WILL and the other species. All insectivorous species move around in loose flocks. A positive association clearly exists between WILL and APAL”. 5 Oct: “WILL is non-aggressive, while APAL, CAM and PRIN are aggressive/territorial, especially towards conspecifics”. 30 Oct: “WILL shows quite a lot of pursuit, both intraspecific and towards other species”. 1 Nov: “WILL has become more aggressive – because of food shortage? The amount of aggression and the relative number of foraging flight excursions are positively correlated”. 22 Nov: “WILL shows much “aggressive” pursuit towards other species”.

The following general notes and comments are considered important in understanding the role of WILL in the community.

(1) The behaviour of trapped APAL, PRIN and RATT in the hand is increasingly vigorous and aggressive. These species all have laterally compressed beaks with black inner sides. Increasingly through the order APAL, PRIN and RATT the bite is strong and the bills are difficult to force open – even with the blade of a knife. The juveniles of the same species have whitish or yellowish innersides of the beak, and are not, or much less aggressive. WILL and CAM have comparatively flat beaks, and in both species the beaks are easy to open even with a finger nail. The adult CAM has a black inner beak, but neither CAM nor WILL are aggressive in the hand. It seems obvious that black is a signal of threat.

(2) Clearly, the behaviour of WILL is by no means sufficient in itself to expel the local warblers from their habitats, and in fact the habitat distributions of Fig. 8 may be interpreted as showing that WILL is expelled from its preferred habitat (groves) by the local birds. However, interference is not only a matter of aggression. Because of its abundance and pursuing behaviour WILL may change the (micro-)habitat distribution of the local warblers.

Preferred vegetation. Clearly, the preferred vegetation of WILL is the *Acacia* (Yellow Fevertree) and, within this tree, its twigs and leaves. However, very often WILL is also observed in other trees (except whistling-thorn acacia) and bushes, and even on the ground (especially in the short grass on the lake shore or on the “lawn” of the floating *Salvinia*-fern. The following notes may be cited:

24 Sep (Stn 2): “WILL likes Oleleswe – which resembles a willow-scrub. However, the scattered *Acacia* trees are clearly “oases” in the Oleleswe scrub”. 31 Oct (Stn 1): “WILL is least common in the dense and green middle part of the area which includes many *Rhus* bushes”. 6 Nov (Stn 2): “WILL has a refuge in the Oleleswe, which is avoided/disliked by the numerous APAL. WILL seems to prefer Oleleswe almost as much as *Acacia*”. 22 Nov (Stn 1): “Many WILL in the open bushes (1–2 m high) of Oleleswe, *Psiadia* and *Aloë*”.

Foraging behaviour and micro-habitat distribution. The following notes may be cited:

24 Sep: “Until now, WILL and APAL have had the same habitat and micro-habitat distribution: Green and dense MT-*Acacia* groves rather than the more open and less foliated HT-*acacias*. However, WILL is more restless, the foraging range is larger, and the wings are commonly used in the foraging move-

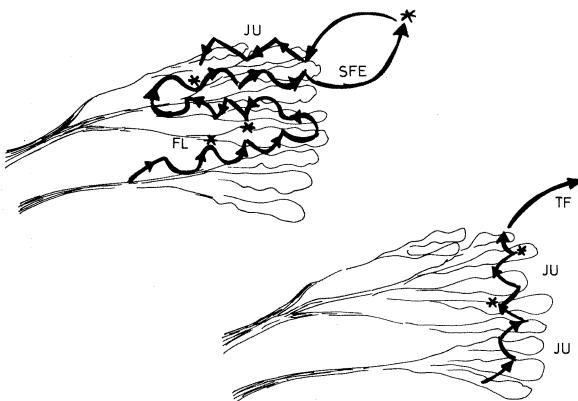


Fig. 11. The upper figure shows the JU/FL/SFE foraging and movement pattern of WILL. The lower figure shows the JU-foraging of APAL. TF means transit flight. Asterisks show points of prey capture.

ments. The food intake movement of both species is normally a PICK. It is remarkable that WILL – apart from a single bird – has not yet been observed in the HT-acacia woodland". 25 Sep (Stn 3): "WILL is now a common bird – up to 5–6 birds in the same "flock" within the same patch of a few trees. WILL is more lively than APAL. The transit flights are longer, and the amount of FL and SFE in the foraging are significantly higher. The foraging speed is higher than in APAL and the foraging movements are more horizontal. A small part of the foraging is on the dry (leafless) branches interior to the twigs and leaves (Figs 11–12). Even when labelled E the foraging is on the average more interior than in APAL. Horizontal turns/tossings in JU are common – unlike the more vertically moving APAL". 29 Sep (Stn 6): "4 WILL were observed in the scattered Acacia trees on the lake shore, but none in the pure woodland area, where 3 CAM and 7 APAL were observed foraging in the tree-tops. This is the complete opposite of the distributions in Feb/Mar 1980". 29 Sep: "In general WILL and APAL have the same habitat and micro-habitat distribution, i.e. MT-acacia groves and small and scattered groups of MT/HT acacias in scrub/grassland. Both species are mostly observed H, M and E,

and APAL is not more I than WILL – contrary to expectation. The foraging behaviour is a little different, as FL/HO are significant components in the foraging of WILL. WILL also turns the head more from side to side, whereas APAL turns/tips the whole body". 12 Oct: "With a single exception WILL does not make SFE/FE to prey in the air. As flying insects are fairly plentiful, the reason should be that the amount of prey on the twigs and leaves is sufficient or in excess. It is not profitable to be a sallying flycatcher in this situation". 24 Oct: "WILL often forages in the bare small branches and twigs in I and the inner part of E. APAL never does so". 24 Oct: "WILL often JU-forages 1–1.5 m inside the "surface" of the Acacia trees. Typically WILL is more I or in inner part of E than APAL, and moves more horizontally within the treetops and twigs/leaves (Figs 11–12). The foraging behaviour of WILL is more variable than the foraging behaviour of APAL". 29 Oct: "SFE is now a common foraging movement". 30 Oct: "More SFE, more aggression, and a habitat shift towards woodland are obvious during the last month". 31 Oct: "The paleoarctic visitors (WILL, SPOT and European Bee-eater *Merops apiaster*) are remarkably active, restless, wing-fluttering and flying compared with their African relatives". 2 Nov (Stn 3): "No WILL were observed in the MT/LT Acacia groves (where APAL is numerous). The few WILL observed were all in tops of scattered HT". 7 Nov: "WILL forages more on the branches (JU, FL, SFE) and more in the air (SFE) than APAL, which JU-forages in the twigs/leaves. Almost all SFE until now have been towards prey sitting on branches and twigs". 11 Nov: "Several WILL on SFE to prey in the air. JU is now used less frequently compared with in Sep/Oct, when JU was almost the only foraging movement". 12 Nov (Stn 3): "WILL in the grove habitat moves around singly or a few birds together – never in "flocks" as in the woodland habitats". 14 Nov (Stn 3a): "Huge numbers of WILL, most FL-foraging, also many HO/SFE. SFE is directed towards prey on the twigs and branches – not towards prey in the air. WILL is obviously preying on flies, and only to a minor extent on Lepidoptera-larvae". 17 Nov: "Within the last weeks it is obvious that WILL takes much more winged prey which are either sitting in the vegetation or are flying in the air. This change is not observed in APAL. In the beginning WILL was foraging much more like APAL". 18 Nov (Stn 6): "Many flying insects in the acacias – and much FL/SFE foraging. However, there were many flying insects earlier in the season without extensive FL/SFE foraging. Most SFE are directed towards prey on twigs and branches. However, a single long (5–6 m) FE towards a prey in the air". 23 Nov: "WILL and APAL have much the same twig and leaf preference. But WILL moves more freely around, also faster and horizontally in and out. APAL moves more elaborately and slowly and moves mostly out- and upwards". 10 Dec (Stn 7): "Only few WILL in HT and the prevailing low FL/HO/SFE-foraging is indicative of few Lepidoptera-larvae high in the trees and comparatively many diptera/beetles low in the trees".

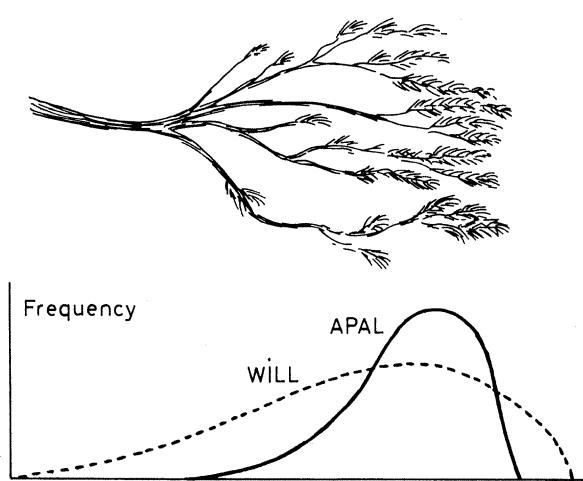


Fig. 12. Frequency distributions of WILL and APAL along an Acacia branch terminating in twigs/leaves. APAL is mostly in the outer layer – as a function of its way of foraging (cf. Fig. 11).

Food. I have many notes on the foraging behaviour of WILL, but almost none on the food actually taken. However, it seems clear that WILL takes many Lepidoptera-larvae and flies, and – judging from the foraging behaviour – more flies and fewer "stationary" prey (e.g. spiders) than APAL. I have several notes of APAL taking spiders or picking in spider webs, but almost none of APAL making SFE into the air after a fly.

Habitat preference in the course of the season. The following notes may be cited:

24 Sep: "Apparently WILL and APAL prefer the same habitat – i.e. MT-groves and not HT-woodland. Maybe WILL first settles in the latter habitat in the course of the season, because of intra-specific competition (when WILL becomes numerous) or because of inter-specific competition". 4 Oct (Stn 7): "21 WILL were registered: the great majority along the lake-shore in luxuriant low tree/bush vegetation. Still not "intruding" into

the true woodland.” 30 Oct: “An obvious shift in abundance from grove habitat towards woodland has occurred during the last month.

First WILL is common at Stns 3 and 2 – i.e. in groves/bushland with scattered MT/LT acacias. Much later WILL becomes numerous at Stn 4 (which is a transient station between groves and woodland) and at Stn 7 (along the lake shore), and finally WILL arrives at the true woodland-habitats (Stns 5, 6 and 7). If the birds are stationary in the Naivasha area after arrival – or if the departures are fewer than the arrivals – this pattern may be perceived as habitat displacement/extension because of intra- and inter-specific competition. The crowns in the HT-woodland form a vacant niche, since APAL, CAM and PRIN are all scarce in this micro-habitat prior to the arrival of WILL (and MASK). The grove/bush habitats (Stns 2 and 3) are much more studded with competitors (APAL, CAM, PRIN, BUFF, RATT and YELL). In this connection it should be observed that the amount of food seems much higher in the woodland (at least at Stn 5) than in the grove habitat (Stn 3”). 13 Nov: “The question is how much within-habitat displacement has occurred? A between-habitat displacement is much more obvious – at least in WILL”.

Summary. In summary, WILL is a (micro-)habitat and foraging generalist which in the course of the autumn shifted away from the presumed most important competitor, APAL. Obvious shifts were: Less singing, more calling, more aggression, more use of wings in foraging, more feeding on flying prey, and a habitat shift from groves to woodland. These are indicative of the presence of intra- and interspecific competition and lack of food.

APAL

Aggression. APAL very often pursues, or is aggressive towards, individuals of its own species. However, this behaviour is directed much less against other species: only five such encounters were observed (towards WILL, VAR, Yellow-bellied Eremomela *Eremomela icteropygialis*, BOU and Greater Honeyguide *Indicator indicator*). The latter two are not obvious competitors and only one *Eremomela* individual was observed at all. APAL is very often alarmed or nervous in the presence of other species, including WILL.

One phenomenon, designated “a snarling pair”, was very commonly observed. A snarling pair consists of a singing bird (drewt – drewt – drewt) and a snarling bird (a – a – a – a). The birds are always adults and presumably constitute the male and the female of a breeding pair in their territory. They seem to defend, not their offspring but their feeding territory. The two birds normally keep close together but may occasionally be more than 20 m and several trees apart. The singing and snarling were easily elicited by the presence of conspecifics or other species (including man). Sometimes almost half of the APAL records in a day were of birds of snarling pairs. The snarling pair moves slowly in the vegetation, showing aggressive postures. When APAL is aggressive or annoyed the central crown feathers and tail are raised, and the breast is protruded, making the small black breast patch much larger and more conspicuous. Single juveniles often snarl and may even pursue adult birds. However, in the hand APAL is a very quiet bird – very reminiscent of a Lesser Whitethroat *Sylvia curruca*. This species too can be very aggressive in the field, in a good feeding place such as a flowering *Ribes sanguinea* bush.

Until the end of September the level of APAL aggression was clearly decreasing, and on 25 Sep I write: “Very little aggression now between APAL. More singing now than in Aug. The feeding of pull/juv – which was often observed in Aug – has stopped”. However on 5 Oct I write: “More excited now since the offspring-feeding period and the arrival of WILL”.

Some other field-notes should be cited: 11 Oct: “Singing often starts when APAL is scared or dissatisfied. When for example 3–4 APAL are close to each other, the tail and head feathers

are raised, whereas in the case of an “isolated” snarling pair there is no tail and head feather raising. Here the singing/snarling “radiates” from the pair – presumably often expressing a general non-directed dissatisfaction”. 22 Oct: “Many snarling pairs are recorded now – especially at Stn 3, creating a basic situation well suited for micro-habitat displacement”.

During the rest of the autumn the level of aggression was high – corresponding to an increased and high density of several species including APAL and WILL.

In retrospect, the widespread and continual singing/snarling of APAL at Stn 3 (groves) during the late autumn may have acted as a shield against intruders – especially APAL-immigrants, many of which may have been forced out into the less preferred woodland-habitat.

Breeding and juveniles. Juveniles were observed during the whole period, constituting about 20–30% of the total number, and no change in the proportion of juveniles was apparent in the course of the autumn. The important point is that local production of juveniles cannot explain the significant increase in density in the course of the season (Tab. 3).

Until about 5 Sep feeding of juveniles was commonly observed at Stn 3. Then there seemed to be a gap until 22 Oct when feeding of juveniles was again observed. Thereafter it was commonly observed. APAL may have two broods – or a very prolonged breeding season? Feeding was particularly noticeable at Stns 3 and 3a, and probably there are no nests or production in the pure woodland habitats.

Foraging behaviour and habitat distribution. Comparisons with WILL are described in the WILL section. Otherwise the following notes may be cited:

18 Aug: “It seems clear that APAL, CAM and RATT are observed higher in the trees than during Feb/Mar 1980 (when WILL was numerous in the area)”. 21 Aug: “APAL resembles a mini-WILL. More FL than I remember from Feb/Mar 1980”. 22 Aug: “APAL prefers foraging in the flowering *Acacia* trees”. 22 Aug: “The general impression is of few birds, i.e. low density (all species) in the tops of HT (*Acacia*)”. 29 Aug: (Stn 6): “There is no doubt that APAL and CAM are much more common now in HT/MT compared with winter 1980 – especially CAM which was not observed foraging in an HT at all in the winter 1980. The question is whether these observations are because of (1) more food in the *Acacia* trees now, or (2) the lack of WILL, i.e. competitive release. (1) could be related to the many flowering trees and the fresh, nutritious leaves. On the other hand the density is highest at Stn 3 where only few trees are flowering (contrary to Stn 6), and many APAL, PRIN, CAM and RATT are observed in the trees of Stn 3”. 5 Sep (Stn 6): “APAL has a tendency to start foraging in the interior (I) in the lower or middle part of a tree and then moves more to the exterior (E) and higher up”. 7 Sep (Stn 6): “APAL, CAM and PRIN tend to forage in MT and the lower flat-topped HT which are in bloom (but the birds do not forage in the flowers)”. Sep 18 (Stn 1): “Surprisingly few APAL in the bushland – all birds seem associated with the scattered *Acacia* trees”. 3 Oct: “When an APAL is observed in B it normally appears to be a juvenile”. 14 Oct: “The transit-flights from tree to tree are normally directed downwards. APAL then starts rather to the interior (I) and moves up- and outwards ending in the extreme outer layer of twigs/leaves”. 29 Oct: “Interior (I) foraging in B is not normally observed”. 31 Oct (Stn 1): “APAL is found on the fringes of the area – in and among the scattered LT/MT acacias. In the central area with dense and green bushes/scrub (*Aloë*, *Rhus*) no APAL are observed”. 6 Nov (Stn 2): “APAL is much more dependent on or associated with *Acacia* trees than WILL. APAL avoids Oleleswe unless these have characters of LT”. 8 Nov (Stn 5): “APAL is found on the fringe of the HT area in the gardens”. 18 Nov (Stn 6): “APAL and CAM are now found only on the fringes of the woodland area – none are observed in the central area, where several birds were regularly observed before the arrival of WILL”. 24 Nov (Stn 3a): “Most APAL on the border/fringe of

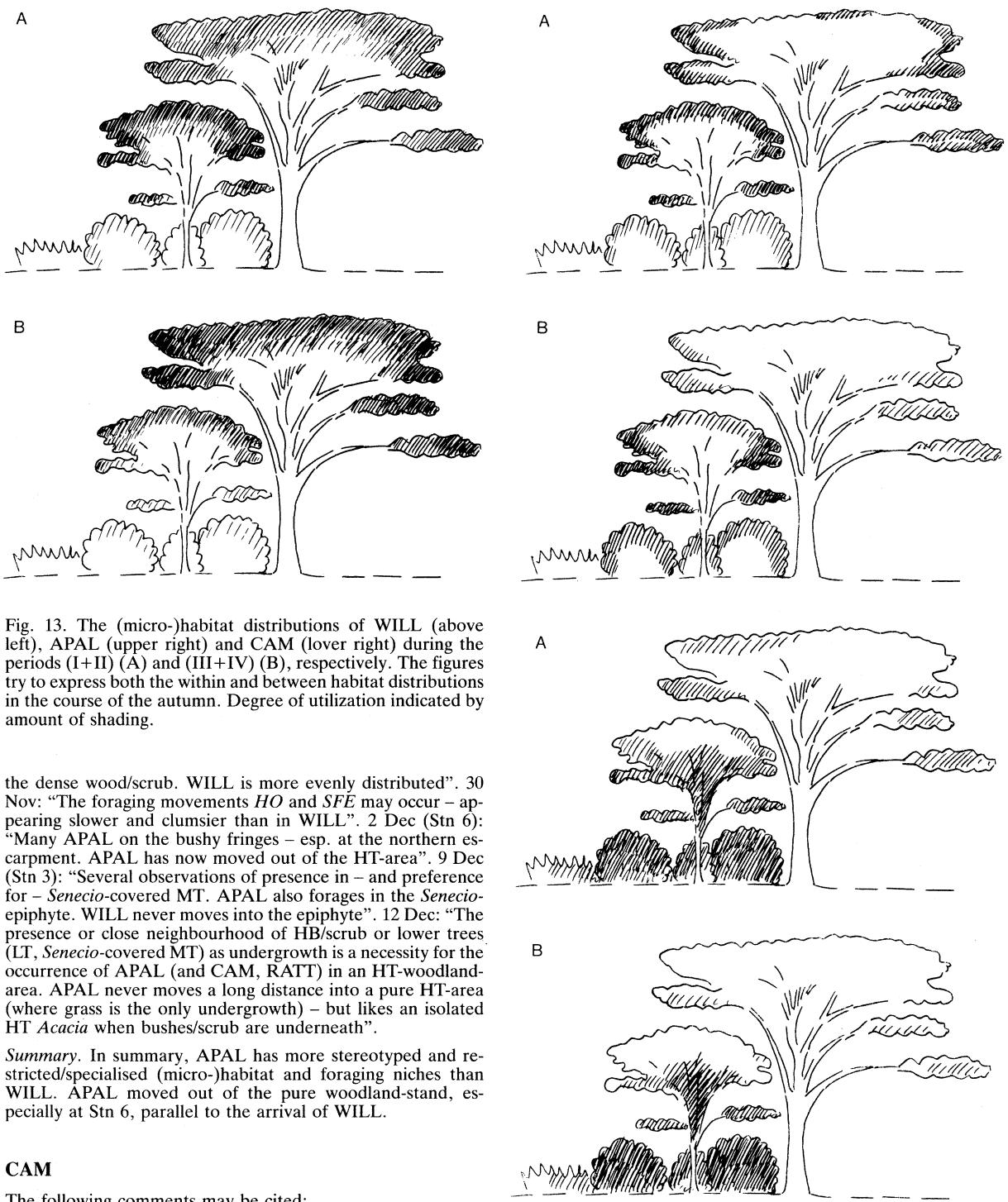


Fig. 13. The (micro-)habitat distributions of WILL (above left), APAL (upper right) and CAM (lower right) during the periods (I+II) (A) and (III+IV) (B), respectively. The figures try to express both the within and between habitat distributions in the course of the autumn. Degree of utilization indicated by amount of shading.

the dense wood/scrub. WILL is more evenly distributed". 30 Nov: "The foraging movements HO and SFE may occur – appearing slower and clumsier than in WILL". 2 Dec (Stn 6): "Many APAL on the bushy fringes – esp. at the northern escarpment. APAL has now moved out of the HT-area". 9 Dec (Stn 3): "Several observations of presence in – and preference for – *Senecio*-covered MT. APAL also forages in the *Senecio*-epiphyte. WILL never moves into the epiphyte". 12 Dec: "The presence or close neighbourhood of HB/scrub or lower trees (LT, *Senecio*-covered MT) as undergrowth is a necessity for the occurrence of APAL (and CAM, RATT) in an HT-woodland-area. APAL never moves a long distance into a pure HT-area (where grass is the only undergrowth) – but likes an isolated HT Acacia when bushes/scrub are underneath".

Summary. In summary, APAL has more stereotyped and restricted/specialised (micro-)habitat and foraging niches than WILL. APAL moved out of the pure woodland-stand, especially at Stn 6, parallel to the arrival of WILL.

CAM

The following comments may be cited:

15 Sep: "CAM clearly prefers dense bushes/shrub, but often moves up into the trees. CAM is often observed foraging especially in the lower and inner part of MT-acacias, especially those covered with the *Senecio*-epiphyte, but also often in the lower, hanging twigs/leaves of an HT-acacia. At Stn 6 also foraging in the flat tops of the flowering HT-acacias". 22 Sep (Stn 5): "Most CAM are observed in the *Solanum* bushes, also many in the *Archyranthus*. Relatively more birds now – com-

pared with Aug – in the bushes/herbs than in the trees". 5 Oct: "Fewer birds now in the trees, and more skulking". 22 Oct: "Decreasing numbers seen – compared with the numbers registered by ear". 1 Dec: "Compared with Aug/Sep relatively fewer birds seen (because the care of offspring is finished?). More skulking now in bushes and scrub".

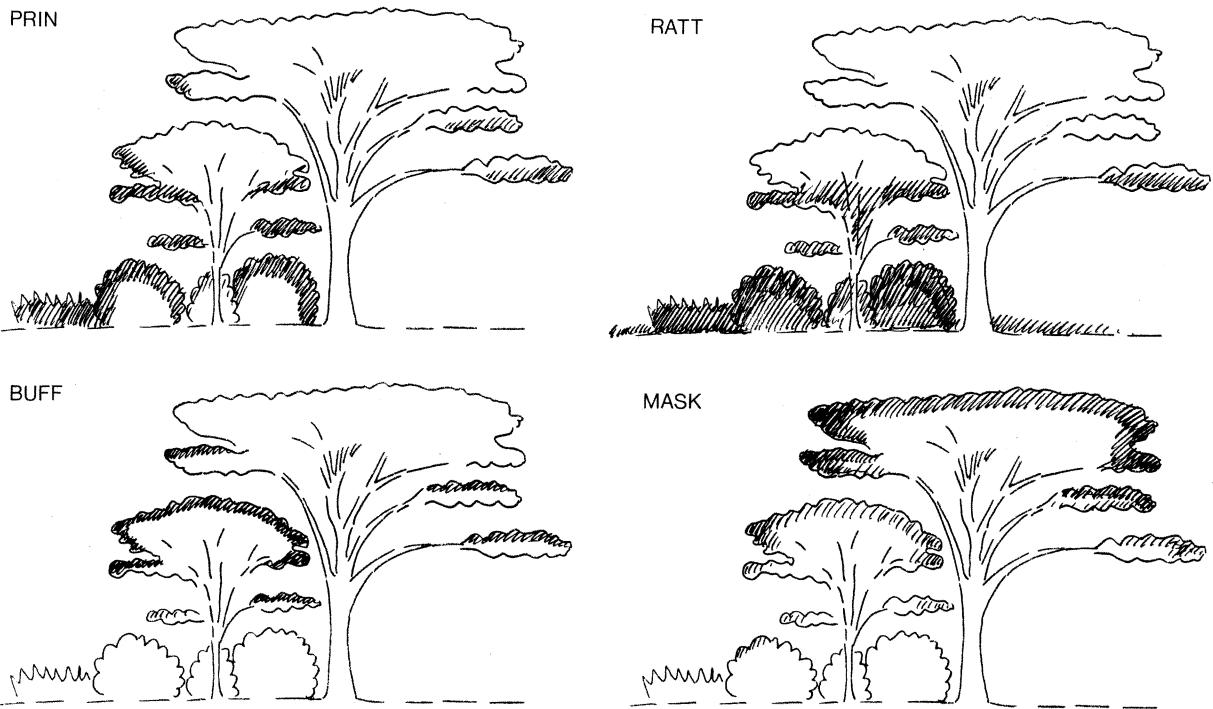


Fig. 14. The (micro-)habitat distributions of PRIN (upper left), BUFF (lower left), RATT (upper right) and MASK (lower right). Degree of utilization indicated by degree of shading.

In summary CAM moved down from the trees and into the bushes about the time (perhaps before) WILL arrived. This may well have been a general response to the increased density of other species in the guild too, or to the food situation.

Presumably the density of CAM was highest in the luxuriant "forest" at Stn 3a, where its song and calls, mixed with the whistlings of many CAP and BOU, contributed to a tropical forest sound.

Many CAM had young in Aug but already in the beginning of Sep feeding of juveniles had ceased and song had decreased significantly. The increase in CAM density during Sep and early Oct (Tab. 3, Fig. 7) is presumably because of local production and not due to immigration (as in the case of APAL).

CAM – like RATT – was not normally a permanent member of the "flocks" that moved around. However, when a flock moved through the home-range of a bird, a pair, or a family group CAM often ascended in the vegetation or sang or called.

The foraging movement in trees was JU – often with a short FL/SFE upwards to the prey item on a small branch or twig. However, much prey was taken by JU, and on the whole less FL was found in CAM than in APAL. The food intake movement usually was a weak slightly upward-directed PICK. CAM mostly foraged on small branches/twigs, not so much among the leaves. In several cases the food taken was a Lepidoptera-larvae.

As in PRIN and RATT the lower parts of the trees were often used as advertising posts. When aroused CAM often flew up into the trees. Pursuits were often observed in the trees, obscuring the true foraging distribution pattern.

It should be emphasized that the call bzeee-- of CAM is similar to the harsher (d)raeae-- of RATT, while the song of CAM is close to the fainter song of APAL. Presumably these vocalizations have inter-specific function and meaning.

PRIN

The (micro-)habitat distribution is shown in Fig. 14 (cf. Tab. 5). The density was highest in the grove habitat, and lowest in the woodland (Tab. 3).

PRIN resembles CAM in being a bird of the bushes (especially in the woodland). To some extent, like RATT PRIN is also a high grass species, especially late in the autumn. Compared with CAM, PRIN prefers lower trees, and forages lower and further out in the trees.

PRIN is a sort of mini-RATT both in morphology and in micro-habitat distribution. Otherwise it resembles an APAL, foraging on the twigs and leaves in the outer parts of bushes and scrub. The normal foraging movement is a JU. SFE was observed a few times. Several Lepidoptera-larvae were seen to be taken, and presumably PRIN is very close to APAL in its food spectrum. A few notes should be cited:

5 Oct (Stn 3): "As usual, foraging is very much on the exterior of the trees – and contrary to other warblers many PRIN are observed in the open 2–4 m high LT acacias". 12 Nov (Stn 3): "Like CAM and RATT, PRIN moves some distance up in the trees when alarmed or when expressing aggression". 21 Nov (Stn 3): "The combination of low bushes, herbs and grass is a much used micro-habitat of PRIN. PRIN often moves into high grass, like a RATT, but unlike WILL, APAL and CAM". 26 Nov (Stn 5): "No PRIN and RATT in the dense wood or scrub (contrary to CAM)".

BUFF

The (micro-)habitat distribution is shown in Fig. 14 (cf. Tab. 5). The density was highest in the grove habitat (Tab. 3). BUFF also had a very narrow micro-habitat distribution: H and M in MT, almost always E, and almost never in B.

The tiny BUFF resembles a small and small-headed WILL. In the hand BUFF also resembles a mini-PRIN. Normally 2–5 BUFF are seen together in a flock – like Long-tailed Tits *Aegithalos caudatus*. BUFF is lively, and forages by horizontal JU and faint PICK. A BUFF stays for long periods and circles within the same small area ($0.5\text{--}1\text{ m}^2$), in and mostly upon the outermost twigs or leaves. BUFF seemingly preys upon minute and stationary animals – but once I observed a bird with a large Lepidoptera-larvae.

RATT

The (micro-)habitat distribution is shown in Fig. 14, and as observed in Tab. 3 the density was by far the highest in the grove habitat, and lowest in the woodland.

RATT resembled PRIN in (micro-)habitat distribution, but foraged lower and more in the interior of the trees. The T-ratio was lower; in fact low bushes, herbs and high grass are the preferred vegetation. Most foraging seemed to occur in the grass and herbs. However, RATT often moved up into the trees to forage, though most of the observations of RATT in trees seemed to be of birds in territorial displays.

There were some seasonal within-habitat trends: The T-ratio decreased in the groves ($P = 0.05$), and shifts towards lower trees were found in both grove and woodland habitats ($P < 0.05$ in both habitats).

Apparently, RATT should not be a close competitor to WILL but it may well have some influence on the (micro-)habitat distribution of WILL through its mere presence, e.g. be part of the “pressure” forcing WILL into the woodland in the course of the season.

VAR

VAR is the most numerous sunbird, and the highest density was found in the bushes/shrub habitat (Tab. 3). VAR was also common at Stn 3a, but scarce in the woodlands outside the gardens with flowering jacarandas or *Leonotis*-beds (Stn 4). In both the grove and woodland habitats VAR was observed H and M and always E in the outermost twigs/leaves in HT/MT – or exteriorly in the herbs/bushes (the T-ratio is about 0.60). There were no shifts in the micro-habitat distributions in the course of the autumn apart from the preference for the flowering jacarandas in November.

In theory, VAR should be a suitable species to study the potential influence of WILL. However, VAR has a nectar refuge. As a matter of fact neither WILL nor other species seem to have an influence on the micro-habitat distribution of VAR.

VAR very often forages in the trees like a small restless WILL with a shorter range of action and more “narrow” and

rapid movements. Vertical SFE loops are often performed. A few notes may be cited:

15 Sep: “A typical foraging movement is a combination of HO and hanging beneath the twigs/leaves with the back downwards (like a tit)”. 24 Sep: “The foraging movement is a FL/HO on the outside of the outermost twigs/leaves – preying on small insects”. 1 Oct: “The foraging movement of WILL (JU/FL/HO) is between VAR (FL/HO/SFE) and APAL (JU/FL). SFE in VAR is never to prey in the air”.

MASK

The (micro-)habitat distribution of MASK is shown in Fig. 14 (cf. Tabs 4 and 5), and as shown in Tab. 3, woodland is the preferred habitat. The seasonal trend in density much resembles that of WILL. MASK is almost never observed in B. In the woodland MASK is observed H and E in HT. Both in the tree size distribution and in the height distribution the variances increased in the course of the season (more MT and more M, $P < 0.001$ in both cases). In the grove habitat MASK is much scarcer (and appears to behave differently). Most MASK were here observed M in MT – also less E. There is a slight tendency ($P < 0.10$) towards lower height in trees in the course of the autumn.

By reason of its large numbers and (micro-)habitat preference one should expect MASK to be a serious competitor to WILL as it seems exclusively to take insect food.

MASK almost always JU-forages in a slow and elaborate way on the outermost twigs/leaves, but also sometimes hangs (like a Siskin *Carduelis spinus*). The feeding movement is normally a PICK. The head is turned down and the neck bent to investigate the undersides of the twigs/leaves. Sometimes MASK may PECK or probe the branches like SPEC. Its foraging behaviour points to MASK taking stationary prey like Lepidoptera-larvae and spiders.

The three common insectivorous weavers MASK, REICH and SPEC together cover the whole micro-habitat range in the woodland habitat. The preferred micro-habitats are almost non-overlapping. MASK is typically a species of large flocks (up to 100 birds), whereas more than 6–8 REICH are seldom observed together, and SPEC are mostly seen singly or in twos or threes. Compared with MASK, REICH forages lower down and hangs more in the outermost twigs/leaves (M and L in HT, and E), and also often forages in the bushes, or on the ground (as the only weaver). Like MASK, SPEC mostly forages H and M in HT but with most birds on the stem or branches (the E-ratio is 0.39 in woodland). SPEC also forages deeper in B than REICH and MASK. SPEC is a sort of Treecreeper *Certhia familiaris* or Nuthatch *Sitta europaea* in its way of foraging, and forms a mini-guild of probers together with the Wood Hoopoe *Phoeniculus purpureus*, TIT and CROM.