Observations of mixed-species bird flocks at Kichwa Tembo Camp, Kenya

Alasdair I V Gordon and Nancy M Harrison

Alasdair I V Gordon Anglia Ruskin University East Road

Cambridge CB1 1PT UK

e-mail: aligee75@yahoo.co.uk

Corresponding author and contact details:

Nancy M Harrison Anglia Ruskin University East Road Cambridge CB1 1PT UK

e-mail: <u>nancy.harrison@anglia.ac.uk</u> Telephone: 0845 196 2524

Abstract

Mixed-species foraging flocks were studied at Kichwa Tembo Camp on the edge the Masia Mara National Reserve in Kenya between July and September 2004. Observations were made on 29 mixed-species flocks, in which 24 species participated. African Paradise Flycatcher *Terpsiphone viridis*, Black-backed Puffback *Dryoscopus cubla*, Grey-backed Cameroptera *Camaroptera brachyura*, Collard Sunbird *Hedydipna collaris* and Cabanis's Greenbul *Phyllastrephus cabanisi* were the most common participants in mixed-species flocks, as well as among the most frequently encountered bird species overall. The Black-backed Puffback was identified as the nuclear species in flocks due to their abundance and frequency with which they were followed by other species. Mixed-species flocks represent another niche dimension in this diverse bird community, but few of these species could be described as flock specialists; most of the birds observed in mixed-species flocks in this study were opportunistic attendant species, including the African Pygmy Kingfisher *Ispidina picta*, not previously described as joining mixed-species flocks.

Introduction

Mixed-species flocks of insectivorous birds are a conspicuous feature of tropical communities worldwide (Rand 1954, Moynihan 1960, Jones 1977, Powell 1979, Wiley 1980), important in structuring avian communities of African forests (Chapin 1932, Vernon 1980), but also evident in open woodland and savannah habitats (Greig-Smith 1978a, Thomson and Ferguson 2007). The high diversity of bird species observed in the tropics has been attributed to the increased number of niches and tighter niche packing (Weins 1989). Tropical species tend to use a narrow range of habitats (Karr 1971, Lovejoy 1974), and may be more specialized in their foraging behaviour (Terborgh and Weske 1969, Stiles 1978) than their temperate counterparts. However comparisons of the feeding behaviour of birds in mixed-species flocks, and apart from them, have found a tendency for species to converge in feeding niches, opposite to the expectation if competition is forcing niche segregation (Hino 1998, Thomson and Ferguson 2007).

Mixed-species foraging flocks are remarkably coherent structures, often involving the same individuals of a small number of species foraging over a well-defined common home range (Greig-Smith 1978a, Munn and Terborgh 1979). The attachment of species to flocks varies, with some species unambiguously flock specialists, whereas many others are ephemeral, opportunistic participants. Typically flocks have identifiable 'nuclear' species which attract birds of other species and are instrumental in the initiation and maintenance of mixed-species feeding flocks (Winterbottom 1949, Rand 1954, Moynihan 1960, Gram 1998). The adaptive value of mixed flocking has usually been attributed to anti-predator effects, aids to foraging, or both (Rand 1954, Morse 1970, Buskirk 1976, Croxall 1976, Diamond 1987, Thomson and Ferguson 2007).

This study aimed to describe the membership of the mixed-species flocks in the context of the local diversity of birds at Kichwa Tembo Camp, Kenya. Behavioural observations were made in order to evaluate foraging strategies within mixed-species flocks and the nature of inter-specific relationships.

Methods

The study was carried out at Kichwa Tembo Camp between mid July and mid September 2004. Kichwa Tembo Camp (01°16'S 35°10'E) is located on a private concession leased from Maasai landlords. The camp is set in the fringe of a riverine forest at the foot of the Oloololo Escarpment on the western border of the Masai Mara Reserve. The riverine forest occurs in the camp, due to the perennial Sabaringo River and the protection the vegetation gains from the surrounding electric fence. The climate is temperate with average temperatures of 26°C during the day and 12°C during the night. Little rain fell during the study period as it was between the 'long rains' in April and May and the 'short rains' in November. The altitude of the camp is 1634m above sea level (CCAfrica 2005).

Observations were made of mixed-species flocks between the 16^{th} July and the 12^{th} of September 2004. A bird was defined to be a member of a mixed-species flock if part of a cluster of three or more birds moving together, maintaining the distance among themselves and preserving discontinuity between areas with and without birds (Berner & Grubb 1985). Once encountered, a flock was followed until birds had dispersed, or contact was lost. Only flocks that met the definition without any ambiguity were followed. Data were collected on foraging behaviour and species composition. Five types of foraging techniques were recorded (following Eguchi *et al* 1993): gleaning, hovering (i.e. catching sedentary prey during the hover), probing, snatching (i.e. jumping upon sedentary prey and snatching it off) and hawking (i.e. flycatching aerial prey). Five categories of the foraging location were recognized: leaf, twig, branch, trunk, air and undergrowth.

Species diversity was quantified using the X-species (McKinnon) lists method. The observer recorded each new species occurrence until he reached a target number of species. The number of species recorded in the list is related to the richness of the local avifauna, and thus for riverine/montane forests of Africa 15-species lists were appropriate (McKinnon & Phillips 1993). Evaluating relative abundance using this method is problematic because of the markedly different detectability of species, but the method is a means of characterising the composition of the avian community and was used in this way to show the context of mixed-species flocks. Observations of mixed-species flocks were made independently of the 15-species lists.

Cole's (1949) coefficient of association (CA) was calculated in order to examine whether the degree of attendance of a given species in a mixed-species flock was influenced by the presence of other species. Thus, CA = (ad - bc)/[(a + b)(c + d)]. The variables are the number of flocks in which both species A and B are present (a), only species A is present (b), only species B is present (c), neither species is present (d). Significance in the associations was established using Chi-squared test ($\alpha =$ 0.05).

Results

Observations were made of 29 mixed-species foraging flocks with a total of 24 different bird species participating, a total of 384 individual birds. African Paradise Flycatcher *Terpsiphone viridis*, Black-backed Puffback *Dryoscopus cubla*, Greybacked Camaroptera *Camaroptera brachyura*, Collard Sunbird *Hedydipna collaris* and Cabanis's Greenbul *Phyllastrephus cabanisi* were seen in more than half of the observed flocks (Table 1). Most of the bird species were observed in a low proportion of the mixed-species flocks. The average flock size was 13.2 birds, which consisted of 5.83 species per flock (range 2-13) with an average of 2.3 birds per species per flock. Most species were represented in a flock by a single individual, or by a pair, however for the Black-backed Puffback and the Cabanis's Greenbul there was a mean number of over 3.5 individual birds per flock.

Independently of the observations of mixed-species flocks, a total of 79 15-species McKinnon lists were made over the two month study period, in which 1185 birds of a total of 111 different species were observed (Appendix 1). Some species such as the Common Bulbul *Pycnonotus barbatus* and the African Paradise Flycatcher were recorded in over 60% of the lists, while many more species were only rarely encountered. Of the 111 species recorded, 18 species were recorded on only one list and 12 species were recorded on only two lists. The four most common participants in mixed-species flocks (African Paradise Flycatcher, Black-backed Puffback, Greybacked Cameroptera and Collard Sunbird) were also among the 7 most frequently recorded species in the McKinnon lists.

The frequency with which the 6 most regular flock participants co-occurred in flocks was scored and Cole's Association Coefficient (Cole 1949) was calculated (Table 2). Fourteen of the fifteen correlations among species pairs were significant. The Blackback Puffback and Cabanis's Greenbul were significantly positively associated with all six of the other species common in flocks.

The foraging technique and foraging location in vegetation among the five most common participants in mixed-species flocks at Kichwa Tembo was compared (Fig 1 and Fig 2). The African Paradise Flycatcher was recorded using hawking 74% of the time as its predominant foraging technique; it was the principal aerial predator among the flock participants. The Grey-backed Cameroptera and Cabanis's Greenbul were seen to snatch their prey over 60% of the time. They were also the only species to forage largely in the undergrowth. The Collard Sunbird was recorded to forage 77% of the time by means of gleaning; their preferred foraging location was on the leaves. The Black-backed Puffback used a wide range of foraging techniques and also varied greatly with regards to foraging location within the vegetation.

Discussion

The African Paradise Flycatcher, Black-backed Puffback, Grey-backed Cameroptera and Collard Sunbird were the four most common mixed-species flock participants, as well as being among the most frequently encountered bird species overall at Kichwa Tembo Camp. These and many of the other participants were as frequently observed apart from mixed-species flocks as in them, a pattern consistent with other reports in which 50% or fewer of the individuals from participating species were found to be active in flocks at any given time (e.g. McClure 1967, Powell 1985). Large flocks contained similar numbers of each species as did small flocks (usually one or two), and appeared to grow in size as the result of more species joining, similar to Greig-Smiths (1978a) findings in Ghana.

Birds described as 'nuclear species' can be recognized by the regularity of their occurrence in flocks, their position in the front of the flock, or the frequency with which they were followed by other species (Winterbottom 1949, Davis 1946, Moynihan 1960, Morse 1970). The most likely candidate which appears to fulfil these requirements is the Black-backed Puffback, which was positively associated with all of the common flock participants. The Black-backed Puffback has several

characteristics which might stimulate following-reactions by other birds: the birds are active, continually moving from perch to perch; they habitually travel in small parties, which might be expected to provide a stronger stimulus than single birds; their calls are loud and distinctive, and might be an effective signal in the relative poor visibility of the riverine forest. Greig-Smith (1978a) identified White-winged Black Tit *Parus leucomelas* as the 'nucleus' species in savannah woodland in Ghana for similar reasons. Through their behaviour Black-backed Puffbacks appear to stimulate positive association, and have been documented as well by Vernon (1980) as forming positive associations with a different suite of species found in *Brachystegia* woodland.

Mixed-species flocks typically coalesce in times of scarcity – the dry season in many tropical regions (Salewski et al. 2003, Croxall 1976) – and flocks may be of benefit both in location of widely dispersed resources, and also in the enhanced security of flock membership when travelling over unknown territory (Buskirk 1976). Protection from predators, when required to search across larger areas is another likely benefit, which explains the many occasional participants. Other foraging advantages are possibly leading birds to join mixed-species flocks at Kichwa Tembo, such as more efficient foraging as the result of the 'beater effect' (Moynihan 1960, Diamond 1987, Hino 1998, Thomson and Ferguson 2007), increased access to resources defended by territorial birds (Moynihan 1960, Diamond 1987), and shared information about the location of food (Krebs 1973, Greig-Smith 1978b).

The 'beater effect' is a convincing benefit for some participants; notably African Paradise Flycatchers would follow other birds, mostly Black-backed Puffbacks, and forage on the insects flushed by these birds. Rand (1936), Croxall (1976), MacDonald and Henderson (1977) also found species highly similar in their behaviour to Paradise Flycatchers catching insects flushed from substrates by the gleaners and snatchers.

One of the mixed-species flocks observed at Kichwa Tembo included an African Pygmy-kingfisher *Ispidina picta*, not previously recorded with such flocks, but documented following columns of driver ants to catch fleeing insects (del Hoyo et al. 2001); bird parties are found following driver ants which are superficially similar but unrelated to mixed-species flocks of birds (Chapin 1932). The African Pygmy-kingfisher was observed following a large flock that was moving through riverine forest not far from the Sabaringo River. It would sit on a low perch scanning the ground for prey, occasionally head-bobbing or tail-flicking. It would dart into the

undergrowth (forest debris) seizing prey and return to a perch where prey would be swallowed whole, before catching up with the flock again. This particular mixedspecies flock was successfully tracked for 45min travelling a distance of about 150m.

Mixed-species flocks at Kichwa Tembo were dominated by opportunistic attendant species, and it is unlikely that any simple explanation is sufficient to account for the flock membership of all species (Wiley 1971, MacDonald & Henderson 1977, Greig-Smith 1978a, Powell 1985). The advantages in terms of predator detection and avoidance are likely to be an important reason a great many species are seen to join flocks fleetingly. These observations differed from those of Thomson and Ferguson (2007) in that relatively few of the participants were hawking for insects. The gleaning and probing behaviours commonly observed, and the activity in the undergrowth may have made these birds particularly vulnerable to predators, and the participation in the flocks would have offered some protection through both increased vigilance offered by some of the less vulnerable group members, and through the dilution effect.

Once birds converge into mixed-species flocks, each species is likely to benefit in its own way from the foraging opportunities which come from the aggregation (Vernon 1980). For opportunist species joining, such as the African Pygmy-kingfisher there is likely to be foraging benefits through the beater effect. The advantages from predator detection and foraging are not mutually exclusive and it is likely both represent selective pressures favouring opportunistic participation, with a differing balance important for different species, or perhaps at different times. A large variety of species were observed as occasional participants, and the selective pressures that have shaped their propensity to join mixed-species flocks must be various (Morse 1970, Buskirk 1976). For the six species at the heart of the flocks, they were also often seen apart, and none of the birds appeared to be obligate participants as documented elsewhere in the tropics.

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Species	Flocks joined	Flock attendance	Mean no. per flock
African Paradise Flycatcher Terpsiphone viridis	26	89.7 %	1.8
Black-backed Puffback Dryoscopus cubla	22	75.8 %	3.8
Grey-backed Camaroptera Camaroptera brachyuran	17	58.6 %	1.9
Collard Sunbird Hedydipna collaris	17	58.6 %	2.5
Cabanis's Greenbul Phyllastrephus cabanisi	15	51.7 %	3.5
Common (Brown-throated) Wattle-eye Platysteira cayanea	13	44.8 %	2.0
Yellow White-eye Zosterops senegalensis	9	31.0 %	2.7
Common Bulbul Pycnonotus barbatus	7	24.1 %	1.9
Black Cuckoo-shrike Campephaga flava	7	24.1 %	1.0
Yellow-rumped Tinkerbird Pogoniulus bilineatus	5	17.2 %	1.0
Tropical Boubou Laniarius aethiopicus	3	10.3 %	1.3
Spectacled Weaver Ploceus ocularis	3	10.3 %	1.3
Grey-capped Warbler Eminia lepida	3	10.3 %	1.0
Sulphur-breasted Bush-Shrike Malaconotus sulfureopectus	3	10.3 %	1.0
White-bellied Tit Parus albiventris	2	6.9 %	2.5
Yellow-breasted Apalis Apalis flavida	2	6.9 %	2.5
Lesser Honeyguide Indicator minor	2	6.9 %	1.0
Arrow-marked Babbler Turdoides jardineii	2	6.9 %	4.5
Green-headed Sunbird Deleornis axillaris	2	6.9 %	1.0
Klaas's Cuckoo Chrysococcyx klaas	2	6.9 %	1.0
Ashy Flycatcher Muscicapa caerulescens	2	6.9 %	4.0
African Blue Flycatcher Elminia longicuada	1	3.5 %	1.0
White-browed (Heuglin's) Robin-chat Cossypha heuglini	1	3.5 %	1.0
African Pygmy Kingfisher Ispidina picta	1	3.5 %	1.0

Table 2: Interspecific association (Cole's coefficient of association) of the six most regular participants in mixed-species flocks at Kichwa Tembo. Significant association are shown in bold type.

	T. viridis	D. cubla	C. brachyura	P. cabanisi	H. collaris	P. cyanea
T. viridis		0.103	-0.190	0.577	0.282	0.128
D. cubla			0.584	0.071	0.208	0.403
C. brachyura				0.172	0.005	0.338
P. cabanisi					0.305	0.314
H. collaris						-0.088
P. cyanea						

Appendix 1: Bird species ranked in order of frequency recorded in 79 '15-species lists' and the proportion of lists in which present.

Rank	Species	% Records
1	Common Bulbul (Pycnonotus barbatus)	86.1
2	African Paradise Flycatcher (Terpsiphone viridis)	60.8
3	White-browed Robin-chat (Cossypha heuglini)	54.4
4	Collard Sunbird (Hedydipna collaris)	50.6
5	Black-backed Puffback (Dryoscopus cubla)	48.1
5	Speckled Mousebird (Colius striatus)	48.1
7	Grey-backed Camaroptera (Camaroptera brachyura)	44.3
8	Black Saw-wing (Psalidoprocne holomelas)	43.0
8	Cinnamon-chested Bee-eater (Merops oreobates)	43.0
10	African Citril (Serinus citrinelloides)	40.5
11	Tawny-flanked Prinia (Prinia subflava)	39.2
12	African Blue Flycatcher (Elminia longicuada)	36.7
13	Northern Black Flycatcher (Melaenornis edolioides)	35.4
14	Yellow-fronted Canary (Serinus mozambicus)	34.2
15	Grey-capped Warbler (Eminia lepida)	30.4
16	Emerald-spotted Wood Dove (<i>Turtur chalcospilos</i>)	27.9
17	Brown-throated Wattle-eye (<i>Platysteira cyanea</i>)	25.3
18	Wire-tailed Swallow (Hirundo smithii)	24.1
19	Purple Grenadier (Uraeginthus ianthinogaster)	22.8
19	Schalow's Turaco (Tauraco schalowi)	22.8
19	Yellow Bishop (Euplectes capensis)	22.8
22	African Pied Wagtail (Motacilla aguimp)	21.5
22	Cabanis's Greenbul (Phyllastrephus cabanisi)	21.5
24	Ring-necked Dove (Streptopelia capicola)	20.2
24	Tropical Boubou (<i>Laniarius aethiopicus</i>)	20.2
24	Yellow White-eye (Zosterops senegalensis)	20.2
27	Brown-crowned Tchagra (Tchagra australis)	17.7
28	Holub's Golden Weaver (Ploceus xanthops)	16.5
28	Marico Sunbird (Cinnyris mariquensis)	16.5
28	Red-rumped Swallow (Hirundo daurica)	16.5
28	White-browed Coucal (Centropus superciliosus)	16.5
28	Yellow-breasted Apalis (Apalis flavida)	16.5
33	Little Bee-eater (Merops pusillus)	15.2
33	Spectacled Weaver (Ploceus ocularis)	15.2
33	Spot-flanked Barbet (Tricholaema lacrymosa)	15.2
33	Winding Cisticola (Cisticola galactotes)	15.2
37	Chin-spot Batis (Batis molitor)	13.9
37	Baglafecht Weaver (<i>Ploceus baglafecht</i>)	13.9

39	Green-headed Sunbird (<i>Deleornis axillaris</i>)	12.7
39	Pale Flycatcher (Bradornis pallidus)	12.7
39	Red-faced Cisticola (<i>Cisticola erythrops</i>)	12.7
39	Stout Cisticola (<i>Cisticola robustus</i>)	12.7
39	Usambiro Barbet (<i>Trachyphonus usambiro</i>)	12.7
44	Blue-spotted Wood Dove (<i>Turtur afer</i>)	11.4
44		11.4
	Common Waxbill (<i>Estrilda astrild</i>)	
44	Sooty Chat (<i>Myremecocichla nigra</i>)	11.4
44	Yellow-throated Longclaw (<i>Macronyx croceus</i>)	11.4
48	African Moustached Warbler (<i>Melocichla mentalis</i>)	10.1
48	Red-necked Spurfowl (Francolinus afer)	10.1
48	Scaly Francolin (Francolinus squamatus)	10.1
51	Black Cuckoo-shrike (<i>Campephaga flava</i>)	8.9
51	Fork-tailed Drongo (<i>Dicrurus adsimilis</i>)	8.9
51	Olive Sunbird (<i>Cyanomitra olivacea</i>)	8.9
51	Sulphur-breasted Bush-Shrike (Malaconotus sulfureopectus)	8.9
55	African Black-headed Oriole (<i>Oriolus larvatus</i>)	7.8
55	Giant Kingfisher (<i>Megaceryle maxima</i>)	7.8
55	Woodland Kingfisher (Halcyon senegalensis)	7.8
58	African Dusky Flycatcher (<i>Muscicapa adusta</i>)	6.3
58	African Pygmy Kingfisher (Ispidina picta)	6.3
58	Amethyst Sunbird (Chalcomitra amethystina)	6.3
58	Ashy Flycatcher (Muscicapa caerulescens)	6.3
58	Klaas's Cuckoo (Chrysococcyx klaas)	6.3
58	Ross's Turaco (Musophaga rossae)	6.3
58	Tambourine Dove (Turtur tympanistria)	6.3
65	Rattling Cisticola (Cisticola chiniana)	5.1
65	Red-eyed Dove (Streptopelia semitorquata)	5.1
65	Violet-backed Starling (Cinnyricinclus leucogaster)	5.1
65	White-bellied Canary (Serinus dorsostriatus)	5.1
65	Yellow-crowned Canary (Serinus canicollis)	5.1
65	Yellow-rumped Tinkerbird (Pogoniulus bilineatus)	5.1
71	Arrow-marked Babbler (Turdoides jardineii)	3.8
71	Black-and-white-casqued Hornbill (Bycanistes subcylindricus)	3.8
71	Bronze Manikin (Lonchura cucullata)	3.8
71	Brown Parrot (Poicephalus meyeri)	3.8
71	Cardinal Woodpecker (Dendropicos fuscescens)	3.8
71	Crowned Hornbill (Tockus alboterminatus)	3.8
71	Double-toothed Barbet (Lybius bidentatus)	3.8
71	Narina Trogon (Adaloderma narina)	3.8
71	White-bellied Tit (Parus albiventris)	3.8
71	White-browed Scrub Robin (Cercotrichas leucophrys)	3.8
71	White-eyed Slaty Flycatcher (Melaenorinis fischeri)	3.8
82	African Emerald Cuckoo (Chrysococcyx cupreus)	2.5
82	African Goshawk (Accipiter tachiro)	2.5
82	African Green Pigeon (Treron calva)	2.5
82	Bronze Sunbird (Nectarinia kilimensis)	2.5
82	Lemon Dove (Aplopelia larvata)	2.5

82	Lesser Honeyguide (Indicator minor)	2.5
82	Lesser-striped Swallow (Hirundo abyssinica)	2.5
82	Pecroral-patch Cisticola (Cisticola brunnescens)	2.5
82	Red-faced Crombec (Sylvietta ruficapilla)	2.5
82	Siffling Cisticola (Cisticola brachypterus)	2.5
82	Swahili Sparrow (Passer suahelicus)	2.5
82	White-headed Barbet (Lybius leucocephalus)	2.5
94	African Fish Eagle (Haliaeetus vocifer)	1.3
94	Black-headed Heron (Ardea melanocephala)	1.3
94	Brimstone Canary (Serinus sulphuratus)	1.3
94	Broad-tailed Warbler (Schoenicola brevirostris)	1.3
94	Grassland Pipit (Anthus cinnamomeus)	1.3
94	Striated Heron (Butorides striatus)	1.3
94	Green-winged Pytilia (Pytilia melba)	1.3
94	Grey Heron (Ardea cinerea)	1.3
94	Grosbeak Weaver (Amblyospiza albifrons)	1.3
94	Malachite Kingfisher (Alcedo cristata)	1.3
94	Nubian Woodpecker (Campethera nubica)	1.3
94	Red-headed Weaver (Anaplectes rubriceps)	1.3
94	Saddle-billed Stork (Ephippiorhynchus senegalensis)	1.3
94	Scarlet-chested Sunbird (Chalcomitra senegalensis)	1.3
94	Slate-coloured Boubou (Laniarius funebris)	1.3
94	Trilling Cisticola (Cisticola woosnami)	1.3
94	Wooly-necked Stork (Ciconia episcopus)	1.3
94	Yellow-rumped Seedeater (Serinus reichenowi)	1.3

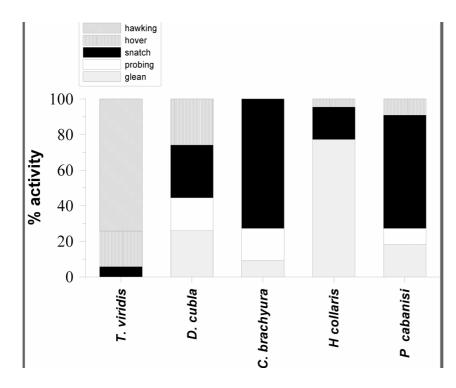


Figure 1: Percentage utilization of different foraging techniques by five species commonly in flocks.

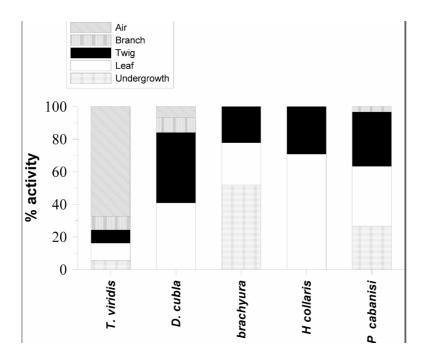


Figure 2: Percentage utilization of different foraging locations by five species commonly in flocks. None of these species were observed foraging on the trunk of trees.