

Habitat Selection by Marico Flycatchers and Chat Flycatchers in the Kalahari Gemsbok National Park

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Habitat selection by Marico Flycatchers and Chat Flycatchers in the Kalahari Gemsbok National Park was studied during September 1985. Marico Flycatchers were found mainly along the rivers and in dune areas vegetated with tree savanna, and in both these habitats were predominantly associated with tall trees. Chat Flycatchers were found mainly in dunes vegetated with low shrubs and along areas of open river terrace. There was little difference in the overall height of the perches selected by the two species, and on the single occasion that they were seen foraging close together neither showed aggression towards the other.

Key words: Marico Flycatcher, Chat Flycatcher, Kalahari Gemsbok National Park, habitat selection.

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Introduction

Since congeneric species are often similar in structure and also in habit, the likelihood of competition between them is greater than it is between more distantly related species. Habitat separation is often given as one of the ways in which closely related species can minimise niche overlap and reduce competition (Pianka 1974). Spatial separation may be in the form of microhabitat selection, whereby congeners utilise different parts of the same vegetation (MacArthur 1958), or species may select distinct habitat types (Johnson 1966; Beaver & Baldwin 1975). Species characteristics, however, may not always have evolved in response to competition, but may also be the product of other selective forces, such as habitat and resource conditions (Wiens 1977).

The *Melaenornis* species-group of flycatchers provides a clear example of habitat separation in closely-related species (Hall & Moreau 1970). Of the three southern African species, the Pallid Flycatcher *Melaenornis pallidus* (Von Müller, 1851) generally occurs in moist broadleaved woodlands (e.g. *Brachystegia* and *Burkea*

woodlands), the Marico Flycatcher *M. mariquensis* A. Smith, 1847, in *Acacia* thornveld and the Chat Flycatcher *M. infuscatus* (A. Smith, 1839) in drier scrub. Although the Chat Flycatcher and Marico Flycatcher show considerable overlap in their geographic distributions, they apparently separate spatially by selecting different vegetation types. For example, in the southern Kalahari the Marico Flycatcher is found mainly in *Acacia* savanna, but where taller growth gives way to more stunted vegetation, such as in areas surrounding the edge of pans, it is replaced by the Chat Flycatcher (Hall & Moreau 1970). In this paper we provide further information on habitat selection by the Marico Flycatcher and Chat Flycatcher in the Kalahari Gemsbok National Park (KGNP).

Methods

Data were collected from transects conducted between 11 – 13 September 1985. Observations were made from a car while driving slowly (ca. 40 km/h) along the park's roads. We had five transects: four followed the general courses of the Nossob and Auob rivers and one crossed over the dunes (Fig. 1). During each transect all Marico Flycatchers and Chat Flycatchers sighted within 50 m of either side of the road were recorded. Each transect was sampled once. When either species was sighted, the car was stopped and note made of the time, kilometer reading, species, number of individuals, perch height estimated to the nearest 0,5 m and habitat type. During the first transect we noticed that Marico Flycatchers often foraged near tall trees

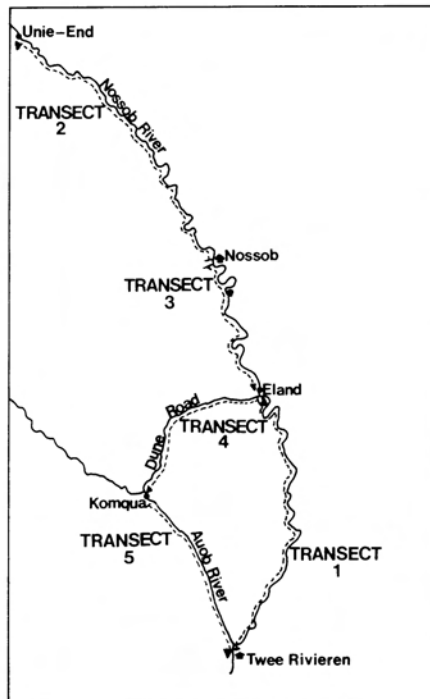


Fig. 1. The position of the five transects in relation to the Nossob and Auob rivers.

(ca. 6 m high), whereas Chat Flycatchers did not appear to be associated with this type of vegetation. In the later transects we examined this further by additionally noting for each sighting whether or not tall trees were present within 50 m of the bird. The length of each transect, and the time of day during which the transects were made, are given in Table 1.

Table 1
The estimated distance (km) travelled through each habitat type and the number of sightings made of Marico Flycatchers and Chat Flycatchers on each transect

Transect No.	Time	Habitat type				Total distance (km)	No. Marico sightings	No. Chat sightings
		RF/RT	P	TS	DLS			
1. Twee Rivieren — Eland	07h45 – 13h00	69	10	12	26	117	13	9
2. Nossob Camp — Unie End	06h50 – 15h19	60	22	29	17	128	6	19
3. Nossob Camp — Eland	07h10 – 08h31	25	—	9	15	49	8	13
4. Eland — Komqua	08h40 – 11h40	—	3	14	39	56	11	19
5. Komqua — Twee Rivieren	11h40 – 14h30	37	21	—	—	58	42	5

The vegetation of the KGNP has been described by Leistner (1967). We divided the habitat observed along the transects into five main categories:

- (i) The riverine fringe (RF), characterised by bare ground and scattered tall trees (mainly *Acacia erioloba* E. Mey.).
- (ii) The river terrace (RT), incorporating the flat area between the river fringe and the elevated dunes. This area had a short ground cover of herbs and grass, and was vegetated in some places either by scattered *Rhigozum trichotomum* Burch. shrubs or a combination of shrubs and small trees (e.g. *Acacia haematoxylon* Willd. and *A. erioloba*).
- (iii) The edges of open treeless pans or plains (P) with scattered *Rhigozum trichotomum* shrubs and the grass *Stipagrostis obtusa* (Del.) Nees.
- (iv) Dunes with tree savanna (TS), where the vegetation included *Acacia haematoxylon*, *A. erioloba*, *A. mellifera* (Vahl) Benth., *Grewia retinervis* Burret and *Boscia albitrunca* (Burch.) Gilg & Ben.
- (v) Dunes vegetated with low shrubs (DLS), mainly *Hermannia* spp. and *Rhigozum trichotomum*, and grasses, mainly *Stipagrostis amabilis* (Schweik.) de Winter; *S. uniplumis* (Licht.) de Winter and *Asthenatherum glaucum* (Nees) Nevski.

The amount of each habitat travelled through during the survey was later estimated from our field notes and the vegetation map of the park (Bothma & De Graaff 1973).

Results

The transects covered a total of 408 kilometres. Overall, we made 65 sightings of Chat Flycatchers and 80 sightings of Marico Flycatchers, involving 83 and 102 individuals respectively.

Table 1 gives the number of sightings of each species, the length of each transect, and the estimated distance travelled through the various habitat types. The river fringe and river terrace habitats were often so intermingled that we were not able to estimate the proportions of the two habitats in any consistent way. It was possible, however, to say whether a bird was in one habitat type or the other.

Figure 2 gives the percentage Chat Flycatcher and Marico Flycatcher sightings made in each of the five habitat categories for all transects. Although both flycatchers were seen in all of the habitats, Marico Flycatchers were found mainly along rivers and Chat Flycatchers on dunes covered by low shrubs. We tested the flycatchers' preferences against the estimated amount of each habitat covered by the transects, and found that Marico Flycatchers apparently avoid open plains and pans, and prefer the riverine fringe and river terraces. Chat Flycatchers prefer dunes with low shrubs. The relationship in both species was significant ($P < 0,001$: Table 2).

We saw more Chat Flycatchers per hour in the early morning than at other times of the day, whereas the number of Marico Flycatchers seen was highest after midday (Table 3). This apparent paucity of Chat Flycatchers after 12h00, in contrast to the relatively high numbers of Marico Flycatchers seen then, is because we spent less time in the open dune habitats at that time of day and more time in the wooded riverine communities. We do not have sufficiently precise information though on the amount of time that we spent in the various habitats at different times of the day to test this pattern statistically.

For 65% of all Chat Flycatcher sightings and 90% of all Marico Flycatcher sightings we noted whether or not the birds were foraging in the vicinity of tall

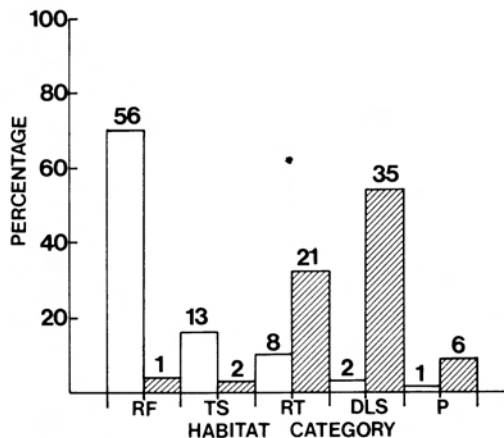


Fig. 2. The frequency of sightings of Marico Flycatchers (open histograms) and Chat Flycatchers (shaded histograms) in the various habitats. See methods section for an explanation of the abbreviations used for the habitat categories. The habitats have been arranged in approximate order of decreasing vegetation height with the tallest vegetation (RF) on the left. Individual sample sizes are given above the histograms. Data represent information gathered from all five transects.

Table 2
The overall number of Marico Flycatchers and Chat Flycatchers observed in each habitat type, and the distance of each habitat covered during the survey. The species are not uniformly associated with the habitat types (Marico: chi-squared = 43,1; df = 3, P < 0,001. Chat: chi-squared = 34,6; df = 3, P < 0,001)

	RF/RT	P	TS	DLS	Total
Amount habitat type (km)	191	56	64	97	408
No. Marico sightings	64	1	13	2	80
No. Chat sightings	22	6	2	35	65

Table 3
Number of Marico Flycatchers and Chat Flycatchers seen in each habitat type during three time periods of the day. The total observation time spent during each time period is also given

Species	Time-period	Habitat type					Total	Hours obs.	Birds hr ⁻¹
		RF/RT	P	TS	DLS				
Marico	06h00–09h00	15		8	1	24	5,1	4,7	
	09h00–12h00	15		11	2	28	9,0	3,1	
	12h00–15h30	47	2	1		50	7,0	7,1	
Chat	06h00–09h00	17	1		19	37	5,1	7,3	
	09h00–12h00	2	2	2	26	32	9,0	3,6	
	12h00–15h30	9	3		2	14	7,0	2,0	

trees. Table 4 shows that we observed significantly more Marico Flycatchers (n = 67) foraging near tall trees than we did Chat Flycatchers (n = 10) (chi-squared = 54,9; df = 1, P < 0,001). Within a species, perch height varied across habitat types (Fig. 3), but did not change with time of day (Table 5). Although

Table 4
The number of sightings made of Marico Flycatchers and Chat Flycatchers in relation to the presence and absence of tall trees. The species are not uniformly associated with this feature of vegetation structure (chi-squared = 54,9; df = 1, P < 0,001)

	Tall trees present	Tall trees absent	Total
Marico	67	5	72
Chat	10	32	42
Total	77	37	114

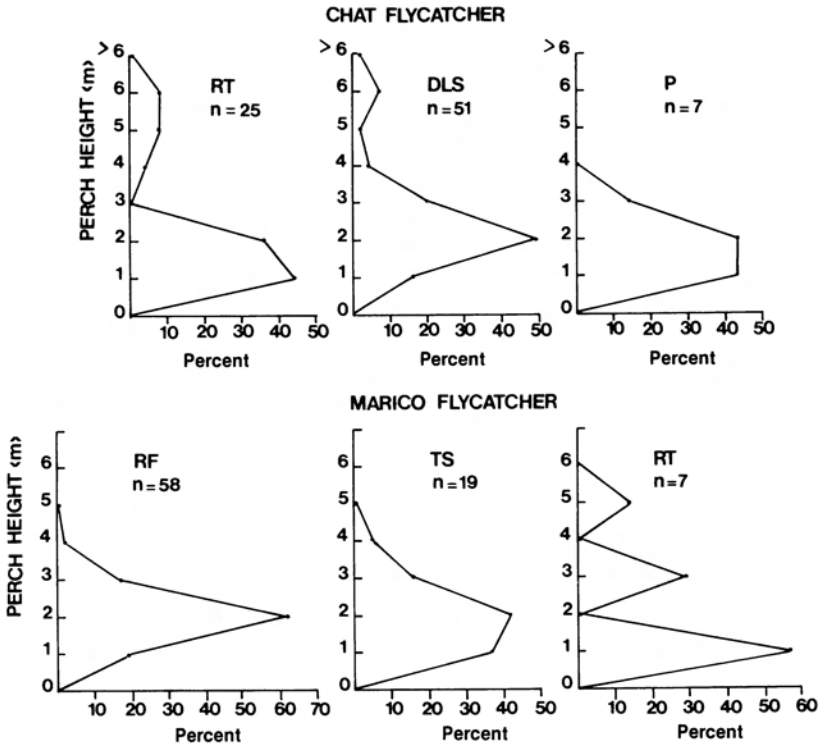


Fig. 3. The percent frequency of perch heights (m) selected by Chat Flycatchers and Marico Flycatchers in the various habitats. For both species, habitats in which there were less than five observations have been omitted.

Marico Flycatchers had access to taller trees, overall there was no significant difference in the median perch height selected by Chat Flycatchers or Marico Flycatchers (Chat: $M = 1,5$ m, $n = 71$; Marico: $M = 1,4$ m, $n = 87$) (Mann-

Table 5
The relationship between the height of perches chosen by Marico Flycatchers and Chat Flycatchers, and the time of day. Data given as medians with lower and upper quartiles in brackets

	06h00 – 09h00	Time of day 09h00 – 12h00	12h00 – 15h30
Marico	n = 22 1,4 (1,0 – 2,5)	n = 22 1,5 (1,2 – 2,0)	n = 43 1,4 (1,2 – 1,7)
Chat	n = 31 1,5 (0,5 – 2,5)	n = 26 1,5 (1,3 – 2,0)	n = 14 1,3 (0,5 – 1,7)

Whitney U-Test, $P > 0,05$). Although we have no data to quantify it, we also noticed that the flycatchers perched at different positions. Marico Flycatchers generally perched on the outside of canopies, usually at the browse line. Chat Flycatchers perched on top of small to medium sized shrubs. This may simply reflect the prevalence of the types of perches available, small shrubs being more common on the dunes than along the rivers, where trees predominated.

We only once observed pairs of Marico Flycatchers and Chat Flycatchers foraging in close proximity to one another, and in this instance neither species displayed any aggression towards the other.

Discussion

Although the flycatchers show a certain amount of overlap, each species has a clear preference for a particular habitat type. Marico Flycatchers were often found foraging near tall trees and were strongly associated with riverine fringe and, in dune areas, with tree savanna. Chat Flycatchers preferred areas vegetated with short scrub savanna. This distribution could be the outcome of competition for similar resources, or if the flycatchers utilise different resources, it could reflect the local availability of their particular food type. It is also possible that in an environment as variable as the Kalahari, resources are not limited relative to the population densities of the two species. In harsh environments, recurrent and unpredictable stress periods (e.g. severe drought) may maintain species' populations below the level at which competition operates (Wiens 1977). If the flycatchers are not food limited, other factors (e.g. the availability of preferred nest sites) may determine their habitat selection. Data are needed to evaluate this last possibility.

The areas selected by Marico Flycatchers have a higher vegetation quality than those selected by Chat Flycatchers. Leistner (1967) reports that the vegetation along the river beds in the southern Kalahari is richer in minerals than the vegetation on the dunes, and that some of the dominant grasses growing in the river beds (e.g. *Panicum coloratum* L. and *Stipagrostis obtusa*) are among the highest quality grasses in the area. The presence of tall trees in areas selected by Marico Flycatchers further suggests an increased availability of water and nutrients. In the central Transvaal, Marico Flycatchers are also found in woodlands situated on nutrient rich soils (Tarboton 1980). In these areas they aggressively exclude the morphologically and behaviourally similar Pallid Flycatcher from the richer areas (Frost *in prep.*).

We only once saw Chat Flycatchers and Marico Flycatchers foraging closely together, and the lack of aggression on that occasion suggested that their habitat separation is not maintained through species interactions. Other studies have shown that closely-related, ecologically similar species can co-exist in the same area without aggression (Barlow & McGillivray 1983; Craig 1984). More information on social interactions between Chat Flycatchers and Marico Flycatchers would help to clarify their ecological relationship.

If habitat separation is not maintained through species interactions, then either resources are not limited, or the flycatchers use different types of food. Since the

vegetation differs between the dunes and the river beds, these areas could support different insect communities. The distribution of the flycatchers in the park therefore might not be the result of competition between them for similar resources but, instead, reflect the local availability of particular prey types on which each species is relatively specialised. Differences in their morphology support this suggestion. Chat Flycatchers are on average 1,5 times heavier than Marico Flycatchers (37 vs 24 g) and also have larger bills (culmen length: 20 vs 13 mm) (Maclean 1985). Nevertheless, some studies have found that morphologically different species can utilise a highly similar assortment of prey types and sizes (Wiens 1977); clearly, data on prey availability and food selection are needed to test these hypotheses.

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