FACTORS AFFECTING HABITAT SEPARATION IN THE PALLID FLYCATCHER *MELAENORNIS PALLIDUS* AND MARICO FLYCATCHER *MELAENORNIS MARIQUENSIS*

by

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I dedicate this work to my father who first taught me to love nature, then gave me the opportunity to study it.

This thesis, unless where specifically indicated to the contrary in the text, is all my own original work. The thesis has not been submitted for a degree to any other university.

Signed by candidate

S.K. Frost

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SUMMARY

Factors affecting habitat separation in Pallid Flycatchers *Melaenornis pallidus* and Marico Flycatchers *Melaenornis mariquensis* were studied from June 1980 to June 1982 at the Nylsvley Nature Reserve in the central Transvaal. The main emphasis of the study, which is divided into two sections, was to determine the effect of habitat and resource conditions on the flycatchers' foraging behaviour (Section I) and other aspects of their ecologies (Section II) with the aim of evaluating the relative importance of these effects in maintaining habitat separation between the two species.

I found that the two habitats occupied by the flycatchers differed (i) in their level of resource availability and (ii) in their ground vegetation height and cover. The latter probably affected the birds' ability to detect ground-living invertebrates, the major prey type selected by both species. Both flycatcher species were sit-and-wait predators and at Nylsvley (as throughout their geographic range) Marico Flycatchers occurred only in *Acacia* woodlands and Pallid Flycatchers in *Burkea* and other broadleaved woodland types found on the reserve. During the wet season *Acacia* woodland had a significantly higher level of resource biomass and abundance than *Burkea* woodland. There was no significant difference between the two habitats in this respect during the dry season. For most of the year *Acacia* woodland had a lower ground cover and shorter grass than *Burkea* woodland.

Even though there was no significant difference in resource availability levels found in the two woodlands during the dry season, throughout the year Marico Flycatchers made significantly more foraging attempts/min. than did Pallid Flycatchers and for seven out of the eleven months that foraging behaviour was studied, Marico Flycatchers had a significantly greater proportion of their perch changes result in foraging attempts. Marico

Flycatchers may have been able to maintain a faster foraging rate than Pallid Flycatchers in the dry season because of the availability of harvester termites *Hodotermes mossambicus* in *Acacia* woodland (most termites in *Burkea* woodland foraged below litter and were therefore generally unavailable to Pallid Flycatchers) and because the shorter and sparser ground cover found in *Acacia* woodland probably made it easier for Marico Flycatchers to detect prey than for Pallid Flycatchers which experienced tall grass and dense cover throughout the year. Marico Flycatchers had significantly shorter periods to wait at a perch before making a foraging attempt or before "giving-up" and trying a new perch than did Pallid Flycatchers. Both species selected mainly small-sized prey items (< 6 mm in length) but overall Pallid Flycatchers took significantly more large prey items in their diet than did Marico Flycatchers. Pallid Flycatchers also perched significantly higher than did Marico Flycatchers, probably because higher perches gave them a clearer view through the taller and denser ground vegetation found in *Burkea* woodland. These results suggest that the flycatchers had adapted their foraging behaviour to match the habitat and resource conditions they experienced.

A more detailed study of one aspect of the flycatcher's foraging behaviour, namely their giving-up time, again showed that ground cover density and height was an important factor influencing search times in both the Pallid Flycatcher and Marico Flycatcher. These results were consistent with the findings of other similar studies on sit-and-wait predators.

Marico Flycatchers foraged more efficiently than did Pallid Flycatchers in that they were able to utilize resources at a faster rate. This may mean that at Nylsvley, Marico Flycatchers excluded Pallid Flycatchers from richer *Acacia* woodland through exploitation competition. Pallid Flycatchers, however, were efficient at exploiting low levels of resource availability in that by perching for long periods they utilized a more energy-conserving foraging mode than Marico Flycatchers which frequently changed perch. The Marico Flycatchers' habit of perching for short periods only may have made it uneconomical for this species to forage in low quality resource areas outside of *Acacia* woodland. This may explain why geographically Marico Flycatchers are confined to a relatively narrow strip of *Acacia* woodland, whereas Pallid Flycatchers occupy a wide range of broadleaved woodlands as well as being able to move into *Acacia* woodland in the absence of Marico Flycatchers.

The effects of habitat and resource conditions extended to other aspects of the flycatchers' ecologies besides their basic foraging behaviour. Marico Flycatchers occupied a small home range of 2-3 hectares and experienced more intra and interspecific interactions than did Pallid Flycatchers which occupied large home range areas of between 10-22 hectares. The level of aggression and aggressive interactions experienced by the birds was an important behavioural difference between the two species. Marico Flycatchers were more aggressive and vocal than were Pallid Flycatchers which were shy and retiring and which seldom interacted with other species. In both species over 90% of their aggressive interactions were on an individual-to-individual basis and involved displacements rather than outright physical aggression. On two occasions, however, Marico Flycatchers were observed to physically fight with Whitethroated Robins *Cossypha humeralis*, a species with which it probably overlapped in its use of prey items. Whenever the two flycatcher species met at woodland boundaries, Marico Flycatchers aggressively excluded Pallid Flycatchers from the *Acacia* woodland which suggests that apart from exploitation competition, habitat separation in Pallid Flycatchers may also have been maintained through interference competition.

The flycatchers also showed some differences in their breeding behaviours. Marico Flycatchers had a longer breeding season than Pallid Flycatchers, they fed their chicks more frequently and were co-operative breeders.

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First and foremost, I would like to thank my husband Peter for his continued encouragement throughout the entire project. I think it is true to say that without his support (which was not only in the form of guidance and encouragement, but also financial) this study would never have been completed. Thank you for your help and understanding, especially during those times when I am sure I was being not so understanding myself.

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CHAPTER 1

INTRODUCTION

In this thesis I discuss some of the factors affecting habitat separation in closely related species. The species studied belong to the genus *Melaenornis*, a group which has several morphologically and behaviourally similar, sympatric species which show clear habitat separation. This chapter begins, therefore, with a general overview of the genus *Melaenornis* and an outline of possible ecological mechanisms maintaining habitat separation. This is followed by sections dealing with the main aim of the study, the study birds and study area, hypotheses tested in the study and finally the chapter contents and layout.

1. Overview of the genus *Melaenornis*

The *Melaenornis* species are large flycatchers with strong legs and a black, brown or grey plumage. Originally the genus included only the Black Flycatchers (*M. pammelaina*, *M. edolioides* and *M. ardesiaca*), their ally the Chocolate Flycatcher (*M. chocolatina*), and the Fiscal Flycatcher (*M. silens*) (Hall & Moreau 1970). Later Clancey (1980) included the genus *Bradornis* which consists of the Pallid (or Pale) Flycatcher (now *M. pallidus*), the Marico Flycatcher (*M. mariquensis*), the Chat Flycatcher (*M. infuscatus*) and the Grey Flycatcher (*M. microrhynchus*). Hall & Moreau (1970) call this group the Pale Flycatcher and its allies. Two groups closely related but not included in the genus are the Forest Flycatcher (*Fraseria ocreata* and *F. cinerascens*) and the Silverbird *Empidornis semipartitus*. The Forest flycatchers are considered closely related because they structurally fall within the range of measurements found for the original *Melaenornis* genus defined by Hall & Moreau 1970 (*i.e.* the Black Flycatchers, Chocolate Flycatcher and Fiscal Flycatcher); and the Silverbird because it is behaviourally similar to the former *Bradornis* group.

A preliminary overview of species distributions, descriptions, habitat preferences and habits (given in

Britton 1980; Hall & Moreau 1970; Maclean 1985) shows that genus members are either allopatric (*i.e.* do not overlap in their geographic distribution) or where sympatric (*i.e.* overlap geographically) usually show some behavioural or habitat differences (Table 1). Of the Black Flycatchers, for example, *M. pammelaina* is found in southern (along the east coast) and central Africa, and *M. edolioides* in northern and northeast Africa (see Hall & Moreau 1970 for a detailed map of all species distributions discussed in this section). Their ranges meet in East Africa, however, without apparent overlap. *M. pammelaina* and *M. edolioides* are typically birds of savanna woodland and cultivation whereas the third member of the superspecies, *M. ardesiaca*, occurs in a small area of central Africa and differs from the other two Black Flycatchers in that it is found on the edges and in clearings of montane forest. The Chocolate Flycatcher also occurs in central and northeast Africa, but being a typically montane bird of forest edges and clearings, it occupies different habitat types than *M. pammelaina* and *M. edolioides*, and where it meets *M. ardesiaca* (the species with which it is most similar in its choice of habitat and habits), it ascends to higher altitudes.

The Fiscal Flycatcher is found in southern Africa (mainly central, southwestern and eastern areas) and occupies drier and more open habitat than the other genus members. The Fiscal Flycatcher also differs from the other members in that it has marked sexual dimorphism with both sexes having bold patterning (see Maclean 1985). Clancey (1980) retains the Fiscal Flycatcher in the genus *Sigelus* but ecologically it is very similar to other *Melaenornis* members (especially the Pallid Flycatcher and its allies discussed below) in that it perches conspicuously and takes food from the ground and to a lesser extent also on the wing (Hall & Moreau 1970; Maclean 1985). Fiscal Flycatchers are sympatric with Black Flycatchers (*M.*

pammelaina), Pallid Flycatchers, Marico Flycatchers and Chat Flycatchers (Table 1). It differs in its choice of habitat with the first two species, and possibly in its choice of food items with the last two. Fiscal Flycatchers have a shorter bill than Chat Flycatchers (Fiscal 13,5 - 17,5 mm Chat 19 - 21 mm) and a slightly longer bill than Marico Flycatchers (Marico 12 - 14 mm) (Maclean 1985). Fiscals may also take more fruit and nectar than Maricos but more data are needed to establish behavioural differences between this species and its sympatric congeners (Hall & Moreau 1970).

The members of the former *Bradornis* species-group show clear habitat separation, especially among birds found in southern Africa (Fig. 1). The members of this group are all very similar in appearance and habits. All have a grey plummage and all perch on prominent branches or bushes and drop to the ground for food. They only occasionally take prey on the wing and in this respect differ somewhat from most of the other *Melaenornis* species discussed above which frequently take aerial prey. Of the three species occurring in southern Africa the Pallid Flycatcher occurs in moister, mainly broadleaved woodlands, the Marico Flycatcher in richer *Acacia*, and the Chat Flycatcher in drier scrub.

In northeast Africa the Pallid Flycatcher is again a woodland bird and the Grey Flycatcher confined to the drier *Acacia* thornveld. Even where the two habitats interdigitate, as in western and southern Kenya, and in Tanzania, Pallid Flycatchers and Grey Flycatchers maintain their habitat preferences (Traylor 1970). This is true also of Pallid Flycatchers and Marico Flycatchers in Botswana (Traylor 1965) and in central Transvaal (Tarboton 1980). Species which have overlapping geographic distributions but which are not in close proximity, cannot interbreed, and do not occur together in the same locality are termed allotopic by Rivas (1964).

TABLE 1

ECOLOGICAL SEPARATION IN THE GENUS *MELAENORNIS*. SEE TEXT FOR REFERENCES USED.

	Mp	Mpall	Me	Ma	Mc	Ms	Mm	Mmic	Mi	F	Es
M. pammelaina	●	B	▨	H	H	H (B)	H (B)	H (B)	H (B)	▨	H (B)
M. pallidus		●	B	H (B)	H (B)	H	H	H	H	▨	H
M. edolioides			●	H	H	▨	▨	H (B)	▨	H	H (B)
M. ardesiaca				●	A	▨	▨	H (B)	▨	?B	▨
M. chocolatina					●	▨	▨	H (B)	▨	?H	H (B)
M. silens						●	?FI	▨	?FI	▨	▨
M. mariquensis							●	▨	MH (?FI)	▨	▨
M. microrhynchus								●	▨	▨	MH
M. infuscatus									●	▨	▨
Fraseria spp.										●	▨
E. semipartitus											●

▨ NO GEOGRAPHIC OVERLAP

⧄ GEOGRAPHIC OVERLAP

SEPARATION BY:

HABITAT:
H = HABITAT
MH = MICRO-HABITAT
A = ALTITUDE
B = BEHAVIOUR

FI = FOOD ITEMS

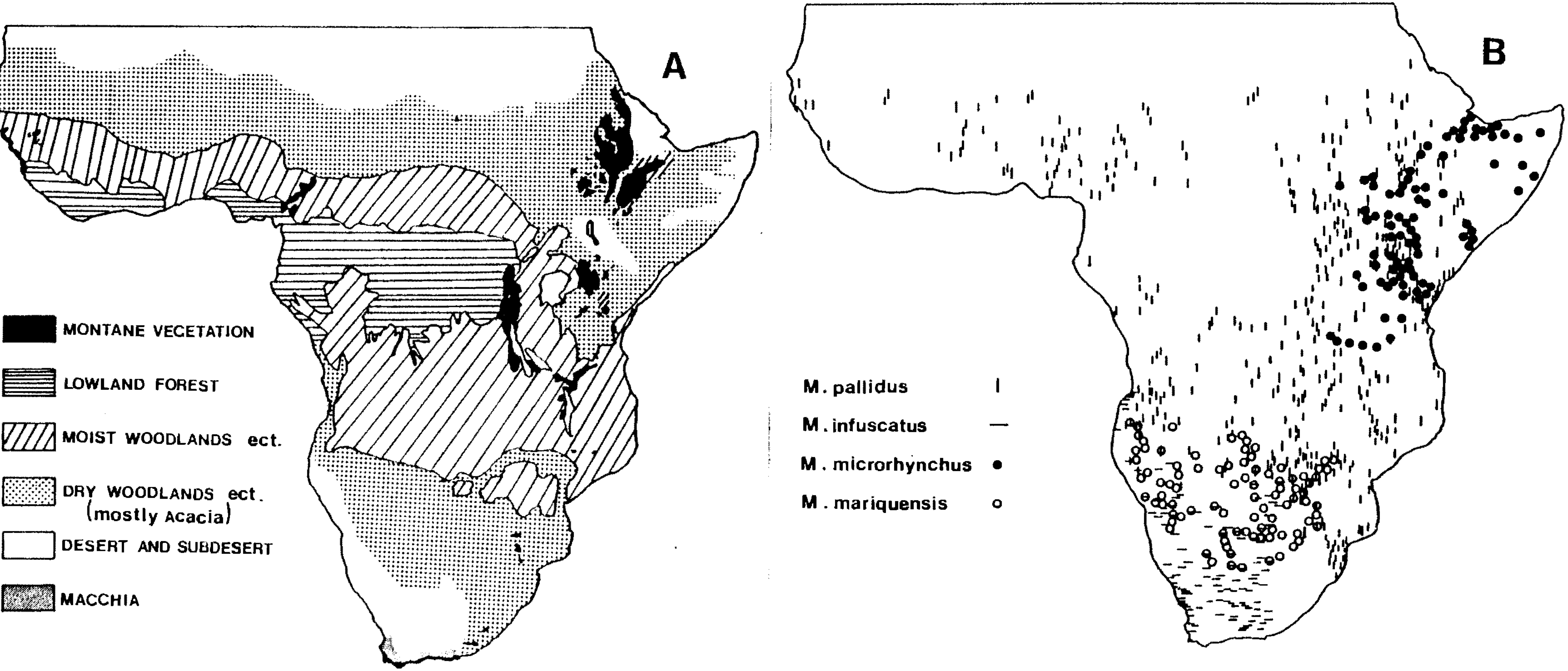

FIGURE 1

(A) A simplified vegetation map of Africa, and
(B) geographic distribution of the Pallid Flycatcher
and its allies. Maps A & B from Hall & Moreau 1970.

In northeast Africa there is considerable size variation between different populations of both Pallid Flycatchers and Grey Flycatchers. Grey Flycatchers occurring in the eastern "horn" of Africa (Ethiopia, Somalia and Kenya) are smaller than those occurring in the Tanzania, Uganda and Sudan regions. In these latter regions Grey Flycatchers overlap geographically with the Silverbird which, like the Grey Flycatcher, is also an *Acacia* thornveld species which forages by perching prominantly and dropping to the ground for food. Whereas the Grey Flycatcher occurs in wooded grassland (*i.e.* predominantly trees), however, the Silverbird occurs in bushed grassland (*i.e.* predominantly shrubs) (Britton 1980); and this difference in microhabitat separation may allow the two species to co-exist.

2. *Possible factors determining habitat separation in closely related species*

Cody (1974) suggests that species can segregate either on a horizontal scale (*i.e.* habitat separation), on a vertical scale (*i.e.* through using different foraging techniques or vegetation strata) or in their choice of prey items. In the genus *Melaenornis* habitat separation is the most common form of species segregation (see Table 1). What are the reasons, however, for habitat separation in closely related species? Some ecologists believe that habitat and microhabitat separation results almost entirely from past and present competitive interactions (MacArthur 1958; Cody 1974; Diamond 1975). The assumptions underlying this theory (as listed by Wiens 1977) are that since the variety and abundance of resources are limited, as populations reach carrying capacities competition for shared resources occur among similar species. Continued co-existence is permitted only by virtue of differences along niche dimensions between species. These differences define the population optima of resource-utilization traits, since individuals of a species that depart from the optimum suffer intensified competition and therefore reduced fitness.

Utilization of different habitats could be one of the ways in which potentially overlapping species avoid competition. The actual processes by which this competition is carried out could be through interference or exploitation competition (see Pianka 1974; Branch 1985). Interference competition occurs when one individual (or species) actively prevents another individual (or species) from using the same set of resources. Interference competition usually involves aggressive behaviour (e.g. fighting, territoriality). Exploitation competition occurs when one individual (or species) utilizes resources so efficiently (i.e. uses more of the resources per unit time) that it becomes uneconomical for another individual (or species) to attempt to use the same set of resources. Exploitation competition need not involve aggression.

Habitat preference is one of the features that go to make up a species characteristics. Wiens (1977) warns, however, against over-emphasising the role of competition in determining species characteristics. He believes that in examining species differences one should not begin only with the premise that the species differ solely to avoid competition with one another. Many of the assumptions underlying competition theory may not always hold true in nature. Resources may not be limited and factors such as environmental variability and predation may keep populations below the levels at which they compete. While not denying the possible existence of competition, Wiens (1977) suggests that ecologists should give equal time to investigating which species characteristics are not simply a means of avoiding competition but which are due to the species' response to the environmental conditions it experiences.

3. Main aim of the study

In this study I consider the behaviour of Pallid Flycatchers *Melaenornis pallidus* (Fig. 2) and Marico Flycatchers *M. mariquensis* (Fig. 3) with the aim of determining factors underlying their habitat separation. These species were chosen because they form one of the examples of allotopy in the genus *Melaenornis* (see Section 1 above). Although the flycatchers are sympatric in the central Transvaal, each species maintains a distinct habitat preference even in areas where their two habitat types interdigitate to form a small-scale mosaic (Tarboton 1980). The habitats chosen by the flycatchers have been found to differ in their vegetation structure, diversity and consumer biomass (Huntley & Morris 1978) and in this respect a study of Pallid Flycatchers and Marico Flycatchers in these areas would provide an ideal opportunity to study both the effect of habitat and resource conditions on the flycatchers' behaviour and species interactions at points of contact.

4. Background information relating to the study area

I carried out my study at the Nylsvley Nature Reserve (24° 29'S; 28°42'E), central Transvaal, where fineleaved and broadleaved woodlands occur side by side, forming a mosaic of Mixed Bushveld (Acocks 1953). I had two study areas: one in fineleaved woodland dominated by *Acacia* species and called *Acacia* woodland; the other in broadleaved woodland dominated by the tree species *Burkea africana*, *Terminalia sericea* and *Ochna pulchra*, and called *Burkea* woodland (Fig.4). Marico Flycatchers occurred in *Acacia* woodland and Pallid Flycatchers in *Burkea* and other broadleaved woodlands (*e.g. Combretum*) found on the reserve (Tarboton 1980).

Tarboton (1980) studied the avian populations of *Acacia* and *Burkea* woodlands and found that *Acacia* woodland had a lower species diversity but higher avian biomass and density than *Burkea* woodland. Besides differing in their

FIGURE 2

The Pallid Flycatcher Melaenornis pallidus. An adult with a fledged juvenile (mottled individual).

FIGURE 3

The Marico Flycatcher Melaenornis mariquensis. Adult tending nestlings.

avian communities, the woodlands differ also in their soils (Harmse 1977), their plant communities and their vegetation structure (Coetzee *et al* 1976). *Acacia* woodland, situated on relatively nutrient-rich alluvial clays, has approximately half the tree density found in *Burkea* woodland (Lubke *et al* 1975; Tarboton 1980), as well as for most of the year, short grass and a sparse ground cover (Figs 5 & 6). Most grasses in *Acacia* woodland are palatable (Coetzee *et al* 1976), and consequently wild ungulates are more abundant here than in *Burkea* woodland (Huntley & Morris 1978). Frequent grazing probably maintains the short ground cover found in *Acacia* woodland, whereas *Burkea* woodland, situated on nutrient-poor sands, has a continuous tree and shrub layer and a tall, dense, ground layer (Figs 7 & 8).

5. Hypotheses tested

In areas in and around Nylsvley, *Acacia* and broadleaved woodlands occur adjacent to one another. Why then do Marico Flycatchers remain in one woodland and Pallid Flycatchers in the other? especially since in areas where Marico Flycatchers do not occur, such as in northern Zululand (Cyrus & Robson 1980), Pallid Flycatchers move into *Acacia* woodlands. Two possible hypotheses are:

(i) At Nylsvley the flycatchers maintain their habitat separation because one species excludes the other through interference competition.

(ii) At Nylsvley the flycatchers maintain their habitat separation to avoid exploitation competition with one another.

In this thesis I concentrate mainly on determining the effect of habitat and resource conditions on the flycatchers' foraging behaviour. By so doing I will attempt to assess the relative foraging efficiency of each species and will therefore be addressing mainly hypothesis (ii). This part of the thesis is dealt with in Section I. Although a comparison of the flycatchers' foraging

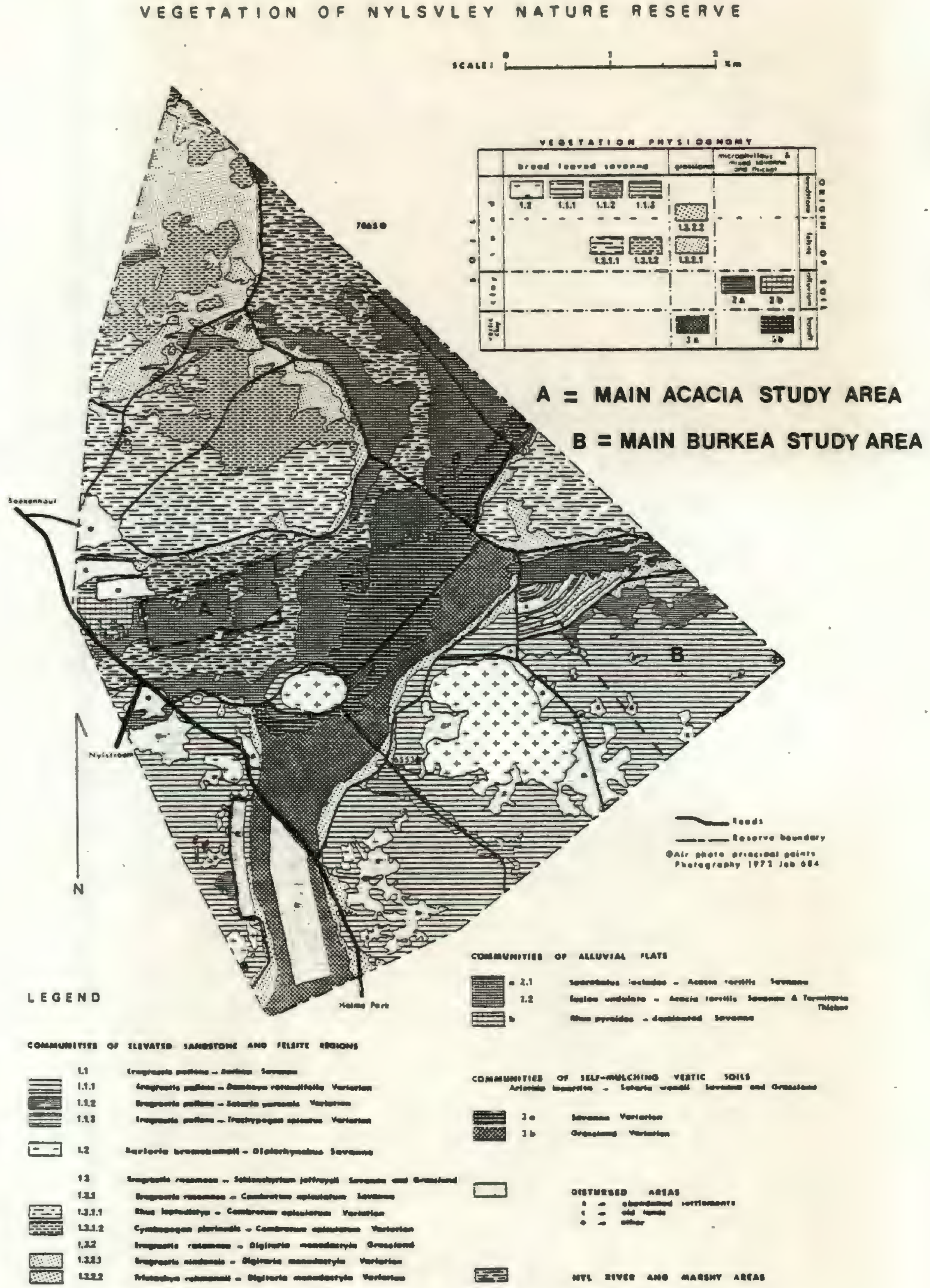

FIGURE 4

Vegetation map of the Nylsvley Nature Reserve showing position of *Acacia* and *Burkea* woodland study areas. Map reproduced from Coetzee *et al* 1977.

FIGURE 5

A view of the Acacia study area in the wet season (January 1981). Note the open woodland and short grass cover. Figure shows woodland area and in the foreground part of a clay pan.

FIGURE 6

A view of the Acacia study area in the dry season (June 1982). Again the figure shows a woodland area and clay pan. Note the lack of grass cover on the pan and the short, sparse grass in the woodland areas.

FIGURE 7

A view of the Burkea study area in the wet season (December 1980). Note that the woodland has several woody vegetation strata and a tall dense grass and herb layer.

FIGURE 8

A view of the Burkea study area in the dry season (June 1982). Note the tall dense grass and herb layer.

behaviour forms the major component of the thesis, I will, however, also consider other aspects of their ecologies (e.g. activity patterns, home range sizes, aggressive interactions and breeding systems) which could be affected by the resource and habitat conditions experienced by the birds (Section II). Part of hypothesis (i) therefore, will be considered in the latter section of the thesis.

6. Chapter contents

The following is a brief outline of the main subjects discussed in each chapter.

(i) Section I: The effect of habitat and resource conditions on the flycatchers' foraging behaviour.

Several studies have found that grass height and ground cover can affect the foraging behaviour of birds hunting for ground-living invertebrates, particularly how high they perch to scan the ground and their foraging rate (Pinkowski 1977; Eiserer 1980; Morrison 1980). In addition, seasonal changes in resource abundance can affect the types of foraging technique used by insectivores (Robinson & Holmes 1982; Greig-Smith 1983), the choice of substrate from which they forage (Gibb 1960), and the variety of prey items included in their diets (Davies 1977; Greig-Smith 1983). In Chapter 2, therefore, I consider similarities and dissimilarities in the flycatchers' foraging behaviour and attempt to correlate these with habitat and resource conditions found in the two woodlands. Aspects of the flycatchers' behaviour studied include how high they perch, the distances they travel between successive perches, how far they fly to retrieve prey items, the variety of foraging techniques used, their foraging substrates, their search times, and the size and variety of prey items included in their diet. Environmental features studied include grass height and ground cover density, the availability of perches, and the relative biomass and abundance of ground invertebrates found in the two woodlands.

In Chapter 3 I consider in more detail the effect of habitat and resource conditions on one aspect of the flycatchers' foraging behaviour, namely their giving-up times. Giving-up time is the period between a flycatcher arriving at and leaving a perch without having made a foraging attempt in the interim (FitzPatrick 1981). I then compare observed giving-up times of Pallid Flycatchers and Marico Flycatchers with those of other sit-and-wait predators (FitzPatrick 1981; Greig-Smith 1983; Moreno 1984) in order to determine whether they are related to the average time the flycatchers wait at a perch before catching prey in the habitat as a whole, or whether they are determined by the visual complexity of the search area.

(ii) Section II: The effect of habitat and resource conditions on other aspects of the flycatchers' ecologies besides their foraging behaviour.

Habitat conditions and levels of resource abundance, however, can affect other aspects of an animal's ecology besides its foraging behaviour. Several studies have found, for example, that levels of resource availability determine not only the time and energy needed to obtain food and the net energy gained from feeding, but also the amount of time and energy birds have available for other non-foraging activities (Gibb 1956; Greig-Smith 1982). Territory size is also often related to food density, with birds in areas of low resource availability generally requiring a larger territory to obtain their necessary food supply than birds in areas of higher resource abundance (Stenger 1958; Davies 1980). In Chapter 4 I consider the flycatchers' time-activity patterns and home range sizes. I also consider intra and interspecific interactions experienced by the birds, including aggressive interactions between the two species.

In Chapter 5 I consider the flycatchers' breeding behaviour; in particular their nests, nest building behaviour, clutch size, incubation, nestling care, and post-fledging behaviour. Again, these are discussed in the light of the possible effect of habitat and resource conditions on the flycatchers' behaviour.

Finally, in Chapter 6 I discuss the relative importance of interference and exploitation competition in maintaining habitat separation in the Pallid Flycatcher and Marico Flycatcher. Reference is made to other similar studies, including an additional example of habitat separation in the genus Melaenornis (Appendix I). I end the chapter by suggesting a future line of study which may shed more light on the overall problem discussed in the thesis.

7. Chapter layout

With the exception of Chapter 6, each chapter contains summary, introduction, methods, results and discussion sections. Although this method of presentation necessitates the duplication of some information, it allows each chapter to be written in the form of a paper. These papers are ultimately intended for publication in the scientific literature.

SECTION I

THE EFFECT OF HABITAT AND RESOURCE CONDITIONS ON THE FLYCATCHERS' FORAGING BEHAVIOUR

CHAPTER 2

A COMPARISON OF THE FORAGING BEHAVIOUR OF PALLID FLYCATCHERS AND MARICO FLYCATCHERS

SUMMARY

The foraging behaviour of Pallid Flycatchers and Marico Flycatchers was studied for one year. Both species were predominantly sit-and-wait predators foraging mainly on invertebrates found on the ground. They took a similar variety of invertebrate types and both preferred small-sized items (< 6 mm long). Marico Flycatchers waited a shorter period before either making a foraging attempt or "giving-up" at a perch. They had a greater proportion of their perch changes result in foraging attempts, and overall made more moves/min. than Pallid Flycatchers. The two flycatcher species occurred in vegetatively different, but adjacent woodlands, and differences between their behaviours could be largely attributed to differences in the levels of resource abundance and biomass available to each, and in the height and density of ground cover each experienced.

INTRODUCTION

The Pallid Flycatcher *Melaenornis pallidus* and Marico Flycatcher *Melaenornis mariquensis* provide an example of habitat separation in two morphologically similar species (Hall & Moreau 1970; Maclean 1985). Both flycatchers are common in the central Transvaal, where this study was conducted, and here, as in other areas where they co-occur, Pallid Flycatchers occupy broadleaved woodland and Marico Flycatchers fineleaved woodland (Tarboton 1980). Although these woodlands are often adjacent to one another, the flycatchers show no overlap in their occurrence (Tarboton 1980) and the question arises as to why they maintain this habitat separation. The woodlands differ with respect to their soils (Harmse 1977), their vegetation structure and diversity (Coetzee *et al* 1976), and their secondary consumer biomass (Huntley & Morris 1978), with the fine-leaved woodland having a higher avian and ungulate biomass than the broadleaved woodland (Huntley & Morris 1978; Tarboton 1980). In this chapter I investigate the extent to which differences in habitat structure and resource availability found in the two woodlands affect the flycatchers' foraging behaviour.

Preliminary observations indicate that both flycatchers are predominantly sit-and-wait predators feeding on ground-living invertebrates. Other studies have found that grass height and ground vegetation cover are important features affecting the foraging behaviour of birds hunting these types of prey. Tall grass and dense cover may lower a bird's ability to detect prey and decrease foraging rates (Eiserer 1980); as well as cause birds which forage from vantage points to select higher perches in order to gain a clearer view through the vegetation (Pinkowski 1977; Morrison 1980). In this study both grass height and ground vegetation cover are measured and compared with the height at which the flycatchers perch, the distance they travel between successive perches and the distance they fly to retrieve prey items. Since foraging behaviour can also be affected by resource characteristics, however, I also determine the relative biomass, abundance, type and size of ground invertebrates found in the woodlands and compare these with certain aspects of the flycatchers' behaviour discussed below.

If ground invertebrate biomass and abundance vary seasonally, one might similarly expect certain seasonal changes in the flycatchers' behaviour. Some studies have found, for example, that temporal change in resource availability may cause predators to alter their foraging tactics (Robinson & Holmes 1982; Greig-Smith 1983). To investigate whether this occurs in Pallid Flycatchers and Marico Flycatchers, I compare the amount of time they spend in sit-and-wait foraging with the amount of time they spend on active gleaning. Changes in resource availability, however, may also cause predators to alter their choice of prey items (Davies 1977) or foraging substrate (Gibb 1960), and to investigate this aspect of the flycatchers' behaviour, I compare the type and size of prey items taken by the flycatchers and the proportion of time they take prey from various substrates (e.g. the ground, trunks, leaves). Comparisons are made between species and within species on a monthly basis.

Finally, I consider the effect of resource availability on the flycatchers' search time per prey item and foraging rate to test whether the species occurring in the habitat with the higher level of resource availability has a shorter search time per prey item and a faster foraging rate (i.e. number of foraging attempts/unit time) than the species occurring in the habitat with the lower level of resource availability (see Pianka 1974; Norberg 1977).

METHODS

1. Study area

The study was carried out between February 1981 and December 1982, in the Nylsvley Nature Reserve (24°29'S; 28°

42'E), central Transvaal. The reserve is 3 120 ha. in extent and situated on gently undulating terrain between 1 080 m and 1 140 m in altitude. The climate is semi-arid with two main seasons: a dry season extends from May to October and a wet season from November to April. The mean annual rainfall is 625 mm. The rainfall in 1981 totalled 471 mm, and in 1982, 602 mm (Fig. 9).

The reserve, vegetated with a mosaic of broadleaved and fineleaved woodlands, is classified by Acocks (1953) as Mixed Bushveld. Coetzee et al (1976) provide a detailed account of its vegetation structure and diversity, and Harmse (1977) has analysed the soils. I had two study sites, one in broadleaved woodland and the other in fineleaved. The broadleaved study site, referred to below as Burkea woodland, is dominated by the trees Burkea africana, Terminalia sericea and Ochna pulchra. It has a continuous grass, shrub and tree cover and is situated on well-drained, nutrient-poor sands. The fineleaved study site, dominated by Acacia species and referred to as Acacia woodland, is situated on poorly-drained, relatively nutrient-rich alluvial clays and characterised by bare clay pans surrounded by scattered thornveld with a short grass cover. Tree density is about 50% higher in Burkea woodland than in Acacia woodland (Lubke et al 1975; Tarboton 1980).

2. Ground vegetation features

I established fifteen permanent plots (2 m x 2 m) in each study site to measure seasonal changes in ground cover and grass height. The plots were monitored every second month between February 1981 and December 1982. In each plot I estimated the percentage canopy cover by grass and herbs, and the percentage cover by leaf litter, as well as measuring the culm height of ten randomly selected grass tufts.

To determine the range of potential perch sites available to the flycatchers, I placed ten 100 m long transects in each study site. A rope, secured at both ends

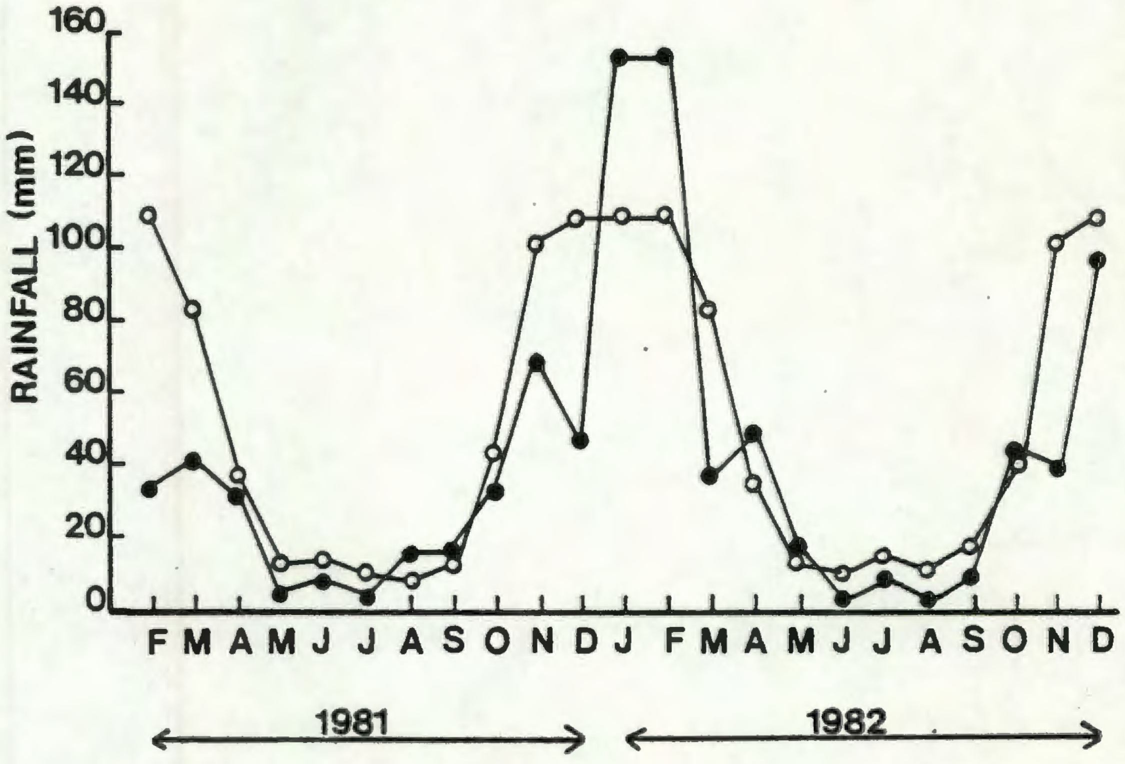

FIGURE 9

Rainfall (mm) recorded at Nylsvley Nature Reserve from February 1981 to December 1982 (closed circles). Open circles give long term mean.

at ca 1,5 m high was drawn tautly along the lengths of the transects, and the height of all branches crossing above or below the rope was measured at the point where it transected the rope.

3. Resource estimation

I collected invertebrates from the two woodlands every second month from July 1981 to June 1982. Fifty samples were taken from each woodland during each sampling period. The samples were obtained by placing a wooden box (0,25 m^2), open at both ends, over randomly selected points distributed along five randomly selected lines, each 100 m long. I obtained the random points by taking fifty numbers from a table of random numbers and finding their position on the 100 m line (e.g. random number 20 = 20 m). Each line was assigned ten random numbers; and the position of the lines was determined by throwing a 100 m long rope along the ground and securing it at both ends.

I collected all grass, herbs and litter in the box and placed them into bags which were individually sealed and marked. Each bag was subsequently sorted in a laboratory where I removed all invertebrates from the vegetation, measured their length, and identified them to class, or in some instances, to order. The invertebrates were then dried to a constant mass, pooled and retained for calorific analyses.

4. Foraging behaviour

Data on foraging behaviour were collected between June 1981 and May 1982. As far as possible I spent equal time observing Pallid Flycatchers and Marico Flycatchers, both of which occurred in groups of between two to five individuals within regular home ranges. I followed a group at a distance of about 20-30 m. This did not alarm the birds, and allowed me to observe clearly their activities through 8 x 30 binoculars. I recorded behaviour onto a tape recorder which ran continuously and which was later re-played to time each event to the nearest second. Most data were collected from four main study groups: two for each species. The birds were not colour-marked. In following a group I concentrated my observations on whichever individual happened to be closest to me, switching to the next nearest when the first moved away or became obscured from view. I only collected data from birds which were not actively engaged in breeding.

Overall I made 41 hrs of observation on Marico Flycatchers and 36 hrs on Pallid Flycatchers. Most of my observations were made in the morning between 09h00 and 12h00 (Pallid = 84% Marico = 76%). As the temporal pattern of observations was similar for both species, and there was no significant difference between morning and afternoon data, I lumped the two data sets for both species. I collected the following information:

(i) Type and size of prey taken, when possible. Prey size was classified in "half bill length" units, the bill length of both flycatcher species being ca 12 mm.

(ii) Mode of foraging used (sit-and-wait, active gleaning, hawking).

(iii) Substrate from which prey taken (ground, leaves, branches, trunks, air).

(iv) Time interval between arriving at a perch and making a foraging attempt (= successful search time).

(v) Time interval between arriving at a perch and leaving that perch without having made a foraging attempt in the interim (= giving-up time).

(vi) Frequency of foraging attempts.

(vii) Frequency of perch changes.

Between September 1981 and February 1982 I collected information on horizontal displacements, perch heights, and distances travelled between successive perches. Horizontal displacement refers to the horizontal distance from the point where a bird was perched to the point where it landed on the ground to retrieve a prey item. I measured horizontal displacement and the distance between successive perches to the nearest cm using a tape measure. Perch heights up to 2,5 m were also measured with a tape measure to the nearest cm, beyond that they were estimated to the nearest 0,5 m. I did not measure individual, isolated distances or heights, but used only those which formed part of a continuous foraging sequence.

As most of the data collected in this study had non-normal distributions, I used non-parametric statistical tests (Siegel 1956). In all cases means are given ± 1 SD and in all tests $p \leq 0,05$ was taken as the accepted significance level.

RESULTS

1. Changes in ground cover

For most of the year, grass and herb cover was higher in *Burkea* than in *Acacia* woodland, and litter cover was consistently much greater (Fig. 10 A & B). Grass and herb cover remained high throughout the year in *Burkea* woodland, but in *Acacia* woodland, where many of the grasses are palatable and heavily grazed, cover was initially high at the beginning of the wet season but declined greatly during the dry season (Fig. 10A). Grass height declined in both woodlands in the dry season, but remained higher in the *Burkea* woodland for most of the time (Fig. 10C).

2. Resource availability

A similar range of invertebrates was collected in both woodlands. Spiders comprised the major group by number, followed by ants and beetles (Table 2). During the wet season, *Acacia* woodland had a significantly higher invertebrate biomass and a greater number of invertebrates per sample than *Burkea* woodland (both tests: Mann Whitney Test, $p < 0,05$) (Table 3). During the dry season there was no significant difference between the two woodlands. In

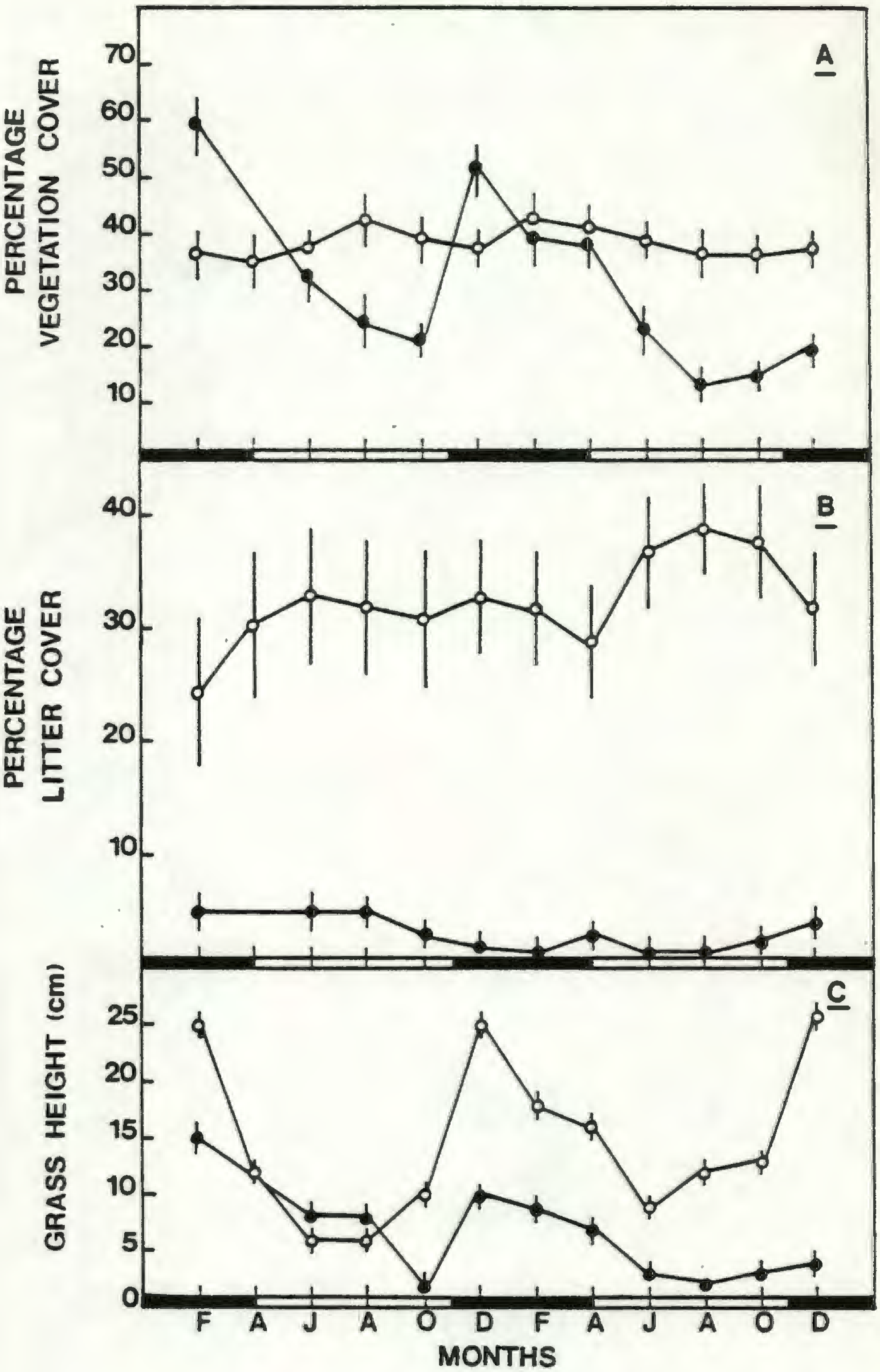

FIGURE 10

(A) The percentage vegetation cover (grass and herbs combined), (B) litter cover and (C) grass height (cm) in the <u>Acacia</u> woodland (closed circles) and <u>Burkea</u> woodland (open circles) plots. Vertical lines denote standard error. Closed horizontal bar indicates the wet season months.

TABLE 2

INVERTEBRATES FOUND IN SAMPLES COLLECTED IN THE *ACACIA* AND *BURKEA* WOODLAND STUDY SITES DURING THE WET AND DRY SEASONS.

	BURKEA WOODLAND		*ACACIA* WOODLAND	
	percentage		percentage	
	wet	dry	wet	dry
Spiders	30	41	29	33
Beetles	17	27	21	46
Antlions	1	5	0,3	2
Ticks	4	5		0,5
Ants	35	4	33	3
Worms	3	3	6	3
Grasshoppers	2	3	3	4
Caterpillars	1	2	0,3	1
Crickets	1	1	1	
Termites	2		0,4	5
Larvae	1		4	0,5
Others	3	9	2	2
TOTAL NO.	560	216	1 818	305

TABLE 3

INVERTEBRATE BIOMASS (mg/0,25 m^2) AND NUMBERS COLLECTED IN THE ACACIA AND BURKEA STUDY SITES. LQ = LOWER QUARTILE, UQ = UPPER QUARTILE.

	INVERTEBRATE BIOMASS				INVERTEBRATE NUMBERS			
	Median	LQ	UQ	Range	Median	LQ	UQ	Range
BURKEA								
Wet season:								
Dec '81*	-	-	-	-	2	0	4	0 - 18
Feb '82	3,0	0	5,9	0 - 68,4	2	0	5	0 - 62
Apr '82	1,4	0	5,5	0 - 54,9	1	0	3	0 - 10
Dry season:								
Jul '81	2,4	0	11,7	0 - 78,8	1	0	2	0 - 10
Oct '81	0	0	4,4	0 - 56,1	0	0	2	0 - 5
Jun '82	1,4	0	5,2	0 - 272,3	1	0	2	0 - 9
ACACIA								
Wet season:								
Dec '81	19,7	5,9	54,3	0 - 163,4	7	5	14	0 - 46
Feb '82	8,8	1,8	26,5	0 - 225,8	4	2	11	0 - 80
Apr '82	29,6	8,5	100,0	0 - 289,2	11	6	20	0 - 73
Dry season:								
Jul '81	3,2	0	12,6	0 - 276,4	2	0	4	0 - 19
Oct '81	0,9	0	3,3	0 - 29,6	1	0	2	0 - 14
Jun '82	2,2	0	9,0	0 - 48,2	1	0	3	0 - 15

NOTE: * Biomass data for samples unavailable.

both woodlands, the samples taken in any month were highly skewed, implying patchy distribution of potential prey. Invertebrates in Burkea woodland had a mean calorific value of 22,7 ± 1,68 Kj/ash free dry gram and those in Acacia woodland 22,5 ± 1,97 Kj/ash free dry gram; these values did not change significantly through the year.

3. Resource consumption

Both flycatchers had similar diets comprising almost entirely animal foods. Small fruits such as Rhus pyroides, Euclea undulata and Solanum sp. comprised 0,7% (n = 6) of the observed diet of Pallid Flycatchers and 0,4% (n = 9) of the observed diet of Marico Flycatchers. Of the animal foods taken, most were too small to be identified (Pallid = 92%, Marico = 97%). Larger items included caterpillars, beetles, spiders, grasshoppers and moths.

At times I could tell when Marico Flycatchers were feeding on ants or termites, as they would repeatedly peck the ground at the same spot during this process. I checked this behaviour on 41 occasions by chasing the bird away from its prey, and found that on 59% of occasions the bird was feeding on ants and for the remaining 41% on termites. Harvester termites Hodotermes mossambicus only occurred in Acacia woodland, where their availability was probably underestimated for at times large numbers were seen foraging for grass. At such times, Marico Flycatchers would stand near the entrance of the termite nest and remove the workers as they emerged. When attacked in this manner, the termites generally retreated into their nest and the flycatchers then departed. During the wet season, ants and termites comprised approximately 8% of the Marico Flycatchers' diet, and during the dry season approximately 6%. Pallid Flycatchers rarely took ants or termites (< 1% of all feeding records).

There was no detectable difference in the size of prey items taken by Marico Flycatchers in the wet and dry seasons ($\chi^2 = 0,64$; df = 1; $p > 0,05$) (Table 4), and

TABLE 4

DISTRIBUTIONS BY SIZE CLASS OF INVERTEBRATES TAKEN BY MARICO FLYCATCHERS IN THE WET AND DRY SEASONS.

	< 6 mm	≥ 6 mm	TOTAL
Wet	410	17	427
Dry	453	14	467
	863	31	894

throughout the year they took proportionally more small prey items (< 6 mm long) than were available in Acacia woodland (wet season $\chi^2 = 42{,}8$; df = 1; $p < 0{,}001$; dry season $\chi^2 = 64{,}1$; df = 1; $p < 0{,}001$) (Table 5).

Pallid Flycatchers also took similar-sized items in both the wet and dry seasons (= 0,07; df = 1; $p > 0{,}05$) (Table 6), although during the dry season alone they took proportionally more large food items than were available in the Burkea woodland (wet season $\chi^2 = 2{,}96$; df = 1; $p > 0{,}05$; dry season $\chi^2 = 8{,}60$; df = 1; $p < 0{,}01$) (Table 7).

Overall, Pallid Flycatchers took proportionally more large prey in their diet than did Marico Flycatchers ($\chi^2 = 8{,}06$; df = 1; $p < 0{,}01$) (Table 8). For both species handling time increased significantly with increasing prey size for items > 1/2 bill length in size (Spearman Rank Correlation Coefficient: Marico $r_s = 0{,}98$; df = 17; $p < 0{,}05$; Pallid $r_s = 0{,}82$; df = 11; $p < 0{,}05$) (Fig. 11). Handling time of smaller items (< 6 mm) was essentially instantaneous.

4. Foraging behaviour

Both flycatchers were predominantly sit-and-wait predators. For each species, active gleaning formed only 1% of all foraging attempts during the wet season and was not recorded at all during the dry. Throughout the year, most prey were taken from the ground, although for both species the proportional importance of ground items decreased slightly during the wet season months (Fig. 12). During the wet season, Marico Flycatchers increased mainly the proportion of foraging attempts made for items on tree trunks, and Pallid Flycatchers increased their number of foraging attempts for items on leaves, trunks, branches and in the air (Fig. 12). Both flycatchers snatched prey from vegetation at similar heights (Table 9).

During most months, Pallid Flycatchers perched significantly higher than Marico Flycatchers (Mann Whitney Test, $p < 0{,}05$) (Table 10). This trend was significant

TABLE 5

COMPARISON OF INVERTEBRATE SIZE CLASSES TAKEN BY MARICO FLYCATCHERS AND THOSE AVAILABLE IN THE SAMPLES COLLECTED IN THE *ACACIA* WOODLAND STUDY SITE.

WET SEASON	< 6 mm	≥ 6 mm	TOTAL
Marico	410	17	427
Acacia	1 525	293	1 818
	1 935	310	2 245

DRY SEASON	< 6 mm	≥ 6 mm	TOTAL
Marico	453	14	467
Acacia	242	63	305
	695	77	772

TABLE 6

DISTRIBUTION OF INVERTEBRATE SIZE CLASSES TAKEN BY PALLID FLYCATCHERS IN THE WET AND DRY SEASONS.

	< 6 mm	≥ 6 mm	TOTAL
Wet	144	12	156
Dry	41	4	45
	185	16	201

TABLE 7

COMPARISON OF INVERTEBRATE SIZE CLASSES TAKEN BY PALLID FLYCATCHERS AND THOSE AVAILABLE IN SAMPLES COLLECTED IN THE *BURKEA* WOODLAND STUDY SITE.

WET SEASON	< 6 mm	≥ 6 mm	TOTAL
Pallid	114	12	156
Burkea	489	71	560
	633	83	716

DRY SEASON	< 6 mm	≥ 6 mm	TOTAL
Pallid	41	4	45
Burkea	151	65	216
	192	69	261

TABLE 8

COMPARISON OF INVERTEBRATE SIZE CLASSES TAKEN BY PALLID FLYCATCHERS AND MARICO FLYCATCHERS. FIGURES REPRESENT DATA FOR ALL TIMES OF THE YEAR.

	< 6 mm	≥ 6 mm	TOTAL
Pallid	185	16	201
Marico	863	31	894
	1 048	47	1 095

TABLE 9

THE MEAN HEIGHT (m) ± 1SD AT WHICH THE FLYCATCHERS SNATCHED PREY FROM LEAVES, TRUNKS AND BRANCHES.

Pallid Flycatcher	n = 12	n = 24	n = 14
	2,7 ± 1,0	1,5 ± 0,9	2,8 ± 1,8
Marico Flycatcher	n = 26	n = 84	n = 41
	2,7 ± 1,3	1,8 ± 1,0	2,6 ± 1,5

TABLE 10

MEDIAN PERCH HEIGHTS (m), DISTANCES FLOWN BETWEEN SUCCESSIVE PERCHES (m) AND HORIZONTAL DISPLACEMENTS (m) OF PALLID FLYCATCHERS AND MARICO FLYCATCHERS.

	PERCH HEIGHT		PERCH DISTANCE		HORIZONTAL DISPL.	
	Pallid	Marico	Pallid	Marico	Pallid	Marico
FEB	*2,0 (n=80)	1,5 (n=55)	10,0 (n=64)	9,5 (n=36)	2,5 (n=33)	3,4 (n=31)
MAR	*2,1 (n=48)	1,4 (n=31)	17,5 (n=23)	10,0 (n=31)	3,0 (n=26)	3,0 (n=31)
MAY	1,8 (n=31)	1,6 (n=30)	7,0 (n=31)	8,0 (n=31)	2,5 (n=31)	2,8 (n=30)
JUN	1,6 (n=31)	1,5 (n=30)	6,0 (n=31)	6,8 (n=31)	*1,8 (n=30)	3,0 (n=31)
JUL	*1,9 (n=49)	1,6 (n=119)	9,5 (n=43)	7,2 (n=55)	2,7 (n=69)	2,3 (n=115)
AUG	*1,9 (n=64)	1,5 (n=108)	9,6 (n=64)	7,0 (n=72)	*3,2 (n=37)	2,5 (n=36)
SEP	*2,1 (n=54)	1,5 (n=60)	9,7 (n=32)	8,0 (n=43)	*3,0 (n=45)	1,6 (n=44)

NOTE: * = significantly different $p < 0,05$.

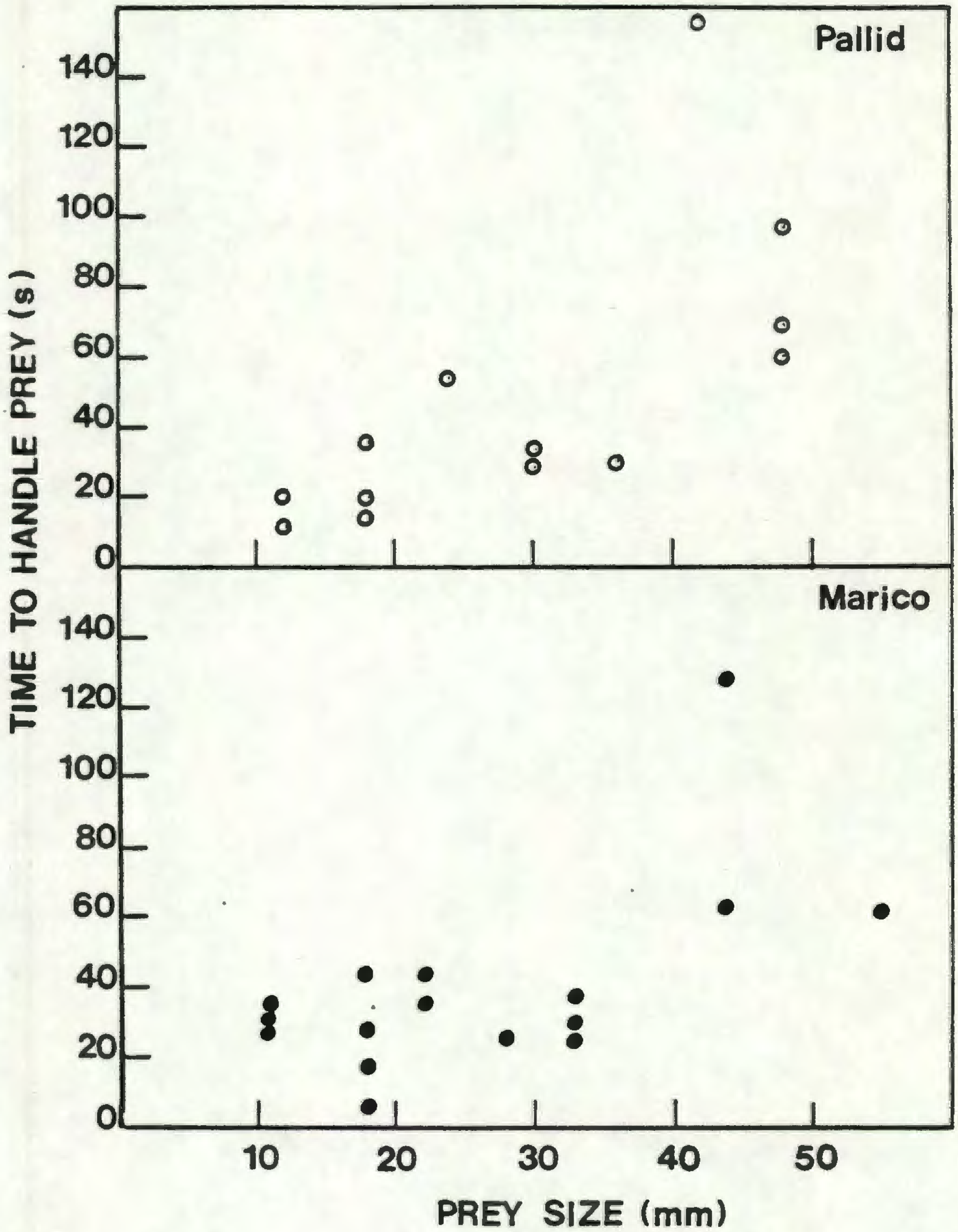

FIGURE 11

The relationship between prey size (mm) and handling time (s). Small items (< 10 mm) have been excluded from the analysis.

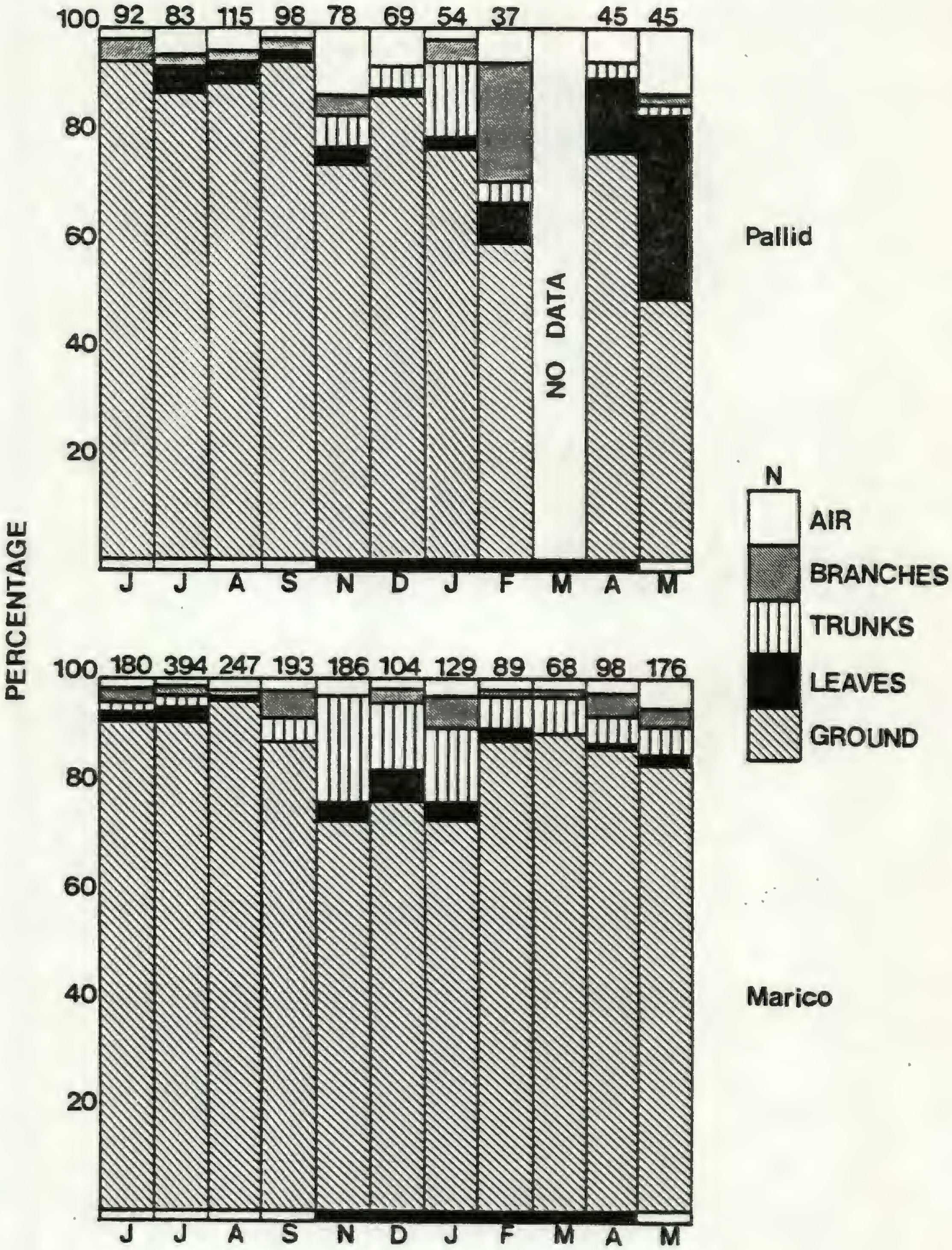

FIGURE 12

The percentage time spent foraging on various substrates. Number of observations given at the top of each column. Black bar at the base of the diagram denotes the wet season.

(Binomial Test p = 0,031). Neither species selected their perch heights in the same proportion that perches were available in their environments (Pallid: $\chi^2 = 136$; df = 9; $p < 0{,}001$; Marico: $\chi^2 = 263$; df = 6; $p < 0{,}001$). The perch height most frequently chosen by Pallid Flycatchers was 0,5 m higher than the common perch height available in *Burkea* woodland, whereas that selected by Marico Flycatchers was 0,5 m lower than the common perch height available in *Acacia* woodland (Fig. 13). The flycatchers travelled similar distances between successive perches (Table 10) and both flew significantly further after making a foraging attempt than they did after finding no prey (Mann Whitney: Pallid z = 3,43; Marico z = 6,75; Both species $p < 0{,}05$) (Fig. 14). Pallid Flycatchers flew significantly further than Maricos for prey during August and September, although in June this trend was reversed (Table 10). For the rest of the months studied, however, the flycatchers showed similar horizontal displacements. For both species, horizontal displacement increased with increasing perch height (Fig. 15).

For all but two months of the year (November and August), Marico Flycatchers had significantly shorter successful search times than Pallid Flycatchers (Mann Whitney Test, $p < 0{,}05$) (Fig. 16); this trend was significant (Binomial Test p = 0,02). For all months of the year except August Marico Flycatchers had significantly shorter giving-up times than Pallid Flycatchers (Mann Whitney Test, $p < 0{,}05$) (Fig. 17); again, this trend was significant (Binomial test p = 0,002). Both flycatchers spent similar amounts of time pursuing prey items (Fig. 18), and neither returned frequently to its previous perch after making a foraging attempt. In Marico Flycatchers, the mean proportion of perch changes that resulted in the bird returning to its previous perch was 0,08 ± 0,03 (data for 11 months; a total of 1751 perch changes) and for Pallid Flycatchers 0,13 ± 0,06 (data for 10 months; a total

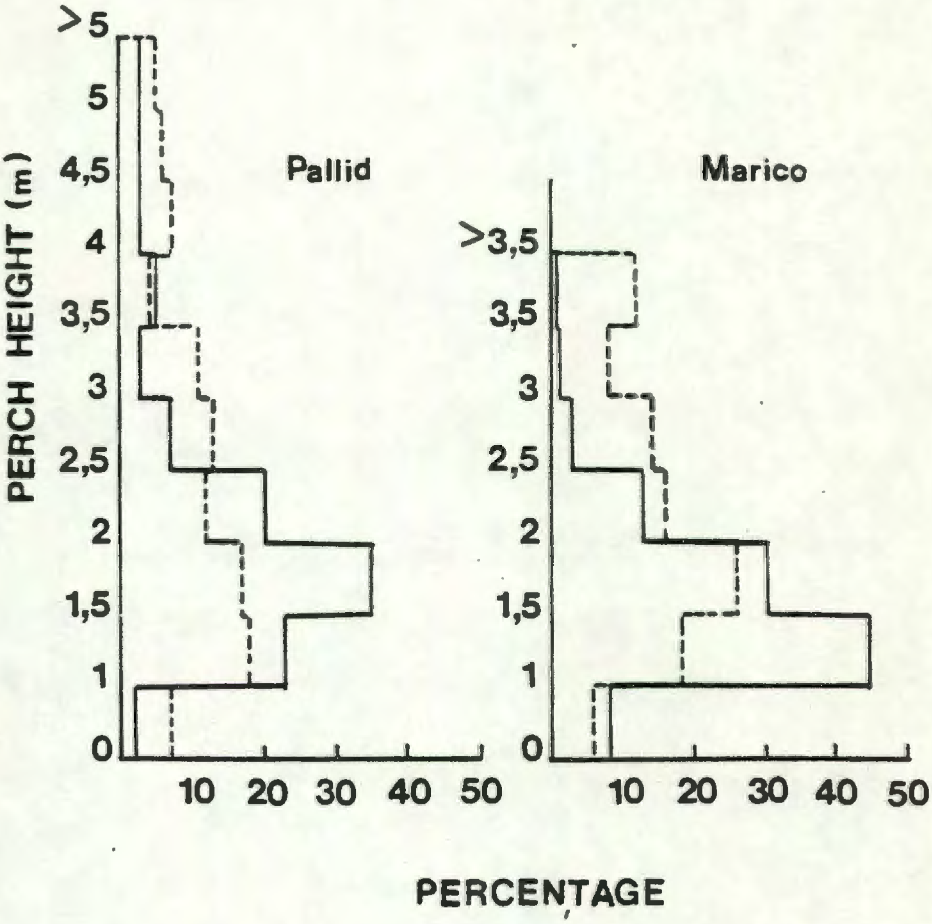

FIGURE 13

The percentage perch heights selected by the flycatchers (closed histograms) and those available in the two woodlands.

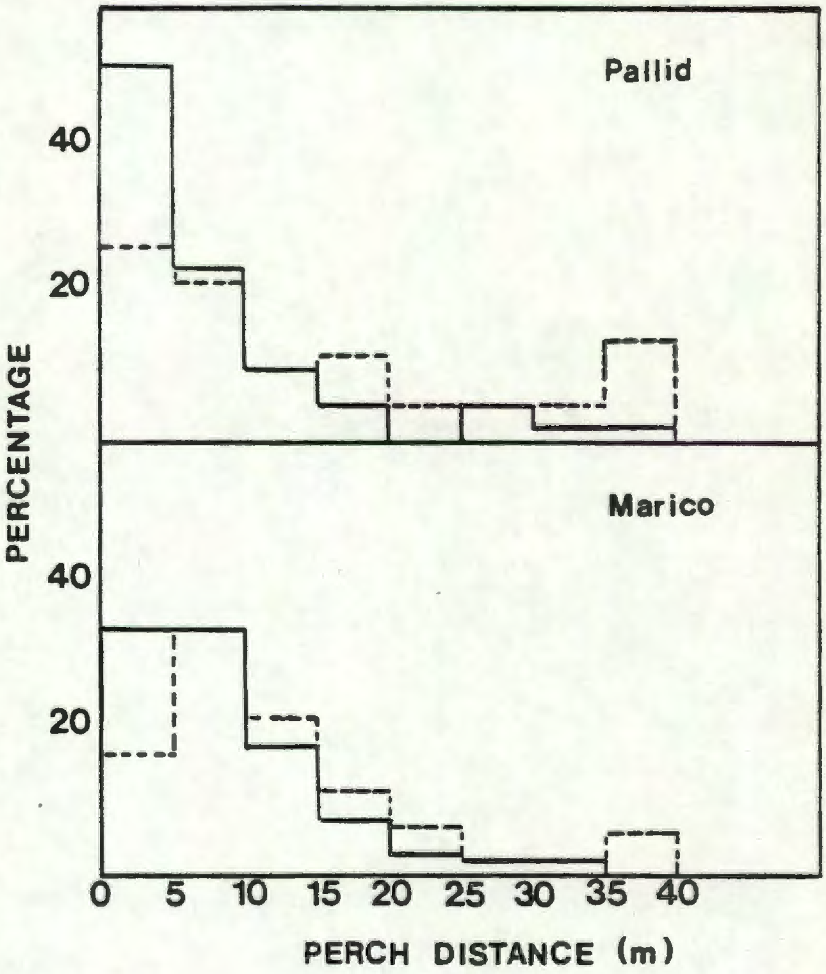

FIGURE 14

Perch distance after successful (closed histograms) and unsuccessful (dashed histograms) searches.

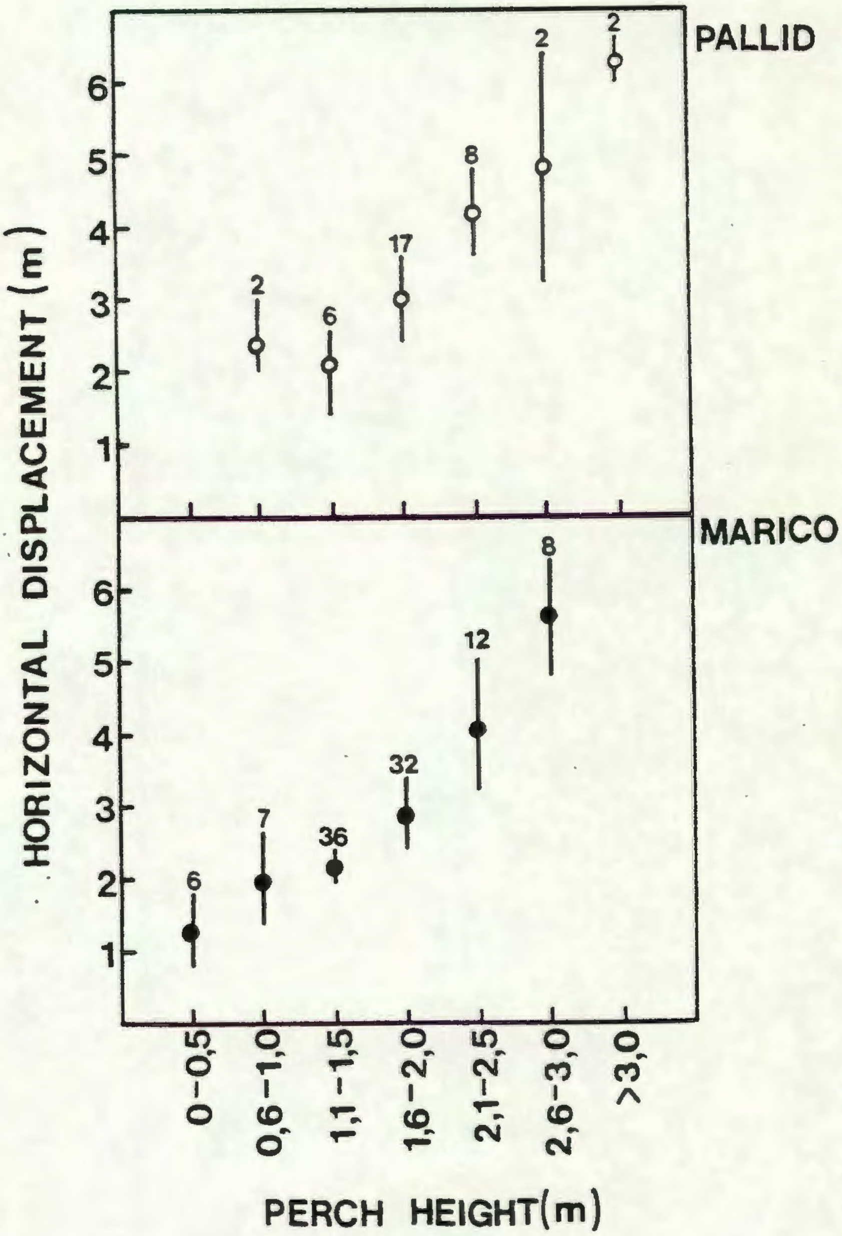

FIGURE 15

The relationship between perch height (m) and horizontal displacement (m). Vertical lines denote standard error. Sample sizes given above each data point.

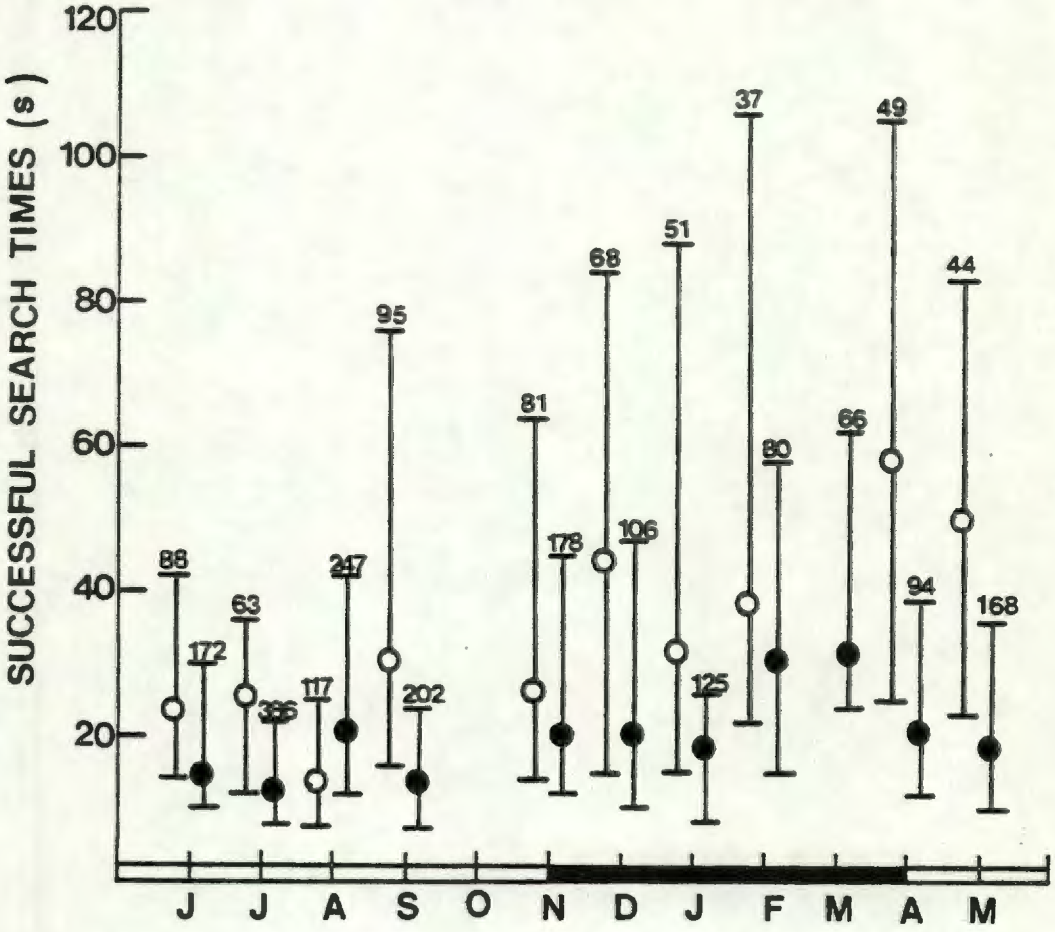

FIGURE 16

Successful search times (s) in the Pallid Flycatcher (open circles) and Marico Flycatcher (closed circles). In each species the horizontal line indicates the median. The top of the vertical line indicates the upper quartile and the bottom the lower quartile. Sample sizes are given above the vertical lines, and the black bar at the base of the figure denotes the wet season. For individual z values see Appendix 2.

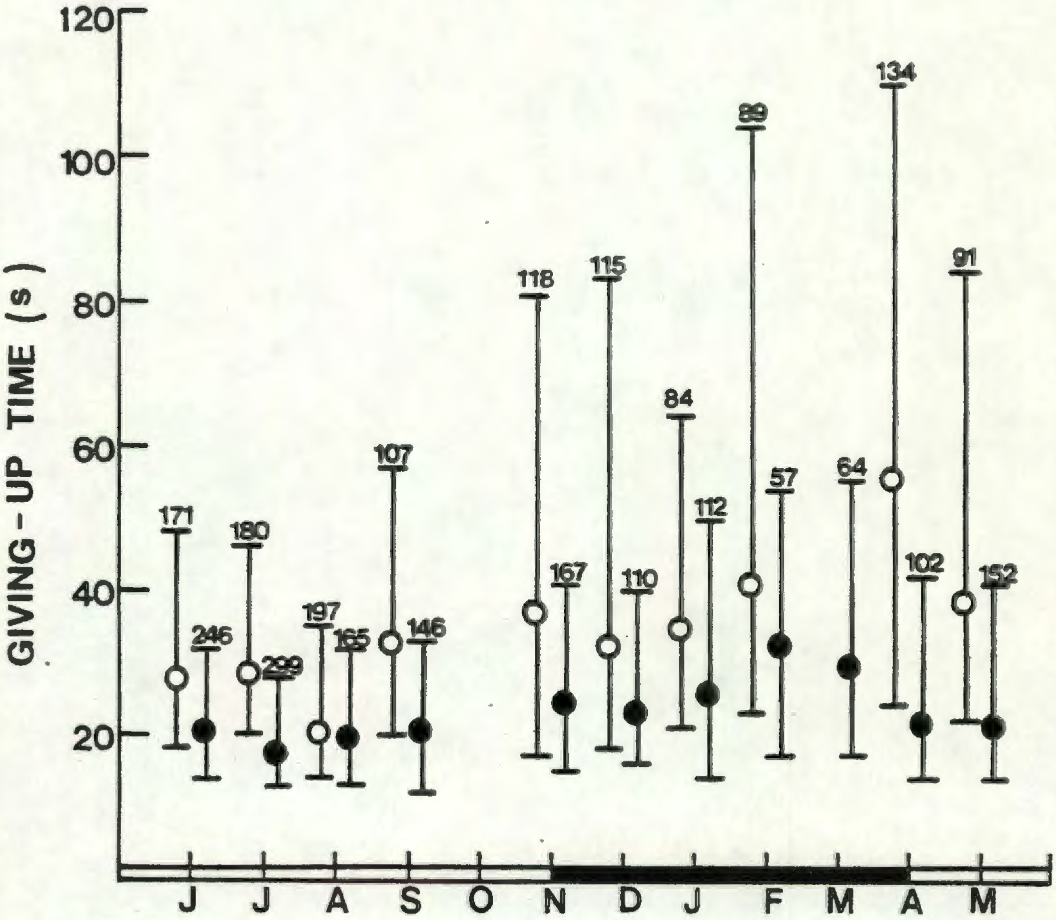

FIGURE 17

Giving-up times (s) in the Pallid Flycatcher (open circles) and Marico Flycatcher (closed circles). Figure notes as for Fig. 16. For individual z values see Appendix 3.

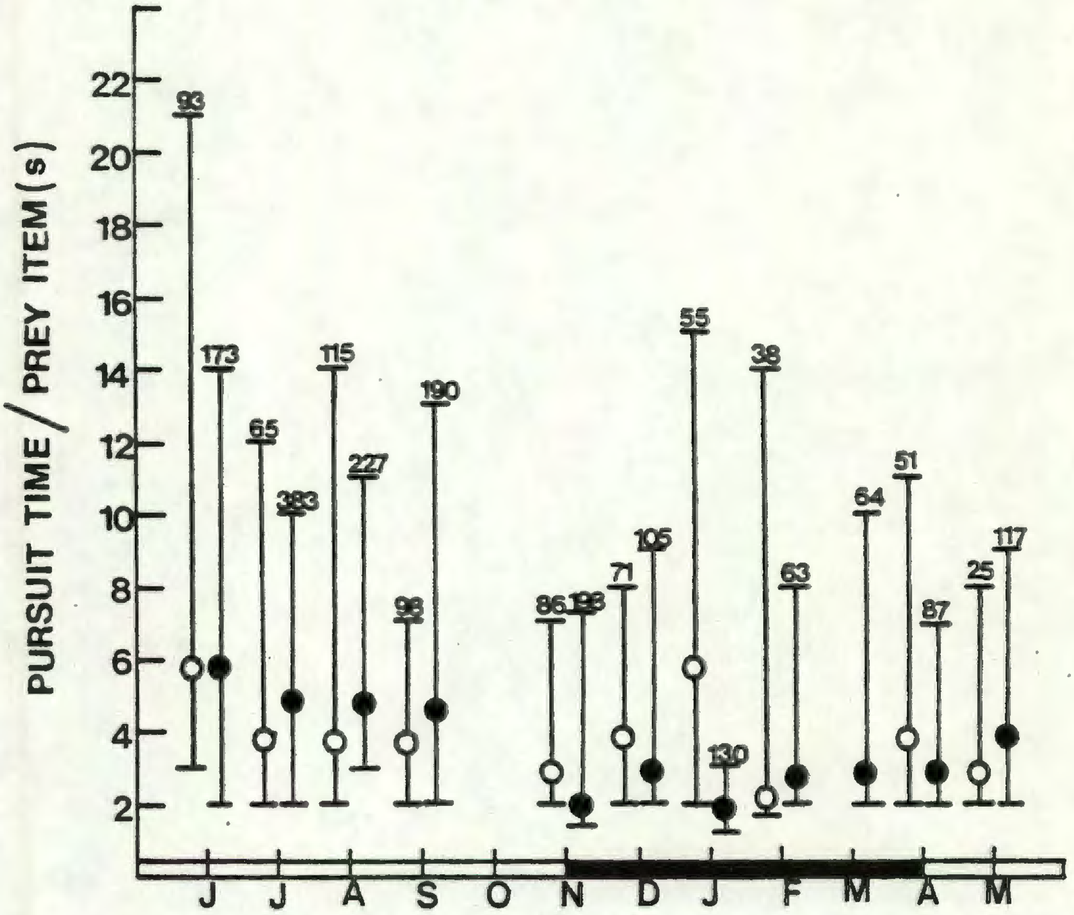

FIGURE 18

Median pursuit time per prey item (s) in the Pallid Flycatcher (open circles) and Marico Flycatcher (closed circles). Figure notes as for Fig. 16. All months except January show no significant difference between the species. For individual z values see Appendix 4.

of 695 perch changes). In both species there was no linear relationship between the probability of the birds returning to the same perch and the length of the previous search time (Spearman Rank Correlation Coefficient $r_s = -0,11$; df = 6; $p > 0,05$).

Throughout the year, Marico Flycatchers made significantly more foraging attempts/minute than Pallid Flycatchers; and for most months had a significantly higher proportion of perch changes result in foraging attempts (both tests: Mann Whitney Tests, $p < 0,05$) (Fig. 19). In both cases the trends were significant (Binomial Test: $p < 0,001$ and $p = 0,016$ respectively). Overall, Marico Flycatchers made more moves/ minute than Pallid Flycatchers (Mann Whitney Test $p < 0,05$) (Fig. 20), and again this trend was significant (Binomial Test $p = 0,008$).

DISCUSSION

Previous studies have shown that morphologically similar species often overlap in their foraging behaviour (Karr & James 1979). Pallid Flycatchers and Marico Flycatchers differ little in their morphologies (Table 11), and have both similarities and dissimilarities in their foraging behaviour (Table 12).

1. Similarities in the flycatchers' behaviour: prey size and foraging techniques.

The flycatchers were most similar in their basic foraging behaviour: both were insectivorous, taking mainly small-sized items; and both caught most of their prey by perching on the outer branches of trees and shrubs and scanning the ground for invertebrates. The flycatchers pounced on their prey, usually killing and eating the prey on the ground before flying to a new perch. The flycatchers' reluctance to return immediately to their previous perch suggests that perch-to-ground foraging may affect the behaviour of local potential prey, which in turn may influence the short-term probability of further hunting

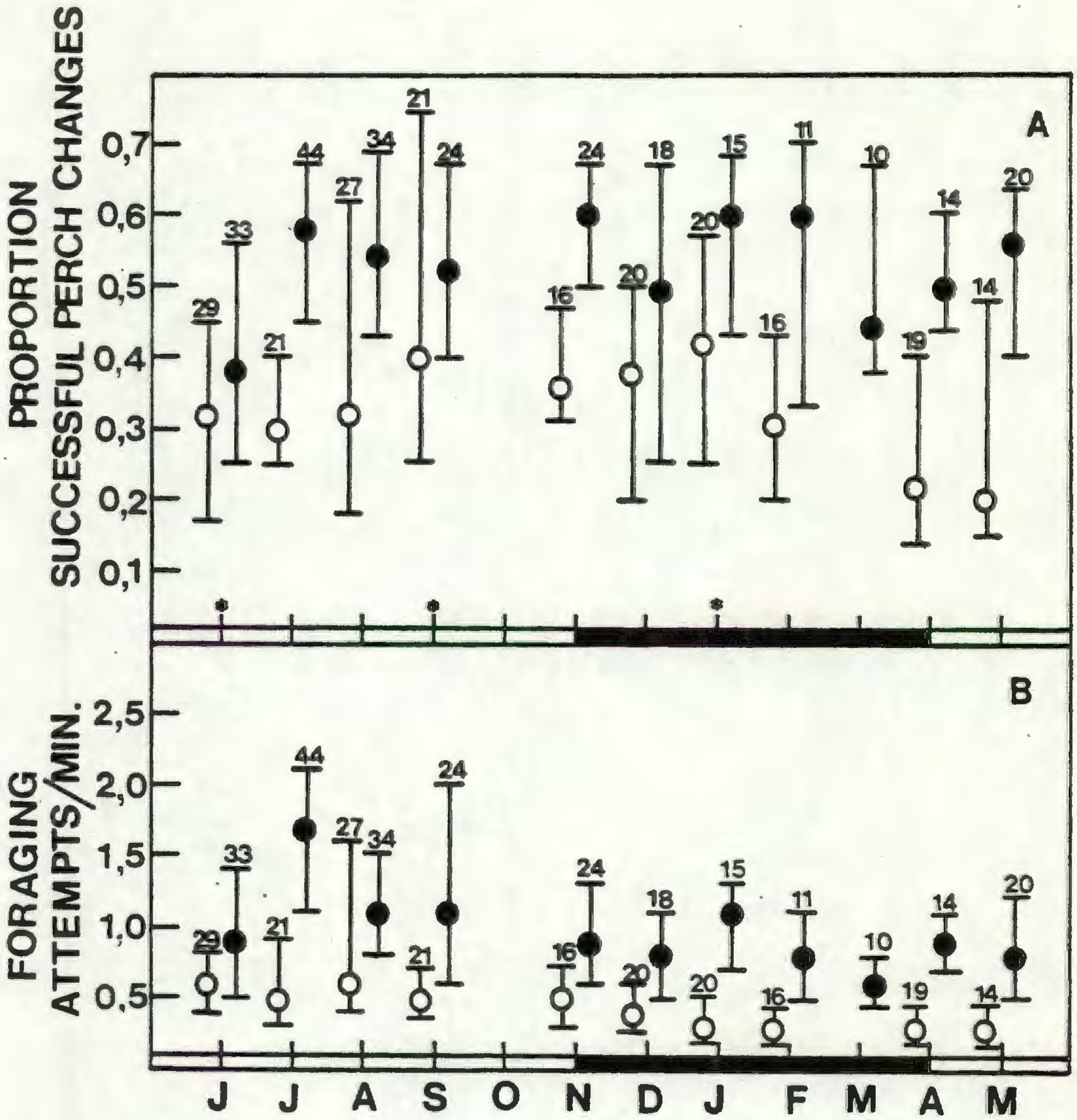

FIGURE 19

(A) The proportion of perch changes which result in foraging attempts and (B) the number of foraging attempts per minute for the Pallid Flycatcher (open circles) and Marico Flycatcher (closed circles). Figure notes as for Fig. 16. Months marked with an asterisk are not significantly different. For individual z values see Appendix 5 & 6.

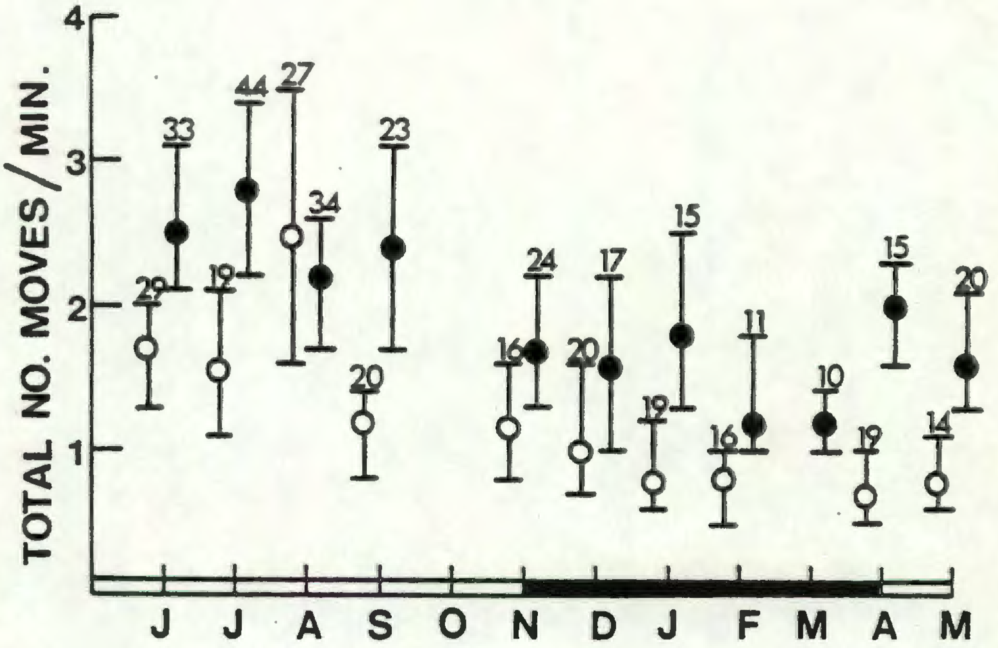

FIGURE 20

Total moves/min. in the Pallid Flycatcher (open circles) and Marico Flycatcher (closed circles). Figure notes as for Fig. 16. August, November and December are not significantly different. For individual z values see Appendix 7.

TABLE 11

MENSURAL (mm) AND WEIGHT (g) DATA FOR PALLID FLYCATCHERS AND MARICO FLYCATCHERS. MEASUREMENTS TAKEN FROM SPECIMENS COLLECTED IN THE TRANSVAAL AND HOUSED IN THE TRANSVAAL MUSEUM. WEIGHT DATA FROM TARBOTON 1980.

	PALLID	MARICO	% DIFFERENCE MARICO VS PALLID
	n = 31	n = 30	
Tail	72,1 ± 4,2	77,6 ± 2,9	+7,6
	n = 31	n = 30	
Wing	89,5 ± 3,2	84,4 ± 3,0	-5,7
	n = 31	n = 30	
Tarsus	19,3 ± 1,1	20,9 ± 2,3	+8,3
	n = 27	n = 30	
Culmen length	12,0 ± 0,8	10,7 ± 0,9	-10,8
	n = 29	n = 30	
Culmen width	4,1 ± 0,4	4,3 ± 0,5	-4,9
Mass (g)	24	23	-4,2

TABLE 12

MAJOR SIMILARITIES AND DISSIMILARITIES FOUND IN THE PALLID FLYCATCHERS' AND MARICO FLYCATCHERS' FORAGING BEHAVIOUR.

SIMILARITIES	PALLID	MARICO
1. Major prey items	Invertebrates	Invertebrates
2. Major prey size	Small	Small
3. Major foraging technique	Sit-and-wait	Sit-and-wait
4. Major foraging substrate	Ground	Ground
5. Other substrates used	Leaves, branches trunks and air	Ditto Pallid but mainly trunks
6. Frequency of return to same perch	Low	Low
DIFFERENCES		
1. Variety of prey types	Includes more large-sized items	Includes harvester termites
2. Successful search time	Longer	Shorter
3. Giving-up time	Longer	Shorter
4. Foraging attempts/min.	Fewer	More
5. Proportion of successful moves	Most months lower	Most months higher
6. Total number moves/min.	Most months fewer	Most months more

success from the same perch. This has been suggested also for other sit-and-wait predators which forage on ground invertebrates from low perches (FitzPatrick 1981; Greig-Smith 1983; Moreno 1984). The flycatchers' habit of suddenly swooping down on prey probably caused invertebrates to scatter and hide, with the result that resources became depressed after the first foraging attempt and the birds were forced to move to a new perch (see Charnov, Orians & Hyatt 1976).

Sit-and-wait predators foraging on aerial prey often use the same perch more than once. In these species the frequency with which they return to their previous perch is inversely related to the length of the search time per prey item (Davies 1977; FitzPatrick 1981). Aerial insectivores probably disrupt their prey less by their foraging actions than do birds which pounce on their victims; and, since a short search time per prey item may indicate a local concentration of prey, it is to their advantage to remain in the immediate search area (FitzPatrick 1981).

Although the flycatchers did not often return to their previous perch, they flew a significantly shorter distance after a successfu search time than after finding no prey. This presumably kept them in the general area of the successful perch, whereas moving further after finding no prey might have increased the probability of travelling beyond an unproductive area. Similar behaviour was reported for Eastern Bluebirds *Sialia sialis* (Pinkowski 1977).

Both flycatchers were sit-and-wait predators throughout the year, and perch-to-ground hunting remained their major foraging tactic throughout. At certain times of the year, however, they varied their proportionate use of other substrates. These changes in the flycatchers' behaviour may have been brought about by seasonal variations in resource availability. The increased grass height and ground cover found in both woodlands during the wet season, for example, may have made it difficult for the flycatchers to detect ground-living invertebrates. This may have forced them to use other foraging substrates during these periods.

During the wet season Pallid Flycatchers decreased the amount of time spent on perch-to-ground hunting and increased the amount of time spent foraging on trunks and branches. During the same period Marico Flycatchers also decreased the amount of time they spent on perch-to-ground foraging; but unlike Pallid Flycatchers, increased their use of trunks more than their use of branches. The flycatchers' different emphasis on trunks and branches may have been due to the different bark structure found in _Acacia_ and _Burkea_ woodland. Most tree species in _Burkea_ woodland have relatively smooth bark compared to _Acacia_ trunks which are fissured and covered with lichens. Rugose barks and barks with epiphytes probably harbour more invertebrates than do smooth barks. At this stage I do not know why Pallid Flycatchers increased their use of leaves in April and May, unless it is in some way connected with a change in leaf structure (furling) and leaf palatability (moving of nutrients) prior to litter fall in the dry season which made leaves more attractive to invertebrates at this period.

2. _Dissimilarities in the flycatchers' behaviour_:

Although the flycatchers showed certain similarities in their basic foraging behaviour, they differed significantly in how long they waited at a perch, the variety of prey items taken, the height at which they perched, and their foraging rates. These differences appear explicable in terms of the habitat and resource conditions each species experienced, whereby relative resource availability in the two woodlands was determined both by total invertebrate biomass and numbers and by the effect of grass height and ground cover on the flycatchers' ability to detect prey.

2.1 Search times:

Marico Flycatchers had shorter successful search times and giving-up times than Pallid Flycatchers, and a greater proportion of their perch changes resulted in foraging attempts, both in the wet season, when ground invertebrate biomass and abundance was significantly higher in *Acacia* woodland than *Burkea*, and during the dry season, when there was no significant difference between the two woodlands. The lower ground cover and shorter grass found in *Acacia* woodland during the dry season must provide better visual conditions for Marico Flycatchers to detect prey relative to Pallid Flycatchers, which experience tall grass and dense ground cover throughout the year in *Burkea* woodland. Marico Flycatchers were also able to forage on termites, which were generally unavailable to Pallid Flycatchers since most termites in *Burkea* woodland forage under litter or under protective soil tunnels (Ferrar 1982). Additional access to resources unavailable to Pallid Flycatchers may have also made it possible for Marico Flycatchers to make more foraging attempts in the dry season than Pallid Flycatchers.

2.2 Variety of prey items:

The number of large invertebrates included in the flycatchers' diet could have been influenced by their search time per prey item. Throughout the year Marico Flycatchers selected proportionally more small-sized items than were available in *Acacia* woodland, whereas Pallid Flycatchers took prey in the same proportion as they occurred in *Burkea* woodland during the wet season, but took proportionally more large prey than were available in the dry season. Since Pallid Flycatchers had longer search times between foraging attempts, they may have been less able to bypass large items, especially during the dry season when resources were low. Marico Flycatchers had a relatively short waiting time between foraging attempts, however, and could probably therefore ignore difficult and more time consuming items in favour of waiting for smaller, more easily handled prey (see Pianka 1974).

2.3 Perch heights:

Tall grass and dense cover may not only lower a bird's ability to detect prey and decrease foraging rates (Eiserer 1980), but may also cause birds which forage from vantage points to select higher perches to gain a better view through the vegetation. Loggerhead Shrikes *Lanius ludovicianus*, for example, tend to select higher perches when ground cover increases (Morrison 1980). Marico Flycatchers, however, used the same average perch height in the dry season when ground cover was low, and during the wet season when ground cover increased. Pallid Flycatchers also used the same perch height throughout the year, but overall selected higher perches than Marico Flycatchers. Higher perches probably allowed Pallid Flycatchers to scan a wider area of ground than low perches, as well as giving them a clearer view through the denser vegetation found in *Burkea* woodland.

2.4 Foraging rates:

Finally, the flycatchers differed in their foraging speeds, with Marico Flycatchers making more moves per minute than Pallids. This finding is consistent with the hypothesis that predators in food-rich areas should use fast, energy-demanding, foraging modes (*e.g.* running, changing perch often) so as to bring them into contact with as many prey items as possible, and predators in food-poor areas should use a slower, more energy conserving technique (Norberg 1977).

3. Conclusion

In conclusion therefore, those aspects of the flycatchers' behaviour which were similar relate mainly to their basic foraging pattern and to certain constraints imposed by their morphology (*e.g.* their optimal prey size) and foraging technique (e.g. the effect of perch-to-ground foraging on prey behaviour and the frequency with which the flycatchers returned to the same perch). Differences in their behaviour, especially their rate of energy intake and foraging velocity, appear to be brought about by the different resource availability and habitat conditions experienced by the birds; which suggests that environmental conditions can have a marked effect on the flycatchers' behaviour. Each species appears to have developed a foraging behaviour suited to the level of resource availability it experienced. Overall, however, Marico Flycatchers foraged more efficiently than Pallid Flycatchers in that they utilized resources at a faster rate and for most of the year made fewer moves per foraging attempt than did Pallid Flycatchers. This suggests that one of the reasons why the flycatchers maintained their habitat separation could have been that Marico Flycatchers excluded Pallid Flycatchers from richer Acacia areas by utilizing the resources found there so efficiently that it was uneconomical for Pallid Flycatchers to attempt to use the same set of resources. Marico Flycatchers, therefore, may have excluded Pallid Flycatchers from Acacia woodland through exploitation competition (see Pianka 1974).

In areas of northern Zululand where Marico Flycatchers do not occur, Pallid Flycatchers are found in Acacia woodland (Cyrus & Robson 1980). A study of Pallid Flycatchers' foraging behaviour in these woodlands would allow one to assess to what extent the birds alter their behaviour in the absence of a competitor and in richer resource areas. By so doing one could also determine whether behavioural traits are species-specific or habitat induced.

CHAPTER 3

GIVING-UP TIMES IN THE PALLID FLYCATCHER AND MARICO FLYCATCHER

SUMMARY

Pallid Flycatchers *Melaenoris pallidus* and Marico Flycatchers *M. mariquensis* are sit-and-wait predators which perch on trees and scan the ground for invertebrates. The flycatchers occurred in adjacent woodlands which differed in ground vegetation height and complexity, and for part of the year also in resource biomass and abundance. I studied giving-up times, the time spent unsuccessfully at a perch before moving to a new one, in the flycatchers to determine whether search times were related to the average time birds wait for prey in the habitat as a whole, or to the vegetation complexity of the search area. Comparisons made between species and within species on a seasonal basis showed that (i) throughout the year Pallid Flycatchers, which experienced taller grass and denser ground cover, had longer giving-up times than Marico Flycatchers which experienced shorter grass and sparser cover; and (ii) both species increased their giving-up times when grass height increased. The results, which are consistent with those found in other similar studies, suggest that giving-up times in the flycatchers are primarily determined by the vegetation height and complexity of the search area.

INTRODUCTION

The Pallid Flycatcher *Melaenornis pallidus* and Marico Flycatcher *M. mariquensis* are sit-and-wait predators which perch on the outer branches of small trees and shrubs and scan the ground for invertebrates (Chapter 2). A problem facing such birds is how long to remain at a perch before "giving-up" and moving to a new one. Optimality models (*e.g.* Krebs, Ryan & Charnov 1974; Charnov 1976) derived for active searchers (*e.g.* gleaners such as *Parus* spp.) predict that a bird should give-up in an area and try a new patch when its rate of prey capture in that particular area drops below the overall rate of prey capture it can expect for the habitat as a whole. These models cannot strictly be applied to passive searchers such as the Pallid Flycatcher and Marico Flycatcher, however, because, since they usually leave a perch either before having made a foraging attempt or immediately after the first foraging attempt (Chapter 2), they have no changing rate of prey capture to use as an index of patch quality. Giving-up times in such species could either be based on the average time they usually wait for prey in the habitat as a whole, or the birds could use some other means of assessing the quality of search area around each perch. The first alternative would result in a constant giving-up time for a particular habitat and time; the second would give a random distribution of giving-up times (FitzPatrick 1981).

Studies of giving-up times in wild sit-and-wait predators have found that (i) there is no constant giving-up time longer than the average successful search time (*i.e.* search time ended by a foraging attempt); (ii) giving-up times and successful search times usually have similar distributions; (iii) both occur irrespective of the time already spent at a perch; and (iv) birds often leave a perch before the probability of sighting a prey item has declined (FitzPatrick 1981; Greig-Smith 1983; Moreno 1984).

FitzPatrick (1981) suggested that the most satisfactory hypothesis explaining the lack of a single optimal giving-up time in sit-and-wait foragers is that perches vary randomly along some continuous distribution of complexity or attractiveness, and that immediately after arrival at a perch a bird can assess how long it will take to search the surrounding area. If a prey item is spotted during the search, the bird makes a foraging attempt; if not, it gives-up when the allotted search time has elapsed. In this way visually simple areas will be searched faster than visually complex areas.

In this chapter, I consider determinants of giving-up times in Pallid Flycatchers and Marico Flycatchers, two similar species which occur in different but adjacent woodlands in the central Transvaal (Tarboton 1980). Marico Flycatchers occur only in _Acacia_ woodland, which for most of the year has shorter grass and a sparser ground cover than the _Burkea_ woodland inhabited by Pallid Flycatchers. In both woodlands, grass height increases during the wet season. At the same time, ground vegetation cover increases in _Acacia_ woodland, but remains approximately the same throughout the year in _Burkea_ woodland. Invertebrate biomass and abundance increase in both woodlands during the wet season; and although _Acacia_ woodland has significantly greater resource levels than _Burkea_ woodland during this period, there is no significant difference between the woodlands during the dry season. Both flycatchers take mainly small invertebrates (< 6 mm long), but, overall, Pallid Flycatchers include significantly more large prey items (> 6 mm) in their diet than do Marico Flycatchers (Chapter 2).

Given the differences in ground cover and resource levels, I predict that: (a) if the flycatchers' giving-up times are related to the average time birds wait at a perch before finding prey in the habitat as a whole, Marico Flycatchers should have shorter waiting times than Pallid

Flycatchers during the wet season but not during the dry season, and (b) if giving-up times are determined by the complexity of the search area, Marico Flycatchers should always have shorter giving-up times than Pallid Flycatchers because the relatively shorter grass and sparser ground cover found in Acacia woodland should tend to make it easier for them to detect prey.

Unless the birds switched to highly cryptic prey, a change of diet should have little effect on search times since it should take the same amount of time to search an area visually irrespective of prey type. Comparison of search times within a species, therefore, should further indicate whether giving-up times are primarily influenced by resource levels or vegetation complexity. If search times are determined by resource levels alone, the flycatchers should have shorter search times in the wet season. If they are determined by vegetation conditions, then an increase in ground vegetation density and grass height during the wet season should result in both longer successful search times and giving-up times since it would then be more difficult for the birds to detect prey.

METHODS

Data were collected between June 1981 and June 1982 in the Nylsvley Nature Reserve ($24^{o}29'S$; 28^{o} 42'E), central Transvaal. I had two study sites, one in Acacia woodland and the other in Burkea woodland (see Chapter 2 for a description of the study areas). There were two main study groups, one for each species, giving a total of five Pallid Flycatchers and three Marico Flycatchers. Approximately equal time was spent observing each species (Pallid = 36 hrs, Marico = 41 hrs).

I followed birds at a distance of 20 - 30 m and recorded their activities on a tape recorder which was allowed to run continuously. The tapes were later replayed and each activity timed with a stop-watch to the nearest second. A successful search time was defined as the interval between a bird arriving at a perch and making a foraging attempt. Giving-up time was defined as the interval between a bird arriving at a perch and leaving that perch without having made a foraging attempt in the interim. Using these two measures the following were analysed:

(i) The distribution of successful search times and giving-up times in the form of survivorship lines calculated by plotting on semi-logarithmic graph paper the number of perching periods of duration t, expressed as a percentage of all observed perching periods in the relevant category. If departures from perches occur randomly, i.e. independently of the time already spent on the perch, the resulting graph would show an exponential decay in the form of a straight line with a negative slope.

(ii) The relationship between the probability of sighting prey and the proportion of giving-up times. The probability of sighting prey was calculated by dividing the number of foraging attempts occurring at time t by the number of times a bird was observed to wait at least t seconds on a perch. The proportion of giving-up times was calculated by dividing the number of giving-up times falling in each time category by the total number of giving-up times observed.

In each of the above, the behaviour of Pallid Flycatchers and Marico Flycatchers was (a) compared to the behaviour of other sit-and-wait foragers (discussion section only), (b) compared between the species and (c) compared within each species on a seasonal basis.

RESULTS

In both species, successful search times and giving-up times had similar distributions which, when expressed as survivorship lines, gave approximately straight lines with negative slopes (Figs 21 & 22). Comparison of giving-up times between the species shows that Pallid Flycatchers had

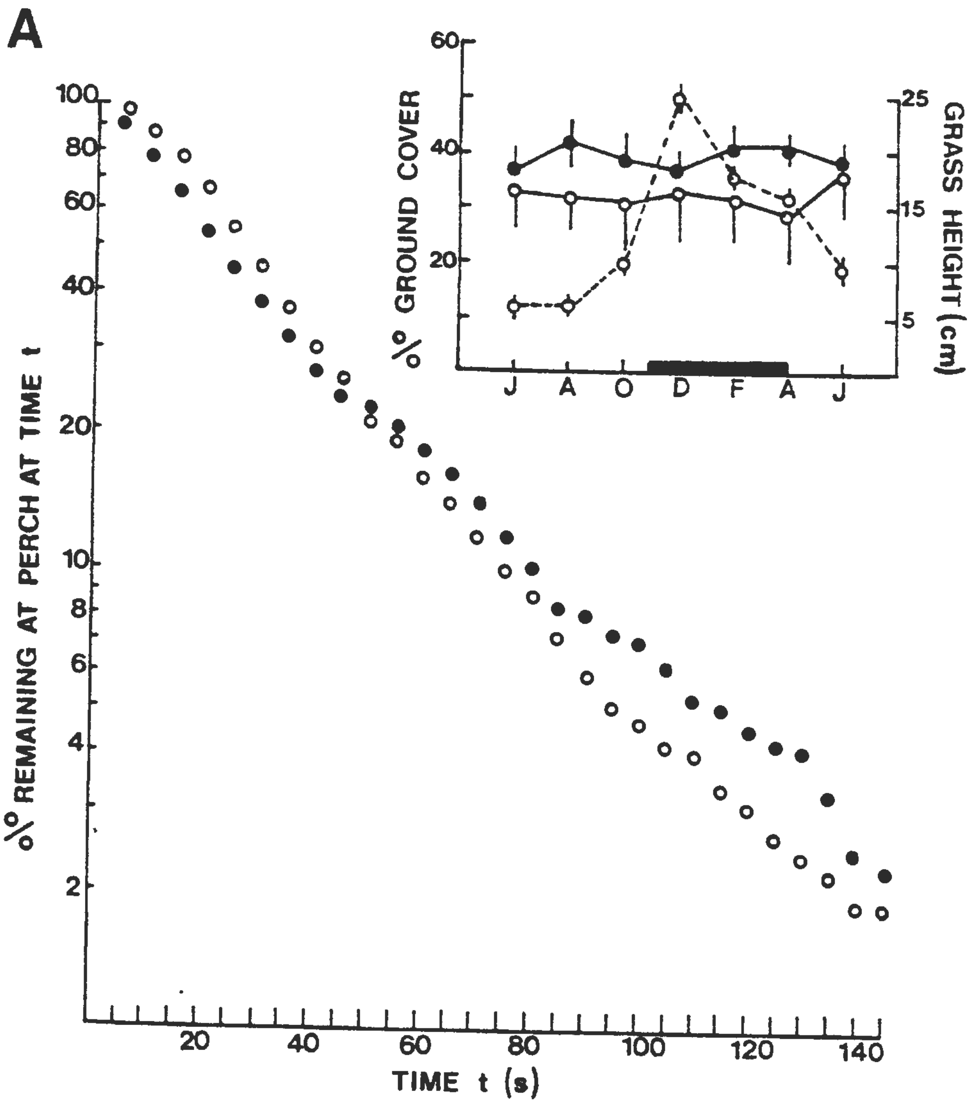

FIGURE 21

The percentage number of Pallid Flycatchers still searching the ground from a perch at the end of each time interval during (A) the dry season and (B) the wet season. Insert gives the mean (± 1 SE) percentage ground cover (● = grass + herbs; O = litter) and mean grass height (cm) (O- -O) for fifteen permanent plots in Burkea woodland (data from Chapter 2). Black horizontal bar denotes wet season.

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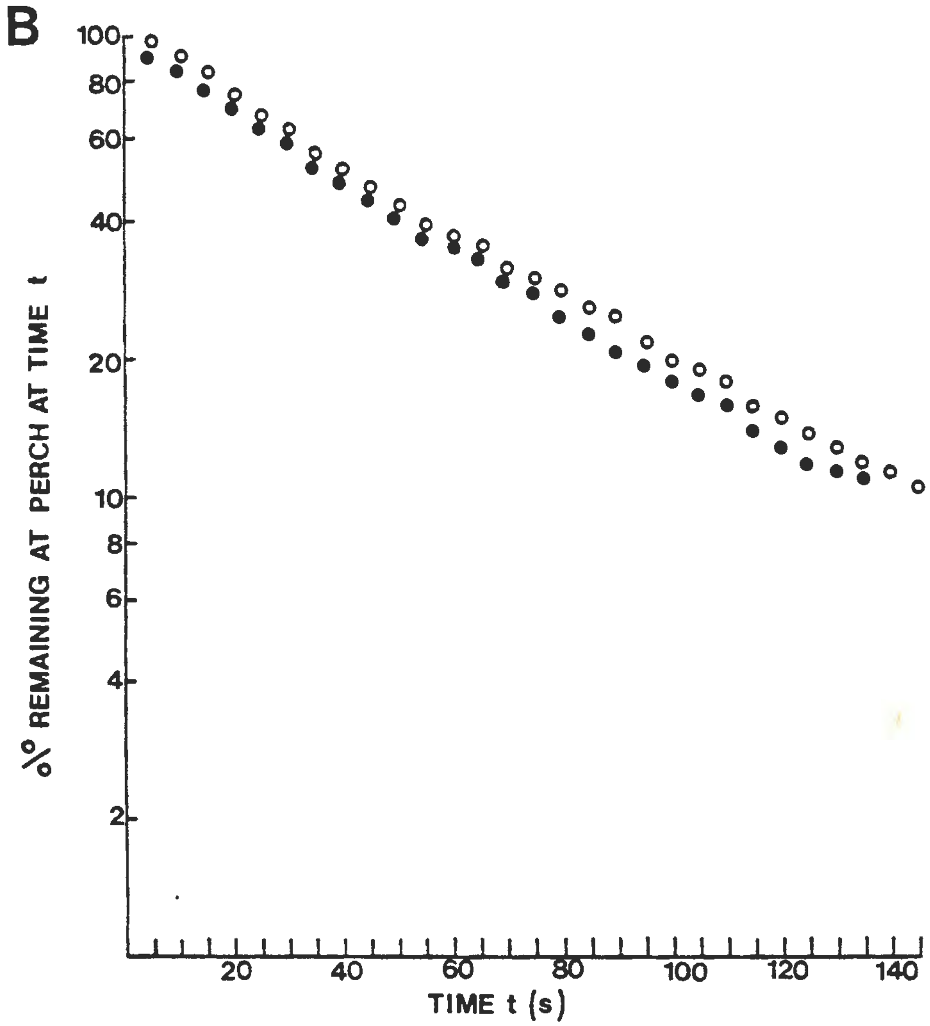

FIGURE 21 continued

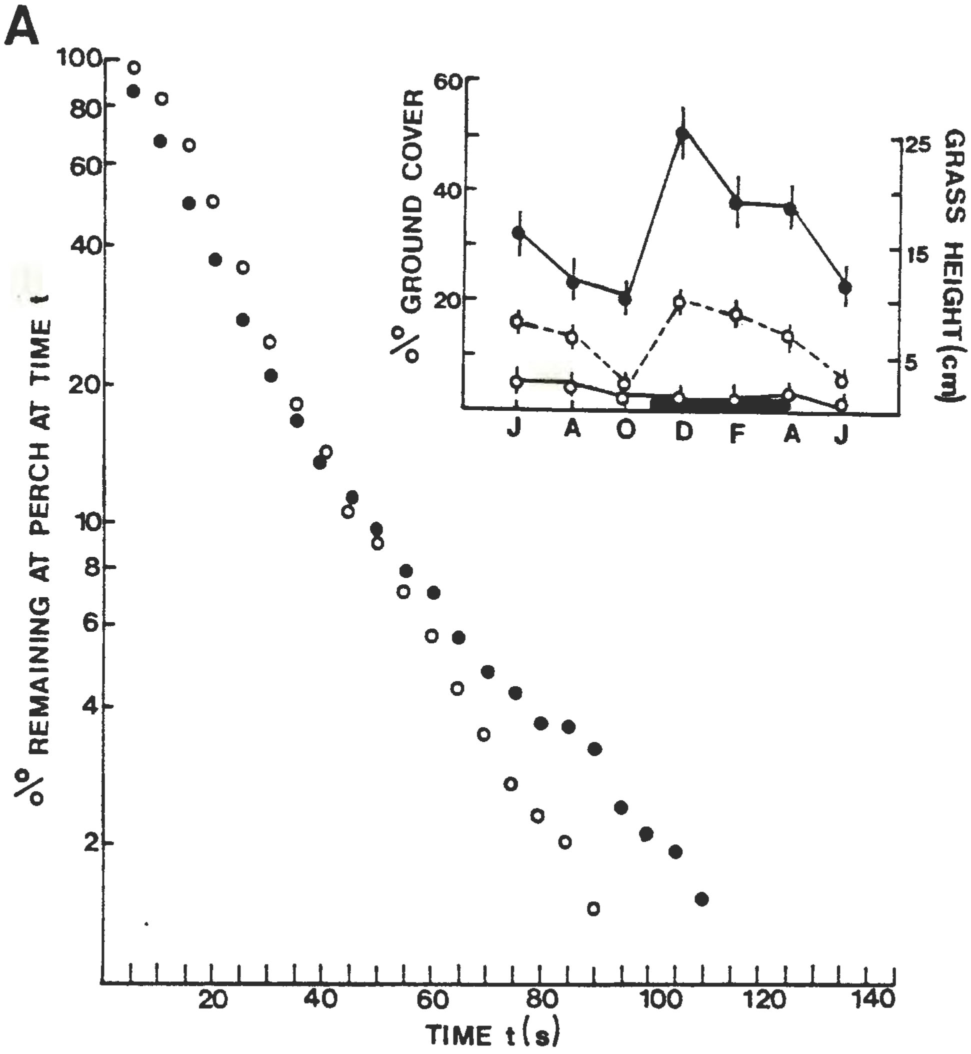

FIGURE 22

The percentage number of Marico Flycatchers still searching the ground from a perch at the end of each time interval during (A) the dry season and (B) the wet season. Figure notes as for Fig. 21.

Continued . . .

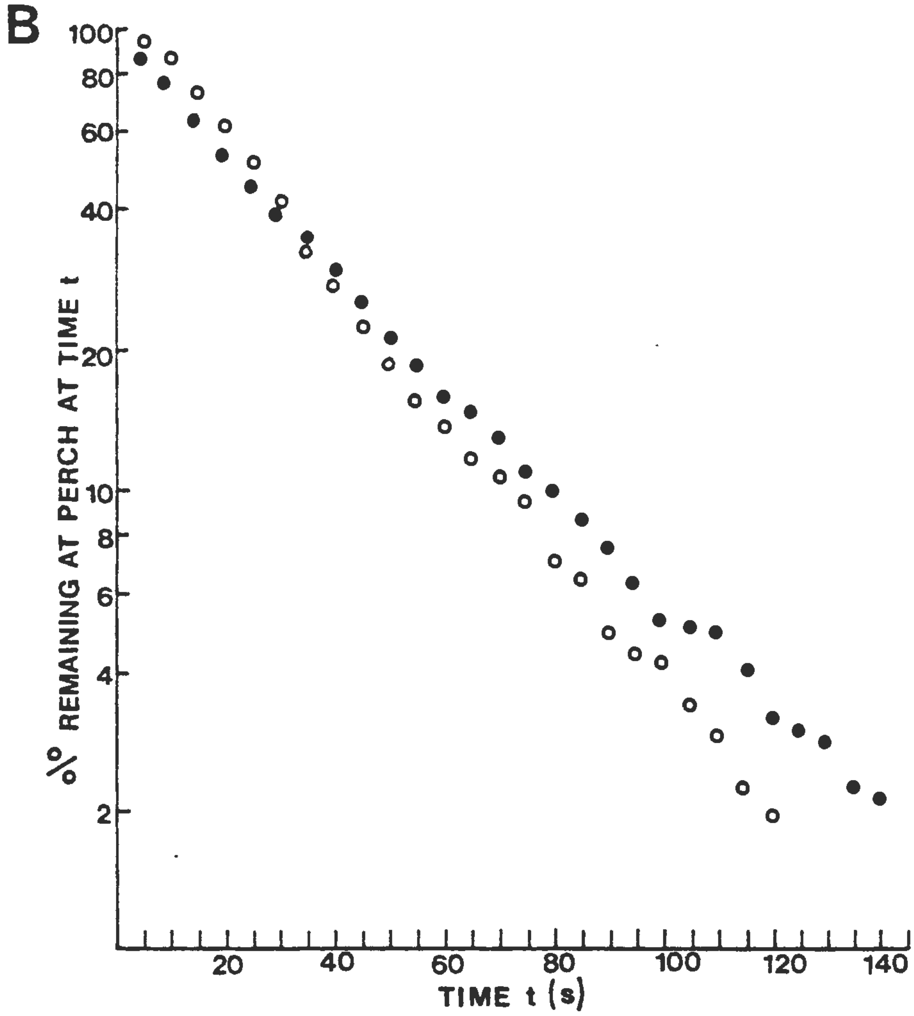

FIGURE 22 continued

consistently longer giving-up times than Marico Flycatchers, the magnitude of difference between the two species being greater in the wet season than in the dry season. Comparison of giving-up time within a species shows that in both giving-up times increased in the wet season. The magnitude of seasonal differences within a species were greater for Pallid Flycatchers than for Marico Flycatchers.

In both species there was a closer relationship between peak proportion of giving-up time and peak probability of sighting prey in the wet season than there was in the dry season. Throughout the year, however, the majority of Pallid Flycatchers left a perch before the probability of their sighting prey had dropped below 0,2 (Fig. 23), and the majority of Marico Flycatchers before the probability of their sighting prey had dropped below 0,1 (Fig. 24).

DISCUSSION

1. <u>Comparison with other sit-and-wait predators</u>:

The results of this study indicate that the Pallid Flycatcher and Marico Flycatcher visually searched an area for prey already present and did not wait at a perch for prey items to come into their view. If the birds waited at a perch for prey they would have had a constant giving-up time determined by their average waiting time for prey in their habitat as a whole. Instead, in both species, the distribution of successful and unsuccessful search times were similar and both occurred irrespective of time already spent at a perch. In addition, most birds left a perch before the probability of their sighting prey had markedly declined which suggests that giving-up times occurred as soon as the birds had finished searching a particular area. These findings are consistent with other observations made on wild sit-and-wait predators (FitzPatrick 1981; Greig-Smith 1983; Moreno 1984).

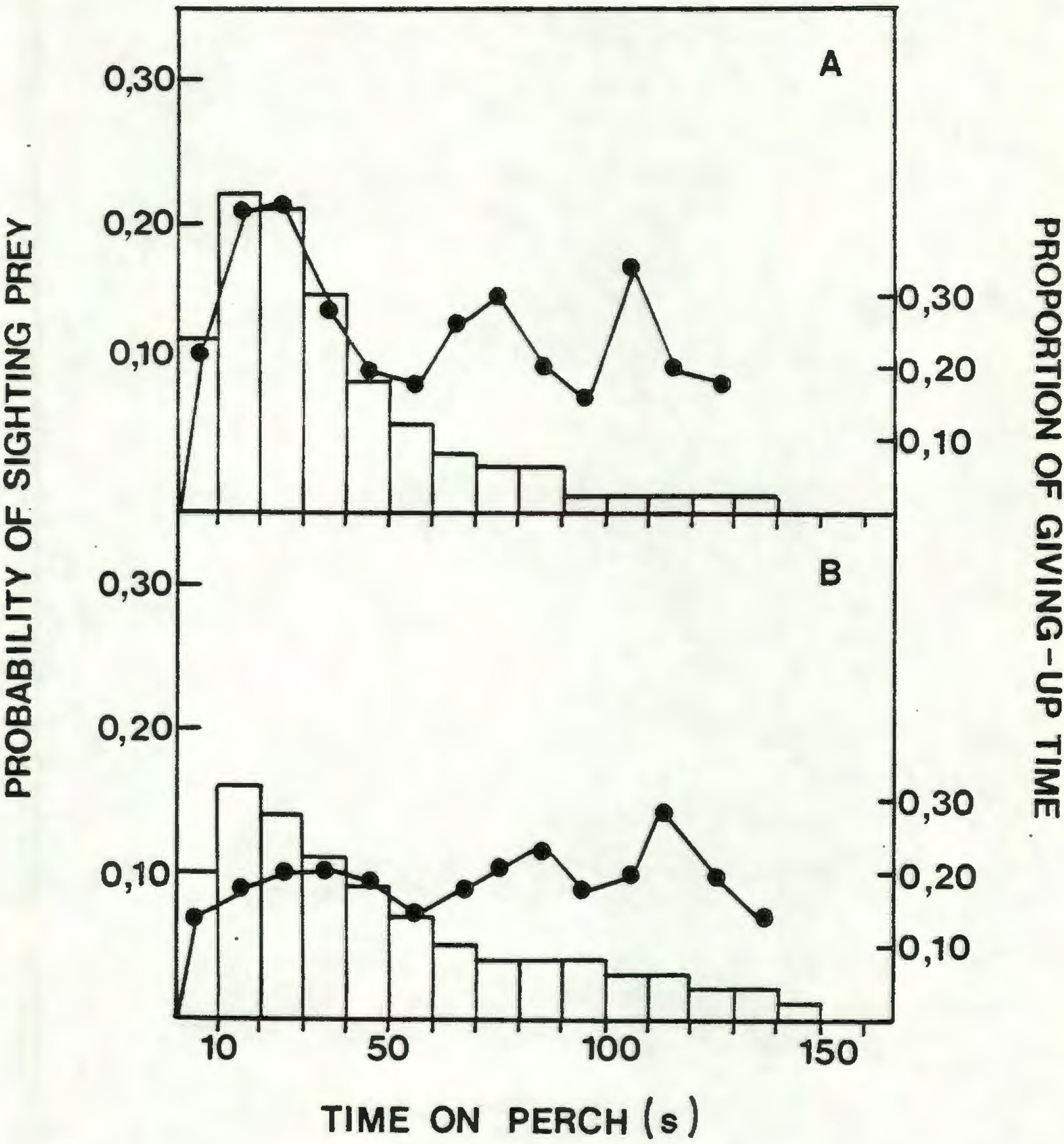

FIGURE 23

The probability of sighting prey (histogram) and the proportion of giving-up times (closed circles) relative to the time spent on a perch (s) by Pallid Flycatchers in (A) the dry season and (B) the wet season.

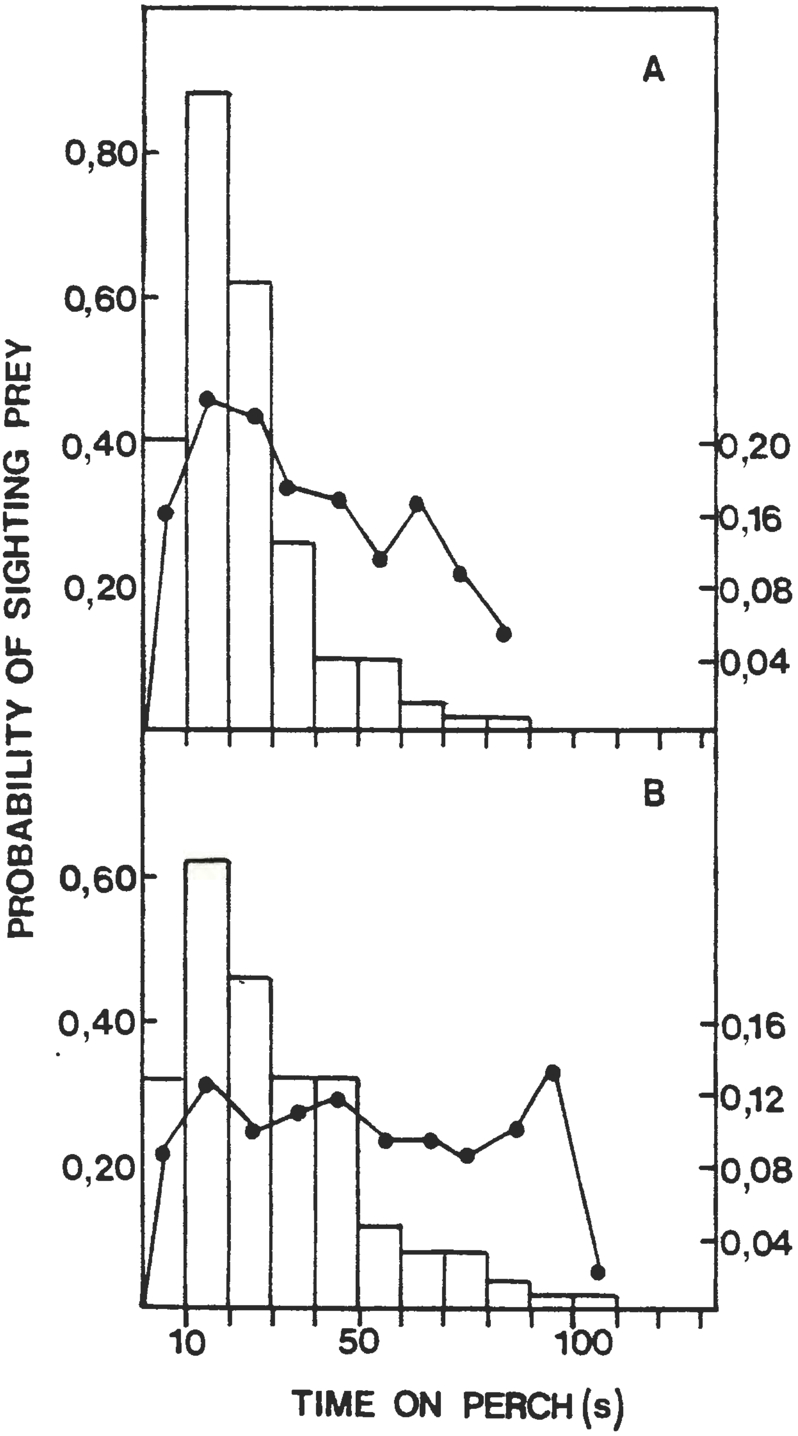

FIGURE 24

The probability of sighting prey (histogram) and the proportion of giving-up times (closed circles) relative to the time spent on a perch (s) by Marico Flycatchers in (A) the dry season and (B) the wet season.

2. Comparison between the species:

Comparison of giving-up times between the species suggests that search times were primarily influenced by the height and density of the ground vegetation cover. For most of the year *Burkea* woodland had taller grass and denser ground cover than *Acacia* woodland (Chapter 2), and throughout the year Pallid Flycatchers had longer giving-up times than Marico Flycatchers.

The magnitude of difference between the two species was greater in the wet season than in the dry season, and again this may have been due to a difference in ground cover conditions found in the two woodlands. Although grass cover reached a peak in *Acacia* woodland during the wet season, since many of the grasses were palatable and heavily grazed (Coetzee *et al* 1976), it rapidly declined. This reduction in ground cover, together with the significantly higher resource abundance found in *Acacia* woodland during this period, may have made it easier for Marico Flycatchers to search for and detect prey than it was for Pallid Flycatchers which, since grasses in *Burkea* woodland were less palatable, experienced high ground cover throughout the wet season.

3. Seasonal comparison within species

Further comparison of giving-up times within a species tends to support the idea that search times were primarily affected by ground cover. In both species successful search times and giving-up times increased in the wet season when grass height and ground cover density increased. The flycatchers also increased their use of other substrates during this period (Chapter 2), presumably because they found it difficult to detect ground invertebrates. Although resource biomass and abundance increased in the two woodlands during the wet season, since this increase coincided with the increase in ground vegetation height and cover, resource availability may have actually been lowered. Since Marico Flycatchers experienced greater seasonal fluctuations in ground cover and resource abundance than Pallid Flycatchers, one might have expected them also to show a greater seasonal difference in their search times. This was not true, however, for Pallid Flycatchers, which experienced relatively stable conditions throughout the year, showed a greater difference between their search times in the wet and dry season than did Marico Flycatchers. At this stage I can offer no explanation for this pattern.

4. A modification of FitzPatrick's hypothesis?

Finally, FitzPatrick (1981) suggests that predators assess and allocate a search time to search areas immediately after arriving at a perch, and if no prey is sighted, birds wait at the perch until the allocated time has expired. I suggest that birds do not allocate search times to search areas, but that their time at a perch is simply determined by how long it takes them to search an area visually. If this latter hypothesis is correct, birds are released of the added burden of pre-deciding how long to wait at an area. Although these two hypotheses are probably difficult to distinguish in the field, the latter is the more parsimonious.

SECTION II

THE EFFECT OF HABITAT AND RESOURCE CONDITIONS ON OTHER ASPECTS OF THE FLYCATCHERS' ECOLOGIES BESIDES THEIR FORAGING BEHAVIOUR

CHAPTER 4

ACTIVITY PATTERNS, HOME RANGE SIZES AND AGGRESSIVE INTERACTIONS IN THE PALLID FLYCATCHER AND MARICO FLYCATCHER.

SUMMARY

Activity patterns, home range sizes and aggressive interactions of Pallid Flycatchers and Marico Flycatchers were studied for one year at the Nylsvley Nature Reserve, central Transvaal. Overall, Marico Flycatchers (i) spent significantly less time foraging than Pallid Flycatchers, and (ii) had smaller home range sizes (2-3 ha. compared to 10-22 ha. found for Pallid Flycatchers). For both species, over half their interactions were intraspecific, and these occurred mainly (>90%) within groups as opposed to between neighbours. Marico Flycatchers, however, experienced more intra and interspecific interactions/hr than did Pallid Flycatchers. For both species, most aggressive interactions were carried out on an individual-to-individual level and involved birds being chased away from perches or prey items. These interactions were called displacements and whereas there was no significant difference in the number of displacements initiated by the flycatchers, Marico Flycatchers were themselves more frequently displaced by other species than were Pallid Flycatchers.

INTRODUCTION

The Pallid Flycatcher *Melaenornis pallidus* and Marico Flycatcher *M. mariquensis* are similar in appearance and general behaviour, and replace one another ecologically throughout their range (Hall & Moreau 1970). At the Nylsvley Nature Reserve in the central Transvaal, where this study was conducted, Marico Flycatchers occur only in fineleaved *Acacia* woodland and Pallid Flycatchers in broad-leaved *Burkea* woodland (Tarboton 1980). Both flycatchers perch on trees to scan the ground for invertebrates. Both take mainly small items (<6mm long), but Pallid Flycatchers catch prey less often and have longer search times (Chapter 2). These differences appear largely due to the level of resource biomass and abundance available to the birds, and to the effect of grass height and ground cover density on their ability to detect prey. For most of the year *Acacia* woodland has shorter grass and a sparser ground cover than *Burkea* woodland, and during the wet season a significantly higher invertebrate biomass and abundance. During the dry season there is no significant difference in resource levels found in the two woodlands (Chapter 2).

Resource abundance can affect other aspects of an animal's ecology besides its basic foraging behaviour. Resource availability determines, for example, the time and energy needed to obtain food as well as the net energy gained from feeding. These in turn determine how much time and energy an animal has available for other non-foraging activities (Gibb 1956; Greig-Smith 1982). Territory size is also often related to food density, with birds in areas of low resource availability generally requiring a larger territory to obtain their necessary food supply than birds in areas of higher resource abundance (Stenger 1958; Davies 1980).

In this chapter I consider the hypothesis that the flycatchers differ in their activity patterns, home range sizes, and aggressive interactions; and that these differences are correlated with different levels of resource biomass and abundance available to the birds. I predict that, for at least during the wet season, Marico Flycatchers (i) spend less time foraging, and (ii) since it is more economical to defend rich resources than poor ones (Davies 1980), have more aggressive interactions (as defined below) than Pallid Flycatchers. If in the flycatchers, home range size is inversely related to food density as it is in other species (Stenger 1958; Davies 1980), I predict that (iii) both species of flycatchers decrease their home range size in the wet season when resource levels increase in the two woodlands, and (iv) Marico Flycatchers have a smaller home range than Pallid Flycatchers in the wet season.

METHODS

The study was carried out between June 1981 and June 1982. I had two study sites, one in broadleaved *Burkea* woodland and the other in fineleaved *Acacia* woodland. Both have been described elsewhere (Chapter 2). The climate at Nylsvley is semi-arid with a dry season (May-October) and a wet season (November-April).

I had two main study groups, one for each species, comprised of three Marico Flycatcher adults and five Pallid Flycatcher adults. A total of 41 hrs of observations were made on the Marico Flycatchers and 36 hrs on the Pallid Flycatchers. Additional information on two other groups, consisting of two Pallids and two Maricos, were gathered less frequently. I followed the birds at a distance of about 20-30 m and recorded their behaviour onto a tape recorder which was allowed to run continuously. The tapes were later re-played and each activity timed with a stop-watch. Activities were divided into five categories:

(i) Foraging, *i.e.* search time plus pursuit time.
(ii) Time spent on aggression.
(iii) Preening.

(iv) Resting, i.e. times when birds "sat down" on a perch and appeared relaxed as opposed to standing upright and actively searching.

(v) Vocalising.

Since short observation periods tend to over represent common activities, I restricted the analysis of activity patterns to those observations lasting five minutes or longer. Using only these periods gave a total of 31 hrs for Marico Flycatchers and 29 hrs for Pallid Flycatchers (79% and 81% of the total observation periods respectively). Most of these observations took place in the morning between 09h00 - 12h00 (Marico 79%, Pallid 86%). Activity data were compared between the species:

(i) On a monthly basis i.e. for each species, all observations ≥ 5 mins. were combined for each month to give an overall percentage time spent on each activity for that particular month. Month by month comparisons were made between the species using a Binomial Test.

(ii) On a seasonal basis i.e. for each species, all observations ≥ 5 mins. were treated as individual units. For each observation I calculated the percentage time spent on each activity and categorised it as either falling in the wet season or dry season. Season by season comparisons between the species were then made using a Mann Whitney Test (e.g. wet season: Pallids vs Maricos).

The mean percentage time spent foraging by each species in the wet and dry season was calculated by summing the percentage time spent foraging in each of the individual units described in (ii) above. Seasonal comparisons within a species were also made using the units described in (ii) above, but in this instance the units were not summed and in each species, wet season activity data were compared to dry season activity data using a Mann Whitney Test (e.g.

Maricos: wet season vs dry season). In all tests $p \leq 0{,}05$ was taken as the accepted significance level.

I defined aggressive interactions as disputes over foraging areas either between individuals (intraspecific or interspecific) or between intraspecific groups. These disputes could take the form of chasing, physical fights or vocalisations. Aggressive interactions were analysed for all observation periods, and included:

(i) Number of interactions/hr divided into intraspecific and interspecific interactions. For each species, the number of interactions occurring in each observation period were expressed as number of interactions/hr. These values were summed for each month to give a mean number of interactions/hr. Comparisons between the species were made on a monthly basis using a Binomial Test. Intraspecific interactions were either intra-group or inter-group interactions. Note was made of the different characteristics of each of these two interactions, but for the sake of between-species comparisons the two categories were combined. Again, $p \leq 0{,}05$ was taken as the accepted significance level.

(ii) The nature of the interaction (e.g. chasing, fighting).

(iii) The species involved in the interaction.

(iv) Whether the interaction was won or lost by the flycatchers.

Home range boundaries were plotted onto maps. The *Burkea* woodland was staked out with marked poles every 100m. The *Acacia* woodland had no poles but positions could be plotted on a 1/4000 aerial photograph which provided clearly recognisable land marks.

RESULTS

1. Activity patterns

There was no significant difference between time spent foraging in the morning and afternoon periods (both flycatchers' Binomial Test p > 0,05). Overall the flycatchers spent more than 70% of their time hunting (Fig. 25), although in both species foraging time decreased significantly in the wet season (Pallids: Mann Whitney z = 2,78 p < 0,01; Maricos: Mann Whitney z = 4,39 p < 0,01) (Table 13). Pallid Flycatchers spent significantly more time foraging than Marico Flycatchers in both the wet (Mann Whitney z = 3,75 p < 0,01) and the dry season (Mann Whitney z = 2,59 p < 0,01) (Table 13).

2. Intraspecific interactions and home range size

A large proportion of Pallid Flycatchers' interactions were intraspecific (59% of a total of 37 interactions) and, as neither study group had home range areas abutting that of other Pallid Flycatchers, all intraspecific interactions were made within the groups. Intraspecific intra-group aggression took the form of individuals chasing members of the same group away from prey items or perches. These interactions lasted only a few seconds and ended once the chased bird had left the immediate vicinity of the aggressor. The chases, which occurred on an individual-to-individual basis, were more a form of displacement than outright physical aggression. The main group, consisting of five adults had a home range area of *ca* 22 ha., and the second group consisting of two adults an area of about 10 ha. Home range size did not vary through the year.

Marico Flycatchers had significantly more intraspecific interactions per hour than did Pallid Flycatchers (Binomial Test p = 0,01) (Table 14). Again, intraspecific interactions comprised a large proportion of the overall interactions experienced by Marico Flycatchers (52% of 115 interactions), and occurred mainly (97%) within groups as opposed to between neighbours. Intraspecific intra-group

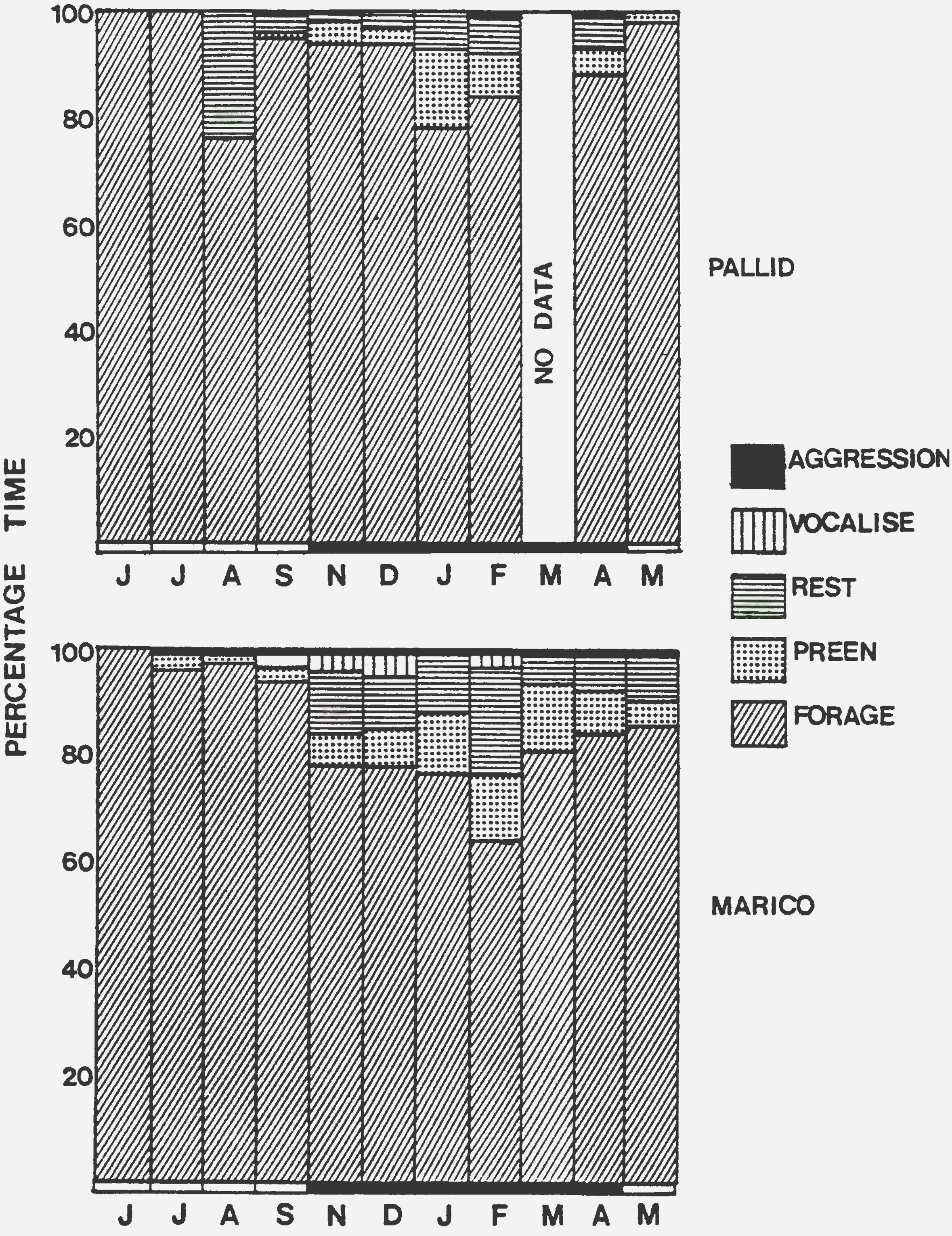

FIGURE 25

The percentage time spent on each activity by the flycatchers during each month of the study period. Data for October 1981 are missing for both species, and March 1982 for Pallid Flycatchers.

TABLE 13

THE MEAN PERCENTAGE (± 1 SD) TIME SPENT FORAGING BY PALLID FLYCATCHERS AND MARICO FLYCATCHERS IN THE WET AND DRY SEASON.

	PALLID	MARICO
	n = 80	n = 86
Wet season	90,6 ± 17,6	79,1 ± 25,6
	n = 58	n = 83
Dry season	96,7 ± 12,1	95,4 ± 11,0

interactions in Marico Flycatchers were similar to those which have been described for Pallid Flycatchers above. Both study groups, consisting of three and two adults, had home range areas of about two to three hectares. Although both of these abutted neighbours, I observed only three aggressive interactions between groups. These occurred on a group-to-group basis (i.e. involved all members of a group at the same time) and usually took the form of groups vocalising to one another across a common boundary. Marico Flycatchers also maintained the same home range area throughout the year.

Comparison between the species shows that, apart from having different sized home ranges, the flycatchers used their foraging areas in a different manner. Pallid Flycatchers covered only part of their home range in a single day, and seldom foraged in the same place more than once a day. The group with an overall area of ca 22 ha., for example, usually covered about 15 ha. in a day. Marico Flycatchers foraged systematically over their entire home range area, frequently re-visiting the same parts several times a day.

3. Interspecific interactions

In both flycatcher species, interspecific interactions occurred on an individual-to-individual basis and, as with intraspecific intra-group interactions, were in the form of individuals being displaced from perches or food items. Interspecific interactions took only a few seconds and ended once the chased bird had left the immediate vicinity of the aggressor. Both Pallid Flycatchers and Marico Flycatchers lost interactions with species heavier than themselves and won those with species of a similar weight or lighter (Table 15 and 16). The flycatchers were more often themselves chased from perches or food items (Pallid = 88%, Marico = 97%) than they themselves did the chasing. Pallid Flycatchers experienced significantly fewer displacements per hour than did Marico Flycatchers

TABLE 14

THE MEAN NUMBER OF INTRASPECIFIC INTERACTIONS/HR EXPERIENCED BY PALLID FLYCATCHERS AND MARICO FLYCATCHERS.

	PALLID		MARICO	
	INTERACTION/HR	OBS. PERIOD (HR)	INTERACTION/HR	OBS/ PERIOD (HR)
June	0	3,1	2,10	3,4
July	1,54	2,6	1,30	5,3
Aug	0,36	2,8	3,20	5,0
Sept	1,20	3,3	5,80	3,3
Nov	0	3,6	1,80	4,9
Dec	1,39	3,6	3,00	3,0
Jan	0,54	3,7	1,90	3,7
Feb	0	4,2	3,30	3,6
Mar	-	0	0,80	2,5
Apr	0,68	5,9	0,80	2,4
May	0,69	2,9	6,10	4,1

TABLE 15

SPECIES WHICH INTERACT AGGRESSIVELY WITH PALLID FLYCATCHERS. DENSITY VALUES FROM TARBOTON (1980), WEIGHTS FROM TARBOTON (1980) AND MACLEAN (1985). THE PALLID FLYCATCHERS' WEIGHT AND DENSITY ARE GIVEN AS A COMPARISON.

SPECIES	WT. (g)	DENSITY Birds/100ha	INTERACTION WON	INTERACTION LOST
Pallid Flycatcher *Melaenornis pallidus*	24	7	-	-
Striped Kingfisher *Halcyon chelicuti*	45	3	0	6
Forktailed Drongo *Dicrurus adsimilis*	48	7	0	4
Fiscal Shrike *Lanius collaris*	40	?	0	1
Yellowthroated Sparrow *Petronia superciliaris*	26	10	0	1
Brubru *Nilaus afer*	25	7	0	1
Tawnyflanked Prinia *Prinia subflava*	9	13	2	0

TABLE 16

SPECIES WHICH INTERACT AGGRESSIVELY WITH MARICO FLYCATCHERS. DENSITY VALUES FROM TARBOTON (1980), WEIGHTS FROM TARBOTON (1980) AND MACLEAN (1984). THE MARICO FLYCATCHERS' WEIGHT AND DENSITY GIVEN AS A COMPARISON.

SPECIES	WT.	DENSITY	INTERACTION	
	(g)	Birds/ 100ha.	WON	LOST
Marico Flycatcher *Melaenornis mariquensis*	23	57	-	-
Whitebrowed Sparrowweaver *Plocepasser mahali*	39	45	0	78
Crimsonbreasted Shrike *Laniarius atrococcineus*	44	16	0	9
Redbacked Shrike *Lanius collurio*	30	19	0	6
Pied Barbet *Lybius leucomelas*	32	8	0	4
Masked Weaver *Ploceus velatus*	24	?	0	1
Crested Barbet *Trachyphonus vaillantii*	77	11	0	1
Forktailed Drongo *Dicrurus adsimilis*	48	18	0	1
Whitethroated Robin *Cossypha humeralis*	24	8	2	0
Whitebrowed Scrub Robin *Erythropygia leucophyrs*	20	90	1	0
Titbabbler *Parisoma subcaeruleum*	16	29	1	0
Greyheaded Sparrow *Passer griseus*	27	?	1	0

(Binomial Test p = 0,001), but there was no significant difference between the number of interactions initiated by the flycatchers (Binomial Test p = 0,17) (Table 17).

Marico Flycatchers were displaced mainly by Whitebrowed Sparrowweavers _Plocepasser mahali_ (Table 16) and were themselves most aggressive towards Whitebrowed Scrub Robins _Erythropygia leucophyrs_ and Whitethroated Robins _Cossypha humeralis_. Both robins usually foraged in thickets but occasionally came out into the open to feed on termites. Interactions with Whitethroated Robins resulted in physical fights won by the Marico Flycatchers.

Interactions between Marico Flycatchers and Pallid Flycatchers were observed on three occasions. In each case the interaction, which took place where the two woodlands adjoined, were initiated by the Marico Flycatchers and followed the same pattern. All interactions were on a group-to-group basis (_i.e._ the entire group of Marico Flycatchers aggressively attacked the group of Pallid Flycatchers in question). On seeing the Pallid Flycatchers, the Marico Flycatchers called loudly and flew over to the Pallids, chasing them further into the _Burkea_ woodland. The Pallid Flycatchers made a silent and hasty retreat. After evicting the Pallids from the immediate area, the Marico Flycatchers returned to the _Acacia_ woodland to forage, stopping every now and then to call. At no time did Pallid Flycatchers act aggressively towards Marico Flycatchers and on each occasion there were equal numbers of Marico Flycatchers and Pallid Flycatchers involved in the interaction.

DISCUSSION

Similarities found in the flycatchers' behaviour were (i) both spent a large proportion of their time hunting and (ii) in both species over half their interactions were intraspecific and involved mainly members of the same group. Dissimilarities in the flycatchers' behaviour were

TABLE 17

THE MEAN NUMBER OF INTERSPECIFIC INTERACTIONS/HR IN WHICH PALLID FLYCATCHERS AND MARICO FLYCATCHERS WERE CHASED BY OTHER SPECIES (LH COLUMN), OR THEY THEMSELVES INITIATED THE CHASES (RH COLUMN). OBSERVATION HOURS THE SAME AS FOR TABLE 14.

	PALLID		MARICO	
	NO. INTERACTIONS/HR		NO. INTERACTIONS/HR	
	DISPLACED	DISPLACES	DISPLACED	DISPLACES
June	0,65	0	0,88	0
July	0	0	3,58	0,38
Aug	0,36	0	3,60	0
Sept	0,30	0	2,73	0
Nov	0,28	0	1,84	0,20
Dec	0	0	2,00	0
Jan	0	0	1,62	0
Feb	0,48	0,48	2,78	0
Mar	-	-	0,40	0
Apr	1,02	0	3,75	0,42
May	0,34	0	2,68	0

(i) the size of their home range areas and (ii) their overall level of aggressive interactions.

1. Foraging time and intraspecific interactions

Although Marico Flycatchers spent significantly less time foraging than Pallid Flycatchers, both flycatchers spent a large proportion of their day hunting and had little time available for non-foraging activities. Other sit-and-wait predators also spend a large proportion of their time hunting *e.g.* Blue-bellied Rollers *Coracias cyanogaster* (85% of their time) (Thiollay 1985). Since passive searchers perch for long periods, relative to active searchers they probably require less energy to hunt and may also be able to carry out other activities, such as keeping sight of mates, at the same time (Schoener 1971). Both flycatchers spent significantly less time foraging during the wet season, when resource biomass and abundance increased in the two woodlands (Chapter 2).

In both flycatchers, over half their interactions were intraspecific and occurred mainly within a group. Nevertheless the flycatchers remained in groups throughout the year which suggests that the benefits of group living outweighed any possible disadvantage. There are several advantages accruing to birds foraging in a group (Rand 1954; Moynihan 1960; Cody 1971). These include a possible reduction in predation risk (the "many eyes" theory) and a greater foraging efficiency, especially where resources are renewable but patchily distributed, as was the case in the *Burkea* and *Acacia* woodland (Chapter 2). Groups of birds are also more likely to be able to evict large competitors than are single individuals (Bertram 1979). Three Marico Flycatchers, for example, chased a Fiscal Shrike *Lanius collaris* from their foraging area. In this instance the entire Marico Flycatcher group acted as a unit to evict an interspecific competitor. Fiscal Shrikes are about 18 g heavier than Marico Flycatchers (Maclean 1985), and as they also feed on invertebrates found on the ground they probably overlap with the flycatchers for some of their prey items. Birds which forage in groups are also sometimes co-operative breeders (Gaston 1978). I have observed all members of a Marico Flycatcher group feeding and defending the young, and this may also be true of Pallid Flycatchers (Chapter 5).

2. Home range area and aggressive behaviour

In the two Pallid Flycatcher groups studied home range size varied with group size. The larger Pallid Flycatcher group consisting of five adults had twice the home range area of the smaller group consisting of two adults. There was no relationship between group size and home range size in the two Marico Flycatcher groups studied. In this species both groups, consisting of three and two adults, had a home range area of two to three hectares.

Neither species decreased their home range size in the wet season when resource levels increased in the two woodlands. A between-species comparison, however, showed that Marico Flycatchers had a smaller home range size than Pallid Flycatchers both in the wet season when resource biomass and abundance was significantly higher in *Acacia* woodland and during the dry season when there was no significant difference between the two woodlands. During the dry season Marico Flycatchers still maintained a significantly higher foraging rate than Pallid Flycatchers (Chapter 2), and this may have allowed them to occupy a smaller home range size during this period. Possible reasons for Marico Flycatchers having a higher foraging rate than Pallid Flycatchers during the dry season have been discussed in Chapter 2.

Territory size may also be influenced by competitor pressure from co-occurring species and habitat quality (Yeaton & Cody 1974; Franzblau & Collins 1980). In some species, however, whereas these factors may be proximate stimulii regulating territory size, food density remains the underlying ultimate factor (Franzblau & Collins 1980).

At Nylsvley, not only was avian density higher in Acacia woodland than Burkea woodland (Tarboton 1980), but Acacia woodland covered a smaller area than Burkea woodland. In the Pallid Flycatcher and Marico Flycatcher therefore, overall species density and the availability of suitable habitat probably acted together with food density to determine home range size.

Kaufmann (1983) defines territory as a "fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others who have priority elsewhere or at another time". He adds that this priority of access must be achieved through social interaction. By this definition neither species were strictly territorial as they seldom interacted with neighbouring groups. I do not know, however, to what extent territory boundaries had already been established and were now simply maintained by the owner's presence. Marico Flycatchers were vocal during foraging, and this may have signalled to other groups that the area was occupied. In addition, there may have been little value to intruders in using areas where they had no knowledge of recent foraging paths used by the owners as they would waste time and energy hunting in resource depressed sites (Davies & Houston 1981). Although Pallid Flycatchers gave a soft "ziz" call when disturbed, they did not give a frequent contact call between group members as did Marico Flycatchers.

Both flycatchers interacted with species which also fed on ground-living invertebrates (Maclean 1985). Marico Flycatchers experienced more interspecific interactions than Pallid Flycatchers, possibly because of the higher avian density found in Acacia woodland compared to Burkea woodland (Tarboton 1980). Overall, although there was no significant difference in the number of interspecific interactions initiated by the flycatchers, Marico Flycatchers were generally more aggressive than Pallid

Flycatchers. They experienced more intraspecific interactions than Pallid Flycatchers, some of their interspecific interactions involved physical fights, and when the two flycatcher species met at woodland boundaries, Marico Flycatchers aggressively excluded Pallid Flycatchers from the relatively richer Acacia woodland. It was probably easier and more economical for Marico Flycatchers to defend the small, relatively food-rich areas than for Pallid Flycatchers to defend large, food-poor areas (see Davies 1980).

In conclusion, the results of this study indicate that the Pallid Flycatchers' and Marico Flycatchers' activity patterns, home range sizes and aggressive interactions were affected by the resource and habitat conditions the flycatchers experienced in their respective woodlands.

CHAPTER 5

OBSERVATIONS ON THE BREEDING BEHAVIOUR OF THE PALLID FLYCATCHER AND MARICO FLYCATCHER.

SUMMARY

Between September 1980 and January 1981, observations were made at the Nylsvley Nature Reserve, central Transvaal, on the breeding behaviour of the Pallid Flycatcher and Marico Flycatcher. Both species used similar plant material to build small, open, cup-shaped nests. Marico Flycatchers built flimsier nests than did the Pallid Flycatchers, and always lined their nests with feathers. Both species placed their nests in the upper canopy and outer branches of small trees and shrubs. Pallid Flycatchers had a clutch of two to three eggs and Marico Flycatchers a clutch of three. Pallid Flycatchers had an incubation period of 17 days and a fledging period of 14 days; both parents fed the chicks and about 17% of the food brought were large visible prey items. Marico Flycatchers were co-operative breeders. Adults and juveniles from a previous brood fed chicks and all food items brought to the young were too small to be identified. The flycatchers also differed in the rate at which they brought food to their chicks; the Marico Flycatchers being able to bring a greater number of food items to their chicks than could Pallid Flycatchers.

INTRODUCTION

To date only a few workers have considered the breeding behaviour of the Pallid Flycatcher *Melaenornis pallidus* and Marico Flycatcher *M. mariquensis*. Brooke and Borrett (1972) suggested that Marico Flycatchers may be co-operative breeders; and Beesley (1972) observed two adult Pallid Flycatchers feeding a third sitting on a nest and interpreted this as a possible case of polygamy.

As an adjunct to a study of the flycatchers' foraging behaviour, carried out in the central Transvaal, I recorded information on birds found breeding. The information gathered includes details of the nests, nest building activities, incubation, and nestling care and provides some new insight into the flycatchers' breeding behaviour. Information from other sources (the Southern African Ornithological Society's Nest Record Cards, and Tarboton unpublished data) are included to give an overall view of the flycatchers' breeding behaviour in the Transvaal as a whole.

METHODS

Observations were made at the Nylsvley Nature Reserve (24°29'S; 28°42'E), between September 1980 and January 1981 during a wider study of flycatcher behaviour conducted between June 1980 and June 1982. Marico Flycatchers occurred in fineleaved *Acacia* woodland and Pallid Flycatchers in broadleaved *Burkea* woodland (Tarboton, 1980). I had study sites in each of these two woodlands (Chapter 2). Most observations were confined to four study groups: two for each species. I visited the groups three to four times a week and recorded any courting or nesting behaviour observed. Nests with eggs or chicks were watched for up to six hours at a time. On other days I walked through the study areas noting the position and condition of any new nests found, as well as recording any aspect of breeding behaviour seen (e.g. birds carrying nesting material). These data were included in the analyses.

Additional data for birds found breeding in the Nylsvley area between 1974 and 1984, were supplied by W.R. Tarboton (unpublished data). For further descriptions of nests I analysed information available in the Southern African Ornithological Society's Nest Record Cards (NRC), and used part of their summarised data to obtain comparative information on clutch sizes. Data on NRC cover the 1912-1969 period. For further data on breeding seasonality I considered data given for the Transvaal as a whole (Kemp, Kemp & Tarboton 1985). Throughout the chapter means are given ± 1 standard deviation.

RESULTS

1. Courtship behaviour

Pallid Flycatchers began courtship in September. During this month one member of the pair, presumably the male, was often seen perched near the top of a tree giving a high pitched warbling song. The female did not join in with the song at this stage but continued to forage and preen nearby. Copulation and the first signs of nest building were observed in mid-October, and as breeding progressed the female also sometimes sang the courtship song with the male who by then usually perched close to the nest to give his song.

I saw no obvious courtship behaviour in the Marico Flycatcher prior to finding their first nests, already with eggs in mid-October.

2. Nest site and nest construction

I found six Pallid Flycatcher nests during November and December 1980. All were situated along firebreaks, burnt in June 1980, which contained low trees and shrubs. Three nests were placed in *Strychnos pungens*, two in *Ochna pulchra* and one in *Terminalia sericea*. Five nests were positioned 2-3 m above ground level (2,4 ± 0,5 m) and the remaining one 5 m up in a tall Terminalia sericea. Four nests were placed at the top of small, slender bushes and two were in the outer branches of trees about half way from the canopy. All were exposed to the sun. The nest itself was a small cup averaging 6,9 ± 0,3 g dry weight (n = 3). The cup dimensions (n = 3) were: inner diameter = 5,4 ± 0,1 cm, wall thickness = 1,0 ± 0,1 cm, and cup depth = 3,4 ± 0,5 cm. The outer wall was made of twiglets about 1 mm thick, and the inner cup was lined with fine rootlets less than 1 mm thick. All nests were found in Burkea woodland.

Tarboton (unpublished data) gives dimensions for two nests : outside diameter = 9,8 ± 0,4 cm, inside diameter = 6,0 cm, total depth = 6.5 ± 0,7 cm, and cup depth = 4,0 ± 0,7 cm. Other Pallid Flycatcher nests found in the Nylsvley area (n = 13) (Tarboton unpublished data) were also in broadleaved woodland. The nests were placed in the upper canopy, fork, and outer branches of small trees and shrubs, and were found in Ochna pulchra, Strychnos pungens, S. cocculoides, and Combretum apiculatum. Two nests were made of weeds, and one of rootlets. All were lined with fine rootlets.

Only one Pallid Flycatcher nest is described for the Transvaal on the NRC. The nest was found in the Kruger National Park, in the outer branches of an Acacia tree, in Acacia thornveld. The nest was a frail, ragged cup of grass stems.

Nine Marico Flycatcher nests were found between October 1980 and January 1981. All were in Acacia woodland. Mean nest height was 3,4 ± 1,1 m. Seven nests were in Acacia tortilis, one in Acacia mellifera, and one in Boscia albitrunca. All were placed in the outer branches of the trees. The nest was a small open cup weighing 5,2 g dry weight (n = 1). The cup dimensions (n = 1) were: inside diameter 2,7 cm, wall thickness 0,5 cm and cup depth 2,0 cm. The outer wall was made of soft stems, twiglets and strips of bark ca 1 mm thick. The inner cup was lined with fine rootlets, similar to those found in Pallid Flycatchers' nests, and with feathers.

Other Marico Flycatcher nests found in the Nylsvley area (n = 11) (Tarboton unpublished data) were also in *Acacia* woodland. The nests were placed in the upper canopy and outer branches of trees and shrubs, and were found in *Euclea undulata*, *Dichrostachys cinerea*, *Acacia nilotica*, *A. karroo*, *A. mellifera*, *A. tortilis* and *A. erioloba*. Nine nests were either in leafless bushes or in trees just coming into leaf. The nests were small, flimsy cups constructed of twiglets, grass and weeds. All were lined with feathers. Tarboton (unpublished data) gives dimensions for three nests : outside diameter = 7,8 ± 0,3 cm, inside diameter = 5,0 cm, cup depth = 2,5 cm, and total nest depth (n = 1) = 5,0 cm.

All nests described on the NRC for the Transvaal (n = 15) were found in *Acacia* woodland. The nests, which had a similar construction to those described above, were placed in the upper or outer branches of *Acacia tortilis*, *A. robusta*, and *A. karroo*.

3. *Nest building behaviour*

I observed two pairs of Pallid Flycatchers building nests. In each, one bird carried the material and was closely followed by the second which gave the courtship song. Similar behaviour was observed by Tarboton (unpublished data). I assumed that the female carried the material and was followed by the male. Only one nest was completed. It took seven days from start to finish, and was built by only one bird (presumably the female) while the presumed male perched nearby and either gave the courtship song or waited quietly for the female to finish before following her on her next trip to collect material. On two occasions I saw pairs of Pallid Flycatchers chase a Grey Hornbill *Tockus nasutus* that came close to their nest.

I have no comparable data on nest building behaviour among Marico Flycatchers.

4. Clutch size and incubation

Of the six Pallid Flycatcher nests found, two contained a clutch of three and two a clutch of two. Data from this study, combined with data from other nests found in the Nylsvley area (Tarboton unpublished data), give a modal clutch size of three (range 2-3) (Table 18). No clutch sizes are given on the NRC for Pallid Flycatchers in the Transvaal.

Incubation data for Pallid Flycatchers were collected from a nest with two eggs. The eggs were laid on successive days and incubation started on the latter and took 14 days. During seven hours of observation (four hours on the third day of incubation and three on the sixth) I saw only one bird, presumably the female, incubating the eggs. The presumed male foraged close to the nest but did not bring food to the female, although he joined her when she left to forage.

All seven Marico Flycatcher nests checked had a clutch of three. These data, together with those collected from other nests in the Nylsvley area (Tarboton unpublished data), give a modal and precise clutch size of three (Table 18). Data from NRC for the Transvaal as a whole also give a modal clutch size of three (Table 18).

I did not document the incubation period in Marico Flycatchers, but gathered data on incubation behaviour from a group comprising three adults (total observation period = 4 hours; age of eggs unknown). Only one bird incubated the eggs, and on three occasions was fed large food items (20 - 25 mm in length) by one other member of the group. When food was brought to the bird on the nest it gave begging calls similar to those made by recently fledged young.

5. Parental care of young

I collected information on nestling care in Pallid Flycatchers from two chicks being fed and cared for by their parents. Both adults fed the chicks (Table 19), apparently bringing only one food item to the nest per

TABLE 18

CLUTCH SIZES IN THE PALLID FLYCATCHER AND MARICO FLYCATCHER. PRECISE CLUTCH SIZES REPRESENT DATA COLLECTED FROM NESTS WHICH WERE VISITED MORE THAN ONCE.

	1	2	3	4	5
Pallid					
Transvaal:					
NRC			no data		
Nylsvley:					
All records		5	9		
Precise clutch only		2	3		
Marico					
Transvaal:					
NRC		3	7	1	
Nylsvley:					
All records	4	2	15	1	
Precise clutch only			5		

TABLE 19

THE NUMBER OF FEEDS PER HOUR AND THE PERCENTAGE LARGE FOOD ITEMS SEEN FED TO TWO PALLID FLYCATCHER CHICKS BY THEIR PARENTS.

AGE OF CHICKS (days)	NO. FEEDS/HOUR	% FEED COMPRISING LARGE (= VISIBLE) ITEMS	OBS. PERIOD (hours)
4	7,0	21	2
5	8,5	18	2
11	6,0	25	2
14	5,5	12	6
Mean:	6,8 ± 1,3		

visit. Most items were too small to identify, but larger ones included worms, centipeds, grasshoppers, caterpillars, and beetles. Both parents either ate or carried faecal sacs away from the nest. Four and five day old chicks were brooded (average brooding period 4,4 ± 3,2 min., n = 17) immediately after 58% of the feeds. Older chicks were not brooded. The chicks fledged after 17 days. Some juveniles remain with their parents for a prolonged period after fledging. For example, three young, fledged at the beginning of 1981, still accompanied their parents at the end of June 1982, even though they had attained adult plumage in the interim.

Nestling care in Marico Flycatchers was observed for two nests belonging to the same pair. The first nest contained three chicks, probably just over one week old when first found. Both parents fed the chicks, and, during three hours of observations, made, on average, 10,3 ± 3,2 visits per hour to the nest. In this and the second nest observed, all food items were too small to identify. The chicks were brooded after being fed (48% of the visits). After fledging, the chicks accompanied the adults on their foraging bouts. The adults gave contact calls ("cheww") and the young a continuous begging call. Initially one adult continued to feed the chicks, but later (ca one month after fledging) the juveniles foraged mainly for themselves and were only fed occasionally by an adult. Thirty-seven days after the first brood had fledged, I found that the group were attending a second nest containing three well-feathered chicks which fledged a week later. The second nest was 200 m from the first and the second clutch must have been started approximately one month after the previous brood had fledged. Both adults and juveniles fed the chicks, and during seven hours of observation made on average 15 ± 5,3 visits per hour to the nest. The adults made 91% of the visits and the juveniles 9%. All birds removed faecal sacs from the nest and defended the chicks against Whitebrowed Sparrowweavers Plocepasser mahali that attempted to approach the nest. Over the midday period, one of the adults shaded the young.

6. Nest Predation

Out of six Pallid Flycatcher nests found, two had a complete clutch of two eggs which in each case resulted in two successfully fledged young. Eggs were taken from three other nests and the remaining nest was initially found empty. Robbed nests were intact, suggesting that snakes had removed the eggs. One pair of Pallid Flycatchers re-nested at least once in a season following a nest failure. Their first nest, built in late October, was robbed; but in early December a new, empty nest was found in their home range area and the pair had a juvenile with them.

For Marico Flycatchers, data on nest predation from two groups gave contrasting results. One group, consisting of three adults, made five nesting attempts between October and January. Although the group defended their nests by mobbing predators (e.g. snakes) with loud alarm calls and by flying at the disturbance, all five nests were robbed of their eggs. Four nests were pulled apart and egg shells found below two which suggests small mammals may have been responsible. Nest material from robbed nests was sometimes included in the new nests; and at one time the birds had built a nest and laid eggs eight days after their former nest had been destroyed. The second pair observed made two nesting attempts. Young fledged from both nests, although the first nest lost one chick from a brood of three and the three young from the second nest were not seen after fledging.

7. Breeding seasonality

For both species, egg laying at Nylsvley was recorded between September and January (pers. obs., Tarboton unpublished data). Considering the Transvaal as a whole, 75% of the breeding records for Pallid Flycatchers fell between October and December, and 75% of breeding records for Marico Flycatchers between September and December (Table 20). There were, however, a large number of outliers on either side of the main breeding months for Pallid Flycatchers.

DISCUSSION

1. Breeding habitat

At Nylsvley, all Marico Flycatcher nests found were in *Acacia* woodland and all Pallid Flycatcher nests in *Burkea* woodland. This suggests that the flycatchers not only foraged in different woodlands (Tarboton 1980; Chapter 2) but also bred in different woodlands. All Marico Flycatchers nests recorded on NRC (n = 56) were also found in *Acacia* woodland. There is only one NRC referring to Pallid Flycatchers found breeding in the Transvaal. This nest was found in the Kruger National Park in an area of *Acacia* woodland where Marico Flycatchers do not occur (Kemp 1974). In other areas of *Acacia* woodland where Marico Flycatchers do not occur, such as in northern Zululand (Cyrus & Robson 1980), Pallid Flycatchers have also been found breeding in *Acacia* woodland (NRC n = 8).

2. Nest construction

Both flycatchers used similar plant materials to build a small, open, cup-shaped nest. Marico Flycatchers, however, built a flimsier nest than did Pallid Flycatchers, and always lined their nests with feathers. Earlé (1983) also found that Whitebrowed Sparrowweavers used a large number of feathers to line their nests, and suggests that feathers may have insulated the nests against the cold nights experienced in some areas. The use of feathers by Marico Flycatchers is presumably a species-specific characteristic since it was recorded in several different geographic areas. In some areas this habit may have the advantage of insulating the otherwise flimsy nests; such as at Nylsvley where *Acacia* woodland is situated on low-lying alluvial

TABLE 20

BREEDING SEASONALITY FOR PALLID FLYCATCHERS AND MARICO FLYCATCHERS IN THE TRANSVAAL AS A WHOLE. DATA REPRESENT INFORMATION FOR THE NYLSVLEY AREA AND OTHER RECORDS GIVEN BY KEMP, KEMP & TARBOTON (1985). DATA REPRESENT THOSE MONTHS IN WHICH NESTS WERE FOUND WITH EGGS. RECORDS HAVE BEEN BACK-DATED TO THE MONTH IN WHICH THE FIRST EGG WAS LAID.

	J	A	S	O	N	D	J	F	M	A	M	J	N
Pallid		5%	5%	50%	20%	5%	10%	5%					20
Marico		2%	11%	30%	26%	20%	9%	2%					46

flats and experiences low night-time temperatures. In other areas, lining the nest with feathers may serve no function or may even be a disadvantage (e.g. overheating the eggs or chicks). Nests recorded for Pallid Flycatchers breeding in Acacia woodland were made of grass and were not lined with feathers. Both flycatchers placed their nests in similar positions in the vegetation.

3. Breeding seasons

In the Transvaal as a whole, Marico Flycatchers had a longer breeding season than Pallid Flycatchers. This trend is also true for Zimbabwe, another area where the two species overlap. In Zimbabwe, 90% of the breeding records for Pallid Flycatchers fall between September and November, and 90% of the breeding records for Marico Flycatchers between August and December (Irwin 1981).

At Nylsvley, the difference in the onset and duration of breeding between the two species may have been linked to a difference in the timing of increased resource availability in the two woodlands. If resources peak earlier in the Acacia woodland compared to the Burkea woodland, for example, Marico Flycatchers could presumably begin breeding earlier than Pallid Flycatchers. The duration of the invertebrate peak would likewise determine the duration of the breeding season. More data are needed, however, on the relationship between resource availability and the flycatchers' breeding behaviour.

4 Co-operative breeding

I only observed co-operative breeding in Marico Flycatchers. Since I was only able to observe breeding in pairs of Pallid Flycatchers, however, and since this species also occurred in groups of 2-5 individuals, I cannot rule out the possibility that Pallid Flycatchers may also have employed co-operative breeding. Where Beesley (1972) saw two adult Pallid Flycatchers feeding a third sitting on a nest and interpreted this as polygamy, it could well have been a case of co-operative breeding. I saw adults feeding an incubating bird in Marico Flycatchers, but did not see the male bring food to the female in the pair of Pallid Flycatchers I observed. My observations on co-operative breeding in Marico Flycatchers confirm the suggestions made by Brooke & Borrett (1972).

I observed both pairs and groups of Marico Flycatchers breeding. Groups were composed of adults and their most recently fledged juveniles, which suggests that group size in Marico Flycatchers was related to the number of young they could successfully rear. All members of the group assisted with breeding. Since both flycatchers had similar clutch and group sizes, Pallid Flycatcher groups may also have consisted of adults and their young.

The advantages of co-operative breeding both to the helpers and the breeding pair are summarised in Brown (1978). In return for remaining with the parents, juveniles may help to defend the home range area, and feed and care for new nestlings. In this study, in one group of Marico Flycatchers juveniles from a previous brood helped feed new chicks. At this nest chicks were fed at a relatively high rate of 15 feeds per hour. The juveniles were responsible for 9% of the feeds. They also removed faecal sacs from the nest, and defended the chicks against possible harrassment by Whitebrowed Sparrowweavers. A second group of Marico Flycatchers, consisting of three adults, did not rear young but all three attempted to defend the nests against possible predators.

5. <u>Rate at which food was brought to chicks and prey size</u>

Finally, the flycatchers observed differed in the rate at which they brought food to the chicks and in the number of large prey items they fed to their young. The pair of Marico Flycatchers observed fed their chicks 25% faster than did the pair of Pallid Flycatchers observed. When the same pair of Marico Flycatchers fed their second brood and were assisted by three juvenile helpers they fed their chicks 46% faster than they did when unaided and 48% faster than the pair of Pallid Flycatchers I observed. The faster feeding rate observed in the Marico Flycatchers compared to the Pallid Flycatchers could have been related to the significantly higher resource abundance found in *Acacia* woodland during the wet season (Chapter 2) or in the case of where the Marico Flycatchers were aided by helpers, in the greater number of individuals bringing food to the chicks. More data are needed to test the generality of this trend.

All food items brought to Marico Flycatcher chicks were too small to be identified, but approximately 17% of those brought to Pallid Flycatcher chicks were large enough to be recognised. Pallid Flycatchers not only fed more large food items to their chicks than did Marico Flycatchers, but also tended to take a greater proportion of large items in their own diet compared to Marico Flycatchers (Chapter 2).

CHAPTER 6

CONCLUSIONS

The results of this study suggest that habitat separation in Pallid Flycatchers and Marico Flycatchers could have been maintained both through interference competition and exploitation competition.

(i) Evidence for interference competition:

I found Marico Flycatchers to be relatively more aggressive than Pallid Flycatchers; and at Nylsvley, where the two woodlands adjoined and the species came into contact with one another, Marico Flycatchers always aggressively excluded Pallid Flycatchers from Acacia woodland. Since the flycatchers overlapped in their use of prey types and sizes; and both were mainly perch-to-ground foragers, interference competition may have been the mechanism by which Marico Flycatchers prevented spatial overlap with Pallid Flycatchers. It would also have been more economically feasible for Marico Flycatchers to carry out this behaviour as opposed to Pallid Flycatchers because, for at least half the year, Marico Flycatchers had access to richer resources.

Both Marico Flycatchers and Pallid Flycatchers could co-exist with other members of the genus Melaenornis if the species concerned differed in its body size or foraging behaviour. In the Kalahari Gemsbok National Park, for example, although Marico Flycatchers came into contact with Chat Flycatchers (Melaenornis infuscatus) they did not show the same aggressive behaviour towards this species as they did towards Pallid Flycatchers. Chat Flycatchers are ca 50% heavier than Marico Flycatchers (Maclean 1985) and may consequently overlap less with Marico Flycatchers in their use of prey types and sizes. In the Kalahari Gemsbok National Park, Chat Flycatchers and Marico Flycatchers were also found in different microhabitat types (see Appendix 1).

At Nylsvley Black Flycatchers (Melaenornis pammelaina) and Pallid Flycatchers occurred in Burkea woodland. In a preliminary study of the foraging behaviour of Black

Flycatchers carried out in March, April and June 1981, I found that, unlike Pallid Flycatchers which during the same months spent 87% of their time on perch-to-ground foraging and 2% of their time hawking aerial prey (the rest of the time being spent on snatching invertebrates from leaves, branches and trunks) (total observation period for Pallid Flycatchers = 18 hrs), Black Flycatchers spent 72% of their time foraging for ground-living invertebrates and 12% of their time on aerial prey (again the rest of the time being spent on snatching prey from vertical vegetation) (total observation period for Black Flycatchers = 16 hrs). Overall Black Flycatchers are on average 33% heavier than Pallid Flycatchers (Maclean 1985). The greatest difference between the two species, however, lies in their culmen width with Black Flycatchers having a culmen _ca_ 75% times wider than that of Pallid Flycatchers (Maclean 1985) which suggests that Black Flycatchers may be more adapted to taking aerial prey than are Pallid Flycatchers. This difference in behaviour may have allowed the two species to co-exist in the same woodland.

(ii) Evidence for exploitation competition:

In exploitation competition the species which depletes the resources the fastest makes it less profitable for other species to utilize the same set of resources (Pianka 1974; Branch 1985). In this study I found that, throughout the year, Marico Flycatchers made significantly more foraging attempts/min. than did Pallid Flycatchers and for seven of the ten months studied made significantly fewer moves per foraging attempt. Marico Flycatchers, therefore, through their more efficient use of resources found in _Acacia_ woodland may have made it uneconomical for Pallid Flycatchers to move into _Acacia_ woodlands occupied by Marico Flycatchers and to attempt to utilize the same set of resources. Pallid Flycatchers, however, by their slow, energy-conserving foraging mode were in a sense equally efficient at utilizing low levels of resource availability.

Pallid Flycatchers also appear to have greater plasticity than do Marico Flycatchers, in that they occur in a variety of broadleaved woodland types (e.g. Brachystegia, Burkea, Combretum, Diphlorhynchus) over a wide range of geographical areas, as well as being able to occupy Acacia woodlands in the absence of Marico Flycatchers (Hall & Moreau 1970; Cyrus & Robson 1980). Marico Flycatchers on the other hand are restricted to a relatively narrow band of Acacia woodland and this may be because their habit of changing perch frequently may not allow them to economically utilize lower levels of resources found in other woodland types. Even in the Kalahari Gemsbok National Park Marico Flycatchers selected richer Acacia sites along rivers (Appendix 1). The Grey Flycatcher (Melaenornis microrhynchus) is also confined to Acacia woodland (Hall & Moreau 1970) and it would be interesting to study this species' foraging behaviour to determine whether it also has a fast foraging rate.

Future Studies

The overall results of this study suggest that habitat and resource conditions play an important role in determining the flycatchers' foraging behaviour (Section I of the thesis). This effect does not appear to be confined to the flycatchers' hunting techniques, but affects other aspects of their life style (Section II of the thesis). Other studies have found that habitat and resource conditions can affect the foraging behaviour, aggressive behaviour, and home range size of closely related or morphologically similar species (see Sherry 1979 for examples) and even the behaviour of species which annually migrate between different habitat types (Walsberg 1977). Before one can assess the relative importance of competition in determining species' behaviours, therefore, one needs to evaluate to what extent species' characteristics are habitat induced or species specific. An important test of this would be to study Pallid

Flycatchers in areas of Acacia woodland where Marico Flycatchers do not occur. Such a study would allow one to evaluate the behavioural plasticity of the species as well as determine which characteristics are habitat-induced and which are species-specific.

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APPENDIX 1

HABITAT SELECTION BY MARICO FLYCATCHERS AND CHAT FLYCATCHERS IN THE KALAHARI GEMSBOK NATIONAL PARK

SUMMARY

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 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.

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 utilize 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* flycatchers provide a clear example of habitat separation in morphologically similar species (Hall & Moreau 1970). Of the southern African species, the Pallid Flycatcher *M. pallidus* generally occurs in moist broadleaved woodlands (*e.g.* *Brachystegia* and *Burkea* woodlands), the Marico Flycatcher *M. mariquensis* in *Acacia* thornveld and the Chat Flycatcher *M. infuscatus* in drier scrub. The fourth species, the Black Flycatcher *M. pammelaina* has a darker plumage than the other three and usually occurs in savanna woodlands, forest edges and exotic plantations (Maclean 1985). Black Flycatchers also differ in their behaviour from the other three species discussed above in that they take prey from the ground, from vegetation and out of the air, whereas the others all mainly take prey from the ground (Hall & Moreau 1970).

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 chapter I provide further information on habitat selection by the Marico Flycatcher and Chat Flycatcher in the Kalahari Gemsbok National Park.

METHODS

Data were collected from transects conducted between 11-13 September 1985. Observations were made from a car while driving slowly (ca 40 km/hr) along the Park's roads. I had five transects: four followed the general courses of the Nossob and Auob rivers and one crossed over the dunes (Fig. 26). 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 I noticed that Marico Flycatchers often foraged near tall trees (ca 6 m high), whereas Chat Flycatchers did not appear to be associated with this type of vegetation. In the later transects I 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 21.

The vegetation of the Kalahari Gemsbok National Park has been described by Leistner (1967). I 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).

(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

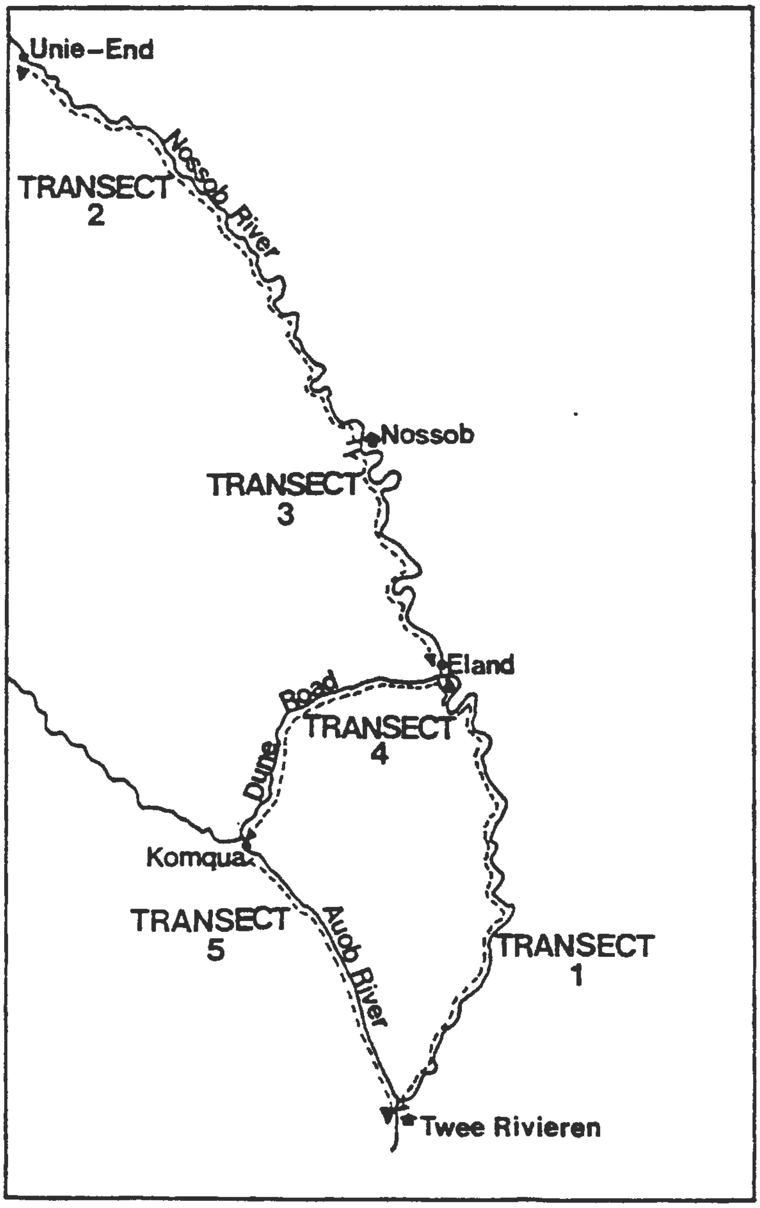

FIGURE 26

The position of the five transects in relation to the Nossob and Auob River.

TABLE 21

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

herbs and grass, and was vegetated in some places either by scattered *Rhigozum trichotomum* shrubs or a combination of shrubs and small trees (*e.g.* *Acacia haematoxylon* and *A. erioloba*).

(iii) The edges of open treeless pans or plains (P) with scattered *Rhigozum trichotomum* shrubs and the grass *Stipagrostis obtusa*.

(iv) Dunes with tree savanna (TS), where the vegetation included *Acacia haematoxylon*, *A. erioloba*, *A. mellifera*, *Grewia retinervis* and *Boscia albitrunca*.

(v) Dunes vegetated with low shrubs (DLS), mainly *Hermannia* spp. and *Rhigozum trichotomum*, and grasses, mainly *Stipagrostis amabilis*, *S. uniplumis* and *Asthenatherum glaucum*.

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

RESULTS

The transects covered a total of 408 km. Overall, I made 65 sightings of Chat Flycatchers and 80 sightings of Marico Flycatchers, involving 83 and 102 individuals respectively. Table 21 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 I was 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 27 gives the percentage number of 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. I tested the

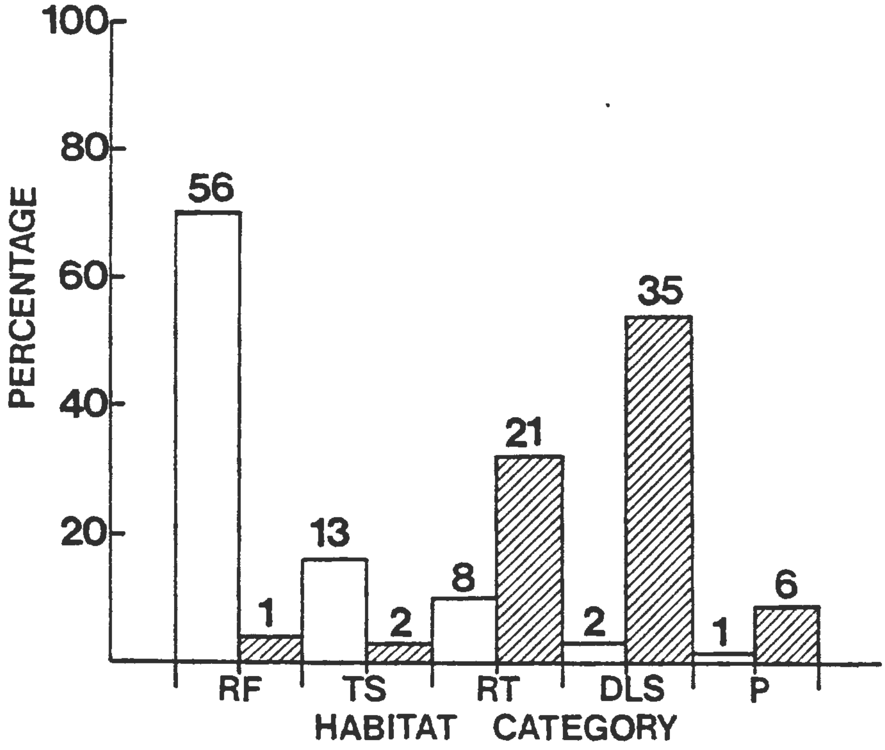

FIGURE 27

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. Sample sizes are given above histograms. Data represent information gathered from all five transects.

flycatchers' preferences against the estimated amount of each habitat covered by the transects, and found that Marico Flycatchers apparently avoided open plains and pans, and preferred the riverine fringe and river terraces. Chat Flycatchers preferred dunes with low shrubs. The relationship in both species was significant ($p < 0{,}001$) (Table 22).

I 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 23). This apparent paucity of Chat Flycatchers after 12h00, in contrast to the relatively high numbers of Marico Flycatchers seen then, is because I spent less time in the open dune habitats at that time of day and more time in the wooded riverine communities. I do not have sufficiently precise information though on the amount of time that I 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 I noted whether or not the birds were foraging in the vicinity of tall trees. Table 24 shows that I observed significantly more Marico Flycatchers ($n = 67$) foraging near tall trees than I did Chat Flycatchers ($n = 10$) ($\chi^2 = 54{,}9$; df = 1, $p < 0{,}001$). Within a species, perch height varied across habitat types (Fig. 28), but did not change with time of day (Table 25). Although 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 Whitney Test, $p > 0{,}05$). Although I have no data to quantify it, I 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

TABLE 22

THE OVERALL NUMBER OF MARICO FLYCATCHERS AND CHAT FLYCATCHERS OBSERVED IN EACH HABITAT TYPE, AND THE DISTANCE OF EACH HABITAT COVERED DURING THE SURVEY.

	RF/RT	P	TS	DLS	TOTAL
Amount of 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 23

NUMBER OF MARICO FLYCATCHERS AND CHAT FLYCATCHERS SEEN IN EACH HABITAT TYPE DURING THREE TIME PERIODS OF THE DAY.

		HABITAT TYPE					HOURS	BIRDS
SPECIES	TIME-PERIOD	RF/RT	P	TS	DLS	TOTAL	OBS.	HR
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

TABLE 24

THE NUMBER OF SIGHTINGS MADE OF MARICO FLYCATCHERS AND CHAT FLYCATCHERS IN RELATION TO THE PRESENCE AND ABSENCE OF TALL TREES.

	TALL TREES PRESENT	TALL TREES ABSENT	TOTAL
Marico	67	5	72
Chat	10	32	42
Total	77	37	114

TABLE 25

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.

	TIME OF DAY		
	06h00-09h00	09h00-12h00	12h00-15h30
	n = 22	n = 22	n = 43
Marico	1,4	1,5	1,4
	(1,0 - 2,5)	(1,2 - 2,0)	(1,2 - 1,7)
	n = 31	n = 26	n = 14
Chat	1,5	1,5	1,3
	(0,5 - 2,5)	(1,3 - 2,0)	(0,5 - 1,7)

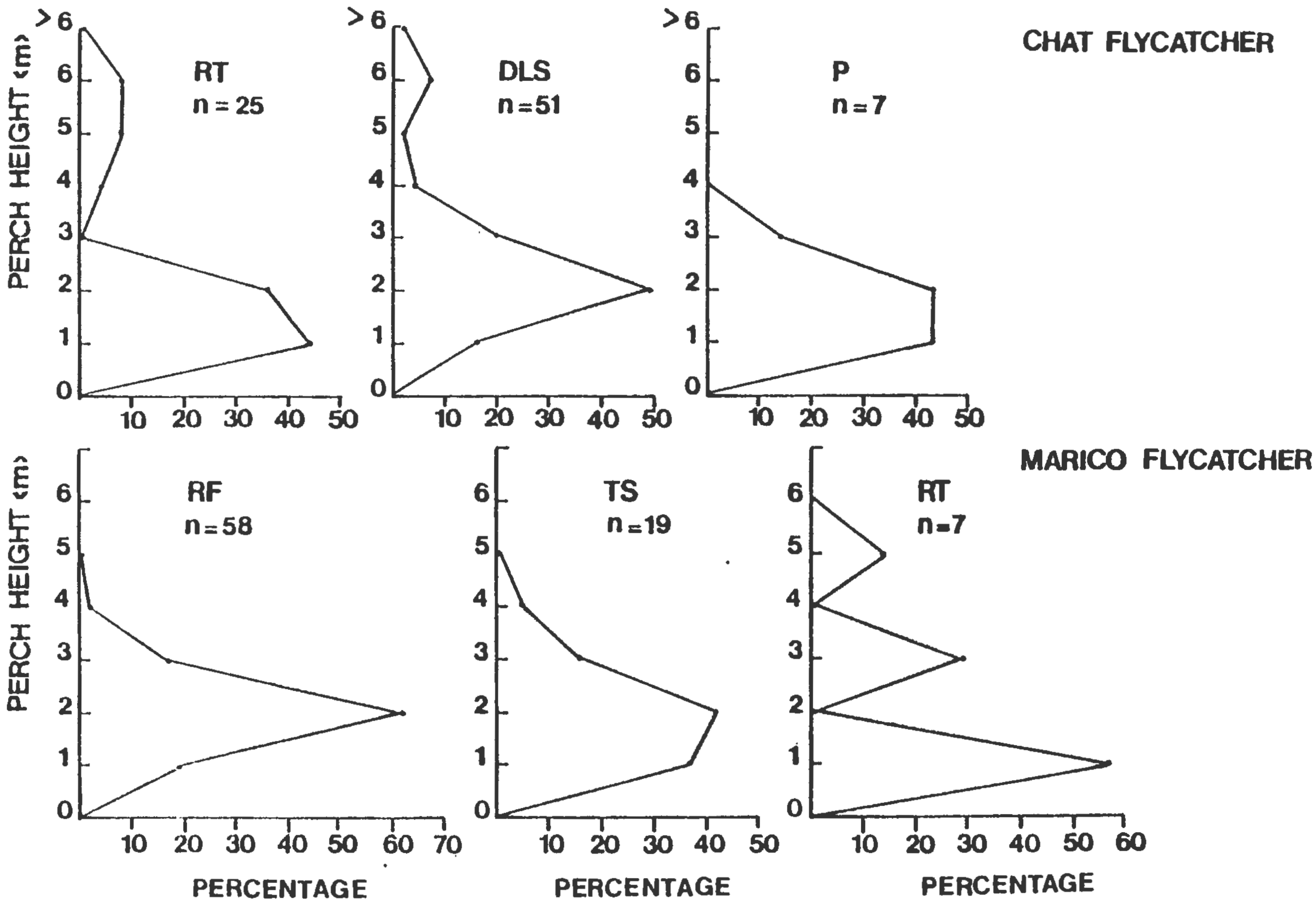

FIGURE 28

The percentage 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.

prevalence of the types of perches available, small shrubs being more common on the dunes than along the rivers, where trees predominated.

I 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 showed a certain amount of overlap, each species had 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 have been the outcome of competition for similar resources, or if the flycatchers utilized different resources, it could have reflected the local availability of their particular food type. It is also possible that in an environment as variable as the Kalahari, resources were 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 were not food limited, other factors (_e.g._ the availability of preferred nest sites) may have determined their habitat selection. Data are needed to evaluate this last possibility.

The areas selected by Marico Flycatchers had 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_ 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 (Chapter 4).

I only once saw Chat Flycatchers and Marico Flycatchers foraging closely together, and the lack of aggression on that occasion suggested that their habitat separation was 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 was not maintained through species interactions, then either resources were not limited, or the flycatchers used different types of food. Since the vegetation differed between the dunes and the river beds, these areas could have supported different invertebrate communities. The distribution of flycatchers in the Park therefore might not have been the result of competition between them for similar resources but, instead, may have reflected the local availability of particular prey types on which each species was relatively specialised. Differences in their morphology support this suggestion. Chat Flycatchers are on average ca 50% heavier than Marico Flycatchers (37 vs 24 g) and also have disproportionately larger bills (culmen length: 20 vs 13 mm) (Maclean 1985). Nevertheless, some studies have found that morphologically different species can utilize 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.

APPENDIX 2

Comparison of the successful search times made by Pallid Flycatchers and Marico Flycatchers.

MONTH	z	p
June '81	2,85	<0,01
July '81	4,83	<0,01
Aug '81	-3,56	<0,01
Sept '81	6,81	<0,01
Nov '81	1,47	>0,05
Dec '81	3,36	<0,01
Jan '82	3,12	<0,01
Feb '82	2,95	<0,01
Apr '82	4,41	<0,01
May '82	3,94	<0,01

APPENDIX 3

Comparison of giving-up times made by Pallid Flycatchers and Marico Flycatchers.

MONTH	z	p
June '81	4,55	<0,01
July '81	6,52	<0,01
Aug '81	0,87	>0,05
Sept '81	4,22	<0,01
Nov ' 81	3,21	<0,01
Dec '81	2,92	<0,01
Jan '82	2,59	<0,01
Feb '82	2,71	<0,01
Apr '82	5,61	<0,01
May '82	4,26	<0,01

APPENDIX 4

Comparison of the pursuit times made by Pallid Flycatchers and Marico Flycatchers.

MONTH	z	p
June '81	1,79	>0,05
July '81	-0,74	>0,05
Aug '81	0,14	>0,05
Sept '81	-1,13	>0,05
Nov '81	1,15	>0,05
Dec '81	0,56	>0,05
Jan '82	4,42	<0,01
Feb '82	0,45	>0,05
Apr '82	1,24	>0,05
May '82	0,59	>0,05

APPENDIX 5

Comparison of the proportion of perch changes that resulted in a foraging attempt in Pallid Flycatchers and Marico Flycatchers.

MONTH	z	p
June '81	0,97	>0,05
July '81	4,74	<0,01
Aug '81	2,71	<0,01
Sept '81	0,67	>0,05
Nov '81	2,87	<0,01
Dec '81	1,72	<0,05
Jan '82	1,30	>0,05
Feb '82	2,17	<0,05
Apr '82	2,71	<0,01
May '82	3,06	<0,01

APPENDIX 6

Comparison of the number of foraging attempts made per minute by Pallid Flycatchers and Marico Flycatchers.

MONTH	z	p
June '81	2,45	<0,05
July '81	5,45	<0,01
Aug '81	2,16	<0,05
Sept '81	3,55	<0,01
Nov '81	3,00	<0,01
Dec '81	3,04	<0,01
Jan '82	2,82	<0,01
Feb '82	3,38	<0,01
Apr '82	4,55	<0,01
May '82	3,64	<0,01

APPENDIX 7

Comparison of the total number of moves made per minute by Pallid Flycatchers and Marico Flycatchers.

MONTH	z	p
June '81	4,27	<0,01
July '81	4,93	<0,01
Aug '81	0,69	>0,05
Sept '81	3,89	<0,01
Nov '81	1,57	>0,05
Dec '81	1,52	>0,05
Jan '82	3,56	<0,01
Feb '82	3,28	<0,01
Apr '82	4,13	<0,01
May '82	3,66	<0,01