ECOLOGICAL FACTORS AFFECTING SOCIAL BEHAVIOUR OF WHITE-BROWED SPARROW-WEAVERS *Plocepasser mahali*.

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An adult male white-browed sparrow-weaver *Plocepasser mahali*.

ABSTRACT

White-browed sparrow-weavers live in territorial groups of two to 12 individuals, comprising a single breeding pair and nonreproductives. Apparent altruism occurs in three contexts: 1) nonreproductives assist in the feeding of chicks of the breeding pair, 2) individuals perform vigilance behaviour while other members of a group feed on the ground, and 3) communal nest-building. This thesis investigates how this sociality and apparent altruism could have arisen among the Plocepasserinae in general, and in white-browed sparrow-weavers in particular.

Although breeding adults are dominant over nonreproductives, no clear rank order was found within groups. Sparrow-weavers have a complex vocal communicatory system. Visual signals are apparently used infrequently. Although individual immatures are accepted by many groups, ritualised agonistic interactions between adjacent groups occur along territorial boundaries.

Each group constructs many nests in a tree: most nests are used for roosting and have two entrances. Consequently breeding nests often have many closeby roost nests. Nests are conspicuous and breeding nests are subjected to high predation levels. Broods in nests with many closely-situated roost nests have a higher fledging success compared with broods with few roost nests nearby. Roost nests apparently act as "dummies" which hinder the location of breeding nests by nocturnal predators. A similar phenomenon appears to affect heavy predation on roosting, full-grown birds: full-growned birds of large groups with many nests disappear at a lower rate than those belonging to smaller groups with fewer nests.

Wind annually destroys a quarter of all nests. To maintain a maximum number of intact nests, they are built on the leeward side of trees. Many bird species attempt to roost in sparrow-weaver nests. Sparrow-weavers show high interspecific aggression, probably as an adaptation to prevent other species from roosting in their nests. Helpers-at-the-nest did not significantly increase the fitness of the breeding pair.

The importance of nocturnal predation in shaping sparrow-weaver sociality is discussed in the light of sociobiological theory. It is concluded that sociobiology underestimates the importance of ecological constraints in giving rise to sociality. The relevance of the above findings to sociality in other plocepasserine species is discussed.

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other university.

Signed on this 28th day of February, 1986

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CHAPTER 1: INTRODUCTION

The Baconian idea of science being a process through which "objective knowledge" is steadily accumulated, has come under severe criticism during the last fifty years (e.g. Kuhn 1962, Popper 1980). These critics are of the opinion that a scientist cannot embark on studying a problem with a completely open and uninformed mind. Cultural, moral and historical factors shape the judgement of any person to such a degree that objective externalisation is not possible. This approach to scientific activity stems mostly from the phenomenological and hermeneutical philosophies that originated in continental Europe during the last century. Biology has traditionally been regarded as a discipline which is relatively far removed from philosophy, and only lately have authors like Grene (1983), Rose, Kamin & Lewontin (1984) and Levins & Lewontin (1985) explicitly emphasised the influence of culture and its associated norms on biological interpretation. During the last decade, two study fields in biology were characterised by a sharp dichotomy in philosophical approach: The first is competition theory, where the idea that interspecific competition results in the diversification of niche characteristics (e.g. Roughgarden 1983), was questioned by authors like Simberloff (1983). The second example is the theory of social behaviour, where the concept of genes or replicators being the unit of selection (e.g. Dawkins 1982), was criticised by scientists who emphasise the contingent aspect of evolutionary change, e.g. Rose, Kamin & Lewontin (1984). Animal behaviour that appears to be altruistic has been interpreted under various paradigms, each shaped by subjective and historical factors. As outlined below, this caused disagreement about the evolutionary forces that shape behavioral traits.

In *The Origin of Species* Charles Darwin discussed the social behaviour of eusocial insects and wondered how sociality could have evolved. He considered the fact that worker castes actually work for the benefit of other individuals as a possible threat to his theory of natural selection. Even after Lorenz and Tinbergen established the study of animal behaviour as a separate discipline, it was generally assumed that behavioural patterns have the function of enhancing the survival of individuals (Tinbergen 1969). However, as Darwin realised, the occurrence

of altruistic behaviour which apparently reduces the fitness of individuals presented a problem. How could a worker bee possibly benefit by raising offspring of other individuals or how can a bird benefit by feeding sibling nestlings?

Advances in the explanation of these phenomena were not forthcoming until V.C. Wynne-Edwards published his controversial book *Animal Dispersion In Relation to Social Behaviour* (1962), in which he proposed that altruistic behaviour is for the good of the species, and not for the good of the individual. He proposed that many commonly-encountered displays, e.g. territorial singing and lekking in birds, are altruistic in that they function as "epideictic" signals that allow individuals to measure their population size so that they can initiate emigration or curtail reproduction before densities are reached at which the available food resources are overexploited. The above book does not give a clear idea of Wynne-Edwards' view of life, but he was probably influenced by the commonly-held view that the interest of the individual is subservient to the interest of society, held by people such as R.A. Fisher (1930) (who had sympathy with the eugenic movement), and E. Marais (1937) who emphasised the 'super-organismic' aspect of society. The reaction to Wynne-Edwards' idea was violent. G.C. Williams wrote a particularly elegant criticism, *Adaptation and Natural Selection* (1966), in which he showed that many behavioural patterns do not have the function of population regulation but can fortuitously cause population regulation as an incidental effect of unrelated processes. Avian territorial singing is thus not an adaptation towards population regulation, but for holding a territory: it may fortuitously be a factor that results in population regulation since the total population size is determined by the total tenure of territories.

Like Williams, J.H. Crook (1964, 1965) disagreed with Wynne-Edwards' theory and suggested that avian social organisations are the by-product of adaptations that allow individual animals to survive. He insisted that adaptations for the efficient procurement of food and for the evasion of predators are the most important factors that determine social behaviour (e.g. Crook 1965, Kummer 1968). Because social behaviour was seen as being shaped by environmental constraints, this could be called the ecological approach to explain social behaviour. They questioned the im-

portance that social behaviour has, in itself, for the survival of populations.

Williams (1966) and Crook (1964, 1965) relied upon individual selection to explain social behaviour and altruism. In contrast, W.D. Hamilton (1964) proposed that altruism may be advantageous to the benefactor through kinship. If benefactor and beneficiary share a number of genes, part of the genetic constitution of the benefactor will benefit from altruism by there being a greater probability of a like copy being transmitted into the next generation. This notion was the centrepiece of the kin selection theory which explained altruism as the result of selection in terms of genes, and not in terms of discrete phenotypes. Sociobiology suggests that social organisation is the vehicle through which an individual maximises the representation of its own genes in the next generation. Individual fitness is *maximised* through the inclusive fitness (Wilson 1975:586) of closely-related individuals. Fitness is not measured as number of offspring but in terms of the number of copies of one's own genes transmitted into the next generation (Wilson 1975), regardless of which individual produces them. This could be called the sociobiological approach to explain social behaviour.

Both these approaches were reactions against Wynne-Edwards' idea of altruism, embodied in the concept of active population regulation. They represent alternate paradigms for interpreting social behaviour. The sociobiological approach works within the paradigm of optimisation of inclusive fitness. Although not explicitly stated by Crook, the ecological approach essentially works within a paradigm of sufficiency. This approach was modelled by H.A. Simon (1962), who stressed that the important point is whether an animal survives to reproduce at all. Williams and Crook dismissed altruism as a fortuitous effect, while Hamilton emphasised that apparent altruism can increase the fitness of the altruist.

The proponents of the two approaches went about their arguments in different ways: it may therefore appear that they did not necessarily address the same question. Crook was primarily interested in whether the formation of flocks or swarms of animals enable more efficient predator evasion or food procurement. Such aggregations are not necessarily stable social units. Sociobiology, on the other hand, arose as an attempt to explain behaviour that appears to reduce the fitness of an individual

within a stable social unit. The following points show, however, that the subject matter treated by Crook does not differ in any fundamental way from that of the sociobiologists.

1. The demarcation between temporary and more permanent congregations of animals is not clear. For example, a kittiwake colony is not just a loose, structureless flock of birds forced together by a scarcity of breeding sites. They have a dominance hierarchy in which dominant birds breed near the centre of the colony (Coulson 1968). Also, buffalo herds are divided into substructures which consist of genetically related individuals (Kruger 1980).

2. The same causative environmental factors have been invoked in both the ecological and the sociobiological approaches. The ecological approach states that the social organisation of animals is an adaptation to achieve one or more of the following: find sufficient food, find a mate and/or avoid predators (Crook 1965). Yet in the sociobiological approach, the environmental constraints model for the explanation of altruistic behaviour such as helping (Emlen 1982a, 1984) postulates mate procurement, predator evasion and territory procurement as the ultimate causes determining whether helping will occur or not.

3. Group formation and altruism are two discrete behavioural phenomena. Yet factors causing altruism within a group of animals have been suggested as the real reason behind the formation of these groups. Emlen (1982a, 1982b) postulated proximate mechanisms (e.g. shortages of territories or mating partners) as causative for the evolution of altruism and once these become clear, the reasons for grouping in the particular species are evident. Similarly, among eusocial insects kin selection (Hamilton 1964) and parental manipulation (Alexander 1974) are the two most widely-quoted sociobiological explanations for group formation.

The ecological approach emphasises the importance of constraints in shaping sociality, whereas the sociobiological approach emphasises maximisation or optimisation of inclusive fitness in causing sociality.

IMPORTANCE OF CONSTRAINTS VS. OPTIMISATION IN SHAPING SOCIALITY

The fundamental difference between the ecological and the sociobiological approaches lies in their assumptions about the mechanisms through which natural selection is viewed to shape sociality. It is not generally appreciated that this is the fundamental issue at stake when explaining the origin and adaptiveness of behaviour. The details about routes to sociality or the importance of parental manipulation vs. kin selection in shaping altruism are unclear unless the basic assumptions about the evolution of such behaviour are explicitly stated. This was done neither by Crook nor by the sociobiologists like Hamilton and Alexander; consequently their assumptions must be extracted from their interpretations.

The assumptions of Crook (1964, 1965) were clear when he wrote about the relationship between social organisation and food supply. Firstly, he saw natural selection as operating on bird populations exposed to adverse environmental conditions. Only the individuals with the highest fitness survive in a population under continuous and severe environmental stress:

> "The relative stability of populations is considered to be due to density dependent mortality, for which the principle cause is food shortage. Clutch size in most species is relatively constant and reflects the largest number of young for which the parents can find enough food." (Crook 1965:184)

He also implied that animals are not perfectly matched to their environment; in fact, the environment eliminates most animals. Many aspects of social behaviour are the effects of such stress factors, e.g. food shortage. Also, when criticising the epideictic function that Wynne-Edwards (1962) attributed to territoriality, and discussing the origin of monogamy in ploceid weavers, he remarked:

> "The monogamous insectivores in tropical forests appear to be close to food shortage at all times. The dispersion of solitary birds or pairs in spaced territories and, in some cases, the apparent tendency to avoid any type of congregation with other

> conspecific individuals may have some effect in controlling population density. Their main value to the individual, however, is probably the provision of a feeding range, in which solitary hunting can occur." (Crook 1964:106)

Finally, when discussing the gregarious behaviour of grassland weavers, Crook argued that species do not necessarily evolve adaptations to exploit superabundances of food. This means that social organisation should not be seen as a characteristic through which *optimum* use of environmental resources is ensured.

> "Overlapping territories, flocking over a wide area, mutual exploitation of the same resources by different species and the occurrence of 'neighbourhoods' in sections of an homogenous landscape leaving large areas, apparently equally suitable, unoccupied though utilised by flocks for foraging, all suggest that territory has no function in density regulation at least in relation to food supplies." (Crook 1964:107)

Crook's distinction between function and effect, resembling that proposed by Williams (1966), is clear. He emphasised that natural selection results merely in the *survival* of some animals and evolution occurs in populations that are under environmental stress.

Sociobiological theory, in contrast, does not emphasise environmental constraints in the course of evolution, although they are sometimes acknowledged. Sociobiological influences are seen as mechanisms through which positive selection for a particular gene or number of genes is enhanced. Natural selection operates on individuals with differences in fitness: the presence of adverse conditions is irrelevant to the argument. The importance of "soft" selection (Wallace 1975) is emphasised: particular phenotypes become common because of the mere fact that differential reproductive success occurs as a consequence of genetic variability. Because of the continual elimination of less successful animals, the mean population fitness tends to increase. Selection would thus operate on differences in fitness irrespective of environmental conditions. Selection is seen as a race among individuals for the greatest reproductive success. In terms of genes, it is a race among the genes of different individuals for the greatest representation in the next generation. More extreme

views see the body of an individual as the "survival machine" through which this struggle for greatest representation is performed:

> "Natural selection favours genes which control their survival machines in such a way that they make the best use of their environment. This includes making the best use of other survival machines, both of the same and of different species." (Dawkins 1978:71)

Life is a continuous arms race among genes, each striving for maximum manipulative power over other genes (Dawkins 1982). When applied to altruism, it means that animals that do not extend their fitness through sociobiological mechanisms will be at a disadvantage compared with individuals that have the trait. This would lead to the fixation of the genotype that maximises inclusive fitness. Similarly, the theories of parental manipulation and reciprocal altruism state that social behaviour is a device through which an animal maximises its personal fitness. Wilson (1975) believed that many examples of social behaviour can be explained on the grounds that genes struggle for the best representation in the next generation of organisms:

> "In the process of natural selection, then, any device that can insert a higher proportion of certain genes into subsequent generations will come to characterise the species" (Wilson 1975:3)

According to the sociobiological view, natural selection is an optimising process that constantly seeks out the fittest "survival machines". This process results in a continuous increase in the overall fitness of the population, and implies that the social organisation of animals allows them to make optimum use of environmental resources. This argument, in contrast to that of Crook, emphasises that natural selection results in the *optimisation* of population fitness.

Among the sociobiologically orientated, Emlen (1982a, 1984) came closest to recognising the importance of environmental constraints in the evolution of altruism. He suggested that many birds cannot breed because of a lack of breeding sites or mates, or because of high risks incurred in breeding. If the probability of successful reproduction is low enough,

unmated individuals are hypothesised to "make the best" of their effective sterility by aiding their parents in raising chicks. According to this view, altruism did not evolve as an adaptation for mere survival, but for the maximisation of the inclusive fitness of the nonreproductives. Emlen therefore shared the view of the other sociobiologists.

The ecological and sociobiological approaches could be reconciled if one were to argue that natural selection by definition operates on *fitness differences brought about by environmental pressure*. In this process many animals die, resulting in selection for and enhancement of some character. However, it is precisely the interpretation of natural selection that differs between the two approaches. Crook never discussed optimisation of characters, whereas the sociobiologists have never stressed that, because of adverse environmental factors, many animals neither survive nor reproduce at all.

One of the main issues concerning the adaptiveness of characters relates to the diversity of available genetic material. Are all genetic variations adaptive? Many geneticists of the fifties and later (e.g. Dempster 1955, Dobzhansky 1955) argued that the large number of alleles/locus are maintained by superior fitness of heterozygotes. Using Haldane's (1957) principle of "segregation load" (Crow & Kimura 1970:303), Kimura (1968) argued that no population would be able to withstand the decreased fitness brought about by such widespread heterosis. He calculated that for a population of half a million animals satisfying Haldane's assumptions, each parent would have to leave about $3,27 \times 10^6$ offspring for one offspring to survive and reproduce! This argument was countered by Maynard Smith (1968) and others who pointed out that Haldane's arguments were based on two assumptions. First, selection acts independently and in a multiplicative way on different loci; second, the relative fitnesses of genotypes can be used to estimate the reproductive capacity of populations composed of such genotypes. The first assumption appears not to be the general rule (Lewontin 1974:202), and Maynard Smith (1968) doubted the validity of both assumptions.

Regardless of the validity of the arguments on segregation load, it does appear that many alleles at the same locus have equivalent fitness values. Harris (1970, quoted in Lewontin 1974) stated that 43 of 59 variant alpha and beta haemoglobin chains are without known physiological effects, at

least in the heterozygous states in which they are found. The same appears to be true for a large number of the electrophoretic variants that are known today. Experimental data suggesting that some allozymes do have fitness effects (e.g. McDonald *et al*. 1977, van Delden *et al*. 1978) are difficult to interpret for two reasons: the influence of background genes could not unequivocably be disregarded (see Lewontin 1974:250), and the relevance of laboratory conditions (under which fitness differences were obtained) to natural conditions is obscure.

It has been suggested (e.g. Lewontin 1974, Futuyma 1979) that a large amount of nonadaptive variation exists. Kimura (1968, 1983) argued that most neutral molecular variation arises through mutation. Genetic drift causes neutral mutations of low frequency to disappear in many cases, but in some cases drift can even cause a mutant allele to penetrate throughout the whole population. This process through which genetic variation is maintained has no adaptive role; it has no evolutionary consequence except for causing a wide range of variation to be present at speciation events when natural selection operates on a subset of the gene pool (Kimura 1983:326-7).

These points of view hold fundamental implications for the interpretation of the adaptive value of traits: all the characters of an animal need not affect its fitness. This corresponds with the view of Williams (1966), who emphasised that many characters of animals (whether they affect fitness or not) are effects due to unrelated biological processes. Williams' most important thesis is that the adaptive significance of a character should not be attributed to any higher level of organisation than is demanded by the evidence: when considering individual characters, one should distinguish between 1) consequences or effects which arise incidentally and 2) means evolved for reaching specific goals or mechanisms for performing particular functions. Because this distinction between function and fortuitous effect has not always been made, Gould & Lewontin (1979) endorsed this point of view. Accordingly three classes of characters can be distinguished:

1. Adaptations are characters that evolved over a long period of time for a specific function. Examples are the eye for seeing, limbs for locomotion and nest-building behaviour for breeding.

2. Preadaptations yield particular advantageous results as fortuitous effects of unrelated biological processes. Gould & Vrba (1982) termed such characters "exaptations". The main aim of Williams' (1966) book was to show that mechanisms with a supposed group-selectionist function were nothing more than fortuitous effects of unrelated social processes. If overpopulation were indeed prevented through epideictic behaviours (Wynne Edwards 1962), these behaviours could be treated as preadaptations, but they did not evolve for the purpose of population regulation.

3. Effects are the fortuitous by-products of unrelated processes and do not affect the fitness of an individual. Curio (1980) reported that the anti-predator aggression of male great tits, *Parus major*, is more intensive and long-lasting than that of females. Assuming that this phenomenon is an adaptation for the optimisation of reproductive fitness, Curio attributed his observations to some, as yet undiscovered, determinant of sex-specific altruism. The observed sex-difference might, however, be the fortuitous effect of higher androgen levels in males than in females. Androgens are not specifically part of a mechanism which makes animals aggressive, but are involved in a mechanism for producing sperm cells as an end product; the high level of male aggression towards intruders is thus likely to be incidental and not adaptive. If this sex difference in behaviour were advantageous, the phenomenon could have been classed as a preadaptation; otherwise it would be a pure effect.

In many respects the arguments of Kimura (1983) and Williams (1966) are complimentary; one deals with molecular variation and the other with macroscopic variation. Both stress the point that many characteristics are nonadaptive: they arose either through mutation or as incidental consequences of unrelated processes. The observed frequencies of such characters within a population are governed by chance and sampling error. These points of view are in direct opposition to the sociobiological approach which emphasises that all the traits of an animal constitute an *optimum* compromise which *maximises* individual fitness. The designation of a character as an adaptation attaches a very different interpretation to the hypothesised evolutionary history of an animal when compared with the situation in which the particular character is assigned as either a preadaptation or an effect. Adaptations are phenotypic characters that

arise from severe environmental constraints and directly reflect the evolutionary history of a population of animals. Preadaptations and effects originate fortuitously and do not reflect the selective pressures that may have influenced the evolution of the animals under consideration.

OBJECTIVES

This study focuses on the adaptiveness of sociality in the white-browed sparrow-weaver *Plocepasser mahali*. One cannot test directly the general assumptions of either the ecological or the sociobiological approach when using data obtained during a study like the present one. However, an important part of the testing of an hypothesis is the falsification of its predictions, and one could test whether the advantages predicted by the sociobiological approach apply to a particular animal. In this way the present study can contribute towards a better understanding of the conflicting aspects of the ecological and sociobiological approaches towards explaining behaviour.

Sociobiology views selection as operating on two components of fitness: 1) the individual fitness contribution of an animal itself and 2) the fitness contribution due to kin or reciprocal altruists (Wilson 1975). The orthodox view of natural selection, as is typified by the ecological approach, takes only the first of the above two fitness components into account (e.g. Lack 1954).

The first objective of this study was to investigate how the social system of white-browed sparrow-weavers could have arisen. This problem raises the following two questions: a) Were the fitness contributions of kin, offspring or reciprocal altruists significant in the formation of sparrow-weaver sociality, or could fitness characteristics of individuals alone account for the observed social behaviour? b) Is sparrow-weaver social organisation an incidental effect of adaptations moulded by individual selection on birds under severe environmental stress, or is it a mechanism through which the fitness of each individual within the group is maximised (i.e. is there any evidence of optimisation)?

The second objective of this study is to use the combined source of published and new knowledge to give a hypothetical outline of how sparrow-weavers as a taxon evolved. If sociality, so characteristic of these birds, is an adaptation, the origin of the social system needs to be viewed against the background of speciation events within the genus.

VIEWS ON SPECIATION

Any study that focuses on the origin of an animal species presupposes particular views on the nature of species and the process by which species in general originate. One of the crucial questions in this study is how present sparrow-weaver characters relate to the evolutionary past of these birds. The following section explains the views adopted here when considering the speciation process.

Speciation represents the most significant event in the evolutionary process (Mayr 1963:424). Several models have been postulated as to how speciation occurs (e.g. Mayr 1963, White 1978, Bush 1981). Futuyma & Mayer (1980) and Paterson (1981) argued that the allopatric speciation model, urged strongly by Mayr (1963), is the only one that is at present unambiguously supported by experimental and field data. This stand was assumed during the present study. According to the allopatric speciation model, a new species arises when the geographic distribution of an ancestral species becomes divided into discrete components. If the environment in one of these areas changes, environmental pressures may result in selection of some genetically-based phenotypic variants in a remnant population, thus bringing about adaptation to this new environment. This may result in the formation of a new species (Mayr 1963). Wright (1931) emphasised the importance of small population size for the establishment of novel genes by means of sampling error or genetic drift; this so-called "Sewall Wright effect" is likely to be highly relevant to genomic changes during speciation.

Mayr emphasised the importance of environmental factors like food availability and predation in speciation. The allopatric model implies that newly-arisen species occupy habitats that differ markedly from those of

their parent species. Paterson (1982a) postulated that each species is characterised by a particular "preferred habitat", the habitat within which a population can survive. During speciation the preferred habitat of a derived species changes from that of its ancestors. The preferred habitat of a species is a constant characteristic during the evolutionary life of that species. Paterson (1978, 1980) postulated that the gene pool of a species is delimited by their common mate-recognition system. This system, in which the sexes are co-adapted, is characterised by strong stabilising selection which results in long-term stability of phenotypic traits. The abovementioned views of Wright, Mayr and Paterson, and the results of palaeontological studies like those of Eldredge (1971) and Williamson (1981) all conform to the concept of species arising relatively abruptly (Eldredge & Gould 1972) during periods when populations have been reduced to small isolates. Species are characterised by a large degree of stasis in both phenotype and genotype, while speciation occurs during short, punctuational events.

The above views lead one to believe that the characteristics of present-day sparrow-weavers are almost identical to those of their conspecific ancestors just after speciation. The corollary to this assumption is that the habitat of present-day sparrow-weavers closely approximates that in which the species evolved.

Common characteristics among different genera within the Plocepasserinae can be used as indicators of the biology of the ancestral plocepasserine species. Although convergent evolution could have resulted in similar characteristics in different genera, it is unlikely to have occurred in all or most of the taxa. If stasis after speciation is accepted and one then considers characters common to *Plocepasser* species, an idea of traits of the original Plocepasserine stock before the origin of *Plocepasser mahali* can be obtained. Hypotheses on the evolution of the Ploceidae have been advanced by Moreau (1960) and Crook (1963), and these ideas can be integrated with the existing knowledge of plocepasserine adaptations to describe how the Plocepasserinae may have come into existence.

STRUCTURE OF THIS THESIS

Chapter 2 gives a descriptive outline of the social system of sparrow-weavers. Group sizes and composition, home range, bonding within groups and inter-territory movements will be described. This information is vital for evaluating the validity of any sociobiological mechanisms that may operate among sparrow-weavers. The communicatory signals of a species are often adapted to its preferred habitat and therefore reflect the environment in which the species evolved. Signaling is also an important constituent of altruistic behaviour; therefore the communicatory patterns of sparrow-weavers are discussed in Chapter 3. The adaptiveness of the communicatory behaviour to the preferred habitat of the birds is investigated and anti-predator behaviour is also discussed. Chapter 4 investigates the nesting biology of sparrow-weavers. The thermal and other microclimatic characteristics of sparrow-weaver nests is examined with the object of determining if and how they could improve sparrow-weaver survival. Altruism related to nest building, and environmental factors that influence the building of sparrow-weaver nest structures are considered. Chapter 5 considers the influence of environmental factors on sparrow-weaver breeding activities. This chapter also describes mortality patterns among the different sparrow-weaver age groups. The mortality rate is relatively high and it could be an important force in shaping sparrow-weaver sociality. The preferred habitat of a species is an important source of information about its evolutionary history and Chapter 6 therefore describes the preferred habitat of sparrow-weavers. The distribution of sparrow-weaver colonies is related to floristic and physical features of the environment. This chapter also investigates whether the food taken by sparrow-weavers is restricted to any specific part of the environment. Chapter 7 discusses the adaptive characteristics of the sparrow-weaver social system. The relative importance of anti-predator vigilance behaviour, nest building behaviour, chick-feeding behaviour and improved feeding ability will be compared to the importance of sociobiological mechanisms in the shaping of sparrow-weaver sociality. Chapter 8 discusses the combined data about environmental factors that significantly affect sparrow-weavers, e.g. nesting requirements, predation and food availability. This information is then employed in an attempt to determine how and where the

Plocepasserinae in general, and white-browed sparrow-weavers in particular, originated.

From the above discussion it is clear that the emphasis of this study is on adaptation *sensu* Williams (1966). Indeed, any study of fundamental zoology would be meaningless if it did not (at least ultimately) attempt to identify adaptations of animals and place them in an evolutionary perspective.

CHAPTER 2: THE SOCIAL ORGANISATION OF WHITE-BROWED SPARROW-WEAVERS.

INTRODUCTION

In this chapter I aim to describe sparrow-weaver social organisation in detail, as this forms the basis for the interpretation of data presented in the chapters that follow.

This study deals with sociality among weaverbirds (Ploceidae). Three African weaverbird subfamilies are fairly closely related: the true weavers (Ploceinae), the sparrows (Passerinae) and the social weavers (Plocepasserinae) (Sushkin 1927). The plocepasserine subfamily comprises eight species belonging to four genera, all confined to the more arid parts of Africa. These genera are the sparrow-weavers *Plocepasser* (four species), the social weavers *Pseudonigrita* (two species), and the two monotypic genera, the sociable weaver *Philetairus* and the rufous-tailed weaver *Histurgops*. Although the subfamily have morphological characteristics of both the sparrows and the weavers, it differs from these by being highly social in nature. The basic plocepasserine social unit often comprises a breeding pair and their offspring (Maclean 1973, Collias & Collias 1978, 1980, Lewis 1982a). The birds often feed in groups and all co-operate in nest building activities. Helping in the form of subadult birds that assist breeding pairs to raise chicks appears to be another characteristic of this subfamily (Maclean 1973, Collias & Collias 1978, Lewis 1982a).

The white-browed sparrow-weaver *Plocepasser mahali* is widespread throughout the more arid parts of southern and eastern Africa. Sympatric congeners occur in Kenya and Ethiopia. Because these social birds are conspicuous and locally very common, they are good subjects for the study of social behaviour. Sparrow-weaver social behaviour is interesting from two points of view: first, the complex plocepasserine social organisation referred to in the previous paragraph is atypical of the Ploceidae (sparrows and weaverbirds). Second, sparrow-weavers engage

in extensive helping behaviour during breeding. Sociobiological arguments could be invoked to explain this unusual social behaviour.

White-browed sparrow-weaver social organisation has not been widely studied. Collias & Collias (1978) published an account of dominance hierarchies and breeding behaviour in Kenyan white-browed sparrow-weavers. There, birds occur in groups of two to six animals, the nucleus of the group being an adult breeding pair. Some of the additional birds help with nest building and care of chicks and fledglings. Each sparrow-weaver group builds approximately 20 nests in a large tree. Most of the nests have two entrances and are used for roosting. Lewis (1981, 1982a, 1982b) conducted a three-year study of white-browed sparrow-weavers in the Luangua Valley, Zambia, and found that non-reproductive group members were mostly siblings or half-siblings. Large sparrow-weaver groups had a higher level of reproductive success compared with smaller groups. Group size and measures of habitat quality were, however, interrelated to such a degree that the separate effect of group size could not be determined. Subadult sparrow-weavers from large groups were more likely to disperse and join small groups than were sparrow-weavers from small groups. This suggests that very large groups are disadvantageous. In some instances adult birds appeared to have been driven from their territory by one or more invaders.

With reference to the previously-published works of Collias & Collias (1978) and Lewis (1982a, 1982b), more intensive investigations into the reasons for sparrow-weaver sociality were launched. The following questions were examined and are described below:

1. What is the average group size of white-browed sparrow-weavers in the Bloemhof area, and how does this compare with the abovementioned published data?

2. How does the population density, group size and average territory size at Bloemhof compare with the published figures?

3. How tight are the social bonds within a sparrow-weaver group in terms of time spent together and rates of interactions?

4. How frequently do individuals move from one group to another?

The peculiarities of sparrow-weaver social organisation will be emphasised and compared with those of birds with similar social organisations, as well as with observations on sparrow-weavers made in other parts of Africa.

THE STUDY AREAS

Sparrow-weavers were observed in two areas: the area immediately south of the Bloemhof Dam (27°40'S, 25°39'E) in the north-western Orange Free State, South Africa, and at the Daan Viljoen Game Reserve (22°32'S, 16°58'E) near Windhoek, South West Africa (Figure 1). The Daan Viljoen data form a minor part of the total information, i.e. only about 4% of the total number of observation hours. A short description of each area follows.

The Bloemhof study area is semi-arid with an annual rainfall of 420mm concentrated into two rainfall peaks in November and in March. The topography is flat and the vegetation is Kalahari Thornveld (vegetation type 16a2; Acocks 1975). *Acacia erioloba* is the dominant tree in the area and *Eragrostis lehmanniana, Eragrostis tricophora, Brachiaria nigropedata* and *Tragus koelerioides* are dominant grasses.

The Daan Viljoen area is also relatively arid with an annual rainfall of 410mm falling mainly in December. The topography is hilly and covered with Highland savanna (Giess 1971). The dominant trees are *Acacia hereroensis, Combretum apiculatum* and *Acacia reficiens*. The dominant grasses are *Anthephora pubescens, Brachiaria nigropedata, Cymbopogon* spp. and *Heteropogon contortus*.

The two study areas have similarities in vegetation, with *Acacia erioloba, Anthephora pubescens, Brachiaria nigropedata* and *Heteropogon contortus* being common to both. Many plant genera are also shared by the two localities and are representative of the habitat in which white-browed sparrow-weavers occur in other parts of Africa. With the exception of the *Collophospermum mopane* woodland of Zimbabwe and Zambia,

FIGURE 1. Views of the study areas at Bloemhof (Upper photog aph) and Daan Viljoen (Lower photograph). *Acacia* spp. trees are common at both sites.

white-browed sparrow-weavers are restricted to arid and semi-arid *Acacia* woodland (Mackworth-Praed & Grant 1963).

The Bloemhof study area was divided into two sections:

1. an area of approximately 2 km² in which behavioural observations were made. Nine sparrow-weaver groups resided in this section. Each group was visited, when possible, at least three times a week. This will be termed the intensive study area, and is illustrated with an aerial photograph in Figure 33.

2. a region about 18 km² surrounding the intensive study area was used to study the breeding success and mortality of sparrow-weavers. This area included 27 sparrow-weaver groups.

An intensive ringing program was initiated in both sections. Gathering of additional information about the characteristics of sparrow-weaver nests and nest trees, as well as a removal experiment were performed on farms immediately south of the Bloemhof study area. Sparrow-weavers were collected in areas adjacent to, but at least 6 km away from the above areas.

METHODS

When studying animal social organisation, a knowledge of the age and sex of each observed animal is essential for the interpretation of social acts. The ability to identify each study animal individually is therefore vital.

Individual identification: During the period July 1982 to February 1984, 154 Bloemhof sparrow-weavers were captured and ringed with a numbered metal ring and two plastic colour-rings: this represented 81% of the total sparrow-weaver population in the study area. As from December 1982 this enabled the identification of all 46 individuals in the intensive study area.

Determination of sex and age: Earle (1983) reported that sparrow-weavers can be sexed by bill colour: males have black bills compared with the

pinkish-brown bills of females. In order to test this statement, 73 sparrow-weavers were shot and sexed by dissection. Only one of the birds did not conform to the above criterion. Therefore, all birds were sexed according to this rule. Sequences of alternate calling between an adult male and its mate also made it easy to sex the calling birds and enabled confirmation of sex-identification on the basis of bill colour. The absolute age of individuals that fledged during the study period was also known. Juveniles could be identified by light-coloured marks on their culmens as well as by their distinctive calls. Individuals were divided into three age classes: juveniles (younger than six months), immatures (older than five months but not mated) and adult (mated) birds.

Observations on behaviour: When observing behaviour, it is important to ensure that differential conspicuousness does not cause biases in data collection. Differences in plumage, calls or perch sites can contribute to such bias. For this reason behavioural data were collected using the focal animal sampling method (Altmann 1974), whereby the activity of colour-ringed sparrow-weavers at instants two minutes apart was recorded. Visual observations of predetermined individuals were made for a predetermined duration (usually 30 minutes). Sparrow-weaver activity centred around the trees in which roost nests and breeding nests had been built. To locate a specific individual for observation, the nest tree of its group was visited. If the required individual was not near the nest tree, the areas known to be frequented by the bird were searched. The above method did not always result in continuous 30-minute periods of observation, as the focal animal often flew out of sight and had to be located again before observations could continue. All behavioural events relating to nest building, grass collecting, and intraspecific as well as interspecific social interactions, were recorded. Home range sizes were calculated by using the locations where sparrow-weavers had been observed and the locations of agonistic interactions between neighbouring groups.

RESULTS

Group composition and sex ratio: Sparrow-weavers occur in groups ranging in size from two to nine birds, and they are all active within the same home range and around a single tree in which all breeding and roosting nests are built. Accurate sizes of 34 such sparrow-weaver groups were obtained at Bloemhof through visual observation and nocturnal capture of the birds. Sizes of 30 groups at Daan Viljoen Game Reserve were obtained through visual observation. Group sizes at Bloemhof averaged 3,4 birds compared with 5,0 at Daan Viljoen, a significant difference ($z=3,76$; $p<0.001$, Figure 2). Counts were made during August 1983 at Daan Viljoen and during September to November 1983 at Bloemhof. These numbers refer to group sizes before the start of the breeding season at Bloemhof and presumably also at Daan Viljoen. No signs of breeding were observed at Daan Viljoen, nor were any signs of recent breeding found. One group that disbanded before September 1983 at Bloemhof, is also included in the analysis.

The sex ratio of the overall population does not differ from an expected 1:1 ratio; 80 females and 84 males were handled at Bloemhof. These data were obtained from 52 fully grown sparrow-weavers that were shot and 112 such birds that were ringed.

Groups commonly consisted of a single breeding pair associated with offspring of one or both parents (Figure 3). More than two breeding adults in the same group were never observed. The number of attendant non-breeders varied between none and five at Bloemhof, with up to seven being recorded at Daan Viljoen.

Home range size: The home range sizes of nine sparrow-weaver groups at Bloemhof and four more at Daan Viljoen were determined through visual observation. Table 1 shows that home ranges at Daan Viljoen appear to be slightly larger than those at Bloemhof. Statistical treatment of such small samples is not feasible.

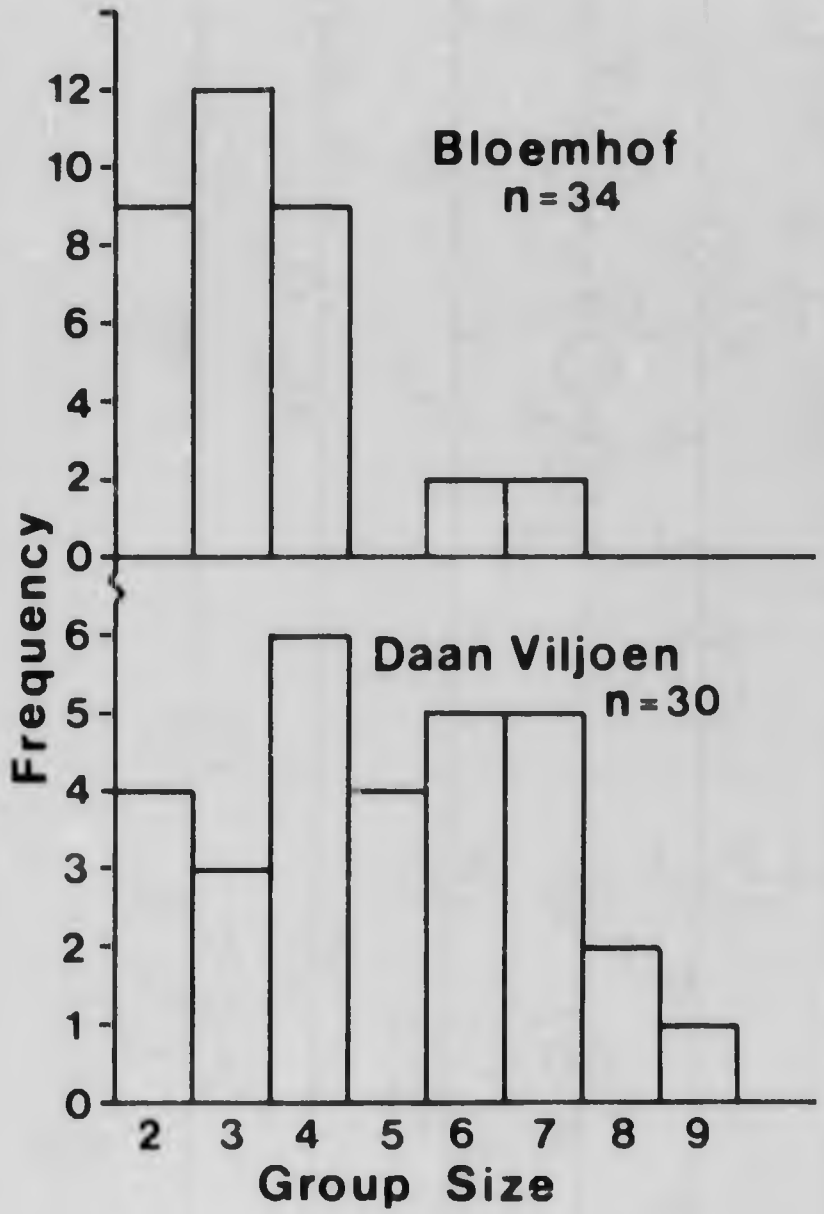


FIGURE 2. White-browed sparrow-weaver group sizes. Groups at Daan Viljoen tended to be somewhat, but not statistically significantly, larger than at Bloemhof.

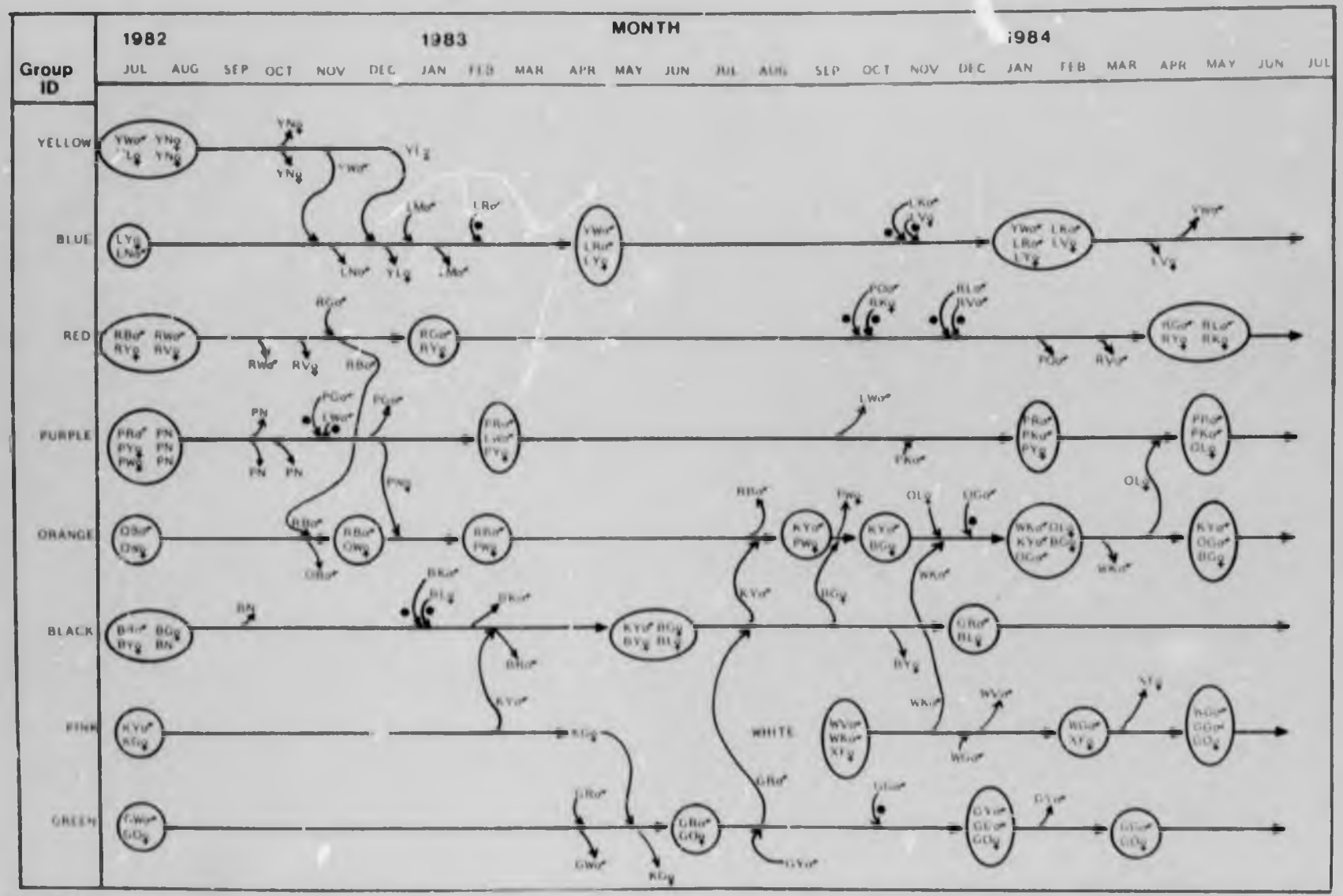


FIGURE 3. The membership of groups, based on observation of colour-ringed individuals during the study period. Individuals are identified by letter combinations and group memberships at particular times are indicated inside ellipses. Arrows show individual inter-group movements, recruitment or disappearances and dots represent recruitment through breeding.

TABLE 1

White-browed sparrow-weaver territory sizes as determined from visual observations of sparrow weaver groups.

Study area.	Sample size	Minimum size (Ha)	Maximum size (Ha)	Average size (Ha)
Daan Viljoen	4	6,97	20,29	12,08
Bloemhof	9	3,85	14,50	7,27

TABLE 2

The frequency of agonistic interactions among members belonging to different age groups within sparrow-weaver groups during 548 focal animal observation hours.

INTERACTION TYPE: Chasing/fleeing:	Chasing	Pecking
Adult/Adult	2 *	2
Adult/Immature	7	5
Immature/Immature	2	2
Immature/Adult	0	0
TOTAL	11	9

* This behaviour occurred shortly after pair formation.

Social bonding within groups

Hierarchical dominance ranks have been observed in many vertebrates that occur in groups or flocks (e.g. Collias 1943, Schenkel 1947, Sade 1967). The occurrence of dominance in the group-living sparrow-weavers was investigated. Social relationships can be measured in two ways:

1. The number of friendly or aggressive social interactions between two individuals gives some idea of the nature of the social relationship between the two animals.

2. The amount of time that two individuals spend together gives an indication of the strength of the social bond between them.

Social interactions: No form of affiliative or mutualistic behaviour (e.g. allopreening) was observed among the study animals. Two forms of agonistic behaviour were observed:

1. Chasing behaviour was observed on 11 occasions when one member of a group chased another over a short distance, usually about ten metres. This behaviour was not accompanied by any other overt acts of aggression or obvious ritualised behaviour.

2. One group member pecked at another on nine occasions. It is suspected that pecking was stimulated by the colour rings, as it was invariably orientated towards the rings of another bird which usually responded by pecking back at the legs and body of the aggressor.

Table 2 summarises the above observations, made during 548 observation hours. Intragroup agonistic behaviour is rare and usually occurs between an adult and an immature sparrow-weaver. Such interactions rarely occurred among adults. Those that did, occurred between pair members immediately after pair formation. It is therefore clear that a dominance hierarchy, based on agonistic encounters within a social group, is not present.

Amount of time that two individuals spend near each other: Sparrow-weavers often perch in a tree near fellow group-members. The

amount of time that each sparrow-weaver spent perched within 1m of one or more fellow group-members was recorded. When two birds spend a large proportion of time together, no functional significance should be attached to their proximity to each other. It is probably greatly affected by the activities of the birds before they perched near each other, and of the availability of suitable perching sites in a tree. However, if one assumes that the proximity of two birds denotes a lack of aggression between them, the amount of time that two birds spend near each other could be used as an absolute minimum measure of non-aggression.

Proximity measurements among sparrow-weavers were made only while they were perched, because the birds were then not obscured by vegetation and could be clearly seen.

As depicted in Table 3, breeding pair members consistently spent a larger proportion of time near each other than near immatures. The proportion of time that adults spent with each individual immature in a group decreased as group size increased. Immature sparrow-weavers spent about equal fractions of time near adults and near other immatures.

Judging from the low incidence of agonistic behaviour between group members (Table 2), as well as from the distribution of time spent near other group members (Table 3), there is no clear indication of a group hierarchy. However, the breeding pair is relatively strongly bonded and is dominant in agonistic interactions with immatures of the same group.

Inter-territorial relations

Sparrow-weaver breeding pairs were sedentary and kept to fixed territories. The members of a group used the whole territory and interacted with members of adjoining territories. Figure 4 depicts the locations of territories and nest trees during November 1983. Adults were never seen far from their territories. Some territory boundaries changed during the winter: groups with the smallest feeding areas enlarged their territories or even established new territories closer to preferred feeding sites (Chapter 6).

TABLE 3

Proportion of time that adult and immature sparrow-weavers spent near other individuals. Only perched birds are included in the analysis. Groups of different sizes are compared. Chi-squared tests were performed on the observed fractions of the raw data to determine whether birds of a specified age group spent more time close to its peers compared with the time spent close to the other age group, the calculated probabilities being indicated in the table. Sample size represents the number of two-minute scans for each class. Observed fractions indicate the percentage of time spent near birds of particular age classes. Fractions per individual indicate the mean percentage of time spent near each individual of that age group with which the focal animal associated.

ASSOCIATION:	GROUP SIZE : NO. OF IMMATURES :	3 1	4 2	5 3
ADULTS:	Sample size	2157	935	655
Adult/Adult:	Observed fraction:	12.3%	11.1%	11.3%
	Fraction per individual:	12.3%	11.1%	11.3%
Adult/immature:	Observed fraction:	8.2%	10.6%	14.2%
	Fraction per individual:	8.2%	5.3%	4.7%
	Statistical significance:	0.05	0.05	0.05
IMMATURES:	Sample Size	1110	679	609
Immature/adult:	Observed fraction:	15.5%	24.0%	15.1%
	Fraction per individual:	7.8%	12.0%	7.6%
Immature/immature:	Observed fraction:	N/A	11.5%	15.1%
	Fraction per individual:	N/A	11.5%	7.6%
	Statistical significance:	N/A	n.s.	n.s.

N/A = Not applicable since 1-immature groups have no immature/immature associations.

Interactions among adult sparrow-weavers of neighbouring territories were restricted to calling matches on their common boundaries (Figure 4), especially on boundary sections close to their nest trees. Adults also engaged in calling matches when they encountered unknown sparrow-weavers within their territories, and often chased such individuals. Colour-marked individuals that moved into the territories of foreign groups were always immatures. During 62 instances where foreign sparrow-weavers were chased, the aggressors were either adults or immature territory inhabitants. Although adults did more chasing than immatures, no sex or age group showed a statistically higher propensity for such behaviour (Table 4). On many occasions, however, juveniles or immatures belonging to foreign groups were tolerated. The foreign youngsters fed or perched with the territorial group. It appears that adult sparrow-weavers are sedentary, but that a certain amount of cross-territory movement by immatures takes place.

Interspecific aggression

White-browed sparrow-weavers chased birds belonging to other species on 162 occasions during the 548 observation hours. Territorial males did most of the chasing (Table 4). The species that were chased belonged to a wide variety of genera, both insect-eating and seed-eating (Table 5). A few common species, however, were not chased. These included the fork-tailed drongo *Dicrurus adsimilis*, the crimson-breasted shrike *Laniarius atro-coccineus* and Cape glossy starling *Lamprocolius nitens*.

Because more than half of the birds chased by sparrow-weavers could not be identified, it is quite probable that the frequencies given in Table 5 are not representative. Laughing doves were easily identifiable while fleeing from sparrow-weavers, whereas some of the finches were impossible to identify under such conditions. Table 5 does show that sparrow-weavers behave aggressively towards a wide range of birds, many of which do not utilise the same food categories as sparrow-weavers.

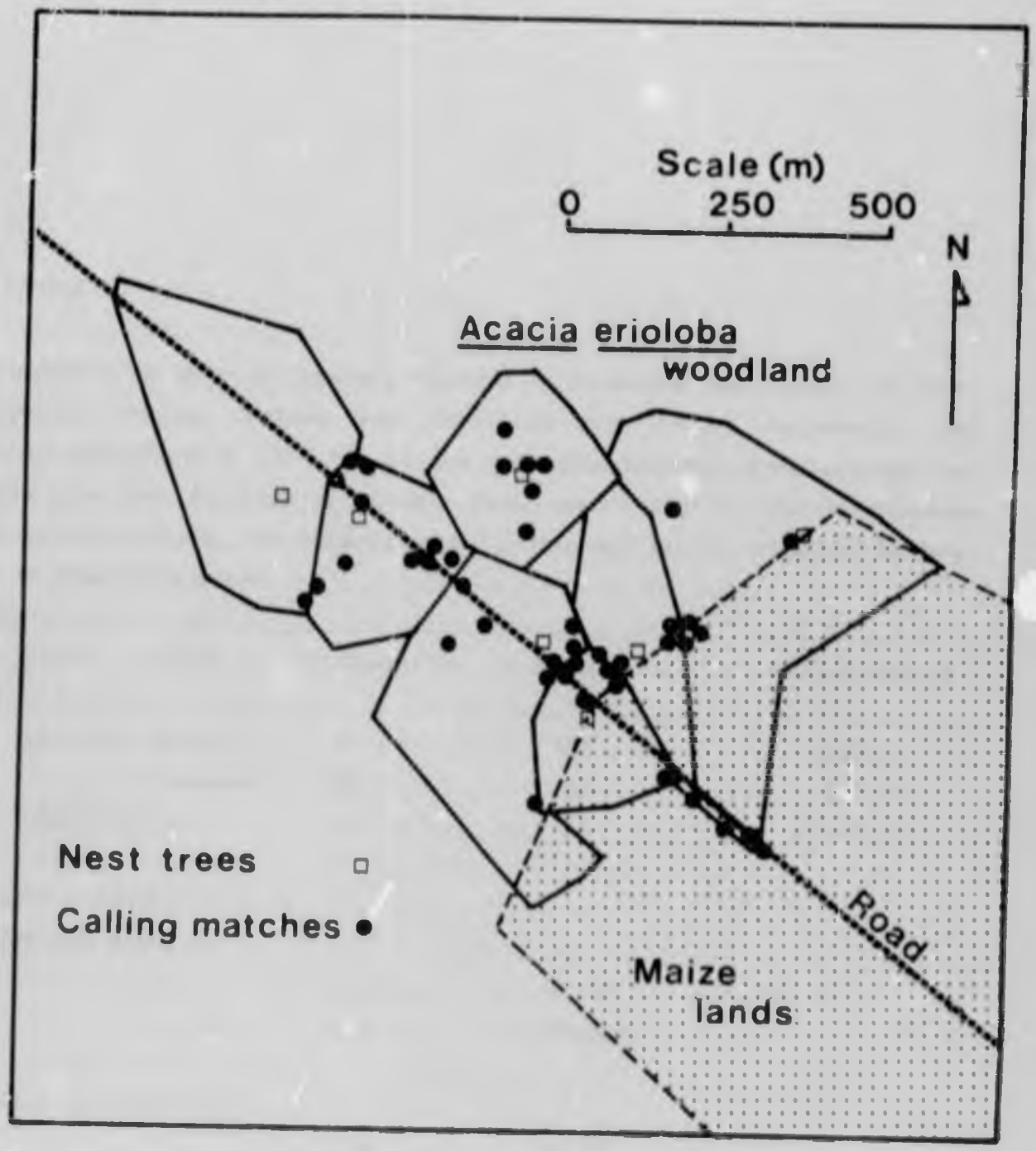


FIGURE 4. The localities of inter-group calling matches. The territories of seven groups at Bloemhof during 1982-84 are indicated by black lines. Calling matches normally occurred near territorial boundaries. The group holding the territory in the central, upper part of the diagram interacted with unknown, non-marked birds well inside their territory.

TABLE 4.

Incidence of sparrow-weavers chasing conspecifics and birds of other species. Males, females and immatures are treated separately, and chi-squared values (d.f.=1) on the raw data compare different age and sex groups. Because of a very small sample size for female immature sparrow-weavers, the observations for this age group could not be broken down into sexes.

Ch sing animals	Intraspecific	Interspecific	Observation h
ADUL ales	27	102	218,2
es	23	39	177,3
IMMAT S:	12	21	149,5
SEX DIFFERENCES AMONG ADULTS:			
χ^2	0,02	17,62	
p	n.s.	<0.001	
AGE DIFFERENCES			
χ^2	2,30	20,36	
p	n.s.	<0.001	

TABLE 5

Bird species that were chased by white-browed sparrow-weavers during 545 focal animal observation hours.

Species being chased		Number of observations
Diederik cuckoo	*Chrysococcyx caprius*	1
Laughing dove	*Streptopelia senegalensis*	11
Namaqua dove	*Oena capensis*	2
Black-collared barbet	*Lybius torquatus*	2
Kalahari scrub robin	*Erythropygia paena*	2
Grey tit	*Parus afer*	5
Penduline tit	*Anthoscopus minutus*	1
Tit-babbler	*Parisoma subcaeruleum*	1
Marico flycatcher	*Bradornis mariquensis*	8
Ground-scraper thrush	*Turdus litsipsirupa*	1
Cape sparrow	*Passer melanurus*	4
Grey-headed sparrow	*Passer diffusus*	2
Red-headed finch	*Amadina eryhrocephala*	8
Black-cheeked waxbill	*Estrilda eryrhronotos*	2
Masked weaver	*Ploceus velatus*	4
Sociable weaver	*Philetairus socius*	12
Yellow canary	*Crithagra flaviventris*	4
Unidentified species		98

Long-term intergroup movements

Twenty observations of intergroup migrations were made during the period July 1982 to May 1984. Except in one case when two birds migrated together, a single bird was always involved. Membership histories of the nine sparrow-weaver groups in the intensive study area are depicted in Figure 3. Figure 5 shows that only 25% of the 17 known immature and adult birds that migrated actually changed their status, with one adult individual even losing status. The population comprising the nine groups in the intensive study area never exceeded 29 birds at any particular time: roughly a third of the population was therefore involved in intergroup movements annually. This also means that on average each of the nine observed groups received about one immigrant per year. Because of the small sample size these figures are only rough indicators of the magnitude of intergroup drift. The reasons for the above movements were diverse and not always clear. For example:

- Three sparrow-weavers migrated after the dominant male in the group had died or migrated, leaving a female by herself or with one juvenile.

- Three birds migrated as immatures to obtain breeding status in the respective destination groups.

- Six immature sparrow-weavers migrated between groups without any clear cause or change of status.

- The social status of three birds was unknown at the time of their migration, so that circumstances surrounding their movements could not be determined.

- Five migrants were breeding males that had held territories and had been mated. Each one assumed the position of a breeding male in the destination group.

Migration by adult males: All cases of adult male migration (n=5) occurred during the normal breeding season (July to February). In three instances

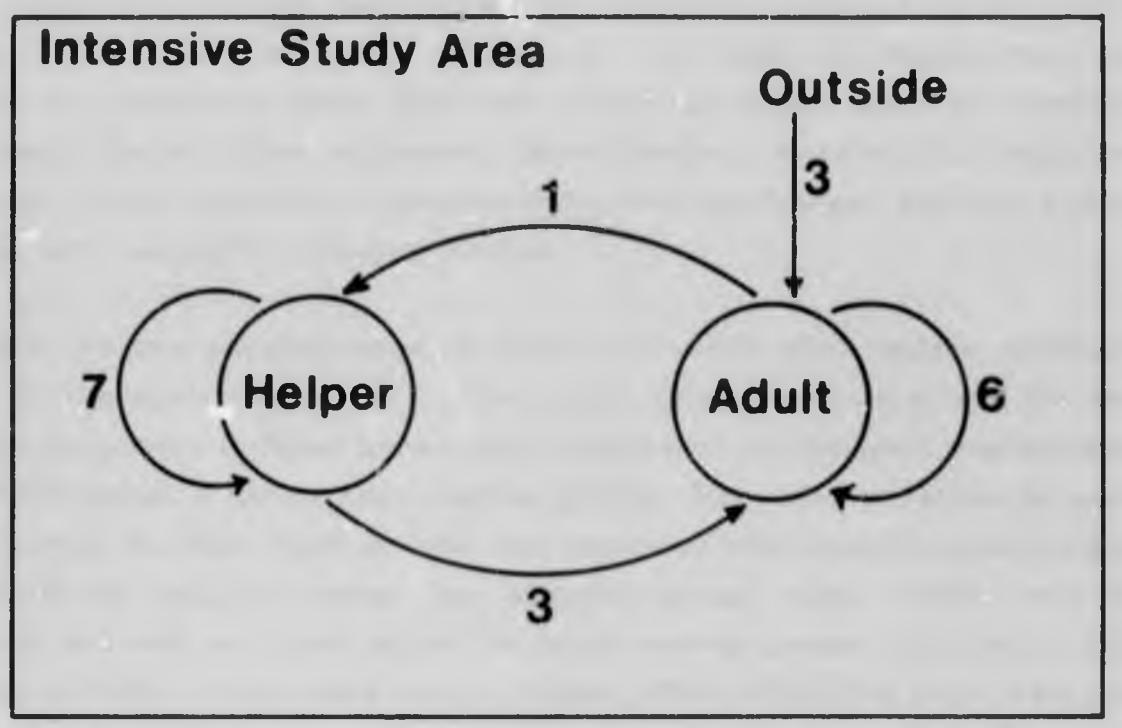


FIGURE 5. Social status of migrant sparrow-weavers before and after intergroup migration. Numbers indicate the sample sizes for the different types of change in social status, represented by the arrows. The social status of a migrant individual before and after migration are respectively indicated by the tail and the head of an arrow.

the breeding male that was replaced was never seen again and the replacement arrived when the adults of the destination group had nestlings. These migrants helped with the rearing of the chicks of the destination groups. The remaining migrations by adult males were precipitated by the emigration of the adult male of the destination group. Two males migrated to larger groups, one to a group of the same size and two to a group of smaller size. It would appear that the dominant male position within a group is sought after, because a chain reaction involving four male sparrow-weavers was observed during August 1983, when male RB in group ORANGE was replaced by KY which was replaced by GR which was in turn replaced by GY (Figure 3). All these movements occurred after the respective males had been in groups which made no breeding attempts for an extended period. Their breeding success after migration varied: three resulted in unsuccessful breeding attempts and two had at least one successful breeding attempt.

There are two possible ways in which one adult may replace another: either the adult in the destination group dies or emigrates and the resulting vacancy is filled by an adult immigrant; or the adult migrant may actively expel an adult from another group. Two field experiments were performed to shed light on the importance of the first of these modes. During the breeding season two adjacent groups were sought, one of which had not yet bred while the neighbouring group had chicks. The birds of both groups were colour-ringed, after which the adult male was removed from the group with chicks. For the first experiment, a breeding group with nestlings was chosen; in the second experiment the breeding group had recently-fledged young. Both experiments were performed outside the study area. In the first experiment, the male from the non-breeding group filled the vacancy in the neighbouring breeding group within 24h. He helped with the rearing of the chicks in the destination group. The deserted adult female of the source group in turn found a new mate after 10 days. In the second experiment, the adult male of the non-breeding group occupied the vacancy in the adjoining group within four hours. He did not desert his original mate, however, and occupied both territories, spending roughly equal amounts of time in each territory. After 21 days had elapsed, an unknown male expelled him from the breeding group and he returned to his original mate. These results show that adult males are rapidly replaced after death or emigration. The results do not, however, discount the alternate mode of

replacement, i.e. expulsion of the original territory holder by a migrant. Despite extensive searches, none of the replaced males was ever seen again. This fact would indicate that these birds had not been expelled but had emigrated or died.

DISCUSSION

Population characteristics: The population density of sparrow-weavers at Bloemhof and Windhoek is lower than reported for other areas in Africa (Table 6). This table also shows that the average group size remains fairly constant regardless of population density and geographic region. The highest densities were found by Collias & Collias (1978) in Kenya, who studied sparrow-weaver groups in the vicinity of a tourist camp. This site may have been responsible for unnaturally high population levels. However, observations made during the present study show that birds are not attracted to human buildings or activities, suggesting that Kenyan populations in general have densities an order of magnitude higher than their Southern African counterparts. The relatively low population density in the Bloemhof study area may indicate that the western Orange Free State is not optimal white-browed sparrow-weaver habitat. This impression is supported by the fact that the mean territory size at Bloemhof (7,2 ha; Table 1) was much larger than those reported by Collias & Collias (1978), Lewis (1981) and Vernon (1983), all of whom measured mean territory sizes of less than 4 ha. The relatively large mean territory size found at Daan Viljoen could be an artefact of the small sample size (Table 1). Bloemhof is situated near the south-eastern edge of the white-browed sparrow-weaver geographical distribution. This site is also situated in relatively dense, moist vegetation, compared with the rest of the geographic range of these birds. Lewis (1981) indicated that Zambian sparrow-weavers avoid tall, densely-matted vegetation. This study yielded similar results (Chapter 6), indicating that vegetation density may be critical in the distribution of sparrow-weavers. The relatively low sparrow-weaver density at Bloemhof (Table 6) may reflect the suboptimal character of the habitat.

TABLE 6

The population densities of white-browed sparrow-weavers in different parts of Africa.

Locality	Birds/sq.km	Groups/sq.km	Average group size	Reference
Bloemhof	29	8	3,4	This study
Windhoek	41	8	5,0	This study
Zimbabwe	839	129	4,5-6,3	Vernon (1983)
Zambia	108	26	4,2	Lewis (1982a)
Kenya	1702	276	4,9	Collias & Colias (1978)

Population sex ratio: It has been suggested that the complex social structures of many co-operatively breeding birds are mechanisms to accommodate an excess of males in the population (Rowley 1965, Maynard-Smith & Ridpath 1972, Tarboton 1979). Neither this nor any other field study of white-browed sparrow-weavers revealed any excess of either sex in the overall population. The trapping method followed during this study entailed removing sparrow-weavers from their roost nests at night. As nearly all the birds of a specific group are captured in this way, bias in estimating the population sex ratio is minimised.

Social bonding and intergroup movement: The relatively constant sparrow-weaver group size (Table 6) suggests that the forces shaping sparrow-weaver sociality do not show marked geographical variation. It is noteworthy that interactions occur rarely among members of the same social unit. If a continual conflict of interest for the procurement of food, nests or mates does not occur, there is no reason why a finely-graded social rank order with a concomitant high frequency of interactions among group members should occur.

Lewis (1982b) found that migrant sparrow-weavers tended to move from large groups to small ones. Since an individual in a small group has a larger probability of breeding than one in a large group, he concluded that the intergroup movement of Zambian sparrow-weavers could be interpreted in terms of breeding opportunity for the migrant: it was anticipating a long-term chance to breed. This study did not suggest such anticipatory movements. Five birds were forced to migrate after one of the breeding adults of the group had disappeared. Of the 20 intergroup movements during this study, 12 represented direct replacements of breeding adults by either immature or adult birds. Of the seven juvenile migrations, five were from outside the intensive study area. The observed high rate of intergroup movements would cause many groups to have one or more members unrelated to one or both of the breeding pair. The acceptance of immatures in a foreign group and their help to unrelated birds must influence arguments involving kin selection in group formation. This point is pursued in Chapter 7.

CONCLUSION

No major differences were found between the social organisation of white-browed sparrow-weavers of this study and those observed by Collias & Collias (1978) and Lewis (1981, 1982a, 1982b) in other parts of Africa. This facilitates the use of information gathered by these authors to augment data from this study. White-browed sparrow-weavers have a group size intermediate between that of the highly social Plocepasserinae (e.g. the sociable weaver *Philetairus socius* (Maclean 1973)) and the pair-living weavers (e.g. *Malimbus rubriceps* (Crook 1964)). Both the number and intensity of social interactions between sparrow-weavers of the same group are very low. However, fixed territories are defended and members of each group form a relatively cohesive unit, with group members spending a significant amount of time together. Despite sparrow-weaver groups being highly territorial, a large amount of intergroup movement takes place and immature birds, in particular, are often tolerated. The existence of cohesive social units, each without a fixed rank order, raises questions relating to the methods and importance of communication within a sparrow-weaver group.

CHAPTER 3: COMMUNICATION AND SIGNALLING PATTERNS

INTRODUCTION

A communicatory infrastructure is required for the maintenance of any stable social organisation, because the different roles in a specific social situation (dominant/submissive; breeding/nonbreeding; sexually mature/immature) must be identifiable to all the component members. One cannot study social behaviour without studying communication.

The signals of a species are related to the environment in which it lives: several authors, e.g. Morton (1975), Wiley & Richards (1978), Marten & Marler (1977) and Marten *et al*. (1977), have postulated that the structure of avian acoustic communication is related to the environment. The higher attenuation of sounds in the range 1 to 10 kHz in forests appears to have played a role in causing the calls of forest birds to have a lower frequency when compared with birds that live in open grassland (Morton 1975). Modulation of vocalisations is distorted by dense vegetation, and forest birds tend to have relatively unmodulated sounds (Morton 1975, Wiley & Richards 1978). The height above ground at which an animal calls also affects the attenuation and distortion of calls (Marten & Marler 1977), so it is possible that the elevation of an animal's preferred call site also imposes restrictions on the mode of communication.

Components of the environment may play an important role in visual communication. During the breeding season, male Jackson's Whydahs *Euplectes jacksoni* each display at a tuft of grass surrounded by a ring of beaten down grass. The dimensions of the ring and tuft are remarkably constant (van Someren 1945, cited in Crook 1964). Van Someren found that the central tuft of grass is vital for the location of a male by a female, as tuftless rings went unnoticed. The bowers of bowerbirds (Gilliard 1969) appear to have the same function as the display rings of Jackson's Whydah. The nests of ploceine weavers also form a vital part of their courtship display (Crook 1964). Courtship feeding, when one member of a pair presents a food item to its mate (e.g. in terns) involves the environment (Alcock 1979). In all these cases particular components

of the environment are integrated into the signals. A significant change in the environment of a particular organism would thus, of necessity, lead to a change in its signalling system. The communicatory characteristics of a species could therefore be an important source of information about its evolutionary history because it often reflects characteristics of the environment in which speciation occurred (Paterson 1982a).

The above statements suggest that two related aspects are important for determining the nature of the relationship between communicatory behaviour and the environment. First, the environment imposes restrictions on modes of communication: a restricted set of communicatory possibilities is available upon which natural selection can operate. For a highly social forest animal with a high rate of communication, visual signals would be less advantageous than auditory signals, since the dense foliage interferes with long-distance visual communication. If it were important for passerines to communicate over as long a range as possible, one might expect relationships between habitat and call frequency to be related as suggested by Morton(1975). The assumption that most signals need to have the maximum possible range (e.g. Cosens & Falls 198-) is wrong. Many signals, e.g. those emitted during precopulatory or aggressive behaviour, function at short range and no need exists for these signals to have long-range characteristics (See Chapter 8). Second, each environment offers particular possibilities or "raw material" which could be incorporated into animal signals. For instance, use of dry grass stems for agonistic display purposes is more likely to occur in an arid habitat. In fact, use of such stems is impossible in forest or marine environments. Similarly, the use of small fish for courtship feeding is restricted to animals that hunt in aquatic habitats.

The most important factors shaping communicatory behaviour are the restrictions and potentials of the genotype and phenotype of an animal. Natural selection cannot produce any conceivable communicatory pattern in response to environmental possibilities, but is limited by the genetic variation in the population. As long as particular communicatory characteristics are adequate for efficient communication in a particular habitat, the species may survive and reproduce in that habitat, even though the communicatory behaviour is not the most advantageous possible. It is even possible that some features of avian vocalisations are neither adaptive nor preadaptive, and therefore do not qualify as communication. This

point of view contrasts with that of the Beau Geste hypothesis (Krebs 1977). Krebs postulated that the great diversity of calls of individual songbirds is an adaptation to deceive neighbours that the territory of the caller has more occupants than those actually inhabiting it.

Because communicatory behaviour has been implicated as sometimes being altruistic in nature, it is central in sociobiological theory. For example, alarm calls have commonly been explained as altruism (e.g. Sherman 1977). Because altruism would usually be expected in social organisms, any study of apparent altruism should therefore include communicatory behaviour.

The major problem encountered during studies of animal communication is the functional interpretation of each specific signal. The concept of communication assumes that information is conveyed and has three aspects (Beer 1977, 1982):

1. What information is being conveyed? This is the semantic aspect of communication (Morris 1938, quoted in Beer 1977).

2. What are the effects of the communication on the recipients? This is the pragmatic aspect (Morris 1938).

3. The syntactic aspect of communication (Morris 1938) concerns the physical structure of the particular signal, and its analysis normally presents fewer problems than unravelling the other two aspects of communication.

In field studies of animals, the distinction between the semantic and pragmatic characteristics of communication usually fades, since we can only deduce the meaning of communication by observing its effects on the recipients. The only way of doing this adequately is under experimental conditions, where a signal can be manipulated in a controlled way and the reaction of the recipients observed. In this respect, the concept of a bioassay for the evaluation of a signal is critical. The only other information that may give some idea of the function of a signal is the contextual information about each communicatory act, either in terms of time and place or in terms of preceding behaviour of participants. However, such information alone is usually not sufficient to interpret the

functional significance of a signal because of the lack of knowledge about the reactions of recipients of the signal. The experimental manipulation and bioassay of sparrow-weaver signals was outside the scope of this project, leaving only contextual information as a guide to the functions of particular signals. The objectives of this chapter therefore relate mainly to the syntactic and pragmatic aspects of communication among sparrow-weavers. These are:

1. To quantify aspects of the sparrow-weaver communication system, and to compare it with that of closely-related birds. This information could provide some idea of the environments in which sparrow-weavers evolved, and thus about their evolutionary relationships. A significant amount of space is devoted to the description and comparison of signals of sparrows (Passerinae), weavers (Ploceinae), and sparrow-weavers.

2. To determine to what extent the environment is involved in sparrow-weaver communication. These data are used for the same purposes as the previous point.

3. To determine whether altruism is involved in the communicatory system of sparrow-weavers, for instance in anti-predator behaviour. This information helps in an understanding of why sparrow-weavers live in groups.

METHODS

Because communication normally involves several simultaneous events, many avian communication studies have not been quantitative in nature, relying on verbal descriptions of sounds or postures (e.g. Collias & Collias 1959, Crook 1964). Animal sounds have several dimensions e.g. amplitude, frequency and modulation. Visual signals usually involve simultaneous movements of several parts of the body. For this reason the use of sonagraphic techniques combined with multivariate analyses of sounds (Sparling 1978), and of special methods, e.g. Eshkol-Wachmann movement notation (Golani 1976) for describing movements, represents a

significant advance in the quantification of communicatory behaviour. Difficulties in quantifying behaviour were also encountered during this study, especially since the amount of material available for comparison is small. Communicatory variables were quantified in the following ways:

Vocal communication: The calls of sparrow-weavers were recorded on magnetic tape at a speed of 19 cm/s using a UHER 4000 tape recorder coupled with an Electret microphone and a 70 cm parabolic reflector. Tape recordings were usually made while carrying the recording equipment during periods of visual observation. In some instances the tape recorder was left below the nest tree of a group and recordings made by means of a remote switch.

The following method was used to quantify the amount of time that sparrow-weavers spend calling. Because sparrow-weavers call continuously for several minutes, it is impossible to demarcate a specific call. The quantification of calls by counting was therefore impossible. The relative occurrence of call types was calculated by noting the last call type to be emitted during a two-minute observation period. If no calls were emitted, the period was noted as quiet. If the last call was of type 3 even though type 2 calls occurred during the period, the type 3 call was noted.

Visual communication: Because sparrow-weavers do not often engage in communication with a strong visual basis, it was not possible to photograph these events. When such signalling was observed, the behaviour was immediately recorded in written form. Some of these descriptions were used as the basis for drawings that depict the respective behaviours.

Quantification of behavioural characteristics: The proportion of time that particular sparrow-weaver age/sex classes spent performing intra-group behaviours was determined via focal animal sampling (Chapter 2) where the behavioural types were recorded at two minute intervals. The amount of vegetation cover at the site of a feeding bird was estimated on a five point scale. Colour photographs, taken beforehand, ensured consistent classification of vegetation cover. The immediate environment where feeding was observed (grassland, maize field, road) was also noted.

RESULTS

Vocal communication

White-browed sparrow-weavers have a large vocal repertoire consisting of at least eight calls (Figure 6). They call actively and were silent during only 22% of 9013 two minute observations of perched birds. The proportion of quiet two minute periods did not differ between adults and immatures (χ^2=0,67; df=1). This very crude measure suggests that, on average, the pause between calls is less than three minutes. More detailed observations would have shown that the inter-call period is substantially shorter than three minutes.

The structural characteristics of the eight call types that were distinguished and recorded in the field (Figure 6) are summarised in Table 7. The behaviour accompanying these calls is described as follows.

Type 1 (Alarm call): Repetitions of this brief chirp, rich in harmonics, were emitted whenever a predator such as a mongoose, snake or a human approached a group of birds too closely. The call was also emitted by vigilant sparrow-weavers that perched in trees while fellow group members were feeding. From the context of this call, it is assumed that it is an alarm reaction to predators.

Type 2 (Contact call): A sparrow-like chirp, longer than type 1, with a band width of 6500 Hz was emitted whenever two or more sparrow-weavers were flying. The same call was sometimes emitted by a vigilant bird perched atop a tree, when it was commonly associated with type 1 calls. It appears that call type 2 was emitted when the birds had a slight tendency to flee and possibly helped them to locate each other while flying.

Type 3 (Territorial call): A complex song with frequencies up to 6000 Hz was emitted by perched sparrow-weavers. The song consisted of two

TABLE 7

Characteristics of sparrow-weaver calls:
B = bandwidth
L = lower frequency limit
H = higher frequency limit
D = duration of one call
Har = no. of harmonics
En = energy level on scale of 5

Figures are based on measurements of at least five sonagrams for each call type; the exceptions being call type 4 (3 sonagrams) and type 5 calls (one sonagram obtained, but often heard).

Call type	B(kHz)	L(kHz)	H(kHz)	D(s)	Har	En
1	7	0,5	7,5	0,1	5	5
2	6,8	1,2	8	0,25	3	5
3	7	0,5	7,5	0,55	0	5
4	2	1	3	0,35	0	3
5	3	1	4	0,15	0	5
6	0,5	7	7,5	0,55	0	4
7	6	2	8	0,1	0	5
8	1,7	0,3	2	0,2	0	1

main parts: a) two wide-band frequency sweeps followed by b) a low-pitched trill. The whole call was normally emitted by a single bird. On occasions, when members of a breeding pair perched close to one another, there was a distinctive duet during which the male emitted the two wide-band sweeps followed by a low-pitched trill emitted by the female (Figure 6).

These calls were also emitted when adjacent sparrow-weaver groups participated in calling matches on their common territory boundary. Type 3 calls were characteristic of adult sparrow-weavers perched atop their nest tree. It appeared that the calls were associated with activities of territorial advertisement and defence.

Type 4 (Low volume territorial call): Perched adults emitted a call that resembled type 3 calls but sounded much softer. Type 4 calls had the same basic structure as type 3 calls. The frequency sweeps were simpler and the low-pitched trill appeared to be frequency-modulated to a higher frequency than type 3 calls. Type 4 calls were emitted singly, as opposed to type 3 calls that were emitted in multiples. The context of type 4 calls was much the same as that of type 3 calls, except that type 4 calls were never heard during territorial conflicts among neighbouring groups. The frequency of this call did not exceed 5000 Hz.

Type 5 (Sparrow-like chirp): Perched adults sometimes emitted a short, distinctive chirp which consisted of a single frequency sweep. Although regularly heard, only one sonogram of this call could be obtained. The structure of this call was similar to the second wide-band sweep of type 3 calls. Contextual information did not suggest the function (if any) of type 5 calls.

Type 6 (Soliciting call): Chicks emitted a high-pitched "tweet" that had the apparent function of inducing adults to feed them. During mating a very similar call was emitted by the male immediately before copulation.

Type 7 (Mating call): During the breeding season, males perched on their nest trees and emitted a very complex and high-pitched song. The song consisted of frequency sweeps that were compounded to form series of warbles (Figure 6). The frequency of these songs often exceeded 7000 Hz and did not appear to have a large energy concentration below 2000

Hz. On two occasions females perched adjacent to males that were emitting this call, after which the male attempted to copulate. This was the only call type showing seasonal variation in occurrence. The calls were very common during the months August and September (early breeding season), uncommon during July and from October to January, and were totally absent during the period February to June.

Type 8 (Close-range call): When more than one sparrow-weaver was perched in the same tree, a harsh, low-pitched call was often heard. This call was not accompanied by any specific activity on the part of the caller or its near neighbours and it was of much lower amplitude than call types 3, 4 and 5.

The calls emitted by vigilant and non-vigilant sparrow-weavers were compared with respect to the exposure of the call site. The short type 2 and type 4 calls were more commonly emitted by non-vigilant birds perched on an exposed site, whereas type 5 calls were more often emitted by non-vigilants perched inside tree canopies (χ^2=157,45; df=7; p<0,001). These differences were not evident in vigilant sparrow-weavers.

Constancy in calls: The communicatory value of a signal can lie in one of two characteristics: either the signal is absolutely constant, ensuring its recognition, or the signal is variable to indicate some continuous quality, e.g. the fight/flight tendency of an animal. Type 1 calls have characteristics of the second group: the rate at which alarm calls are emitted reflects the immediacy of danger. Constancy in a behaviour such as a vocalisation suggests that the behaviour does have communicative value; it is not an incidental effect or an ancestral evolutionary hang-over.

The only sparrow-weaver call that was recorded sufficiently often to allow analysis of call variability, was the type 3 (territorial) call. Ninety-one such calls emitted by ten individual sparrow-weavers were analysed sonagraphically. Most of the measured characters were not normally distributed, necessitating the use of nonparametric statistical techniques. A Kruskall-Wallis test on the Wilcoxon rank sums for the different individuals was performed to obtain a probability of inter-individual variation being statistically significant (Table 8). The test shows that a large degree of inter-individual constancy exists for this call type. The last

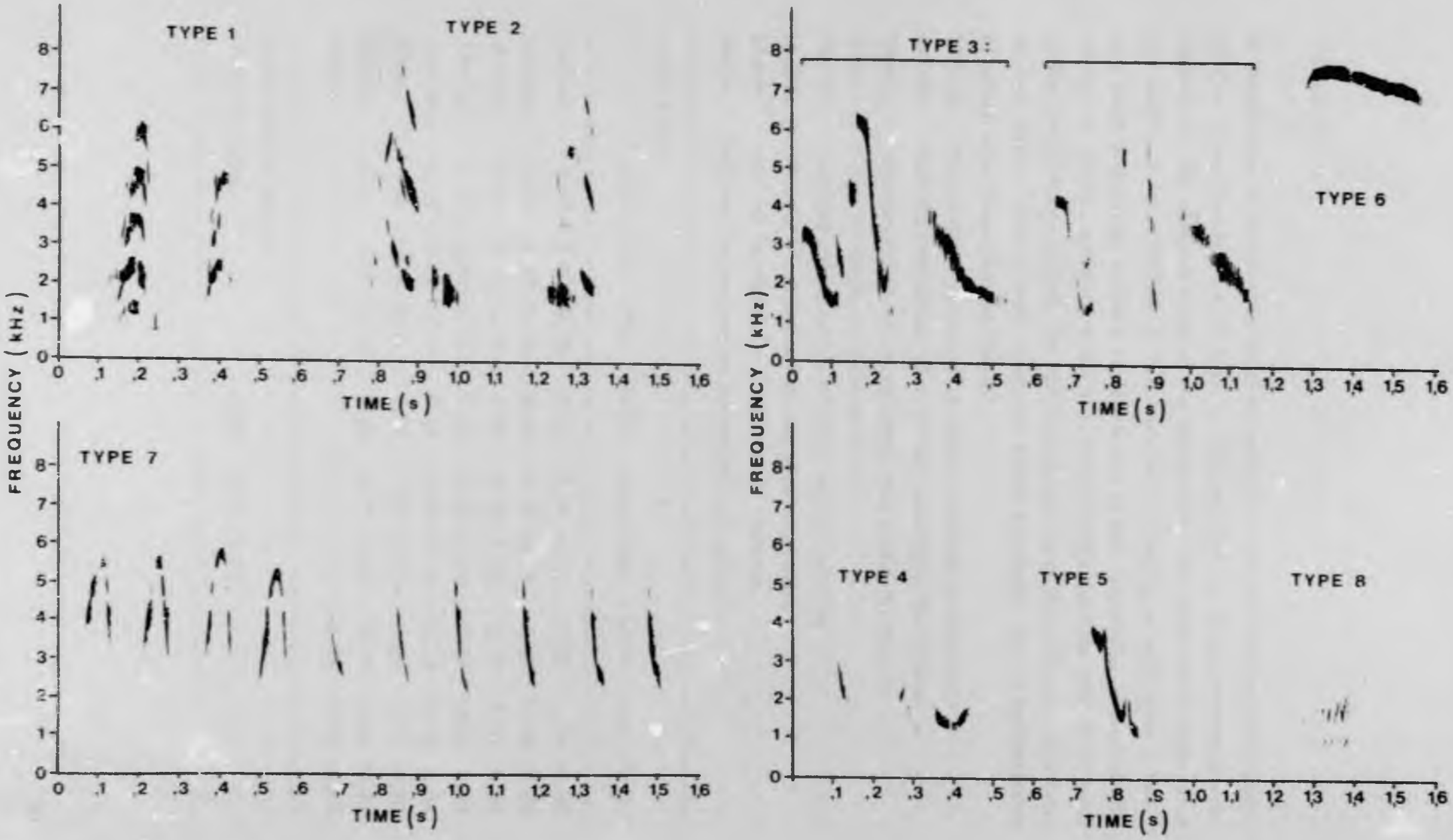


FIGURE 6. Sonagrams of sparrow-weaver calls.

TABLE 8

A comparison of inter-individual as opposed to within-individual variation in the characteristics of 91 type 3 calls emitted by 10 sparrow-weavers. Results of two statistical tests are presented. The sums-of-squares of a parametric 1-way ANOVA of the raw data, relating to individual (Indiv) and inter-individual (Inter) variation are given. Secondly, a probability (Prob) is given resulting from a Kruskall-Wallis test on the rank sums of the individuals, testing the null hypothesis that the calls of individuals do not differ. Type 3 calls comprise three syllables, the characteristics of which are presented separately.

Hifreq =Highest frequency of syllable, excluding harmonics .
Lofreq =Lowest frequency of syllable, excluding harmonics.
Bandw =Bandwidth of whole syllable, excluding harmonics.
Time =Time duration of syllable (ms).
Hinflec =Amount of inflection at high end of syllable.
Linflec =Amount of inflection at low end of syllable.
Shape =No. of segments in sonagram of syllable.
Width =Widest instantaneous bandwidth of syllable.

SYLLABLE	1			2			3		
	Indiv	Inter	Prob	Indiv	Inter	Prob	Indiv	Inter	Prob
Hifreq	2,87	2,64	0,58	2,15	2,94	0,21	0,91	2,94	0,00
Lofreq	0,22	0,29	0,10	0,15	0,32	0,01	0,06	0,05	0.66
Bandw	3,06	2,44	0,70	1,91	3,18	0,13	0,74	2,31	0,00
Hinflec	0,26	0,08	0,95	0,24	0,30	0,29	0,09	0,05	0,78
Linflec	0,23	0,15	0,71	0,11	0 07	0,74	0,12	0,16	0,24
Time	1118	639	0,51	1177	685	0,49	1536	6245	0,00
Shape	0,64	0,26	0,74	0,40	0,98	0,02	0,12	0,07	0,81
Width							0,16	0,63	0,00
FOR WHOLE CALL:									
Total duration				3368	9419	0,02			

syllable of the call exhibited the largest degree of inter-individual variation, with four of the measured parameters differing significantly among individuals. The second syllable varied among individuals by being either a single frequency sweep or by having a break midway through the sweep. These data indicate that type 3 calls have a high communicatory value. The significance of this is discussed at the end of the chapter.

Visual communicatory patterns

White-browed sparrow-weavers have a number of distinctive body markings (Figure 7) which are potential visual signals. Visual signalling was, however, not a regular means of communication among fellow group members. The only cases of clear visually-based communication occurred during premating behaviour (18 observations) and interterritorial conflict (84 observations in 548 observation h).

Pre-mating and mating behaviour: Mating behaviour was observed on 18 occasions and followed a stereotyped pattern (Figure 8). Both birds lowered their wings slightly and raised their heads and tails, exposing the white rump feathers. The body feathers of the male were puffed out so that the bird assumed a more rounded shape. The female remained motionless while the male performed a dance consisting of to-and-fro lateral movements. During this behaviour he moved one leg to grip the perch about 0,5 cm to one side, followed by a similar movement of the other leg in the same direction. In the process he moved closer to and then away from the female, covering distances of about 30 cm along the perch. This behaviour lasted for a period of 2,5 to 7 minutes. When the male was very close to the female, he quivered his wings in a chick-like manner while emitting type 5 (chick-like) calls. The female simultaneously vibrated her tail in a vertical direction. This behaviour always preceded mating and was followed by a chase during which the male followed the female for about 50m. Mating behaviour was not initiated again after the postmating flight. The white rump of these birds may be an important visual signal during the post-mating flight.

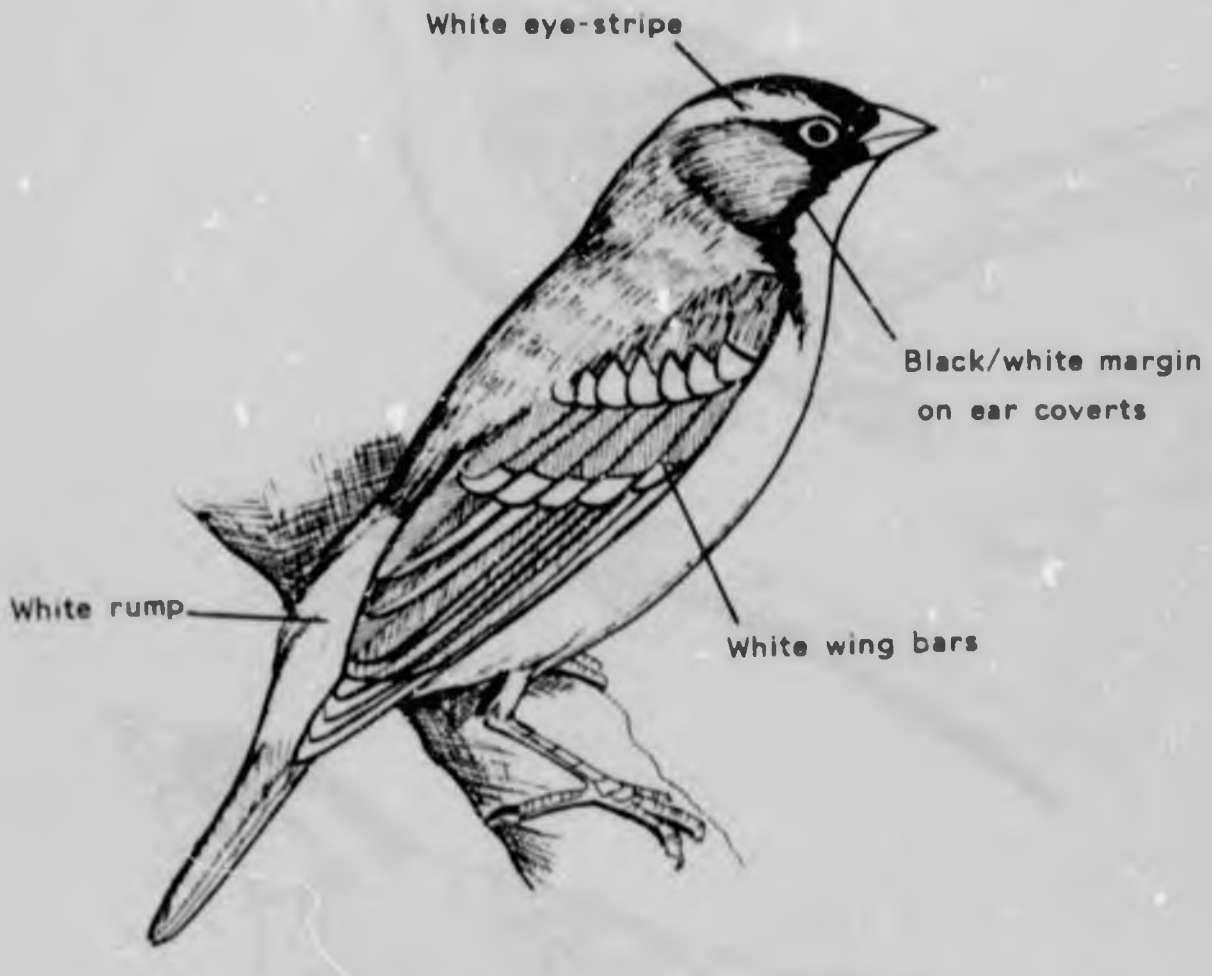


FIGURE 7. Visual signalling marks of sparrow-weavers. These birds have a range of body markings that are potentially useful for visual signalling, the important ones being indicated.

FIGURE 8. Sparrow-weaver mating behaviour, showing the postures of two birds in precopulatory display. The tail of the female vibrates rapidly in a vertical direction and the male quivers his drooped wings while doing a lateral dance (see text).

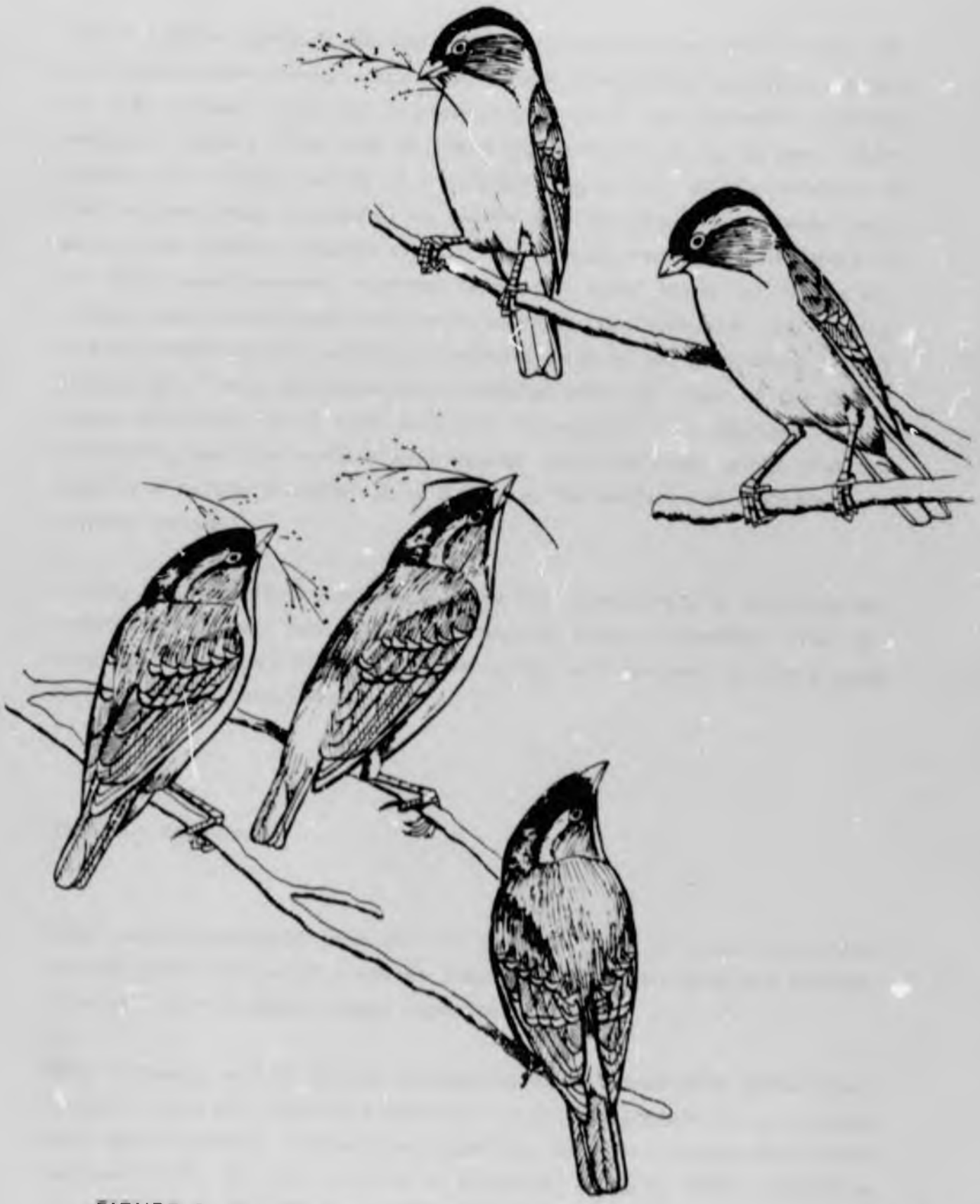


FIGURE 9. A calling match between two sparrow-weaver groups on their common territorial boundary. The groups face each other from neighbouring trees: the grass stems are apparently important visual signals.

Interterritorial conflict: During 548,5 focal animal observation hours, 44 conflicts between groups occurred. These interactions usually occurred on the common territorial boundary (Figure 4) and involved a large amount of calling. The form of these interactions was as follows. After hearing the closeby calling of a neighbouring group, all the members of the resident group assembled on a tree and the two groups faced each other from closely situated trees. Both groups vocalised, with most of the birds simultaneously emitting territorial calls (type 3; Figure 6). Calling was always loud and accompanied by the collection and display of grass stems by both adult and immature birds of the interacting groups (Figure 9). The grass stems were collected after the start of the interaction and were never built into nest structures. The postures of the interacting sparrow-weavers were normal, with the head, wings and tail held in a normal position. In a few cases the white rump feathers were slightly raised.

During 62 interactions between adult territory holders and intruding immature individuals, two instances involved visual signalling. The intruding, submissive bird lowered its wings and exposed its white rump feathers while raising its head.

Vigilance behaviour

When sparrow-weavers feed on the ground, one or more individuals usually perch on top of a nearby tree whence regular calls are emitted. This behaviour is here termed vigilance behaviour.

When compared with birds that perched on top of a tree while fellow group members were NOT feeding (Table 9), a vigilant sparrow-weaver emitted more type 1 (alarm) calls and was quiet for fewer two minute observation periods (x^2=411,6; df=3; p<0,001 at Bloemhof; x^2=70,9; df=3; p<0,001 at Daan Viljoen). Table 9 also shows that the rates of occurrence of call types 2 and 3 are not significantly affected at Bloemhof when the fellow group members of a perched bird descend to feed. At Daan Viljoen, however, the frequency of call type 3 was significantly reduced.

TABLE 9

The calls emitted by sparrow-weavers perched in trees. The composition of calls emitted by vigilant sparrow-weavers whose fellow group members were feeding is compared with the calls of perched birds whose fellows were not feeding. The frequencies are expressed as the percentage of the total calls emitted within each column. Absolute calling rates can be calculated by multiplying an indicated percentage by the sample size indicated in that column.

Study area:	BLOEMHOF		DAAN VILJOEN	
Activity of fellow group member :	Feeding	Non-feeding	Feeding	Non-feeding
No. of observations	1250	4080	82	97
CALL TYPE:				
Quiet	6,9 %	28,4 %	8,5 %	12,5 %
1 (alarm)	21,6 %	6,7 %	73,2 %	12,5 %
2 (contact)	8,2 %	5,2 %	1,2 %	1,0 %
3 (territorial)	63,2 %	59,6 %	17,1 %	74,0 %
TOTAL	99,9 %	99,9 %	100,0 %	100,0 %

Vigilant sparrow-weavers usually perched in an exposed position on top of a tree, while the same birds tended to perch in the shade of the tree when fellow group members were not feeding (χ^2=208,4; ; df=1; p<0,001 at Bloemhof; χ^2=13,7; df=1; p<0,001 at Daan Viljoen).

Vigilance was closely correlated with the physical structure of the habitat in which the group fed (Table 10). Sparrow-weavers feeding in dense grassland had vigilant birds perched nearby during a greater proportion of time than did birds feeding in open grassland (χ^2= 225,3; df=3; p<0,001 at Bloemhof; χ^2=15,2; df=5; p<0,01 at Daan Viljoen).

Figure 10 shows that all age/sex groups contribute towards vigilance behaviour but that adults, and in particular adult males, make the greatest contribution (χ^2=127,9; df=5; p<0,001). These results were obtained from observations made at Bloemhof. The sparrow-weavers at Daan Viljoen could not be classified into age/sex classes.

DISCUSSION

Sparrow-weaver vocal communication

Based on sonagraphic similarities, the different sparrow-weaver vocalisations can be divided into at least 5 groups (Figure 11). Call types 2,3,4 and 7 have a relatively complex structure. The sparrow-weaver vocal repertoire is diverse and complex to the human observer. The fact that type 3 calls possess a large degree of constancy (Table 8), suggests that this call type has high communicatory value. When evaluating constancy as an indicator of the communicative potential of signals, arguments are clouded by the following factors. The fact that a behaviour shows a large degree of constancy does not automatically imply that it has a communicatory function. The low variability could be an effect of some other process, such as pleiotropy. Second many highly social animals can recognise individuals, an ability normally regarded as an advanced social character. A constant signal might make individual

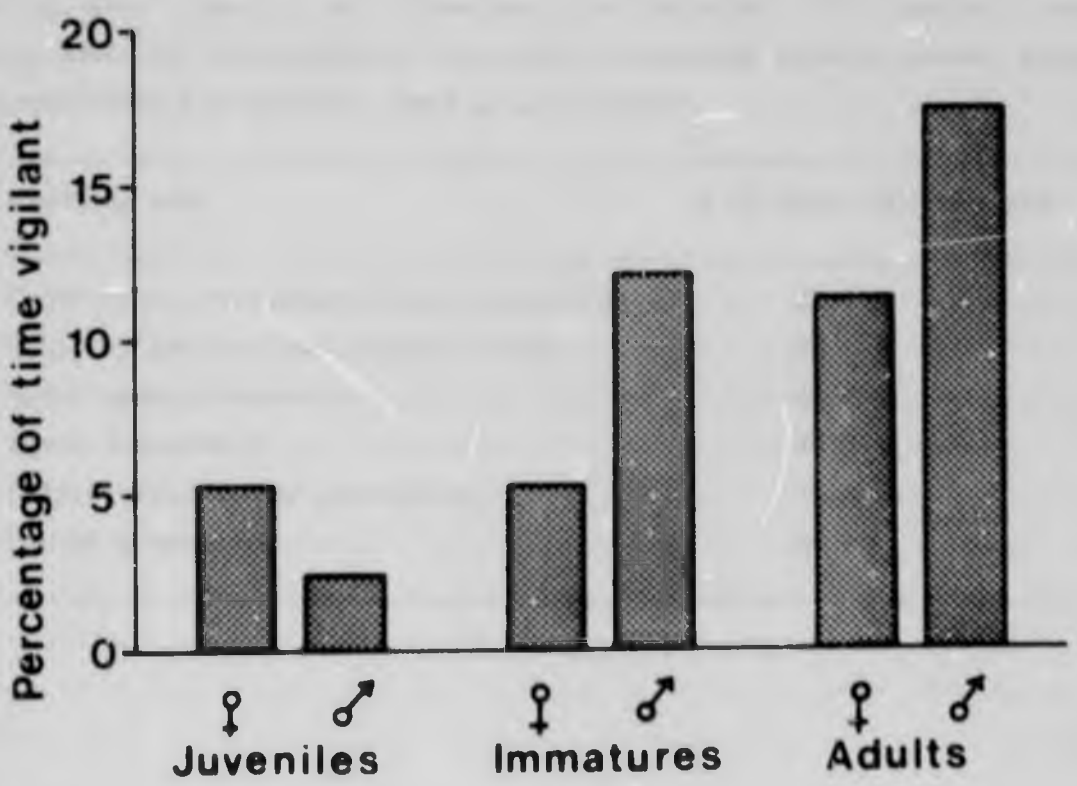


FIGURE 10. Vigilance behaviour by sparrow-weaver age/sex classes. The proportion of vigilance performed by each age/sex class, measured by the fraction of time spent in a tree while other group members are feeding, is represented by the height of the vertical bars. Adult males contribute the most towards vigilance.

TABLE 10

The percentage of time that feeding sparrow-weavers were accompanied by overlooking vigilant birds at Bloemhof. 3291 two minute observations during which feeding was observed, are included. The smallest sample comprised 107 observations for dense grassland feeding sites, because sparrow-weavers seldomly feed in such areas.

Feeding site	% of time with vigilant
Bare area (road, maize field, grassland):	32,7 %
Edge of grass (road, maize field):	54,6 %
Very open grassland:	47,8 %
Open grassland:	44,3 %
Intermediate cover grassland:	79,3 %
Dense grassland:	84.1 %

recognition more difficult and could convey less information than a more variable signal. Beer (1976) showed that although the long-calls of laughing gulls, *Larus atricilla*, are relatively constant; relatively minor differences in the modulation of notes near the start of the call caused the chicks to differentiate between adult calls directed towards them and those not directed towards them. Chicks also differentiated the calls of their parents and those of non-parents. As long ago as 1947, Schenkel showed that the submissive behaviour of wolves, *Canis lupus*, ranged from postures with a depressed tail to lateral recumbancy, allowing the animals to display a wide range in intensities of submission. Variation in a basic signal allows animals to impart much more information than does a completely stereotyped signal. The high constancy of sparrow-weaver type 3 calls (which presumably function partly as territorial advertisement) certainly does not allow for the operation of the Beau Geste hypothesis (Krebs 1977).

The characteristics of large repertoire, constancy (although only proved for one call type) and frequent use of auditory signals suggest that vocal communication in sparrow-weavers is well-developed.

Sparrow-weaver visual communication: It would appear that the distinctive body markings of white-browed sparrow-weavers are used only for communication during mating. During courtship, the raised heads of participating birds accentuate the contrast of the light/dark colour line on the side of the head and neck. The eye-stripe that runs parallel to the lateral neck stripe might further emphasise the position of the bird's head. The light wing bar probably emphasises the lowered position of the wings during courtship. The white rump feathers of both sexes are very conspicuous during courtship and during flight. As far as body markings are concerned, only the rump feathers occasionally seem to play a role in the ritualised interactions between a territory holder and an intruder.

If one considers that visual signals associated with mating or agonistic interactions were emitted at a rate of once every five observation hours, it appears that visual signalling is not as important as vocal signals that are emitted at least once every three minutes. To the human observer, sparrow-weaver vocal signals appear to be much more structurally complex and diverse than visual signals. This does not mean that visual signalling is not vital for sparrow-weavers. It is highly unlikely that the

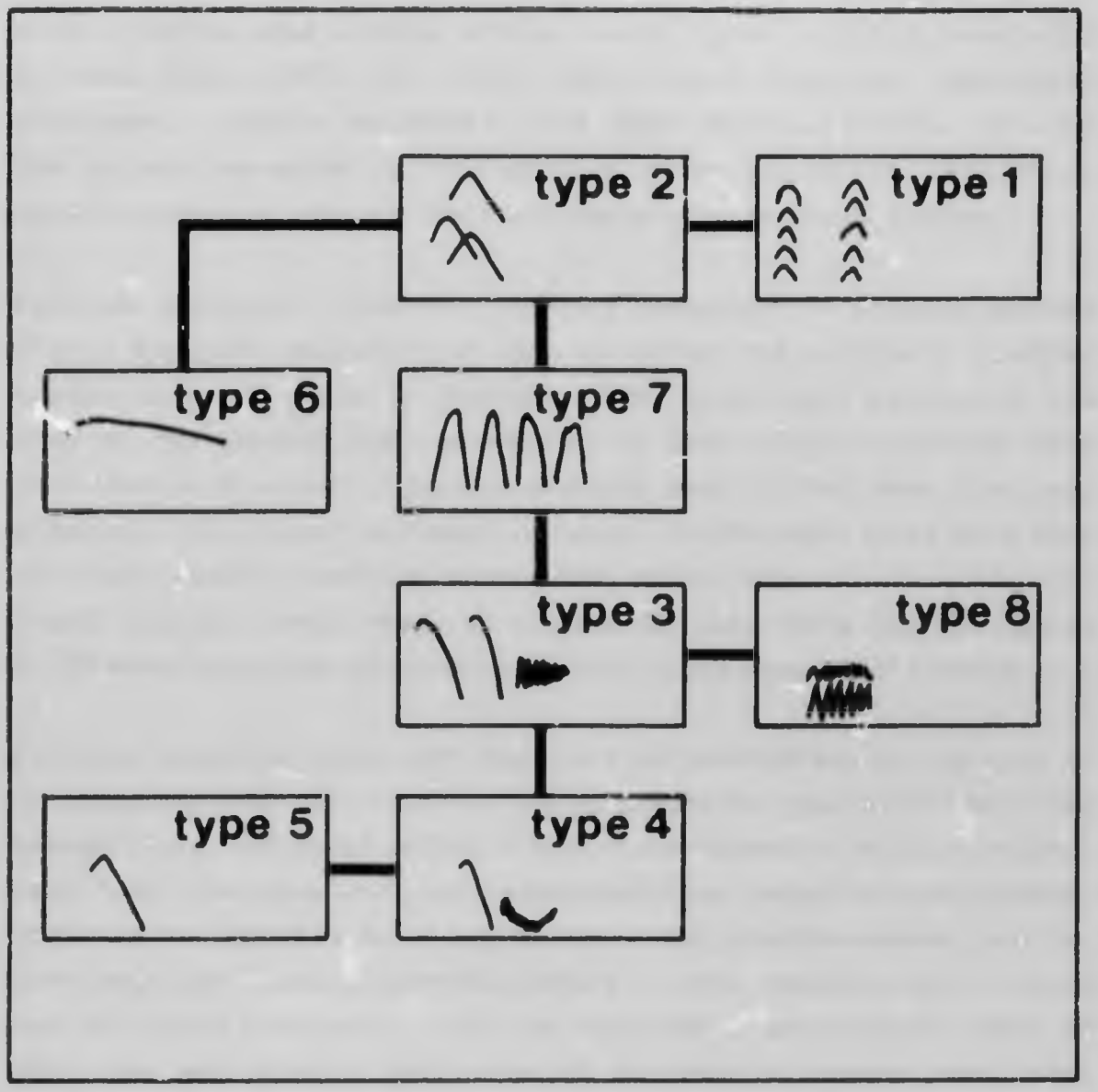


FIGURE 11. Structural relationships among sparrow-weaver calls, based on the comparison of sonagraphs. All the observed calls consisted two basic types of elements, represented by call types 5 and 8, respectively.

birds would be able to mate without visual signals enabling recognition of mates. Smith (1972) and Peek (1972) found that male red-winged blackbirds, *Agelaius phoeniceus*, with dyed shoulder patches were not able to hold territories as efficiently as normal blackbirds. Therefore, visual signals are vital for tne maintenance of some social systems.

Vigilance behaviour: Data on vigilance behaviour in sparrow-weavers (Tables 9 and 10) indicate that vigilance serves the purpose of predator location while the group is feeding and for subsequent warning of the birds on the ground. Sparrow-weavers at Daan Viljoen were much more timid than at Bloemhof (Table 9), probably because they were less used to humans; this caused increased vigilance. The Bloemhof birds were very tame and could usually be approached without disturbance much more closely than the normal observation distance, suggesting that the figures for Bloemhof are close to those occurring in the absence of humans.

Vigilance behaviour would not imply any purposefulness on the part of the vigilant birds. It need not be an adaptation against predation on feeding birds, but could reflect a lack of confidence in perched individuals. Such "nervousness" could conceivably be caused by two agents: predators or interterritorial aggression among sparrow-weaver groups. Overt aggression among sparrow-weavers is rare, usually only occurring near territorial boundaries. Only one observation was made in which an adult male was attacked well inside its territory by another male, when the victim attempted to hold two territories and was ousted from one of the territories by the intruder. Because of its low rate of occurrence, interterritorial aggression does not appear to be the cause of vigilance. Interactions between sparrow-weavers and predators, on the other hand, occurred relatively frequently (Chapter 6). In the light of these observations it appears that vigilance behaviour is indeed an adaptation resulting from predation pressure.

Vigilance behaviour would appear to be altruistic, because an individual sacrifices food and feeding time while other group members forage. Since group members benefit from better predator evasion, this could conceivably be a factor influencing sparrow-weaver group formation (Chapter 7).

Communicatory patterns in other Ploceids

This section deals with characteristics of communication among sparrow-weaver relatives. Species from three subfamilies: the Ploceinae, Passerinae and Plocepasserinae are considered. A comparison of these taxa may allow some conclusions regarding their evolutionary history (Chapter 8).

Weaverbirds (Ploceinae): Crook(1964) reported that ploceine weavers have a diverse array of visual signals which he classified into the following groups:

1. Threat postures, e.g. head forward, tail depressed, song stretch or song bow.
2. Territorial defence, e.g. aggressive dance with or without song bows and lunging.
3. Chasing of female and song approach to female, e.g. pre-mating behaviour in which the male performs a song stretch or a song bow or chases the female for short distances.
4. Nest invitation and nest advertisement in which the male performs a visual display at the nest which apparently attracts the female to the nest structure.

The above behavioural categories are not equally well developed in all the ploceine weavers, some species even lack one or more major components. Many of the weavers, e.g. *Ploceus nigerrimus, P. phillippinus, P.melanocephalus and P. cucullatus*, do have visual signals belonging to all the above categories (Collias & Collias 1959, Crook 1964).

Vocal signalling in the Ploceinae is not well documented. Collias & Collias (1959) noted at least five different calls emitted by breeding *P. cucullatus*. The crude structure of each call can be inferred from the onomatopoeic descriptions given by these authors:

1. Alarm call in response to presence of predators: "kik!"
2. Flight call. "chick!"
3. Call emitted while collecting nest material: "chuck-chuck-chuck!"
4. Territorial call emitted during nest construction: "pee-oh! pee-oh!

swiz-swiz, wheeze, sweeeezzze!"

5. Nest invitation call: "wake, wake-up!"

Crook (1969) surveyed the calls emitted by some 40 ploceine weaver species of Africa and India. He recorded 14 different calls, but observed a maximum of seven of these calls in any one species. Collias (1963), however, identified 15 call variants in captive *Ploceus cucullatus*; the functional classification of these calls was similar to the onomatopoeic outline given above. The descriptions and recordings of weaver calls are probably biased towards sounds emitted close to breeding colonies where the birds are conspicuous. It appears that ploceines have a diverse array of calls. Sonagrams of the territorial calls of *Ploceus cucullatus* are presented in Figure 12, and unlike sparrow-weavers, their calls have a wide bandwidth and are atonal. The vocal structure of ploceine calls is extremely complex. Nearly all the calls noted by both Collias (1963) and Crook (1969) were very similar in all these respects. Crook (1969) suggested that the birds may react to the temporal patterning of these calls rather than to their frequency structure; under experimental conditions ploceine red-billed qualeas, *Quelea quelea*, were seen to respond to white noise as they did to natural calls of the same duration, loudness and temporal patterning.

When compared with sparrow-weavers, ploceine weavers have a visual communication system that is much richer in repertoire and more intricate in structure. The vocal signalling system of ploceine weavers appears to have a relatively constant structure in terms of frequency variations, so that all the calls appear relatively similar on sonagrams. This does not mean that weavers have a simple vocal communicatory system. In fact, they appear to have at least as many functional call types as do sparrow-weavers, which have well defined call types with well-defined tonal variations. The difference between weavers and sparrow-weavers lies in a very large qualitative difference in call structure.

Sparrows (Passerinae): Very little is known about communication in the African sparrows, and no published accounts of either their visual or auditory signals are known. Sonagrams were made from recordings of Cape sparrow *Passer melanurus* calls. All the sparrow calls that were investigated were tonal in nature and consisted of frequency sweeps and

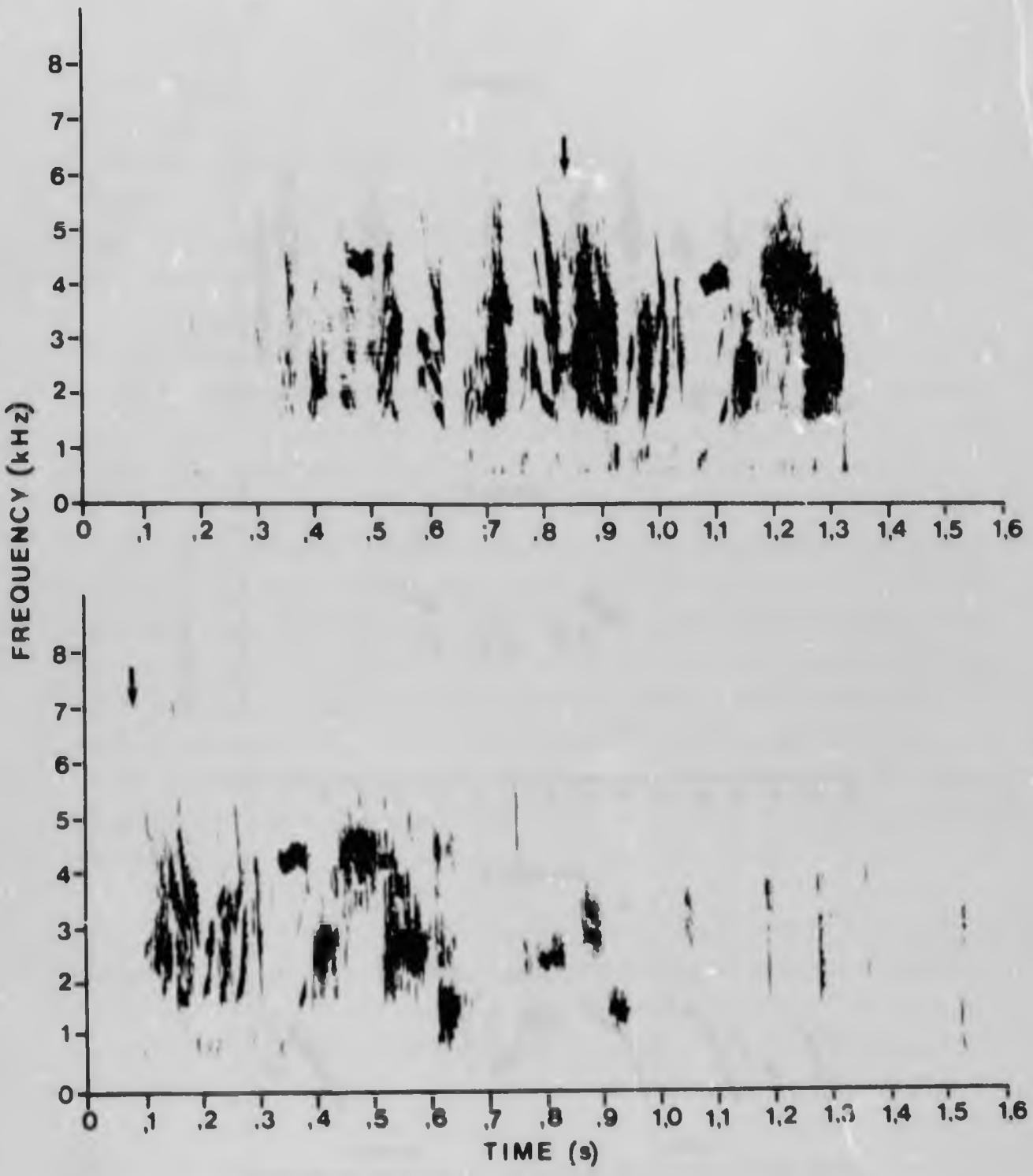


FIGURE 12. Calls of *Ploceus cucullatus*. The two sonagrams show the first parts of two nest advertisement calls made by the same male. Three features of these calls are apparent: 1) their complexity compared with those of sparrow-weavers, 2) their variability in terms of gross elements and 3) their similarity within gross elements, as is apparent in the parts to the right of the arrow above each sonagram. Material from the sound recording collection of the Transvaal Museum.

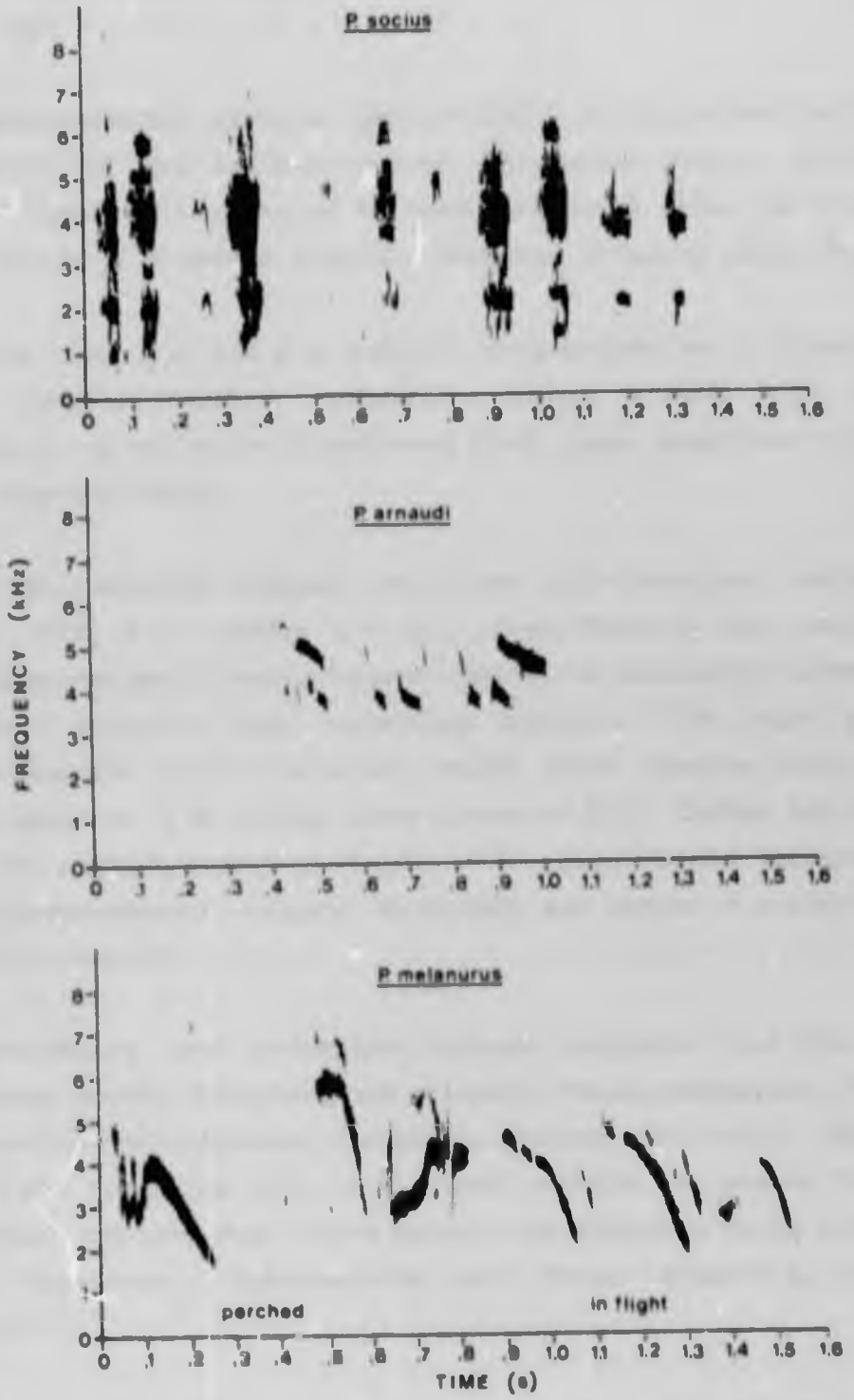


FIGURE 13. Calls of sparrow-weaver relatives. The calls of *Philetairus socius* have similarities with those of the true weavers (e.g. Figure 12). Like sparrow-weavers, *Pseudinigrita arnaudi* and *Passer melanurus* have tonal calls. The perched calls and flight calls of *P. melanurus* are similar to sparrow-weaver type 3 and type 2 calls, respectively.

trills. They thus resemble sparrow-weaver calls in many ways (Figure 13).

Other plocepasserine weavers: Maclean(1973) distinguished ten different vocalisations in the sociable weaver *Philetairus socius*. While at least seven of these calls appeared to have functional value, all except two were based on a somewhat metallic, staccato, chipping note (Figure 13).

The visual signals of sociable weavers have similarities to those observed in the sparrow-weavers: submissive birds crouch with drooping, quivering wings while the threatening birds gape, sometimes with the tail fanned (Maclean 1973).

Surprisingly, sociable weavers with their well-developed social system (Maclean 1973, E.C. Collias & N.E. Collias 1980) do not, as far as the human observer can discern, have a complex communication system, either in terms of visual or vocal signalling patterns. The vocal signals of sparrow-weavers are structurally much more complex than those of sociable weavers. The scanty descriptions of E.C. Collias & N.E. Collias (1980) and a single sonagram of calls of the grey-headed sociable weaver, *Pseudonigrita arnaudi*, suggest their calls are similar in tonality to those of sparrow-weavers.

This preliminary and incomplete survey suggests that the calls of *Plocepasser mahali*, *Pseudonigrita arnaudi*, *Passer melanurus*, *Philetairus socius* and various ploceines (including *Ploceus cucullatus*), fall into two groups: one group has little tonality and includes the genera *Ploceus* and *Philetairus*, whereas the second group has distinctly tonal call and embraces *Plocepasser*, *Pseudonigrita* and *Passer* (Figure 6, Figure 12, Figure 13).

The above judgements on the complexity of communicatory systems of various Ploceidae were based on observations of the repertoire and of the visual or sonagraphic complexity of the signals. A more valid judgement could be made if the function of each call were known, and the occurrence of calls with similar functions could be compared among different species in the weaver family. There is insufficient information about the possible functions of the calls to make such a comparison. From Crook's (1964) interpretation of the ploceine visual displays, it appears that ploceine

weavers have a much more specialised set of visual signals to facilitate mate recognition and pair formation, than do sparrow-weavers. The latter also lack the specialised aggressive postures that weavers show. On these grounds the sparrow-weaver visual communicatory system is very simple, suggesting that their ancestors lived in an environment where long-range visual communication could not function effectively. This point is pursued in Chapter 8.

CONCLUSION

Sparrow-weavers have a very simple visual signalling system used only during territorial conflicts and during mating. It appears to resemble that of other plocepasserines, and is much poorer in repertoire and complexity than that of the ploceine weavers. Within the plocepasserines, sparrow-weaver calls have structural similarities with those of *Pseudonigrita arnaudi*, but differ markedly from those of *Philetairus socius*. In addition, sparrow-weaver calls have large similarities with those of the Passerinae but differ markedly from those of the Ploceinae. The possible origins of these differences are discussed in Chapter 8.

The grass stem display of sparrow-weavers during territorial conflicts represents the only observed case where environmental props are used as part of sparrow-weaver signalling.

Territorial conflicts occur at a very low rate and seem unlikely to have caused the evolution of vigilance behaviour. Vigilance is probably an adaptation against predation and could constitute a form of altruism. Vigilance is not an obvious effect of any other relationship between sparrow-weavers and their environment.

Predation appears to be an important environmental constraint on sparrow-weaver survival. The next two chapters show that sparrow-weaver nests have characteristics that are vital for these birds to avoid predation.

CHAPTER 4: THE BIOLOGY OF NEST BUILDING IN WHITE-BROWED SPARROW-WEAVERS

INTRODUCTION

Sparrow-weaver nests are used both for breeding and roosting and are normally located in a compact group on one side of the nest tree (Figure 14). Although roost nests (with two entrances) and breeding nests (with one entrance) are easy to identify, they often do not serve a single function: roost nests are often converted into breeding nests and *vice versa*. Nest building is an important activity of sparrow-weavers in which all group members participate. Nests have a marked influence on the survival of sparrow-weaver groups (see Chapter 5); communal nest building may therefore be a form of altruism. The selective forces responsible for this altruism could be of prime importance in shaping sparrow-weaver sociality. Because of the survival value to occupants, other species sometimes make use of this valuable resource: e.g. pygmy falcons *Polyhierax semitorquatus* and rosy-faced lovebirds *Agapornis roseicollis* take over the nests of sociable weavers for breeding purposes (Maclean 1973). Use of sparrow-weaver nests by other bird species could affect the survival of the former.

When birds build nests, more than one environmental constraint is often involved in determining the nest site. Some eagle species often nest on cliffs and not in trees, presumably as an adaptation against predation (Brown & Amadon 1968). However, this nest site preference causes chicks to be exposed to a prohibitive amount of shade and cold. Mosher & White (1976) found that golden eagle (*Aquila chrysaetos*) nests are situated on cliffs where the chicks are exposed to the maximum amount of solar radiation, and that this improves survival in a cold environment. Golden eagle nest placement is thus a response to predation as well to ambient temperatures at the nest site.

Nests often yield more advantages to birds than just a safe environment for the eggs and chicks. White *et al.* (1975) and Bartholomew *et al.* (1976) postulated that sociable weaver nests are adaptations through which en-

ergy loss in thermoregulation is minimised during cold winter nights. In ploceine weavers, nests play an important role in pair formation (Crook 1964). Care should be taken when considering benefits resulting from nesting, as a preadaptation or effect could easily be mistaken for an adaptation. Based on the above considerations, the following questions were investigated:

1. How much time do sparrow-weavers spend in nest-building activities, and what is the relative contribution of each age/sex class within a sparrow-weaver group? If the immature age class does a significant amount of nest building, the possibility of altruism arises.

2. How long do nests remain intact after completion?

3. To what extent do sparrow-weaver roost nests affect the nocturnal micro-environment of roosting birds and how do breeding nests affect the micro-environment of incubating or nestling birds during the heat of the day?

4. How often do other bird species make use of the large number of nests that sparrow-weavers build?

The information presented in this chapter was obtained in the Bloemhof study area. The Percy Fitzpatrick Institute of African Ornithology (PFIAO), University of Cape Town, kindly made available some unpublished data that had been collected near Kimberley, 160 km south-west of Bloemhof.

METHODS AND RESULTS

Choice of nest site and number of nests per group

As a first step it was necessary to determine whether sparrow-weaver nests at Bloemhof were built on a particular side (e.g. the northern side

or southern side) of nest trees. A survey of nest site orientation, and other possible parameters influencing the choice of nest sites, was conducted as outlined below. The survey included 4170 nests, built in 167 nest trees and belonging to 105 sparrow-weaver groups.

Condition of nests and orientation of nest sites: In an area where sparrow-weavers were relatively common, a systematic search was made for nest trees. This area included the study area where behavioural observations were made. At every nest tree, the following information was collected from each nest:

1. Nest orientation, i.e. the direction in which the entrance pointed. Roost nests had two entrances at opposite ends of the nest, in which case the most horizontally-situated entrance (most often used by sparrow-weavers) was used as a reference point. A prismatic compass was used to determine nest orientation.

2. Nest site orientation, i.e. the side of the tree on which the nest was located. The nest was aligned with the centre of the nest tree foliage and the direction from the nest to the centre of the foliage was determined using a prismatic compass. This reading was corrected by 180° to give a bearing from centre-of-foliage to the nest.

3. Height above ground, measured in decimetres.

4. The condition of the nest on a scale of 1 to 5 (1=very good condition, 5=collapsed, disintegrated).

5. The building stage of the nest on a scale of 1 to 5 (1=being built, 5=very old). A new, completed nest had a condition code of 1 and a building stage code of 3.

In both the Bloemhof and the Kimberley areas nests tended to be located on the SW side of trees (Figure 15), on average having an orientation of 210° with respect to north. This distribution differed significantly from random (χ^2= 1145; df=2; p<0,002). The orientation of roost nest sites did not differ significantly from that of breeding nests (χ^2= 22,2; df=35; p<0,5). The site orientation of newly-built nests also did not differ sig-

FIGURE 14. A sparrow-weaver nest tree at Bloemhof, showing the clumped distribution of the nests.

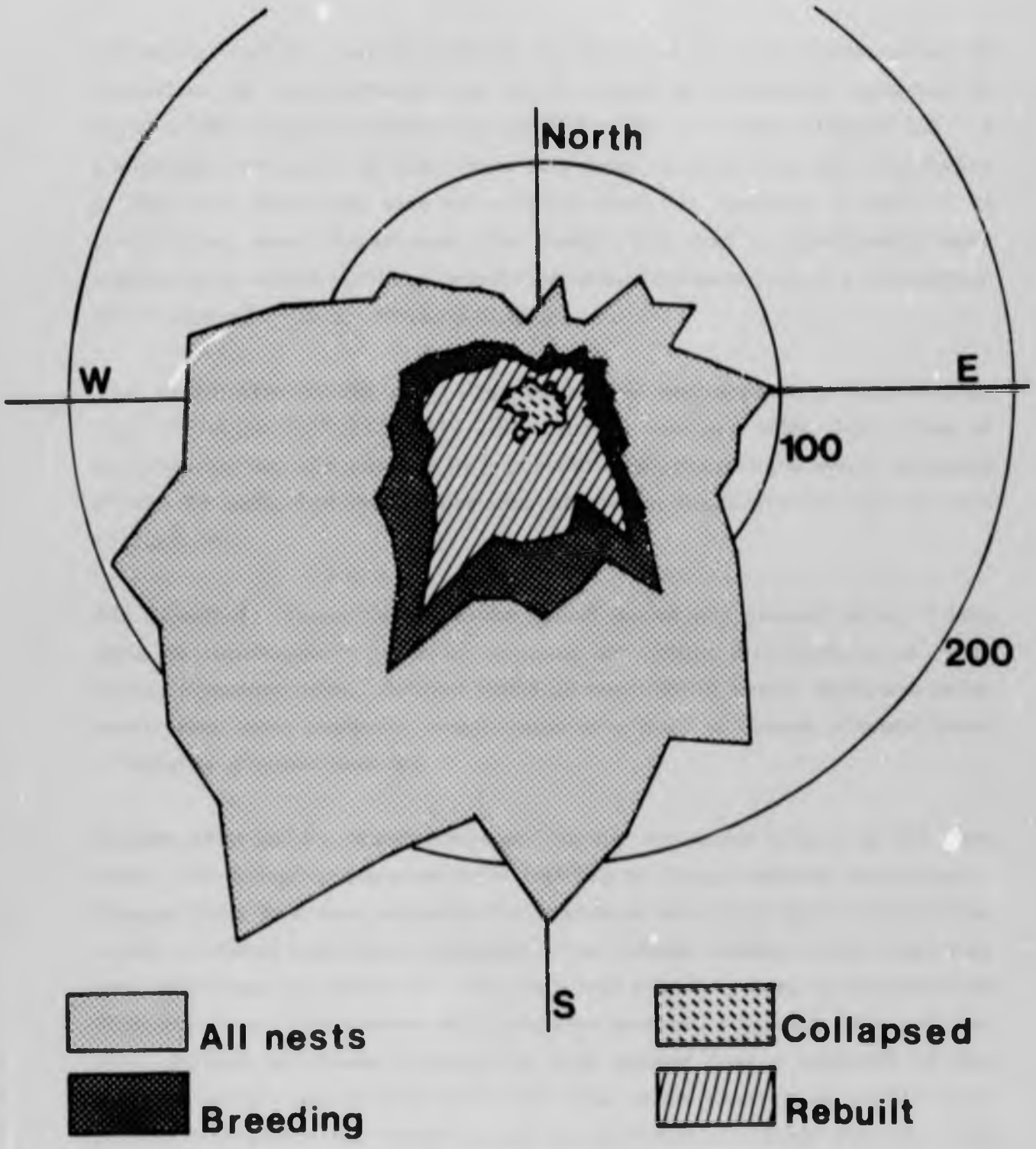


FIGURE 15. Orientation of 4170 nest sites at Bloemhof. The number of observations in each direction is indicated relative to the concentric scale. Nests of all categories, including collapsed and rebuilt nests, are concentrated on the SW side: this indicates a preference for nest sites on the SW sides of trees.

nificantly from the overall pattern at Bloemhof; in fact nests under all conditions of deterioration and at all stages of completion occurred in significantly larger numbers on the SW side of trees (Figure 15). A nocturnal survey of 16 nest trees was made to determine the orientation of the roost nest sites that are actually used for roosting. A total of 64 such nests were found and the roost sites had a significantly more southerly to south-easterly orientation when compared to the orientation of all nests (χ^2=23,2; df=11; p<0,05).

The orientation of 568 nest sites were also measured near Middelburg, Cape Province (31° 28'S, 25° 2'E), during January 1986. Nest sites at this locality was distributed in a bimodal way: nests were mostly situated on the SE side, but many were also placed on the northern side of trees (Figure 24).

At Bloemhof, nests tended to be about 3m above ground level. There were no significant differences between the height distributions of roost nests, breeding nests, defunct nests or newly-built nests. Although many small trees were available, nests were only built in *Acacia erioloba* trees of heights greater than 3m.

Shelter afforded by nearby foliage: During the above survey of 167 nest trees, the following measurements relating to foliage density were made Foliage close to a nest protects the nest from wind and sun, a factor that could influence nest site orientation. The foliage density of the nest tree was calculated by means of a 6m long rod that had been graduated into 10cm divisions. The number of boundaries between adjoining 10cm sections were counted as viewed through the tree foliage from a distance of 20m on the north side of the nest tree. The mean number of visible 10cm section boundaries per metre served as an index of foliage density. The continuity of the tree canopy foliage was classed as continuous or broken and disjunct. Measurements were made of the tree height, canopy height, canopy width and the height of the densest canopy foliage. The number and distance of trees within 100m of the observed nest tree was recorded for each quadrant around the nest tree.

A multiple correlation was performed on the foliage and orientation data collected at each nest tree. Neither the nest site orientation nor the variance in nest site orientation was significantly correlated with either

the foliage density of the nest tree itself or the proximity of nearby trees. Nest site orientation was also not significantly correlated with any of the physical dimensions of the nest tree. Nests tended to be sited 1,5 to 2m below the level of the densest foliage of the nest tree.

Number of nests per group: The number of nests of a sparrow-weaver group and the ratio of number of nests/bird are important factors influencing the survival of a group (Chapter 5). The relationship between the following three factors was analysed: 1) total number of nests in a group, 2) number of birds in a group and 3) the ratio of nests/bird within each group. Each group had many more nests than the number of birds within the group. Table 11 shows that the number of nests per group and per bird at Bloemhof is higher than at Daan Viljoen.

A more detailed analysis, involving known-size groups, was made of the number of nests available to each individual sparrow-weaver at Bloemhof. Data on the number of birds belonging to a group and the number of intact nest structures in their nest tree were obtained for 32 groups over two years, resulting in a total data set of 38 group years. A significant correlation existed between group size and number of nests in their nest tree for each group year (Spearman $r=0,662$; $p<0,0001$). The 38 data points (Figure 16) included 1134 usable nest structures and 127 sparrow-weavers, suggesting a nest/bird ratio of 8,92. However, the slope of the regression equation for this data yields a somewhat lower value: 7,84 ($t=4,741$; $p<0,0001$). This suggests that the ratios of nests/bird as given in Table 11 (calculated using total nest and bird numbers) are higher than the true values. The difference between the ratios for Bloemhof and Daan Viljoen is, however, so large that the above discrepancy does not influence conclusions that follow.

The ratio of nests/bird at Bloemhof was in turn strongly correlated with the total number of nest structures in the nest tree (Spearman $r=0,746$; $p<0,0001$). Thus, trees with many nests offer more nests/bird than trees with few nests. Large groups thus also tend to have more nests per bird compared to small groups. The regression constants for this relationship suggest that groups start off with 2,5 nests/bird and that each additional batch of 10 nests increases the ratio by two nests/bird, so that a colony with 60 nests has a ratio of 14,5 nests/bird. The correlation between

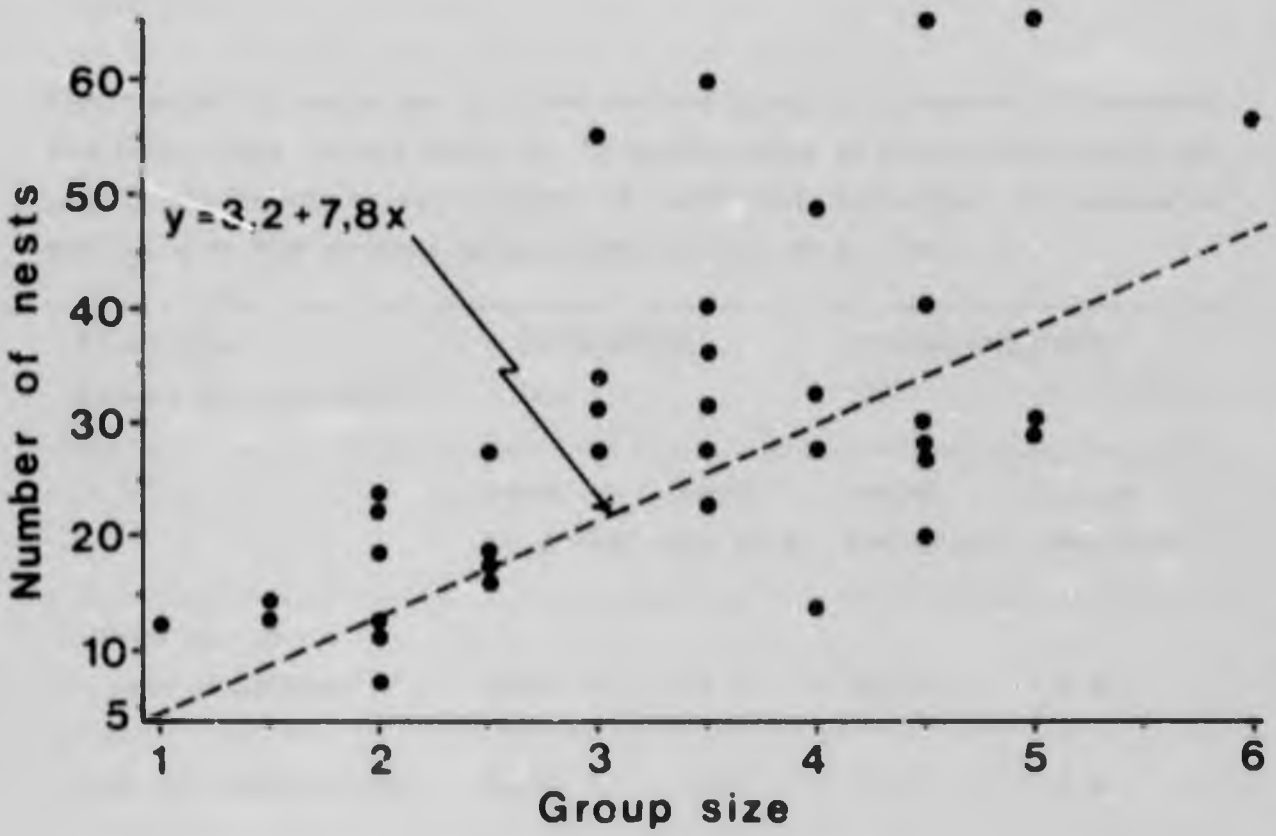


FIGURE 16. Number of nests in the nest trees of sparrow-weaver groups of different sizes. The mean annual values, calculated from six-monthly surveys, are indicated. The linear regression for the data is not entirely realistic: a higher order relationship may be more appropriate.

TABLE 11

The number of nests per sparrow-weaver group as observed at Bloemhof and Daan Viljoen Game Reserve. Breeding nests at Daan Viljoen were not specifically counted. The number of nests per individual is calculated according to the average group sizes arrived at in Table 6.

Study site	BLOEMHOF		DAAN VILJOEN	
Sample size(groups)	105		30	
	nests per group	nests per bird	nests per group	nests per bird
Total no. of nest structures:	38,8	11,4	27,5	5,5
No. of usable nests:	33,7	9,9	17,8	3,6
No. of breeding nests:	5,0	1,5	-	-

group size and nest/bird ratio was, however, not statistically significant (Spearman r=0,144; p<0,39).

Individual sparrow-weavers from large groups collected grass stems at a faster rate than those of small groups (Figure 17). A Kruskall-Wallis test on the rank sums of the grass collecting rates used in this figure showed, however, that the illustrated differences are not statistically significant (χ^2=3,06; df=3; p<0,38); this was due to the wide variances and relatively small sample sizes. The above data, however, suggest a general trend: large sparrow-weaver groups have large numbers of nests, large nest/bird ratios and high nest building activity.

Rate of nest deterioration

The physical environment is assumed to be the major cause of nest deterioration; the process is hastened by a lack of nest maintenance. The rate at which nests deteriorate was determined by using the data from the 167 initially-surveyed nest trees. The 18 nest trees with the widest variance in nest site orientation were selected to obtain a sample of nests which were placed relatively evenly around the circumference of the trees; these 18 trees had 783 nests. The nests were divided into two groups: north-facing (358 nests) and south-facing (424 nests). The condition of each nest was noted as described earlier. This survey was repeated two years after the initial survey. The physical condition or disappearance of each nest was noted. The two-yearly survival rate of 40,9% for north-facing nests differed significantly from the equivalent figure of 54,1% for south-facing nests (Wilcoxon U=57, n=6, m=6, p<0,002).

The effect of nests on the thermal microclimate

Burger & Gochveld (1981) suggested that sparrow-weaver nests are beneficial in that they create a micro-environment that causes the birds

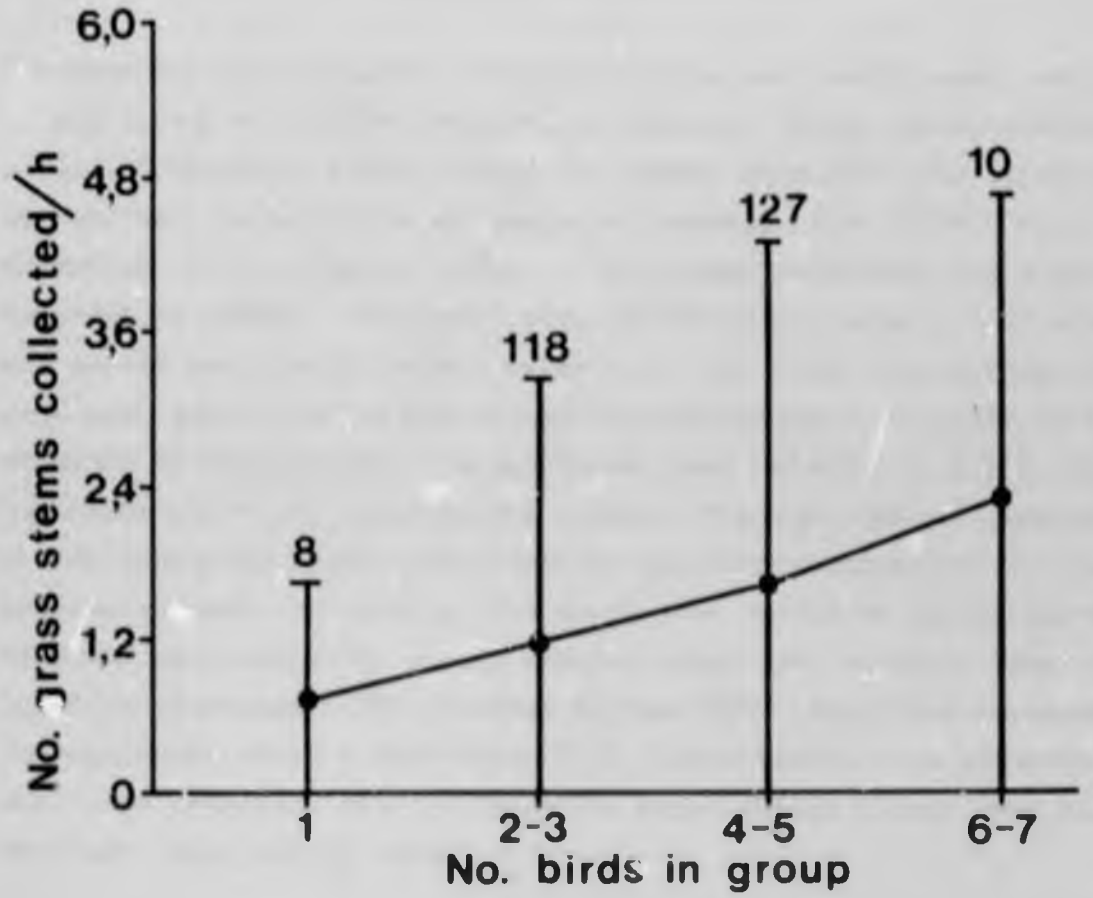


FIGURE 17. Nest building activity of individuals in different-sized sparrow-weaver groups at Bloemhof, expressed as the number of grass stems woven into nests per observation-h. Monthly means and sample sizes are indicated by dots and numbers, respectively, while the standard deviation of observations in each class is indicated by the bars (which all cross the abscissa). Members of large groups tend to spend more time in nest building.

to spend less energy on thermoregulation in a hot environment. If this were the case, one should find that: a) nests have a significant effect on the temperatures that sparrow-weavers experience and b) the savings in thermoregulatory energy are biologically significant. In order to quantify the effect that roost nests have on sparrow-weaver thermoregulation, the following methods were used.

Temperature measurements: Temperatures in and under nests were recorded using four AD590 temperature sensors. These were connected to a Hewlett-Packard HP41C calculator which monitored the sensors and stored their temperatures on magnetic cassette. The PFIAO data from Kimberley were collected using a YSI telethermometer and associated temperature probes. Two nests were monitored at a time in both studies; one sensor was placed inside the nest on the inner roof surface of the nest wall, while another was placed immediately below the nest in a permanently shaded position. Temperatures were recorded to 0,1°C. Breeding nests are mainly used during summer; the high diurnal temperatures at that time could possibly be a thermoregulatory constraint on incubating sparrow-weavers or chicks. Extremely low nocturnal temperatures at Bloemhof occurred only during winter, when the ambient temperature regularly approached 0°C (Weather Bureau 1982). Nocturnal temperatures during summer did not fall below 15°C. Consequently, two separate data sets were collected, one for breeding nests during summer and another for roost nests during winter.

During summer, the effect of orientation in influencing diurnal breeding nest temperatures was determined by monitoring two nests on opposite (NE = sunny and SW = shady) sides of a tree. Differentials between the internal and ambient temperatures of each nest and between the internal temperatures of the two nests were calculated. Nests on the NE side of trees were not exposed to the late afternoon sun because of shade offered by the foliage. For determining the *maximum* effect of foliage on nest temperature, two breeding nests of similar construction were removed from their original sites. One nest was placed on an exposed branch on the north side of a nest tree where it was exposed to the sun for the whole day. The other nest was placed at an identical height below the dense tree canopy, so that it would not be fully exposed to the sun at any time. The difference in the internal temperatures of these two nests was monitored from 10h00 to 14h00 on a day during which the ambient

temperature reached 35°C. The two nests were switched and the procedure repeated the following day.

During winter, two roost nests were monitored at a time, on the NW and SE sides of the same tree. Sensors were placed as during summer. Roosting birds fluff their feathers in winter, and therefore touched the sensor in the nest. Roost nests on the SE side of the tree were not exposed to the late afternoon winter sun because of shade offered by the foliage.

As far as diurnal temperatures are concerned, the greatest amount of thermal stress on birds in breeding nests would occur during the months December to February, when the diurnal ambient temperature is highest (Weather Bureau 1982). Figure 18 shows that the temperatures inside breeding nests on different sides of a nest tree differed very little, usually being within 2°C of one another. The PFIAO data from Kimberley were recorded on an exceptionally hot day when the ambient temperature rose to 40°C, and even under those circumstances the nest to ambient differential of a north-facing nest remained within 3°C of that of a south-facing nest. There was no significant regression between the ambient temperature and differential temperature of north- and south-facing breeding nests (t=0,34 df=1 for intercept; t=1,46 df=1 for slope)(Figure 18). The breeding nests placed below the tree canopy and on totally exposed branches, differed by a mean of only 0,96°C during the period 10h00 to 14h00, during which period the ambient temperature exceeded 31°C. These data suggest that solar radiation has a very small effect on diurnal nest temperatures.

During winter, the roosting birds perched in a hunched posture with their heads tucked back between the wings and with their feathers fluffed: sometimes they touched the temperature sensor. Consequently, a high amount of scatter characterises the ambient to nest temperature differential (Figure 19). The nest temperature was usually above ambient temperature, but usually not more than 6°C higher. A negative regression with a slope significantly different from zero (t=20,2; df=1; $p<0,001$) predicts that at 0°C ambient temperature, the nest is 4,61°C warmer. When individual nest temperature traces were compared with the ambient temperatures at the time, an increasing differential between these two temperatures was often evident as the night became colder (Figure 19).

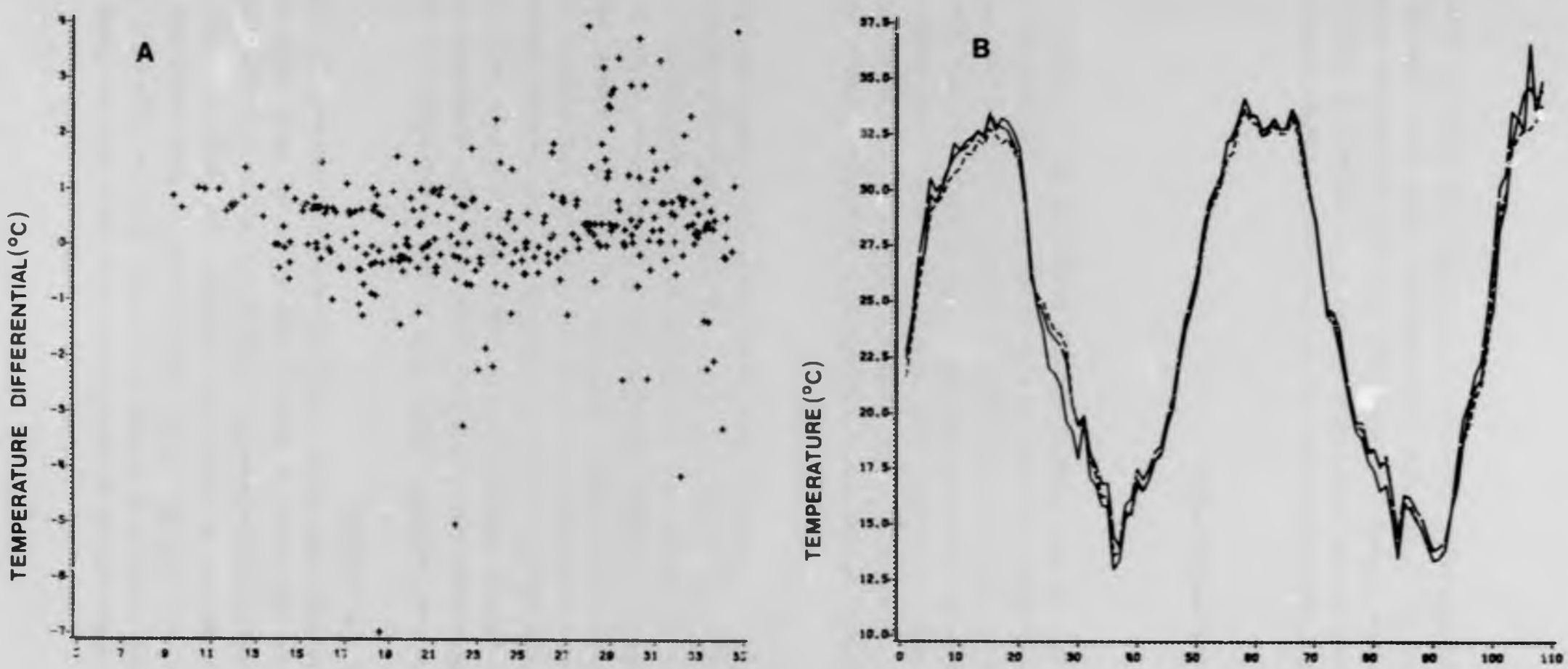


FIGURE 18. Daytime breeding nest temperatures during summer. The temperature differential between north-facing and south-facing nests is related to ambient temperature in A. A 48h trace of the nest temperatures of a north-facing nest (short dashes), a south-facing nest (solid trace) and ambient temperature (long dashes) is shown in B. There are no significant differences between the temperatures in these nests.

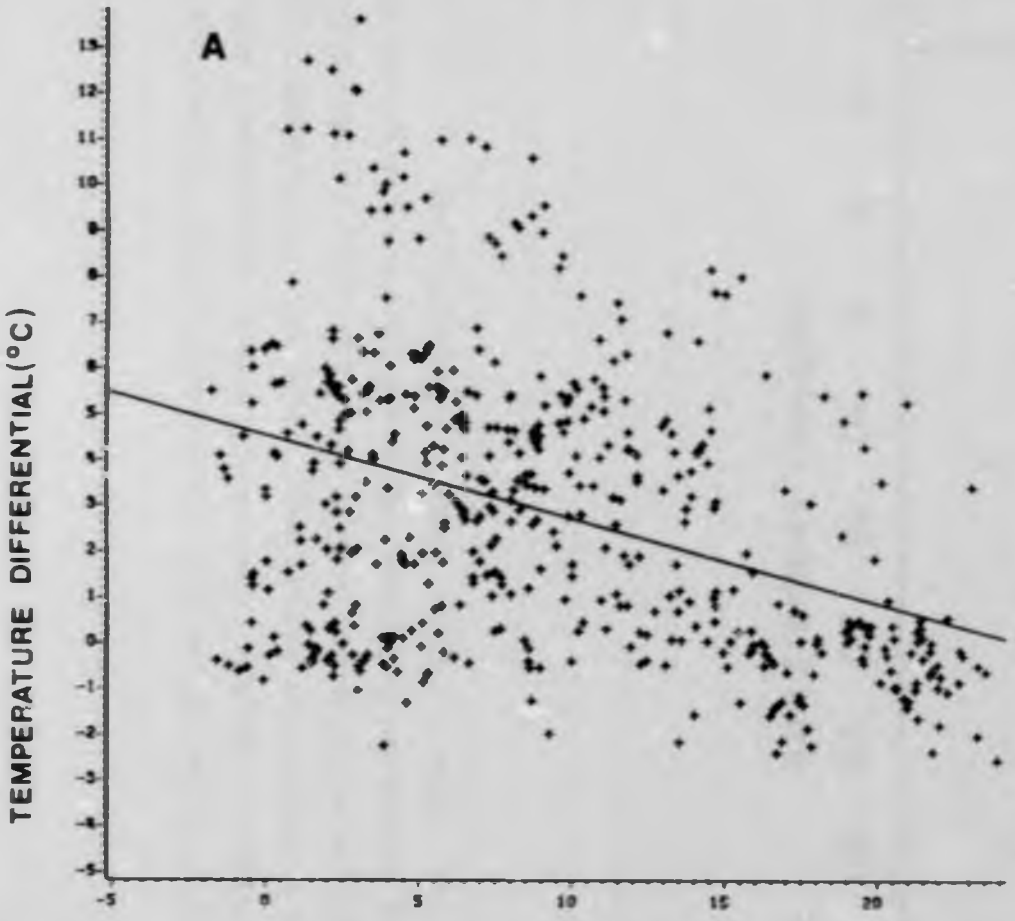
The nest temperatures of west-facing roost nests did not differ significantly from those of SE-facing nests which were not exposed to the late afternoon sun ($t=0,62$; $df=8$); both groups of nests conformed to the results presented in Figure 19. Although the large variation in the internal roost nest temperatures makes interpretation of the data difficult, no evidence was found to indicate that SE-facing roost nests cool at a faster rate than west-facing nests. No nocturnal temperature data from Kimberley are available.

Sparrow-weaver metabolic rates: The oxygen consumption of a group of 20 sparrow-weavers was determined under laboratory conditions using the open-flow method (Decopas & Hart 1957). Measurements were made at 5°C intervals over the range -5°C to 40°C. At each selected temperature, the oxygen consumption of each of ten birds was measured for a 20 min period. During measurement, each bird was kept in a wooden enclosure (volume about 1,5 litres) from which light was excluded as far as possible. Flow of vapour-free air through the box approximated 1 l/min.. Measurements were taken at night between 20h00 and 06h00, when sparrow-weavers normally roost, and experimental birds were presumed to be sleeping.

The laboratory measurements indicate that the thermoneutral zone for these birds extends from approximately 10°C to 30°C (Figure 20). Presumably these conditions are similar to those experienced by a sparrow-weaver roosting in the open. The resting metabolic rate within this range is about 2,5 ml O_2/g/h or 0,0502 kJ/g/h. Below 10°C the oxygen consumption increases at 0,13 ml O_2/g/h/°C, so that the resting metabolic rate at -4°C rises to about 6 ml O_2/g/h (0,121 kJ/g/h).

Humidity in breeding nests

Because sparrow-weavers occur in semi-arid areas, humidity effects might be important for the maintenance of the water balance of these birds. No data were collected at Bloemhof, the only quantitative information being among the PFIAO data from Kimberley. Data were collected using a YSI telethermometer connected to dry bulb, wet bulb and black bulb



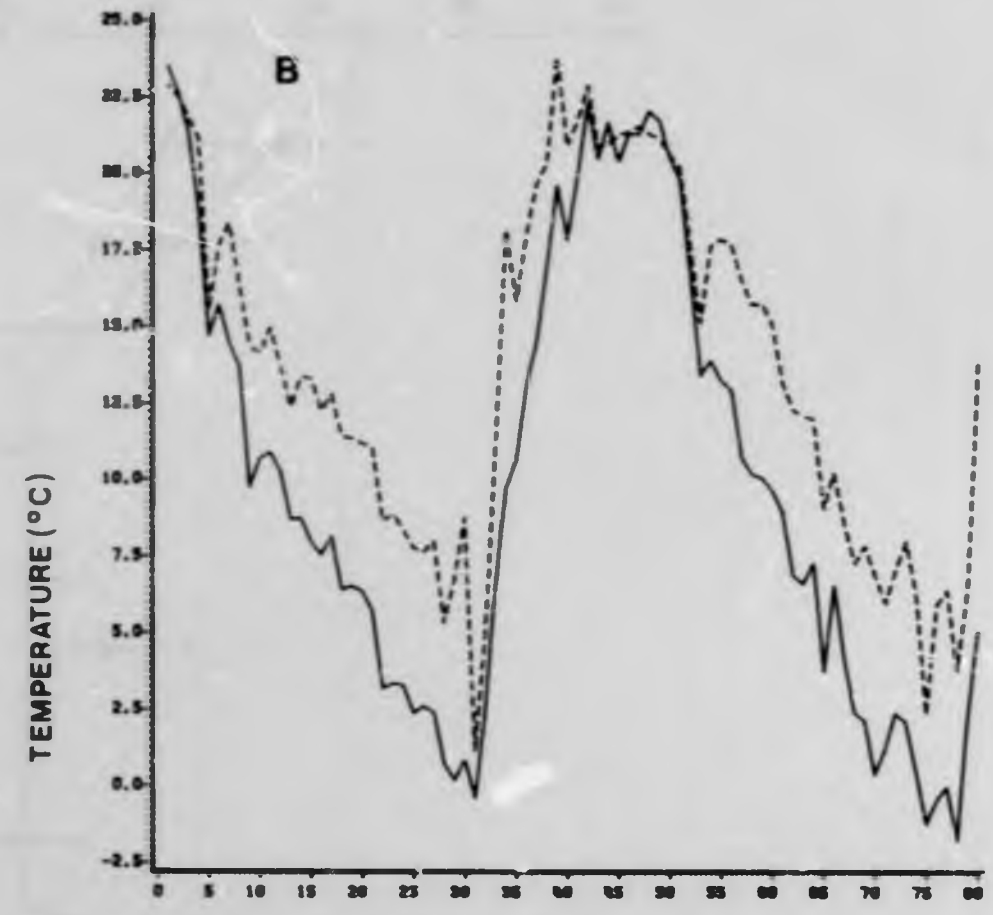


FIGURE 19. Nocturnal roost nest temperatures during winter. The relationship between ambient temperature and the nest-to-ambient differential is shown in A. The large amount of scatter could be due to the varying, but close, proximity of the roosting sparrow-weaver which often fills the whole nest while roosting. A trace of these temperatures over a 48h-period shows how the nest-to-ambient temperature differential often increases as the ambient temperature dreps (B). Nest temperature is indicated by a broken line and ambient temperature by a solid line.

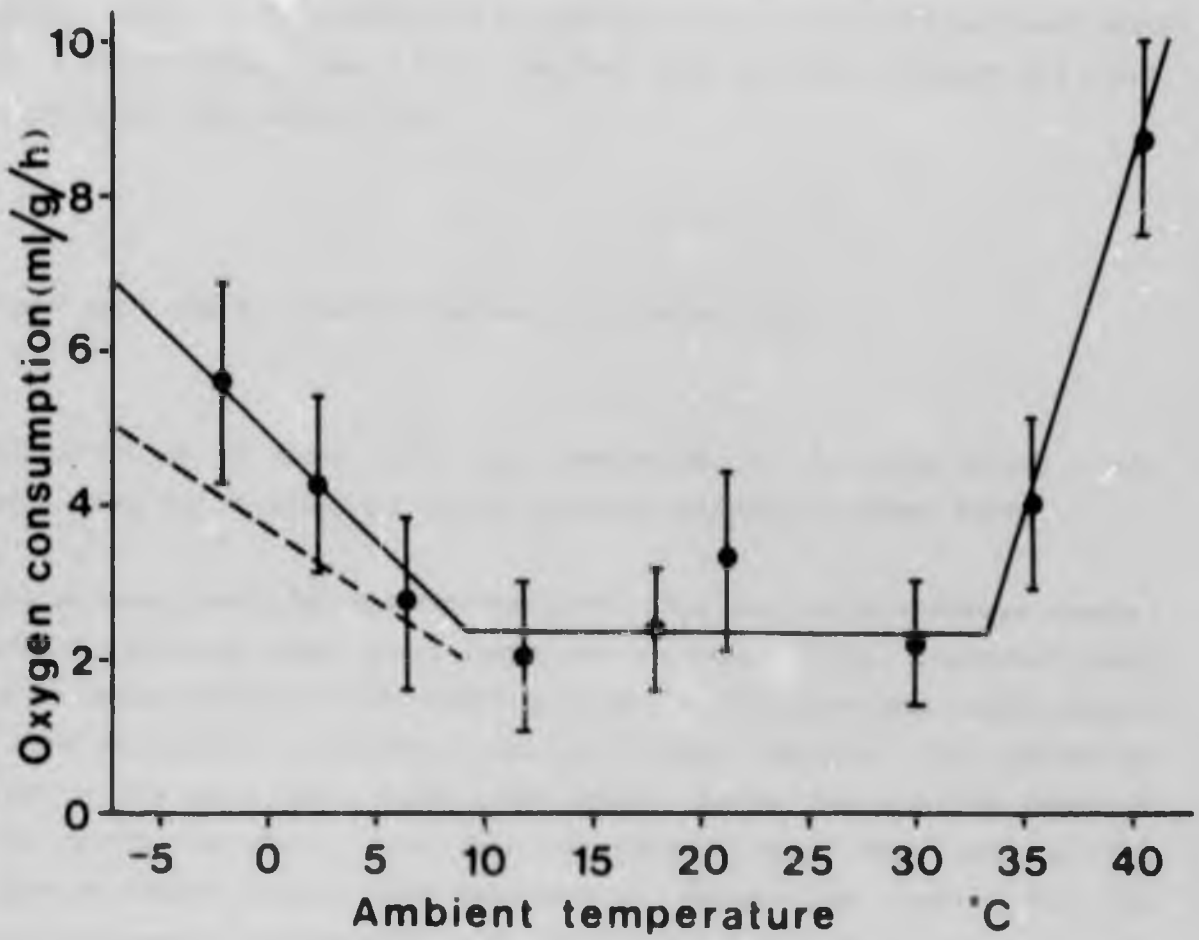


FIGURE 20. Sparrow-weaver resting metabolic rates. The oxygen consumption of sparrow-weavers under laboratory conditions (solid line) indicates that the lower and upper critical temperatures are about 10°C and 33°C, respectively (see text). The broken line indicates the calculated oxygen consumption of sparrow-weavers roosting in nests that conform to the nest-to-ambient temperature differentials indicated in Figure 19.

thermometers in each nest. The humidity in a north-facing nest was compared with that in a south-facing nest on a day when the ambient temperature rose to 40°C, and it was found that the differential in relative humidity between the two nests did not exceed 7% (Figure 21). If solar radiation affected relative humidity through increased nest temperature, the relative humidity in the north-facing nest would be lower than in a south-facing nest. From the few data available (Figure 21), this expectation was not fulfilled.

Roost nest use by sparrow-weavers and other birds.

Nocturnal use of roost nests was determined by recording which nests were used for roosting by either sparrow-weavers or other birds.

Use of roost nests by sparrow-weavers: Sparrow-weavers always roosted singly. Because their roost nests are so conspicuous, predation could be an important factor for roosting birds; in this case one could expect a bird to roost in a different nest each night. However, they tended to roost in the same nests night after night. During two periods (each of one month duration: July and February), roost nest use by two sparrow-weaver groups was recorded on consecutive nights. For 273 sparrow-weaver roost-nights, only 17 changes in the choice of roost nests were observed. This means that sparrow-weavers generally change from using one roost nest to another every 16 nights. The use of roost nests by two individuals from each of the two sparrow-weaver groups during a two week period in summer is depicted in Figure 22, and is typical of the data that were collected. Switches of roost nests occurred at such a low rate that they cannot be considered to be adaptations against predation.

Other bird species roosting in sparrow-weaver nests: The use of nests of active sparrow-weaver groups by other species during 980 non-consecutive nest-nights is depicted in Table 12. At least five species roost in sparrow-weaver nests (but in low densities, as depicted in Table 12). In contrast, when a sparrow-weaver group migrated or died, leaving a vacant nest tree, the nests were rapidly used for roosting by other

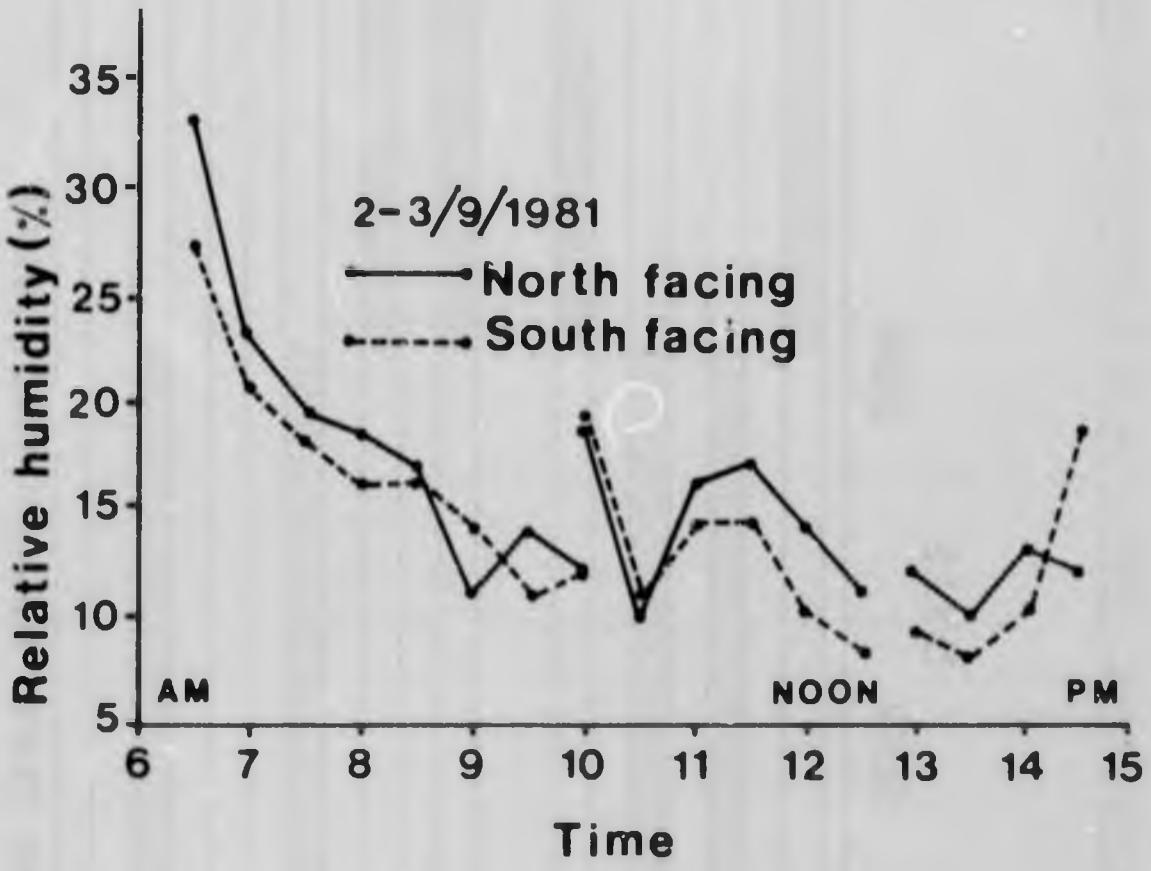


FIGURE 21. Humidity measurements in a north-facing and a south-facing nest. The south-facing nest tended to have a slightly lower relative humidity, being mostly within 3% of the corresponding figure for the north-facing nest. The information was collected at Kimberley on a day when the ambient temperature reached 40°C (PFIAO data). One expects that the humidity in the north-facing nest (which is exposed to the sun) would be lower than in the south-facing nest.

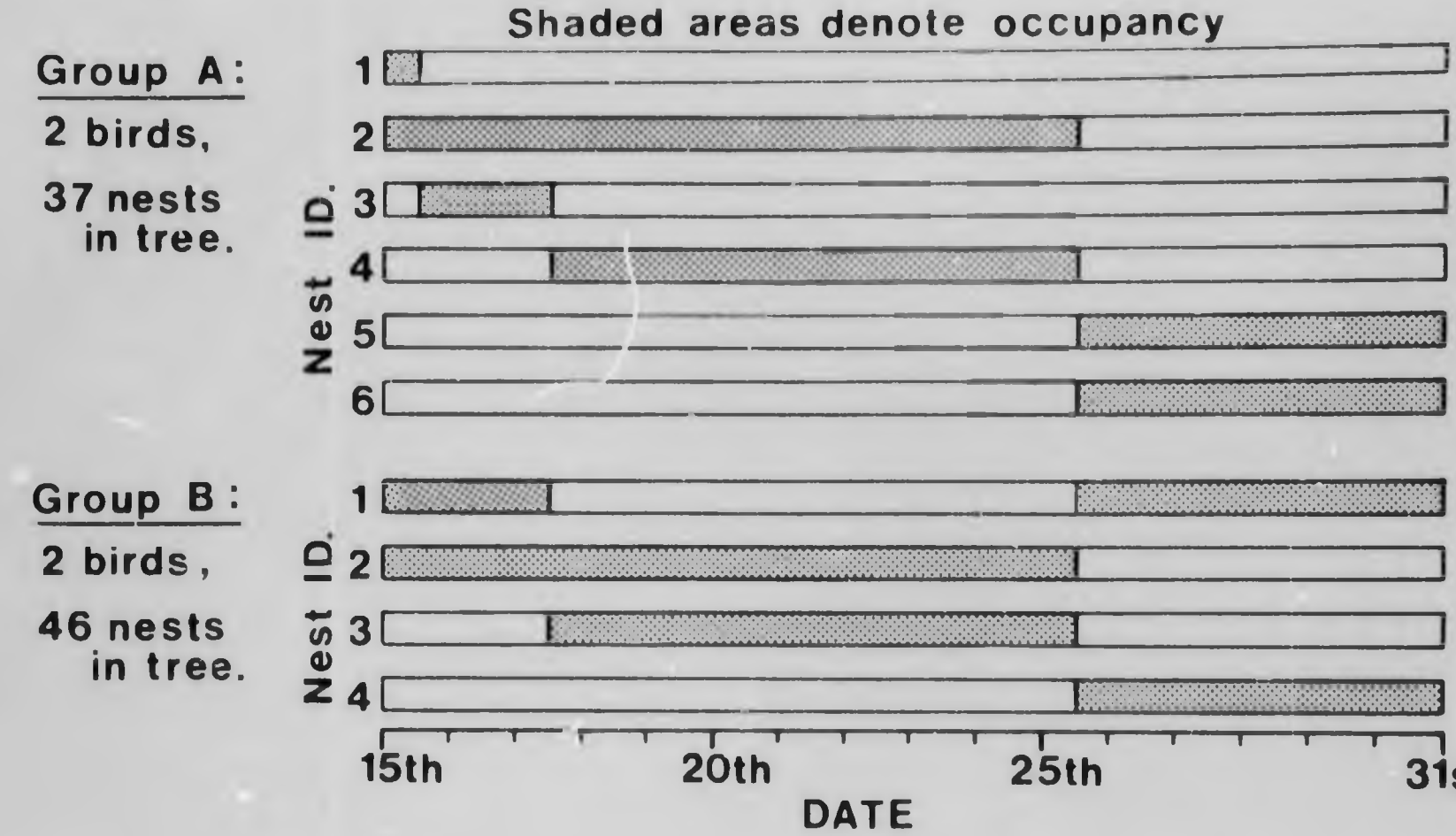


FIGURE 22. Sparrow-weaver roost nest use. Nest occupancy by two sparrow-weaver groups over a period of two weeks during January 1984, is shown. This is representative of the total dataset. Changes in the use of roost nests were infrequent.

TABLE 12

Bird species that use sparrow-weaver nests for roosting. The species in this table were observed when 980 sparrow-weaver nests at Bloemhof, in trees used by sparrow-weaver groups at the time, were searched nocturnally during the period September 1983 to February 1984.

Species		No. birds observed
Black-collared Barbet	*Lybius torquatus*	3
Grey Tit	*Parus afer*	8
Red-headed Finch	*Amadina erythrocephala*	6
Scaly-feathered Finch	*Sporopipes squamifrons*	8
Black-cheeked Waxbill	*Estrilda erythronotos*	7

species, among which the red-headed finch, *Amadina erythrocephala*, was conspicuous. Other species did not use sparrow-weaver nests in occupied nest trees to a large extent. This could indicate that the interspecific aggression noted in Chapter 2 is efficient in stopping other species from roosting in sparrow-weaver nests.

Nest-building contributions by sparrow-weaver age/sex classes:

The most accurate and practical way of quantifying co-operative nest-building activity is to count the number of grass stems that an individual builds into nests. By comparing this figure for all the members of a group, the relative nest building activity of each age/sex class can be calculated. The number of grass stems collected per observation hour was, therefore, determined on a monthly basis through focal animal sampling of each individual. In order to interpret this information in terms of complete nests (to arrive at a number of nest equivalents built by each individual), a knowledge of the number of grass stems/nest is necessary.

The number of grass stems in four roost nests was determined by taking the nests apart and counting the number of grass stems. The total masses of the nests were divided by the total number of their constituent grass stems to arrive at a mean grass stem mass. The masses of 22 more roost nests were determined and the mean number of grass stems per nest was estimated using the data from the four dismembered nests.

The four dismembered nests contained a total of 6950 grass stems, yielding 1737 stems/nest and a mean grass stem mass of 90,63mg. The mean mass of the 32 nests was 156,2g (σ=44,05g), implying that the average nest contains 1621 grass stems.

Contributions towards nest-building activity: Sparrow-weavers were building nests during 738 of 16487 instantaneous focal animal samples, indicating that these birds spend about 4,5% of their time in nest building. I postulate that this overall figure is much higher than that for the Ploceinae or Passerinae. Table 13 shows the contributions of different

age/sex classes towards total nest-building activity. All the sparrow-weaver age/sex classes participated in nest-building. The data on grass-collecting events were analysed by means of separate Kruskall-Wallis tests on the rank sums of the grass collecting rates of birds as classified by age, sex, group size and month of year. Although the difference is not statistically significant (χ^2=0,24 df=1, p<0,63), immature sparrow-weavers contributed more towards nest-building (3,21 grass stems brought to the nest tree per observation hour) than adults (2,63 stems/h). Juvenile sparrow-weavers contributed significantly less toward nest building than the other age groups (χ^2=4,06; df=2; p<0,05), while there was no significant difference between the contributions of the two sexes of all ages (χ^2=0,77; df=1, p<0,37). Group size was not significantly correlated with the relative contribution of any age/sex class.

DISCUSSION

Why [illegible]sts on one side of the tree?

The fact that the site orientation of newly-built nests is very similar to that of old nests, suggests that sparrow-weavers actually prefer to build their nests on the southern aspect of the trees. If a high proportion of collapsed nests had been found on the NE side, it would have meant that differential, weather-induced erosion was responsible for the observed uneven distribution. Several other authors have also noted this preference of sparrow-weavers (Collias & Collias 1964, Mitchell 1966, Mendelsohn 1968, Ferreira *et al.* 1972 and Burger & Gochveld 1981). The following hypotheses could be put forward to explain the observed nest site specificity:

1. The nests are placed on the side of the tree that receives the least sunshine. This would ameliorate the heat load on tne nest while sparrow-weavers make diurnal use of nests, e.g. incubation (Burger & Gochveld 1981, Mendelsohn 1968). The effect of nest placement would be to cool breeding nests.

TABLE 13

The contribution of sparrow-weaver age/sex classes towards nest-building activity at Bloemhof. The estimates on number of nests built/yr assume that each nest consists of 1621 grass stems and that each sparrow-weaver has 3650h to collect grass stems each year (Details in discussion section of this chapter).

Age/sex group		MALE	FEMALE
Adults:	Observation time(h)	218,5	177,3
	Stems collected/h	3,0	2,2
	Nests built/yr	6,8	5,0
Immatures:	Observation time(h)	66,3	31,6
	Stems collected/h	3,1	3,4
	Nests built/yr	7,0	7,7
Juveniles:	Observation time(h)	46,8	4,8
	Stems collected/h	0,9	3,5
	Nests built/yr	2.1	7,8

2. The nests could be placed on the side of the tree that exposes the nests to the afternoon sun. This could warm the nests immediately before a cold night, which would result in the birds having to spend less energy in thermoregulation. The effect of nest placement would be to heat both roost nests and breeding nests.

3. The nests are placed on that side of the tree that receives the least ultraviolet radiation, a factor that could be important in determining the speed at which nests weather and decompose. The effect of nest placement would be to prolong the life of each nest.

4. The nests are placed on the side of the tree which is the least exposed to wind, another factor that could have an important influence on nest weathering and decomposition (Collias & Collias 1964, Mitchell 1966, Mendelsohn 1968). The effect of nest placement would also be to prolong the life of each nest.

5. The above hypotheses involve the designation of nest placement behaviour as an evolved adaptation that would have a direct effect on the fitness of the birds. A fifth hypothesis is that the nest placement pattern is an incidental effect of unrelated processes.

The following sections will consider each of the above hypotheses in turn. The fact that sparrow-weaver nest placement has been studied by a number of people over a very large geographical area facilitates the interpretation of the observed data. When data from the studies by Collias & Collias (1964), Mitchell (1966), Mendelsohn (1968), Ferreira *et. al.* (1972) and Burger & Gochveld (1981) are added to this one, data from eight localities, encompassing latitudes from the equator to 31° South are available. If the observed nest placement was a response to solar radiation, one would expect that the nest placement pattern would differ between localities where characteristics of solar radiation differed. Data from the above five authors and from the present study indicate that nest placement correlates negatively with latitude (Kendall's $r=14$; $n=7$; $p<0.035$). Nests at localities closer to the equator are situated on the NW and W side, whereas nests at localities further from the equator are situated on the SW side of trees. This suggests that the trajectory of the sun does indeed affect nest placement. If nests are situated on the sides of trees that receive the least sunshine, one would expect nests

to be placed around the circumference of nest trees at the equator (Kenya) where all sides of a tree receive an equal amount of solar radiation. However, Collias & Collias (1964) reported that Kenyan sparrow-weaver nests have a very pronounced tendency for being situated on the western sides of trees: this evidence strongly contradicts the solar radiation hypothesis. The observed correlation between nest site and latitude cannot be correlated with any known geographical phenomenon apart from solar radiation. Consequently one should investigate the possibility that the above correlation is a fortuitous effect of unrelated processes.

The effect of solar radiation on nest temperature appears to be minimal (Figure 18). The observed diurnal nest temperatures fall within the thermoneutral zone for white-browed sparrow-weavers, so that even if the temperature differential between north-facing and south-facing nests was larger, the energetic cost to sparrow-weaver thermoregulation would be minimal. The preferred orientation of nests does not conform to the hypothesis of nest placement reducing diurnal nest temperature. The highest ambient temperatures normally occur after 12h00 (Weather Bureau 1982). If any nests were to become overheated, it would be those with a western aspect because they are exposed to solar radiation during the relatively high ambient heat of the afternoon. In the Bloemhof study area, breeding commenced during July when the supposed limitation of high nest temperature would not apply. Unless extreme selective forces operated during speciation, the evolution of an adaptation that effectively lowers the breeding nest temperature during part of the breeding season, seems improbable. There is no evidence of such forces operating at present. For these reasons the hypothesis concerning lowered breeding nest temperatures is rejected.

The temperatures in west-facing roost nests did not differ to any large extent from those of SE-facing roost nests immediately before entry of the sparrow-weavers in the evenings. There was also no evidence that a west-facing nest cooled at a slower rate than a SE-facing nest. The hypothesis concerning heightened roost nest temperatures must therefore also be rejected.

All hypotheses involving the effects of temperature on nest placement have been discarded. The hypothesis concerning ultraviolet radiation

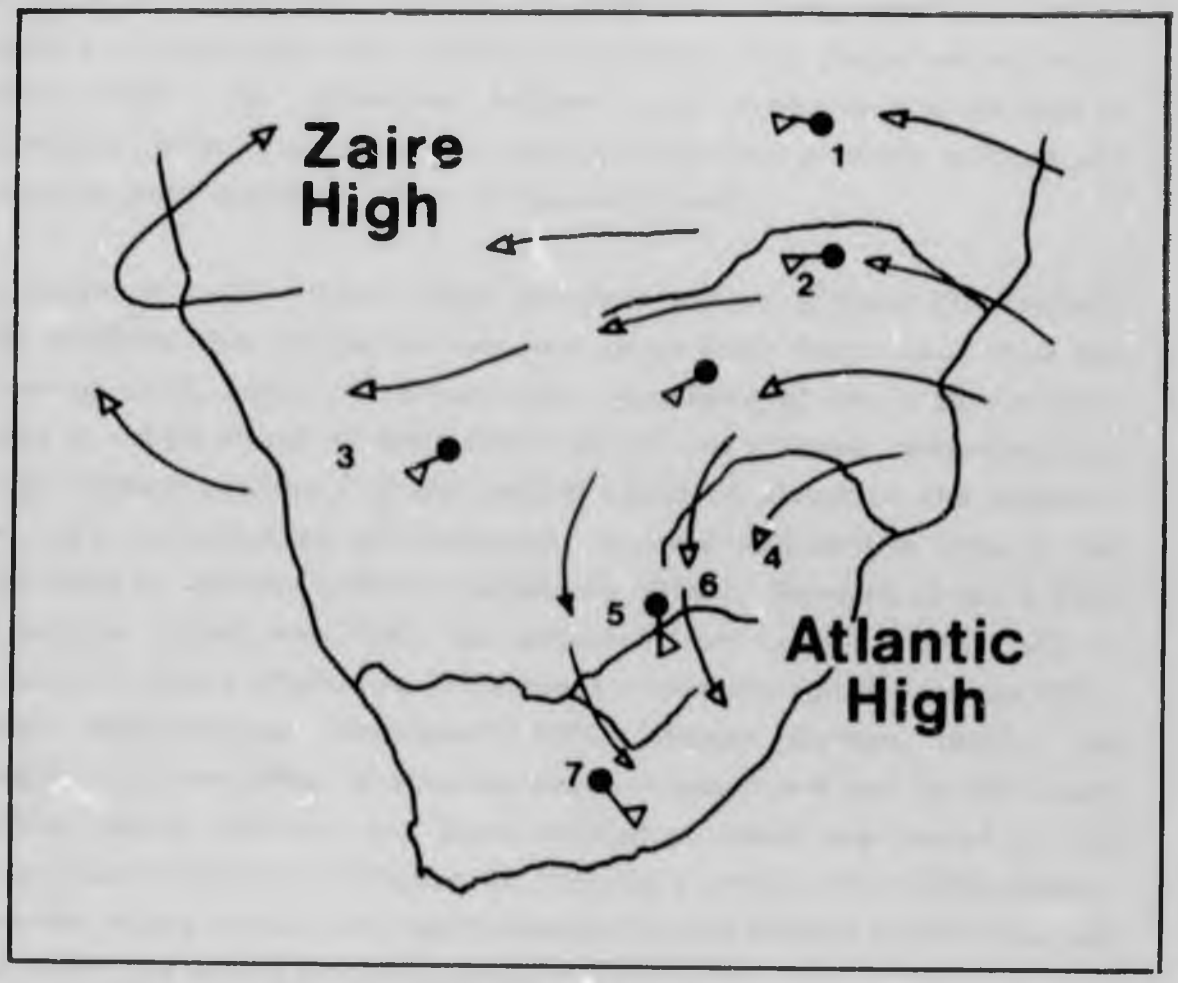


FIGURE 23. Surface wind direction over southern Africa. The combined effects of the south Atlantic high pressure system and the Zaire high pressure system dictate the directions of surface winds in the area (Taljaard 1972). Flags indicate the predicted nest site orientation of sparrow-weavers at various localities, assuming that they build nests on the sides of trees facing away from the prevailing wind. Numbers correspond to the localities shown in Figure 24 where sparrow-weaver nest placement has been quantified.

appears unlikely because of the observed westerly orientations of nest sites near the equator. Because of the significant correlation between latitude and nest site orientation, some other effect of solar radiation coupled with latitude may operate. No such effects are, however, known; therefore it would serve no purpose to explain nest placement as a radiation effect. The correlation between nest placement and latitude is probably an effect because of the strong correlation between latitude and prevailing wind direction. This is discussed next.

The dominant south Atlantic high pressure system (Figure 23, Taljaard 1972) predicts that if sparrow-weavers place their nests away from the prevailing wind, nests on the northern periphery of the high pressure system would be placed on the western to NW side of trees, whereas nests on the western periphery of the system would be placed on the southern side. Data on velocities and directions of wind at localities close to the study sites of Mitchell (1966), Mendelsohn (1968), Ferreira *et al.* (1972) and Burger & Gochveld (1981) was obtained from various weather offices in southern Africa (Zimbabwe Department of Meteorological Services 1981, Zambia Meteorological Department 1974, Weather Bureau 1975). The predictions of the effect of wind on nest placement are met at the seven localities where studies have been conducted: nests are placed on the leeward side of the tree (Figure 24, Kendall's $r=10$; $n=7$; $0.11>p>0.06$). The same figure shows that nest placement is not related to the direction from which the strongest winds blow.

Of the five hypotheses explaining sparrow-weaver nest placement, the wind direction hypothesis best fits the observed data. Particularly useful data were obtained at Middelburg, where the bimodal wind direction pattern would predict a minor nest site preference of NW sides of trees and a major preference of the SE sides. Although the minor peak has a more northerly aspect than expected, the resultant data fitted the prediction remarkably well. None of the above alternative hypotheses allow such a close fit between predictions and results. The advantage gained by building nests on one side of the tree could result either from a preadaptation or an evolved adaptation in a situation where many nests were critical for the survival of a group. This study revealed no adaptation that has the incidental effect of causing these birds to build nests on the side away from the prevailing wind. It therefore appears that sparrow-weaver nest placement is an adaptation that prolongs the life of

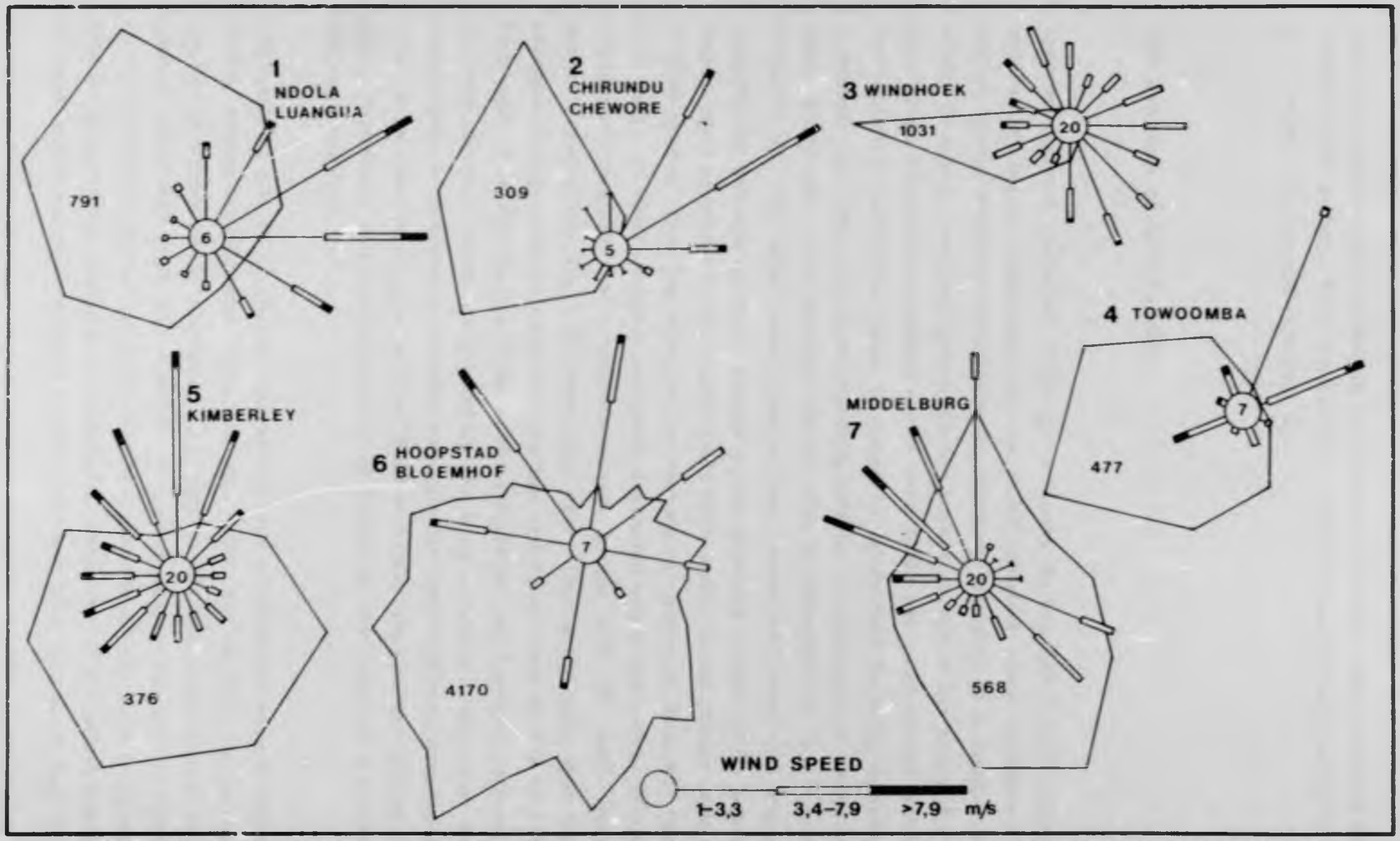


FIGURE 24. Sparrow-weaver nest placement in various wind regimes. The polygons represent the number of nests located on different sides of the nest tree at each locality, while the radial bars constitute wind roses that depict the relative frequencies and wind velocities from various directions. Except for Hoopstad and Towoomba, all wind data were recorded by means of anemographs. The numbers next to each diagram correspond to those mapped in Figure 23. Where two localities are given for a diagram, the top one is the site where wind data were recorded, while nest data were collected at the lower locality. In the other cases both wind and nest data were recorded at the same locality. Source references are mentioned in the text.

nest structures, thus increasing the number of intact nests available for roosting or breeding. The presence of a large number of nests may affect the survival of a group (Chapter 5).

The dynamics of nest-building

Sparrow-weavers collected 1438 grass stems during 548,2 focal animal observation hours. Individuals do not build complete nests themselves, but all group members participate in communal building of a number of nests. If sparrow-weavers are active for a mean period of 10h every day, each group of sparrow-weavers would have 3650h per year during which nest-building could take place. In order to relate nest building activity to annual nest loss, the nest building activity is measured in terms of nests built/year. The average group size at Bloemhof is 3,4 birds (Chapter 2). The focal animal observations conducted during this study suggest the average sparrow-weaver group annually collect 32553 grass stems, corresponding to 20,1 nests built each year. It was shown earlier in this chapter that the average sparrow-weaver group at Bloemhof had 39,7 nests, of which roughly half were destroyed every two years. These calculations suggest that a sparrow-weaver group with 40 nests loses about 10 and builds about 20 nests each year. This would mean that the average sparrow-weaver nest tree has ten additional nests at the end of each year. The discrepancy between the calculated nest building rate and the rate at which nests are eroded by the wind probably stems from an overestimate of the amount of time available for nest-building. The birds tend to be relatively inactive from 13h00 to 17h00. Despite this discrepancy, it appears that in the order of 25 to 40% of the nests of a group are replaced each year.

The usable nests of 32 sparrow-weaver groups at Bloemhof were counted during November 1982 and again one year later. During this period the number of usable nests increased from 928 to 960, an insignificant increase. The fact that the number of useful nests remained constant during the study period suggests that the estimate of the nest building rate in the previous paragraph is excessive. However, if the effort spent in nest replacement is critical for the survival of a group, it may be

important to have several group members participating in nest-building. Nest replacement may therefore be an important factor influencing sparrow-weaver social organisation. The contribution of immature animals is calculated to be in the order of 7 nests/yr/immature (3,21 grass stems/h during 3650 h/yr), compared to a figure of 6 nests/yr/adult (2,63 stems/h during 3650 h/yr). Because the regression constant relating group size to the total number of nests of that group is 7,8; it would appear that the nest building rate of 7 nests/year should be considered a maximum figure.

The contribution of immatures to nest-building: The fact that immature sparrow-weavers make a significant contribution towards the total nest-building activity within a group (Table 13) could play an important role in the group's social cohesion. If the fitness of a newly established breeding pair of sparrow-weavers were reduced on account of a low number of nests available, it would presumably be enhanced if immature birds joined the group. Two immatures in a group of four would build 14 nests/year: for the average group, this is more than the number destroyed by the weather over that time. If nest availability was a severe constraint on sparrow-weaver survival, the presence of immature individuals in a group would clearly have a large effect.

Are roost nests energy saving devices?

Normally the temperature inside a roost nest is higher than the ambient temperature. Because this effect becomes more pronounced as the temperature gets lower, it would have a significant effect on the amount of energy that sparrow-weavers need for thermoregulation. White *et al.* (1975) reported sociable weaver nest temperatures that exceeded the ambient temperature by 5 to 10°C during most of the winter night. The temperature differentials observed by these authors do not differ substantially from those observed in sparrow-weavers during the present study, where the highest recorded temperature differential was 13,5°C. The observed rate of increase in sparrow-weaver metabolic rate with decreasing environmental temperature is about 0,35 ml O_2/g/h/°C below 10°C (Figure 20). This means that roost nests reduce the

sparrow-weaver metabolic rate from around 0,1 to 0,06 kJ/g/h at 0°C. If one considers that the metabolic requirements at 0°C are about twice the resting metabolic rate in the thermoneutral zone, it is clear that the roost nest has the effect of decreasing the energy requirements of a sparrow-weaver by about 32% at 0°C. The use of roost nests outside the winter period would not incur the above advantage to the birds. If roosting in nests is an adaptation towards the reduction of energy spent in thermoregulation during winter, it is conceivable that the evolution of this behaviour could have resulted in a rigid characteristic that does not optimise every aspect of the birds' biology. The habit could be retained because the birds would not survive the metabolic burden that is imposed by cold winter temperatures on birds that roost in the open. The question of whether roost nests constitute an evolved adaptation for energy conservation is deferred until Chapter 7.

Roost nest use by sparrow-weavers and other species: Table 12 shows that other birds use sparrow-weaver roost nests infrequently. The high interspecific aggression reported in Chapter 2 could be an adaptation to reduce the number of individuals of other species roosting in sparrow-weaver nests. This suggestion is supported by the fact that the dominant male of a sparrow-weaver group is the last to go to roost each evening, and he displays a high level of interspecific aggression during the period immediately preceding roosting. No significance is attached to the fact that individual sparrow-weavers sometimes switch from using one roost nest to another (Figure 22). If nocturnal predators had a means of locating continuously used roost nests, switching would clearly be advantageous. Roost nest switching does, however, not occur regularly enough to warrant a special explanation.

CONCLUSION.

The most important finding of this chapter is perhaps the fact that sparrow-weavers appear to need a nest tree with a large number of nests. Also, nests are placed in such a way as to maintain the largest number of usable nests. Large, established sparrow-weaver groups tend to have a larger number of nests/bird compared with small groups. Nest building

is an important activity, occupying some 4,5% of the total sparrow-weaver activity. If nests are a critical resource for sparrow-weavers, the fact that immatures contribute a major share of the total nest building activity could be an important cohesive force in sparrow-weaver groups. The fact that nest erosion causes the disappearance of at least 25% of the nests each year shows that environmental influences could conceivably have a large effect on sociality within sparrow-weaver groups because of the need to replace eroded nests.

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CHAPTER 5: FACTORS AFFECTING BREEDING AND MORTALITY

INTRODUCTION

A knowledge of the ecological constraints operating on a species (factors affecting survival and reproduction) is crucial for an understanding of its evolutionary history. Collectively, these constraints could be termed limiting factors (Andrewartha & Birch 1954), and they are the agents of natural selection. The expectation that adaptations to overcome these limiting factors are fixed at speciation suggests that a study of such mechanisms should provide information as to the environmental conditions prevailing during the emergence of the species.

It could be argued that, since limiting factors are overcome during speciation, they may no longer be detectable. However, I suggest that these were only partially overcome to the extent that the species *survived*. Animal phenotypes do not comprise perfect or optimal solutions to environmental pressures. Some of the observable adaptations and limiting factors would therefore reflect environmental conditions at speciation. This thesis pays special attention to social organisation as an adaptive response to environmental pressure. This chapter details an investigation of the factors limiting sparrow-weaver survival and reproduction in the light of the above approach.

Bissonette (1933) was among the first to realise that ratios of light/dark periods are important in determining the inception of breeding in many animals. He postulated that animals sense the length of day and that this stimulus mediates physiological processes involved in breeding. This theory was confirmed during laboratory experiments in which the light/dark ratios of 24h periods were varied (Lofts 1970). The experimental results of Menaker & Keats (1968) and Barfuss & Ellis (1971) showed that, at least in the case of the house sparrow, *Passer domesticus*, the sensing of daylength is accomplished through the pineal gland which, through altered melatonin secretion, affects the secretion of FSH, LTH and ACTH by the hypothalamus. This mechanism is thought

to be particularly important in temperate regions where variation in daylength is much greater than in the tropics.

As long ago as 1949, Marshall realised that proximate factors other than the number of daylight hours, are significant in the timing of avian breeding seasons. Disney & Marshall (1956) found that *Quelea quelea* was insensitive to photoperiod. These birds were, however, sensitive to the effects of rain, of which the fresh growth of green vegetation appeared important. Maclean (1971) and Immelman (1971) demonstrated that rainfall was an important stimulus of breeding activity in southern African and Australian arid zone birds. They maintained that the proximate stimulus is probably the increased food quality and quantity, and not the rain itself. Skead (1975) and Maclean (1973) found a similar relationship affecting breeding of waxbills in the Transvaal, and sociable weavers in the Kalahari, respectively. Both Maclean (1971) and Immelman (1971) reported inception of breeding within six to 21 days of rainfall; this phenomenon applied to sociable weavers in particular. Collias & Collias (1978), Lewis (1982a) and Earle (1983) found at least partial correlation between rainfall and white-browed sparrow-weaver breeding activity.

The environmental parameters that influence the survival of eggs, chicks and adults appear to differ from species to species, even among communally breeding birds. Emlen (1981) estimated that only 3% of the total nestling mortality of white-fronted bee-eaters *Merops bullockoides* could be attributed to predation, while starvation accounted for 30% of the chick losses. On the other hand, Woolfenden (1978) found that predation was the most important agent of chick mortality in the Florida scrub jay *Aphelocoma caerulescens*. The causes of mortality in animal populations appear to be intimately related to the ecology of the particular populations, and no generalisations can be made. Ricklefs (1969) presented data showing that predation is the single most important source of egg and chick mortality in many bird species.

Colonial-breeding birds have particular problems with regards to predation. Predators probably perform "area-concentrated searches" (Tinbergen *et al.* 1967, Smith 1974) after discovering a profitable food source such as a multitude of breeding nests. The combined aggressive behaviour of many colonial-breeding birds can, however, drive off predators (Kruuk 1964, Andersson 1976). The fieldfare *Turdus pilaris*

often breeds in "neighbourhoods" where several nests are found within a few hundred square metres. Communal defence of these areas by all the breeding birds has been suggested to decrease their nesting mortality (Andersson & Wicklund 1978, Wicklund & Andersson 1980).

The phenomenon of helpers-at-the-nest has received wide attention since its initial description by Skutch(1935). With the exception of Zahavi (1976), nearly all the researchers investigating this phenomenon stressed the advantageous nature of helping behaviour (e.g. Rowley (1965), Woolfenden (1975), Vehrencamp (1978), Emlen (1982a, 1982b)). The same applies to previous studies on white-browed sparrow-weavers (Collias & Collias (1978), Lewis (1982a)). It is conceivable that helping behaviour is sometimes a fortuitous by-product of unrelated processes. If many full-grown birds are present in a breeding group, chick feeding behaviour could be triggered by the stimuli presented by the chicks, irrespective of the adaptive reason why these full-grown individuals remain within the breeding group. It is important to know to what extent helping does improve the survival of the chicks, as this strongly influences arguments about the evolution of this behaviour. The adaptive aspects of helping as a component in the overall biology of sparrow-weavers is discussed in Chapter 7.

With the knowledge that several variables could affect breeding and mortality in this arid-adapted species, the following questions were investigated:

1. What factors affect the inception of breeding activities in sparrow-weavers?

2. What are the important agents of mortality during the breeding season?

3. Does helping have a significant effect on the survival of eggs or chicks?

4. What are the important agents of mortality among full-grown sparrow-weavers?

METHODS

The breeding success of sparrow-weavers in the Bloemhof area was monitored by noting the stage to which each brood survived. The success of each brood was rated on a scale from one to six, representing roughly the number of weeks it takes from egg-laying to the fledging of the chicks:

1 - Clutches that did not survive the first week of incubation.
2 - Clutches not surviving the second week of incubation.
3 - Broods surviving the incubation period but not the first week of the post-hatching (chick) stage.
4 - Broods surviving the first week of the chick-stage, but perishing in the following week.
5 - Broods surviving the second week of the chick-stage but perishing in the final week of the chick-stage.
6 - Broods fledging successfully.

During the breeding season between August 1983 and February 1984, the success of 93 breeding attempts of 37 sparrow-weaver groups was recorded. If broods were inspected regularly, the sparrow-weavers showed extreme alarm behaviour for long periods, resulting that normal behavioural observations could not be done. The manipulation of and disturbance to the nests could also affect predation on the broods. Brood survival was therefore deduced mainly from chick feeding behaviour and nests were not inspected on a regular basis. The disappearance of single chicks from larger broods could thus not be detected. Nest inspections were only performed just before fledging (when the chicks were ringed), as well as after the disappearance of broods. The recording of the disappearances of complete broods, as outlined above, therefore imposes a basic inaccuracy as far as mortality of individual chicks are concerned.

At the stage of hatching (or earlier if the clutch was lost), nests situated close to the breeding nest were counted. These were divided into two classes: completed nests and partially completed or disintegrating nests. All nests within 2m and 4m of each breeding nest were counted, regardless of the tree in which the structures were situated (Sparrow-weaver groups sometimes have nests in adjacent trees). The number of full-grown group members at the time was noted.

Mortality among full-grown sparrow-weavers was recorded by counting the number of surviving birds in each group after one year had elapsed since ringing. The ringing programme was performed in two stages. First, sparrow-weavers in the eight groups inhabiting the central study area were ringed in 1982. Data on the mortality of full-grown sparrow-weavers for two years are therefore available for these groups. Second, birds of 30 groups in the rest of the study area were ringed during 1983 and mortality of the full-grown birds for only one year are available for these groups. As disappearance can result from either emigration or mortality, the importance of emigration in a sparrow-weaver population should be determined. Adult sparrow-weavers have not been observed to move long distances (Collias & Collias 1978; Lewis 1981, 1982a, 1982b; Earle 1983; and this study). Lewis (1982b) found that few birds moved more than 500m from their place of hatching before breeding (average 205m). These observations are supported by data from this study: inter-territory movements normally occurred only between adjacent territories. With one exception, all cases of inter-territory movement (page 33, Chapter 2), where both the source and destination groups of the migrants were known, conformed to the above. However, a bias is possible because short distance movements are much more likely to be observed than long distance movements. The Bloemhof observations do not give any idea of long-term movements (i.e. birth-to-breeding distances), but do indicate the distances involved from year to year. As the disappearance rates were measured annually, the probability is extremely low that an immature bird can drift among colonies and eventually out of the study area during this period. The the study population was separated from nearby sparrow-weaver groups by more than a kilometre: these nearby groups were inspected during December 1982 and January 1984, and no ringed individuals were found. This indicates that movements inside the study area would be more probable than emigration. I therefore assume that mortality accounted for a much larger number of disappearances than emigration, and that the trends observed are primarily the results of mortality.

Climatic data were obtained from the daily rainfall measurements on the Sandveld Nature Reserve, which had a rain meter located 2,5 km north-east of the central study area. Additional information on rainfall was obtained from the farm Rietvlei, 3 km south-east of the central study area. Daily maximum and minimum temperatures were obtained from the

first order weather station located near Hoopstad, 22 km south-east of the study area.

RESULTS

Factors that influence the inception of breeding

The relationship between breeding activity of sparrow-weavers and various environmental parameters in the Bloemhof study area is shown in Figure 25. None of the investigated environmental variables appears to play an immediate role in the initiation of breeding, which started in July and continued until February. Breeding preceded the rainy season by more than a month. Although the breeding activity increased markedly after the start of the rains, no clearly pulsed, correlated relationship was observed. The Bloemhof study area experiences a regular second rainy season during March and April, a period during which I observed no breeding activity. Although breeding appears to have been preceded by increases in the daily minimum temperature (see the shaded areas in Figure 25), this correlation may be fortuitous. Statistical proof would require data collected over a much longer period than two breeding seasons. Daily minimum temperatures probably influence insect abundance and seed production by grasses, factors that could in turn influence sparrow-weaver breeding activity. Once breeding started on a fairly wide scale (e.g. after September 7th, 1983 in the above figure), it continued until the end of the year.

Helping behaviour in raising chicks

According to Collias & Collias (1978), Lewis (1982a) and Earle (1983), helping is characteristic of sparrow-weaver social behaviour. Only seven individuals - four of them immatures - helped breeding birds to feed

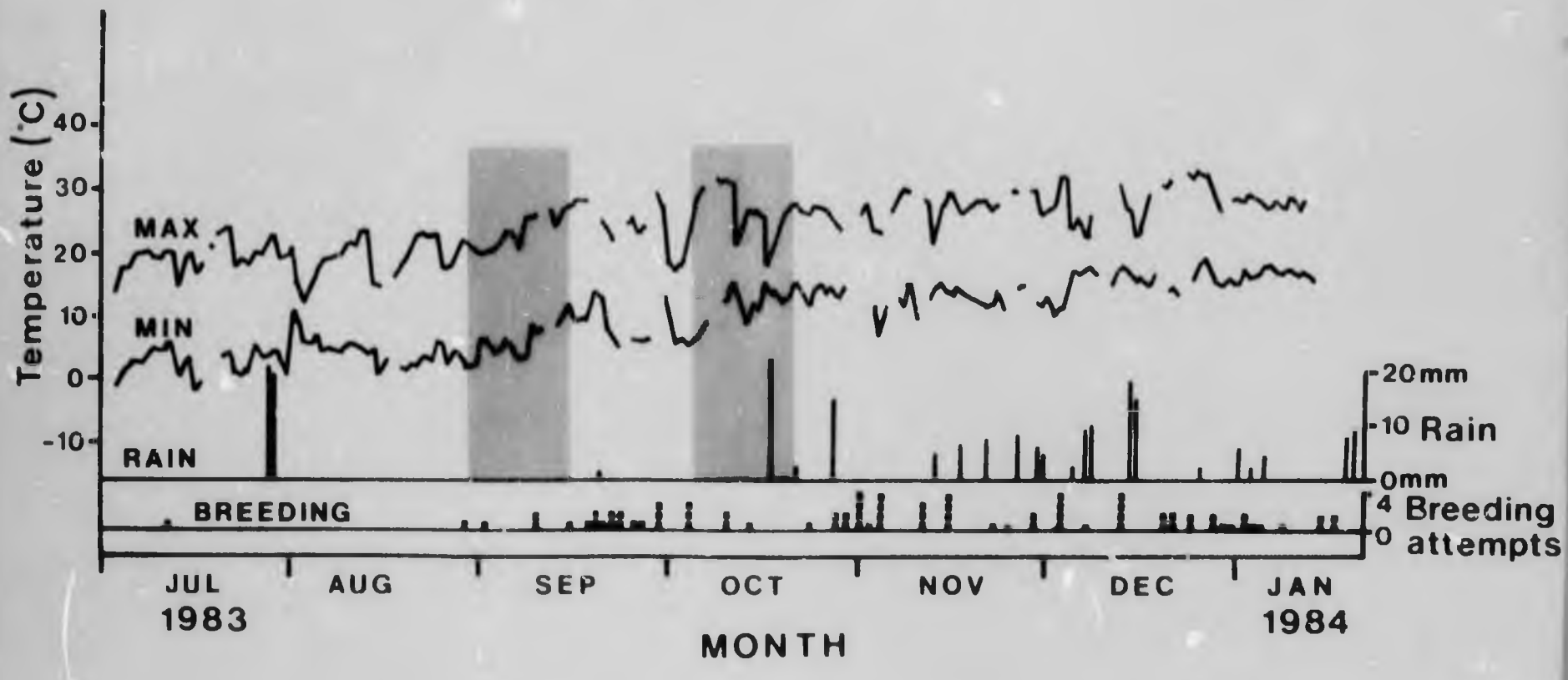

FIGURE 25. The relationship between rainfall, daily maximum and minimum temperatures and the breeding activity of sparrow-weavers at Bloemhof during July to January 1983/4. Breeding activity is expressed as number of clutches laid/day. Gaps in the temperature graphs reflect days on which data were not collected. The shaded portions indicate time spans during which a raise in daily temperature occurred which could possibly affect insect numbers and ultimately sparrow-weaver breeding activity. There is no clear evidence of breeding being triggered by rainfall.

chicks during the present study. These were the only such cases in the nine colonies in the central study area observed over two years. The genetic relationship and helping tendencies of immatures within sparrow-weaver groups with chicks are shown in Table 14. Unrelated birds forming part of a group and that were observed for as long a period as the related birds, did not perform helping. However, both the known related birds (full sibs) did perform helping. The sample size in the tabie is small because of the relatively low breeding success between 1982 and 1984. This prevented statistical treatment of the data.

Table 15 compares the relative contributions to chick-feeding of each age/sex class in no-helper groups as compared to one-helper groups. Helpers of one-helper groups brought 20,3% of the total number of food items to the nest. However, the total feeding rates of these two categories were very similar because the adults in the one-helper groups brought 15,4% fewer food items to the nest than did those of no-helper groups. Adult females brought about twice the number of food items to the nest compared with adult males. When comparing the relative contributions, I assumed that the average nutritive value of food items brought by each group member was identical. The validity of this assumption could, however, not be tested. I also assumed that those feeding events in which the feeding individual could not be identified, did not affect the relative ratios of feeding events among age/sex classes. Because these cases comprise only 1,4% of the total number of feeding observations, this is likely to be true. Fledglings were fed exclusively by their parents.

Because of helping by immatures within a group, and other altruism (e.g. vigilance) by all members, I expected large groups to raise more young successfully than small groups. However, a Kruskall-Wallis test on the Wilcoxon rank sums of the breeding successes of different-sized groups suggested that this is not the case ($x^2=2,27$; $df=3$; $p < 0,52$).

Helping by immigrant adults: In the central study area two cases were observed where helping was performed by immigrant, adult sparrow-weavers that had abandoned their own groups. In two other cases, helping was performed by immatures that had each replaced a breeding adult in a neighbouring destination group. The familial relationships between the members of the affected groups in these cases were not known. It is conceivable that the benefactors could be sibs or

TABLE 14

The correlation between helping behaviour performed by NON-ADULT sparrow-weavers and their genetic relationship to the chicks being fed. Nine such sparrow-weavers were present in five groups that bred and the helping tendencies of these individuals are shown.

Genetic relationship:	Siblings	Unrelated	Unknown
Helping	2	0	2
No helping	0	5	0

TABLE 15

The relative contributions of individuals of different age/sex categories towards feeding of chicks. The contribution of each category is measured in terms of number of visits to the breeding nest per unit time. These comparisons assume equal mean nutritive values for the food items brought by different group members. Age/sex group symbols are: Imm=immature helpers; Ad_M=adult males, Ad_F=adult females; Unid=Feeding individual could not be identified and placed into an age/sex class.

Number of helpers:	1			0		
Number of groups observed:	6			8		
Observation period(h):	38			46		
Age/sex:	Imm	Ad_M	Ad_F	Unid	Ad_M	Ad_F	Unid
No. of visits	80	114	201	11	157	307	1
Feed rate (visits/h)	2,1	3,0	5,3	0,3	3,4	6,6	0
Feed rate of adults (visits/h)			8,28			10,11	
Total feed rate (visits/h)			10,68			10,11	

TABLE 16

The number of diurnal interactions between sparrow-weavers and predator species during 548 focal animal observation hours. An interaction was scored when a predator attacked a sparrow-weaver or if a sparrow-weaver group detected an approaching predator and displayed extreme alarm behaviour.

Predator species		Number of interactions
Mammalian:		
Yellow mongoose	*Cynictis penniciliata*	8
Slender mongoose	*Herpestes sanguineus*	4
Avian:		
Gabar goshawk	*Micronisus gabar*	10
Chanting goshawk	*Melierax musicus*	1
Lanner falcon	*Falco biarmicus*	1
Black-shouldered kite	*Elanus caeruleus*	1
White-necked raven	*Corvulur albicollis*	1
Large bird of prey		1
Snake		1

half-sibs of the adults that were helped. In all these cases the immigrant assumed the position of breeding adult in the destination group which was helped.

Interactions between sparrow-weavers and predators

During the 548 focal animal observation hours, no sparrow-weavers were observed being killed or eaten by predators. The only indication of the relative importance of particular predator species can be inferred from the rates of interactions with individuals of those species (Table 16). Gabar goshawks, yellow mongooses and slender mongooses appear to have the most frequent interactions with sparrow-weavers. On one occasion a slender mongoose climbed around among the nests of a breeding sparrow-weaver group. This caused the sparrow-weavers to perform extreme alarm behaviour, although the mongoose did not attempt to enter any of the nests.

The above observations were made during the day. No data on the importance of nocturnal predators could be obtained. Genets, *Genetta tigrina*, are common in the Bloemhof area and could be important predators.

Predation on sparrow-weaver nests

Forty-three per cent of the 93 observed nests yielded chicks that fledged successfully. As far as could be determined, no chicks or fledglings died of disease or malnutrition. Predation during the two week incubation stage appeared to be relatively low (12,9% of the 93 breeding attempts) when compared to the equivalent figure for the three week nestling (chick) period (44,1 per cent). In 62% of the cases where chicks or eggs disappeared, clear signs of one or more predators were evident. In three instances the predator made a small, neat hole in the side of the nest and snakes were suspected. In two cases the breeding nests had been torn

FIGURE 26. A nest of which the chicks were taken by a predator. More than half of the broods that were unsuccessful resulted in nests with similar signs.

apart and either Gabar goshawks (*Micronisus gabar*) or vervet monkeys (*Cercopithecus pygerythrus*) were suspected. In the remaining cases the nests had a hole of intermediate size in the side or the roof (Figure 26), and the predator could not be identified.

To positively identify the predators responsible for damage to sparrow-weaver nests, eight nest trees with a history of repeated predation attempts were chosen and the ground within 0,6m of the tree trunk was loosened and smoothed so that any mammalian or reptilian predator would leave tracks in the loose sand when approaching the tree. The results were, however, inconclusive. Four of the eight nests were robbed, but no tracks were found in the loose sand near the tree trunk, probably because the small leaves of the *Acacia erioloba* trees mixed with the loose sand near the tree trunk, giving the sand a coarse texture. Consequently, a small snake or mongoose might have crossed the loose sand without leaving any tracks. The identity of predators that robbed sparrow-weaver nests therefore remains obscure. Judging from the diurnal interactions between sparrow-weavers and predators and from the nature of the holes made in nests, I speculate that Gabar goshawks (*Micronisus gabar*), slender mongooses (*Herpestes sanguineus*) and snakes were the most important predators on sparrow-weaver nests. The role of genets (*Genetta tigrina*) as predators of sparrow-weaver nests is unknown, but I suspect it is significant. In many cases nests were intact late in the afternoon but had been robbed by early the following morning, suggesting that predation occurred at night. Many snake species that occur in the area (e.g. the Cape cobra *Naja nivea*) are nocturnal (N.G.H. Jacobsen, *pers. comm.*) and these may also be responsible for predation.

Factors that influence predation on nests

Time of breeding: If predators recognised sparrow-weaver nests as a source of food and if they required a finite time to discover this food, one would expect nesting attempts at the beginning of the breeding season to be more successful than those later in the season. This appears to be the case (Figure 27), although a Kruskall-Wallis test on the Wilcoxon rank sums of the breeding successes classified by month re-

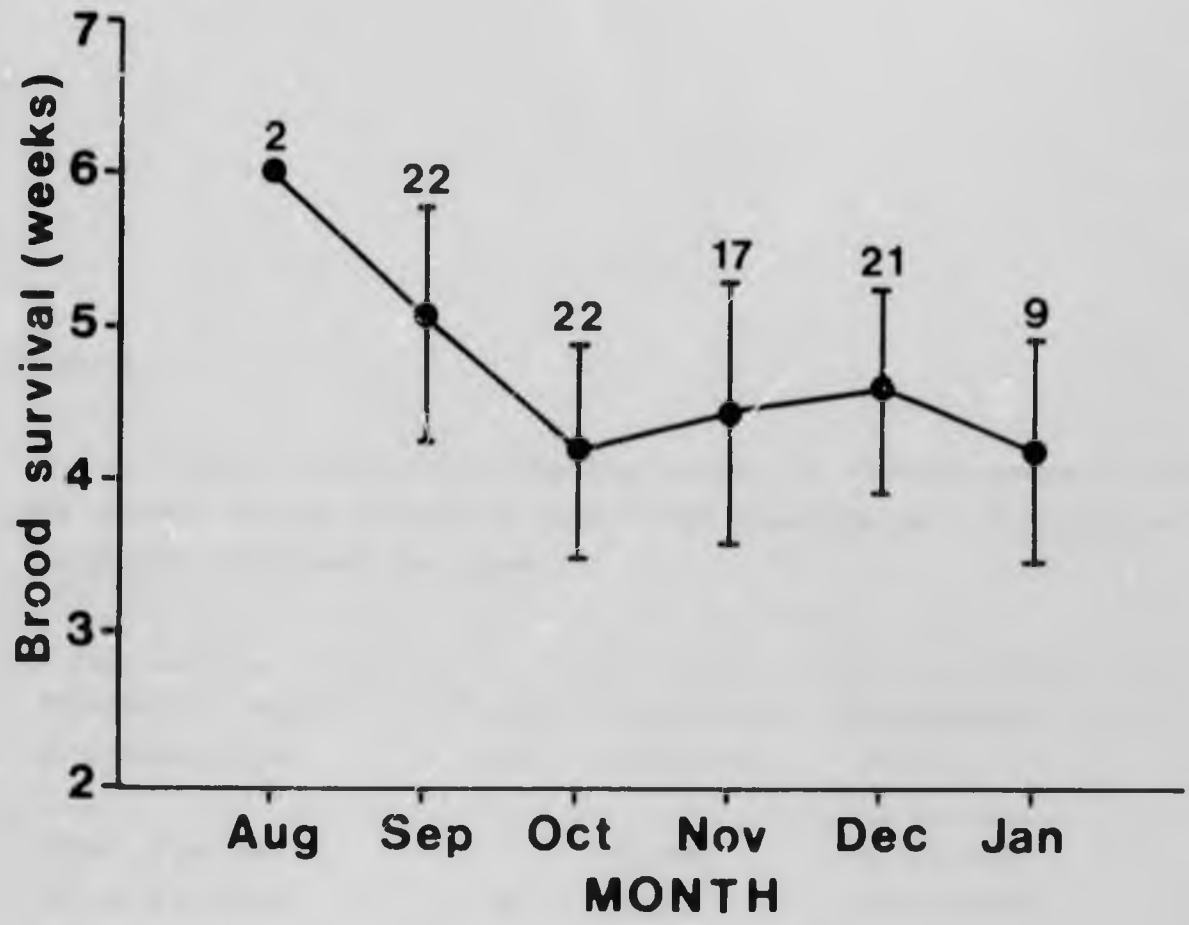

FIGURE 27. Brood survival as a function of the time of year. Although the measured differences are not statistically different, broods near the beginning of the breeding season tended to have a higher survival than late broods. Mean values and sample sixes are indicated by dots and numbers, respectively. One standard deviation of the data within each class is shown by the vertical bars.

TABLE 17

The correlation between the breeding success of sparrow-weavers and the number of nest structures close to the breeding nest. Pearson rank correlation coefficients are given.

Proximity of nests to breeding nest	Sample size	Correlation coefficient	Significance level
Within 2 metres	93	0,286	$p < 0,0056$
Within 4 metres	93	0,383	$p < 0,0002$
In breeding tree	93	0,107	$p < 0,3086$
All nests of group	93	0,150	$p < 0,1518$

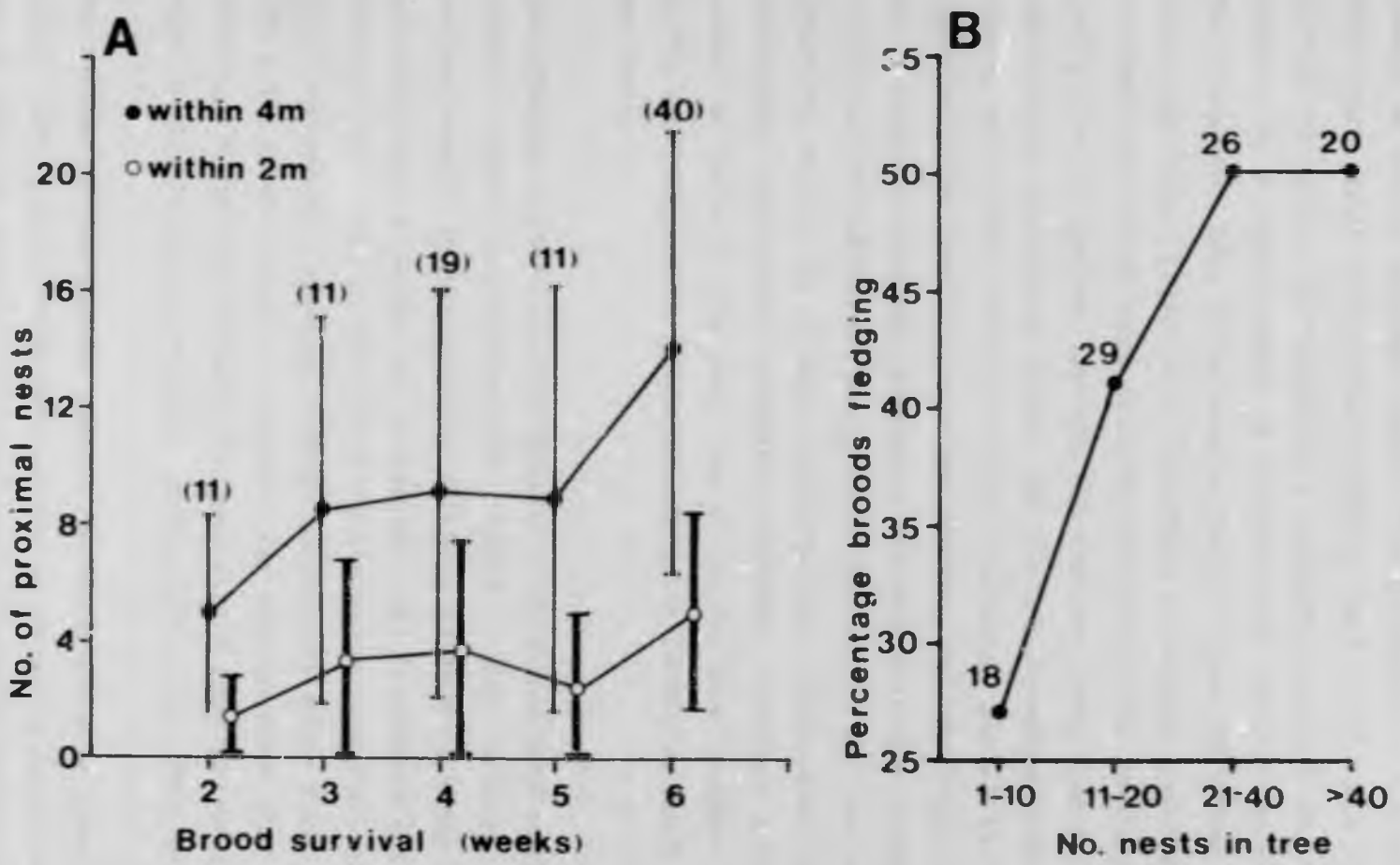

FIGURE 28. The relationship between the number of nests near sparrow-weaver breeding nests and the success of each breeding attempt. Nests that survived the whole nestling period had significantly more nearby nests compared with unsuccessful broods (A). Numbers indicate sample sizes within each class and vertical bars show one standard deviation of that data. Graph B suggests that the number of nests in the nest tree affected the probability of a brood being fledged. By increasing the number of nests in the tree to 30, a group with five nests could double the probability of fledging their brood.

vealed that these monthly differences were not statistically significant (x^2= 7,88; df=5; p<0,16), and the sample size for the first month of the breeding season is very small.

Number of closely situated nests: The proximity of unused breeding or roost nests near the active breeding nest could make the latter more difficult to locate. Consequently I expected active breeding nests surrounded by a large number of neighbouring nests to be more successful than those with only a few nearby nests. Figure 28 shows that this was indeed the case (Table 17). The effect of 'decoy' nests on the survival of broods was much more pronounced during the nestling period than during the incubation period: the Pearson rank correlation coefficient relating nest structures within 4m of the breeding nest to breeding success was 0,201 (p<0,35) for the incubation period as compared to a figure of 0,284 (p<0,017) for the nestling period. Table 17 shows that the correlation between breeding success and the proximity of nest structures around the breeding nest also applies to the number of nest structures within 2m of each breeding nest. There was, however, not a statistically significant correlation between breeding success and the number of nests in the nest tree or to the total number of nests built by the sparrow-weaver group (nests were sometimes built in more than one tree).

The breeding history of each group: If predators with small home ranges preyed upon sparrow-weaver nests, one would expect that sparrow-weaver groups nesting within a predator's home range, would repeatedly be plagued by predation. A Kruskall-Wallis test on the Wilcoxon rank sums of the breeding successes classified by the success of the previous breeding attempt could not show such a relationship (x^2= 4,11; df=3; p<0,25). A similar test also revealed that there was no statistical difference between the success of repeated breeding attempts within a specific sparrow-weaver group (x^2= 3,75; df=4; p<0,44).

The number of full-grown sparrow-weavers within a group: One would expect that groups with many helpers would be more successful than groups with no helpers. A significant difference between the breeding success of sparrow-weaver groups with different numbers of full-grown group members could not be found (Spearman rank correlation coefficient= 0,138; p<0,22; Kruskall-Wallis x^2=2,27; p<0,52). This suggests that

helping does not significantly increase the breeding success of reproductive adults in large groups.

Mortality of full-grown sparrow-weavers

The disappearance of full-grown sparrow-weavers from groups may be attributable to two causes: emigration and mortality. Despite intensive observations and collecting in the surrounding area, no marked animals were observed outside the study area. Animals from the intensive study area were never found in the more peripheral part of the study area. Only one relatively long migration (1,2 km; from peripheral study area into intensive study area) was observed. This suggests that mortality among full-grown sparrow-weavers is a more important source of disappearance than emigration. A better understanding of the causes of these disappearances could be obtained if any factors were found that correlate strongly with the rate of disappearance.

The quantitative assessment of mortality among full-grown sparrow-weavers is complicated by the fact that, despite a high disappearance rate of full-grown sparrow-weavers from their native groups, no predation event was actually observed during the whole study period. Of 120 adult and immature sparrow-weavers that had been colour ringed, only 62 were located one year later. Immatures suffered heavier losses (69%, n=45) than adults (36%, n=75).

The effect of group size: Because of vigilance behaviour (Chapter 3), individuals in large groups may be more successful at evading predators. Large groups also perform more nest building per individual, causing them to have much larger numbers of nests compared with small groups (Chapter 4). The previous section on breeding success suggested that if many nests surround a breeding nest, the success of a breeding attempt is increased, probably because of a decreased probability of predation. The same situation may prevail for roosting sparrow-weavers, causing a higher survival in groups with a large number of nests. The combined effects of vigilance behaviour and large roost nest numbers may cause less severe predation among full-grown birds of large groups, than

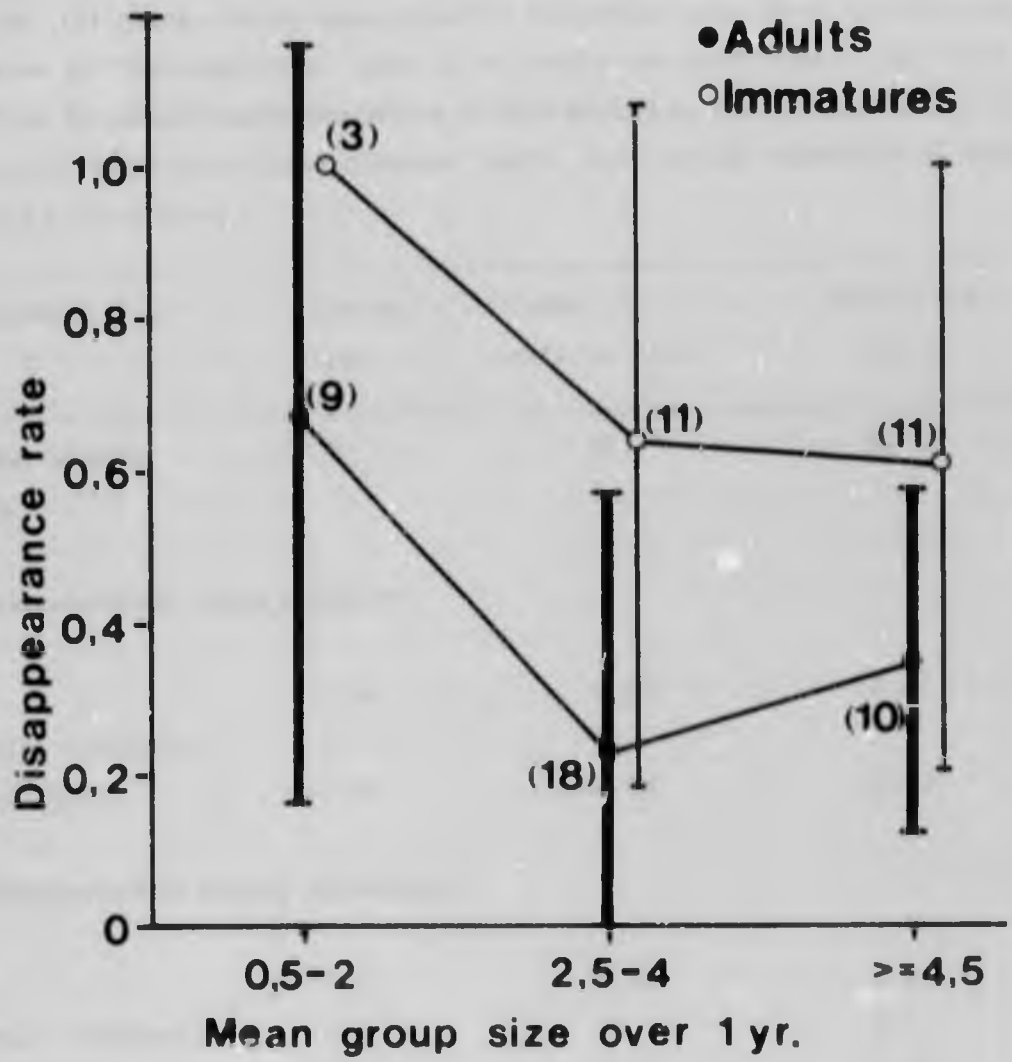

FIGURE 29. The disappearance rates of immature and adult sparrow-weavers as a function of the mean group size. Disappearance rate is expressed as the fraction of individuals of each age class that disappeared from each group over a period of a year. Vertical bars and numbers indicate standard deviations and sample sizes of each class, respectively.

TABLE 18

Statistical analysis of factors possibly affecting the disappearance rate of full-grown sparrow-weavers in the Bloemhof area during 1982-1984. Nonparametric tests were done to determine whether the disappearance rate of full-grown birds was affected by group size, total number of nests in tree or the nest/bird ratio in a particular nest tree. Indicated below are the Kruskall-Wallis statistics of the Wilcoxon rank sums of the 38 data points divided into three classes, with about equal numbers of observations in each class.

Variable:	Group size.	Total nests in tree.	Nest/bird ratio.
Total sample size:	38	38	38
Disappearance among adults:			
χ^2	6,46	6,53	4,47
Degr. freedom.	2	2	2
Probability	<0,04	<0,04	<0,10
Disappearance among immatures:			
χ^2	2,62	8,00	0,24
Degr. freedom.	2	2	2
Probability	<0,27	<0,02	<0,89
Disappearance among all ringed birds:			
χ^2	3,96	6,38	3,42
Degr. freedom.	2	2	2
Probability	<0,14	<0,04	<0,18

is the case with small groups. This effect was statistically significant for adults but not for immature birds (Table 18, Figure 29). A summary of data used in these calculations is presented in Appendix B.

The effect of total number of nests in the nest tree: The disappearance of both adult and immature sparrow-weavers differed markedly among groups with different numbers of nests (Table 18). The mean disappearance rate for groups with less than 22 nests was 92% for immatures and 63% for adults; the corresponding figures for groups with 22 or more nests were 58% and 25%. A summary of data used in these calculations can be found in Appendix B.

The effect of the nest/bird ratio: If surrounding nests close to a roosting sparrow-weaver decreased the risk of location by predators, the correct measure to correlate with disappearance would be the nest/bird ratio of each group. If predation during roosting was an important factor, groups with a large nest/bird ratio should have a higher survival of full-grown birds compared with sparrow-weaver groups that have a smaller nest/bird ratio. Figure 30 shows that the disappearance rates of both adults and juveniles were inversely proportional to the nest/bird ratio of groups. This trend is, however, not statistically significant (Table 18). Appendix B is a summary of data used in these calculations.

DISCUSSION

Stimuli that initiate breeding activity

Rainfall is not the only trigger of sparrow-weaver breeding. The Bloemhof birds, like those studied by Earle (1983) and Lewis (1982a), attempted breeding a number of times before there had been any precipitation. The fact that the first records of breeding (just outside the Bloemhof study area) occurred during the last half of July during both 1982 and 1983, suggests that this is not exceptional. The insects eaten by sparrow-weavers during the present study (see Chapter 6) are well

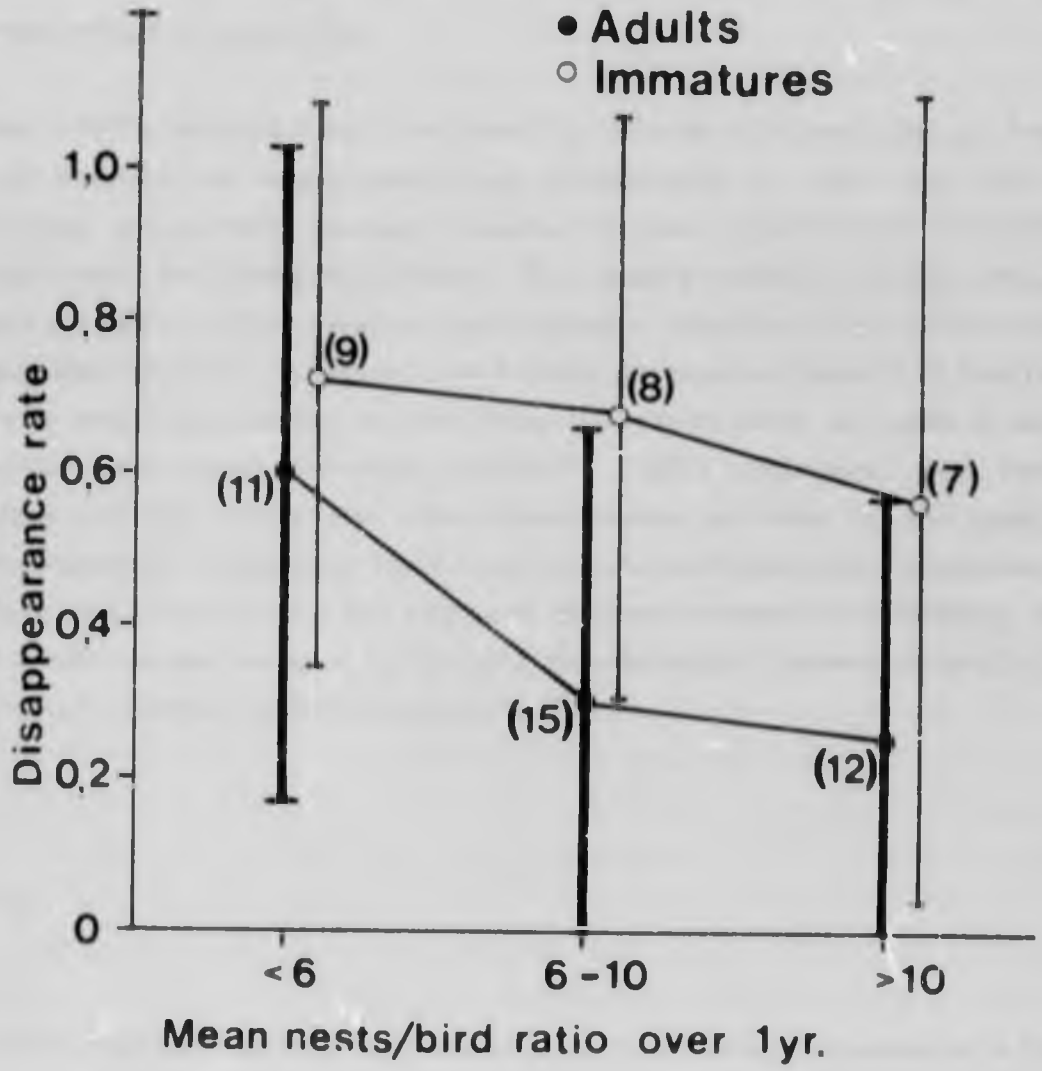

FIGURE 30. Disappearance rates of immature and adult sparrow-weavers as a function of the nest/bird ratio in each group. Disappearance rates are measured as the fraction of each age class that disappeared over a period of one year. Vertical bars and numbers indicate standard deviations and sample sizes within each ratio class, respectively.

adapted to semi-arid conditions: these insects are always available, a fact that could decrease the moisture-dependence of sparrow-weaver breeding. This trend is a clear indication that sparrow-weavers are adapted to an arid environment. An increased supply of insects and seeds after rain probably has a secondary effect in stimulating breeding. The insects fed to sparrow-weaver chicks included a large proportion of larvae, the availability of which would presumably be significantly influenced by the flush of green shoots after rain. Increasing daylength could trigger sparrow-weaver breeding, but a rise in ambient temperature might have the same effect (Figure 25).

Maclean (1971) showed that the breeding season of insectivorous birds in the Kalahari is longer and less constrained by rain than that of granivores, presumably because insects are more consistently available. Judging from its breeding activity, the closely related sociable weaver appears to fall into the granivorous category (Maclean 1971, 1973) which is dependent on rain. However, the following chapter shows that the food taken by sparrow-weavers in the Bloemhof study area includes a large proportion of insects. Following Maclean's (1971) argument, one would therefore predict relatively little dependence on rain in the case of sparrow-weavers. Extensive field observations and laboratory experiments are required to determine the triggers of sparrow-weaver breeding, but these birds do not appear to fit into the situation common in arid-zone birds where rainfall elicits breeding activity.

Helping

The first important observation about helping in sparrow-weavers is that it does not appear to be ubiquitous. The presence of immatures within a sparrow-weaver group does not automatically imply that they will help the breeding adults (Table 14). The available data are too few to make any firm judgement as to whether helping is characteristic of individuals that are related to the breeding pair. Lewis (1982a) is the only person who has reported in a detailed way on helping by sparrow-weavers. One aspect in which the Bloemhof sparrow-weavers differed from those studied by Lewis is that the number of helpers per group was much lower at

Bloemhof than in Zambia where more than two helpers were observed in a number of groups. A group with two helpers was observed only once at Bloemhof, and groups with more than two helpers were never observed. Although Zambian sparrow-weavers have a slightly larger mean group size than that reported during this study (Table 6), Lewis (1982a) reported groups of up to 11 birds (including up to six helpers). The variance in group size is therefore larger in Zambia than at Bloemhof, and groups with many (i.e. more than three) helpers are not a common phenomenon in Zambia. Lewis (Fig. 5 in 1982a) implies that seven of 26 observed groups (or roughly 25% of the observed groups) had more than three helpers. The observed increase in chick-feeding rate in Zambian groups with many helpers may therefore not apply to a large proportion of the sparrow-weaver population.

The second important observation from this study is that helping does not appear to increase drastically the effective feeding rate to chicks in the Bloemhof area. Lewis(1982a) attributed to helpers a significantly increased feeding rate for Luangua Valley sparrow-weaver chicks. This effect was more noticeable among Zambian groups with four or more helpers. At Bloemhof, the group sizes were not big enough to enable such an increase.

These points suggest that the advantages derived from helping is not very important for chick survival. This is in agreement with the lack of correspondence between group size and breeding success at Bloemhof (see the above section "Factors affecting predation on nests"). However, groups may include both helpers and non-helpers. These data are available for the groups in the intensive study area, but not for those in the peripheral study area. The resulting dataset is too small for statistical analysis. Groups with more than one helper were also very scarce at Bloemhof. The analysis of the effect of group size on breeding success did therefore not distinguish between these two classes: a true correlation between breeding success and number of helpers might have been obscured. Helpers could increase chick survival (through feeeding) during dry years when the adults would probably find less food for the chicks. However, present data (this study and Lewis (1982a)) indicate that such breeding seasons do not occur often. If the above effect is operative, it is difficult to see how a strong selective force for helping could exist.

Factors affecting mortality

Brood losses: No chicks were observed to have died of malnutrition or disease. From the holes made in breeding nests, it was assumed that predation is the biggest single cause of mortality among sparrow-weaver chicks. The observed correlation between number of nests close to the breeding nest and brood survival need not imply a cause-effect relationship. Groups with many helpers have many nest structures (Chapter 4), a factor that might fortuitously increase the probability of finding many nest structures close to the breeding nest. It could therefore be argued that if the main effect of helpers in increasing brood survival is through chick feeding, the correlation between brood survival and nearby nest structures may be an incidental effect. Two factors suggest that this is, however, not the case. First, no evidence could be found indicating that helpers do in fact increase brood survival at Bloemhof. Second, Chapter 4 shows that sparrow-weavers have a trait, independent of group size, that contributes to the maximisation of the number of nests per group member. This is the behaviour of building nests on the leeward side of nest trees, which reduces wind-induced nest erosion.

Mortality among full-grown sparrow-weavers: All the data on mortality among full-grown sparrow-weavers was derived from disappearance rates. As explained earlier, I assume that emigration did not contribute greatly to the disappearance of sparrow-weavers from the study area.

From Figures 29 and 30 it appears that the disappearance rate of immatures is higher than that of adult sparrow-weavers. Because of the nonparametric nature of the data and because of the influences of group size and nest/bird ratio, it was not possible to test for the statistical significance of this difference. An obvious reason for such a differential mortality did not emerge from this study. As immatures are more likely to migrate from one group to another (Chapter 2), emigration out of the study area might have played a role in causing this difference. Furthermore, immatures have less experience in predator avoidance: this may cause differences in mortality between the full-grown age groups, as has been found for a number of other bird species (Botkin & Miller 1974).

Two traits of sparrow-weavers could greatly affect mortality among full-grown sparrow-weavers. If predation occurred mainly at night, nest/bird ratio would be the proximate factor affecting survival of full-grown sparrow-weavers. However, if predation occurred mainly during the day, vigilance as an effect of group size would probably be the proximate factor. It is conceivable that one of these factors could be an incidental effect of the sociality of sparrow-weavers. No clear-cut answer to this problem can be offered here. The fact that no predation event was observed during the 548 diurnal observation hours, as well as the circumstantial evidence for nocturnal predation, suggests that most full-grown sparrow-weavers die as a result of nocturnal predation. Nest/bird ratio is, however, correlated with group size. Whichever mechanism operates, convincing evidence exists showing that the number of birds within a group largely influences mortality of full-grown individuals.

CONCLUSION.

The most important finding of this chapter relates to the effect of social structure on sparrow-weaver survival. Predation is a major source of mortality in sparrow-weavers. The most important effect of their social structure is the reduction of predation, among other reasons, as a consequence of the higher nest building activity of large groups. Co-operative breeding of sparrow-weavers at Bloemhof does not appear to increase chick survival: the birds therefore do not fit the predictions of the environmental constraints model (Emlen 1982a, 1984), which predicts that while helpers are unable to breed themselves, they maximise their inclusive fitness through helping.

The ancestors of modern sparrow-weavers may well have been limited by similar, severe, predation pressure, which might have caused the near-extinction of these ancestors. Modern, group-living sparrow-weavers clearly exhibit adaptations moulded by natural selection to survive in the face of high predation.

CHAPTER 6: THE PREFERRED HABITAT OF WHITE-BROWED SPARROW-WEAVERS

INTRODUCTION

The survival and reproduction of animals are both related to particular characteristics of the environment, i.e. they have adaptations that enable them to survive in that particular environment. Therefore, an understanding of the relationship between the adaptations of a species and its environment is necessary for understanding the evolution of that species. Since adaptations evolve in response to the environment (Williams 1966), we can not discuss adaptations without considering the environmental conditions under which they arose.

A difference of opinion exists as to how the tuning between organism and environment arises. Lack (1954), Brown & Wilson (1956), Schoener (1974,1978), Diamond (1978) and Roughgarden (1983) believe that interspecific competition and character displacement force animals to be optimally adapted to a subset of the environment, i.e. the niche of that animal (Hutchinson 1957, MacArthur 1968). The niche of a species is defined by the history of competition of that species and, if interspecific competition is severe enough, this niche may change while a relatively large population of the species exists. This point of view is commonly expressed in textbooks on evolutionary biology e.g. Futuyma (1979:5-). Alternatively, Simberloff (1983), Strong (1983) and Walter, Hulley & Craig (1984) have questioned the importance of interspecific competition in the shaping of either adaptations of animals or the structure of ecological communities. The concept of species' histories following a pattern of punctuated equilibria (Eldredge & Gould 1972, Gould & Eldredge 1977), as well as Paterson's (1982a) recognition concept of species, hold fundamental implications for interpreting the relationship between environment and adaptations. If, following the latter authors, we assume that an animal species does not change dramatically in terms of morphology, adaptations or ecology during the period of existence of that species, we can infer that the present adaptations of a species reflect the environment in which it arose. Also, if we assume that an animal can survive only in an envi-

ronment to which it is adapted, we can infer that the present habitat of a species approximates the environment in which this species originated. There are therefore two sources of information that could be used to gain information on the circumstances in which a species evolved: the present adaptations of that species and the present preferred habitat of the species. These views imply that the niche of a species is defined during speciation and that it remains constant throughout the life of that species. Because the term "niche" has been closely associated with competition theory, the term "preferred habitat" (Peterson 1982b) will be used to describe the habitat to which a species is adapted and in which the fitness of individuals are sufficient for the species to survive.

The features of the habitat that are crucial for sparrow-weaver survival will be investigated so that this information can later be used to reconstruct conceptually the environment in which the social system of sparrow-weavers evolved. Some adaptations in present sparrow-weavers need not, however, reflect environmental constraints when white-browed sparrow-weavers evolved. Indeed, some present adaptations may be evolutionary hang-overs from previous speciation events within the subfamily. The distinction between these two classes of adaptations can sometimes be inferred from a comparison of extant species within a genus or subfamily, but it is often difficult or impossible to make.

The following questions were investigated:

1. Are any particular plant species or genera so essential that sparrow-weavers cannot survive without them? This information could provide an idea of the floristic composition of the environment in which sparrow-weavers evolved.

2. Is any physical feature of the vegetation, e.g. foliage density or ground cover, essential for sparrow-weaver survival? This information could indicate the physical character of the vegetation at speciation.

3. Is the sparrow-weaver diet so specialised that the geographic distribution of the food limits the distribution of these birds? Such specialisation could indicate the environmental constraints at speciation.

METHODS AND RESULTS

The food eaten by sparrow-weavers

The diet of sparrow-weavers was studied by collecting 73 birds during the period July 1982 to July 1983, and a list of the minimum number of each food category (e.g. a grass species or insect genus) in each stomach was compiled. From this, the relative importance of each food category could be ascertained. Because certain food items (e.g. grass seeds) appear to digest at a faster rate than others (e.g. insect exoskeletons), neither volumetric analysis nor analysis of the masses of the food items would yield reliable estimates of their relative importance in the sparrow-weaver diet. Each stomach yielded both plant material and insect material, indicating that both these food sources are important to sparrow-weavers. A total of 761 seeds or fruits and 4371 insects were identified.

A large array of plant items were consumed (Table 19). Maize, *Zea mays*, and wheat, *Triticum aestivum*, were among the most common seeds found in the stomach contents, indicating that sparrow-weavers often feed on cultivated plants. The only wild seeds that were eaten in relatively large numbers are *Urochloa* sp. (probably *Urochloa panicoides*), *Stipagrostis uniplumis*, *Limeum fenestratum* and *Celosia* sp.. These plants grow commonly in disturbed areas.

Insects from three taxa comprised most of the insectivorous part of the diet: weevils (Curculionidae), ants (Formicidae) and termites (Isoptera). These and other insects that are eaten clearly reflect the ground-feeding habits of sparrow-weavers. Table 20 lists the insects that were identified from sparrow-weaver stomachs. Estimates of the numerical importance of the different insect taxa in sparrow-weaver diets, as reflected by counts of insects, shows that termites are most commonly eaten, forming more than 80% of the total insect food (4106 food items). The species *Trinervitermes trinervoides* was the most favoured termite (3710 food items), with *Hodotermes mossambicus* (329 food items) and *Odontotermes* sp. (67 food items) making up the rest of the termite food. The impor-

TABLE 19

Seeds identified from the stomach contents of 73 sparrow-weavers. The "Frequency" column indicates the number of stomachs in which a specific type of seed was found, whereas the 'Occurrence" column indicates the total number of seeds of that species found collectively in all the stomach contents.

Species name.	Frequency	Occurrence
Dactylotinium aegyptium	1	1
Cenchrus sp.	1	1
Chloris gyana	1	1
Cissampelos sp.	1	1
Cleome sp.	1	1
Convolvulus sp.	1	1
Felicia sp.	1	1
Passifloraceae	1	1
Phlox paniculata	1	1
Plantago lanceolata	1	1
Selago sp.	1	1
Setaria sp.	1	1
Sida sp.	1	1
Rubiaceae cf. *Xeromphis*	1	1
Brassica tournefortii	2	2
Eragrostis cilianensis	1	2
Panicum sp.	2	2
Polygonum lapathifolium	2	2
Rosaceae	2	2
Euclea sp.	2	2
Amaranthus sp.	2	3
Grewia sp.	2	3
Rhus sp.	3	3

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Table 19 (Continued)

Species name.	Frequency	Occurrence
Sorghum bicolor	3	3
Digitaria sp.	2	4
Cynodon dactylon	2	4
Echium sp.	3	4
Commelina sp.	3	5
Ipomoa sp.	2	5
Vigna sp.	4	5
Euphorbia sp.	2	6
Tragus sp.	1	6
Gossypium sp.	7	7
Citrillus sp.	8	9
Limeum sulcatum	4	9
Erodium sp.	2	11
Solanum sp.	5	11
Limeum fenestratum	8	14
Oenothera sp.	5	19
Lithospermum sp.	4	23
Gisekia sp.	1	26
Portulaca oleracea	5	28
Celosia sp.	8	36
Sericorema sp.	6	40
Stipagrostis sp.	12	42
Bulbostylis collina	4	47
Eleusine sp.	2	47
Zea mays	47	55
Echinochloa crus-galli	4	63
Urochloa sp.	11	84
Triticum aestivum	19	113
** TOTALS **	216	761

tance of *T. trinervoides* as a food source is emphasised by the fact that 71% of the sparrow-weaver stomachs contained them. Weevils formed the second most commonly eaten insect group (71 food items). These counts represent the minimum numbers of insects taken as deduced from exoskeleton parts recovered, and should be viewed with caution since some of the taxa may be seriously underrepresented. Because insects undergo fragmentation in sparrow-weaver stomachs, reliable counts of commonly-taken food items are not easily obtained, and the data in Table 20 is therefore presented in terms of the number of stomachs containing a particular insect taxon. However, represented in this way, the results do not differ much from estimates of the numerical importance of the different insect taxa.

The insects that are eaten reflect the ground-feeding habits of sparrow-weavers. All the *Trinervitermes trinervoides* taken by the birds were workers; the soldier caste of this species is able secrete a sticky substance that may be poisonous (Buillon 1970). Several times I saw sparrow-weavers dig small holes in the sandy soil at Bloemhof, probably into the foraging tunnels of these insects. Later, I was able to collect termites of the genus *Trinervitermes* from these holes.

To relate these food items to particular aspects of the environment preferred by sparrow-weavers, it was necessary to determine which vegetation types or geographical areas were used most by these birds.

Habitat use by sparrow-weavers.

Sparrow-weaver territories are relatively small and each has at least one nest tree where individuals of a particular group roost and spend a large part of the day (Chapter 2) The distribution of nest trees could thus be used as a crude indicator of the location of sparrow-weaver territories. The positions of 167 nest trees were plotted on a 1:50000 topographical map, and then related to vegetational features and agricultural practices on the map.

TABLE 20

A comparison between the taxonomic groups of insects captured in pitfall traps from January 1983 to May 1983 and the insect remains identified in 73 sparrow-weaver stomachs.

Taxonomic group.	Occurrence in food (No. of stomachs)		Occurrence in traps (No. of insects)	
	Sub-total.	Total.	Sub-total.	Total.
Diptera		1		
Hymenoptera		69		
Formicidae	62			
Vespoidea	7			
Hemiptera		15		
Pentatomidae	14			
Tingidae	1			
Coleoptera		86		
Curculionidae	66			75
Brachycerus			36	
Protostrophus			21	
Synthocos			8	
Rhytirrhinus			2	
Scarabaeidae	12			39
Tenebrionidae	2			331
Carabidae	2			40
Buprestidae	2			
Histeridae	2			2
Chrysomelidae				4
Lampyridae				2
Meloidae				2
Trogidae				1

(Continued on next page)

Table 20 (Continued)

Taxonomic group.	Occurrence in food (No. of stomachs)		Occurrence in traps (No. of insects)	
	Sub-total.	Total.	Sub-total.	Total.
Orthoptera		14		
Acrididae	13			
Gryllidae	1			
Isoptera		71		6
Trinervitermes	52			
Hodotermes	37		6	
Odontotermes	17			
Diverse		2		
Arachnida		3		
** TOTAL **		260		

Habitat use by sparrow-weavers was calculated by plotting each focal animal observation on a 1:10000 map of the central study area and determining which areas were most intensively used.

Of the 167 surveyed nest trees, only two were not camelthorn (*Acacia erioloba*) trees. These were by far the most common trees in the area, other commonly-found trees being *Rhus lancea* and *Ziziphus mucronata* (Viljoen 1979). The observed preference for camelthorn trees could therefore be the effect of their numerical dominance. However, nest trees were not found throughout the thornveld. They were common only around the periphery of this area (Figure 31) where the thornveld adjoined open grassveld or maize lands. Despite intensive search of the interiors of the thornveld regions (A-D, Figure 31), no nest trees were found there.

Sparrow-weavers in the central study area at Bloemhof spent most of their time in the ecotonal areas near thornveld/road or thornveld/maize-land boundaries (Figure 32). Areas frequented inside the thornveld (A-C, Figure 32) were very open with few trees. Although this figure represents sparrow-weaver feeding behaviour, the pattern is identical to that for all the other activities that were mapped.

Floristic composition of sparrow-weaver habitat

Because sparrow-weavers are partial to the ecotonal areas where thornveld borders onto open grassland or disturbed veld, the question arises whether this represents preference for floristic characteristics of the ecotonal areas, or whether these areas have physical or other characteristics that make them desirable. To quantify the character of the vegetation, a detailed botanical survey of the central study area at Bloemhof was undertaken. The taxonomic composition of the grass and herbaceous plants in the area was determined by performing a simplified Braun-Blanquet survey (Mueller-Dombois & Ellenberg 1974) which consisted of fifty randomly-situated sample plots (called *releves* in Braun-Blanquet terminology) of dimensions 5m x 5m (Figure 33). Forty releves were situated in *Acacia erioloba* veld whereas ten were located in disturbed or ecotonal areas. Three additional releves were subjectively

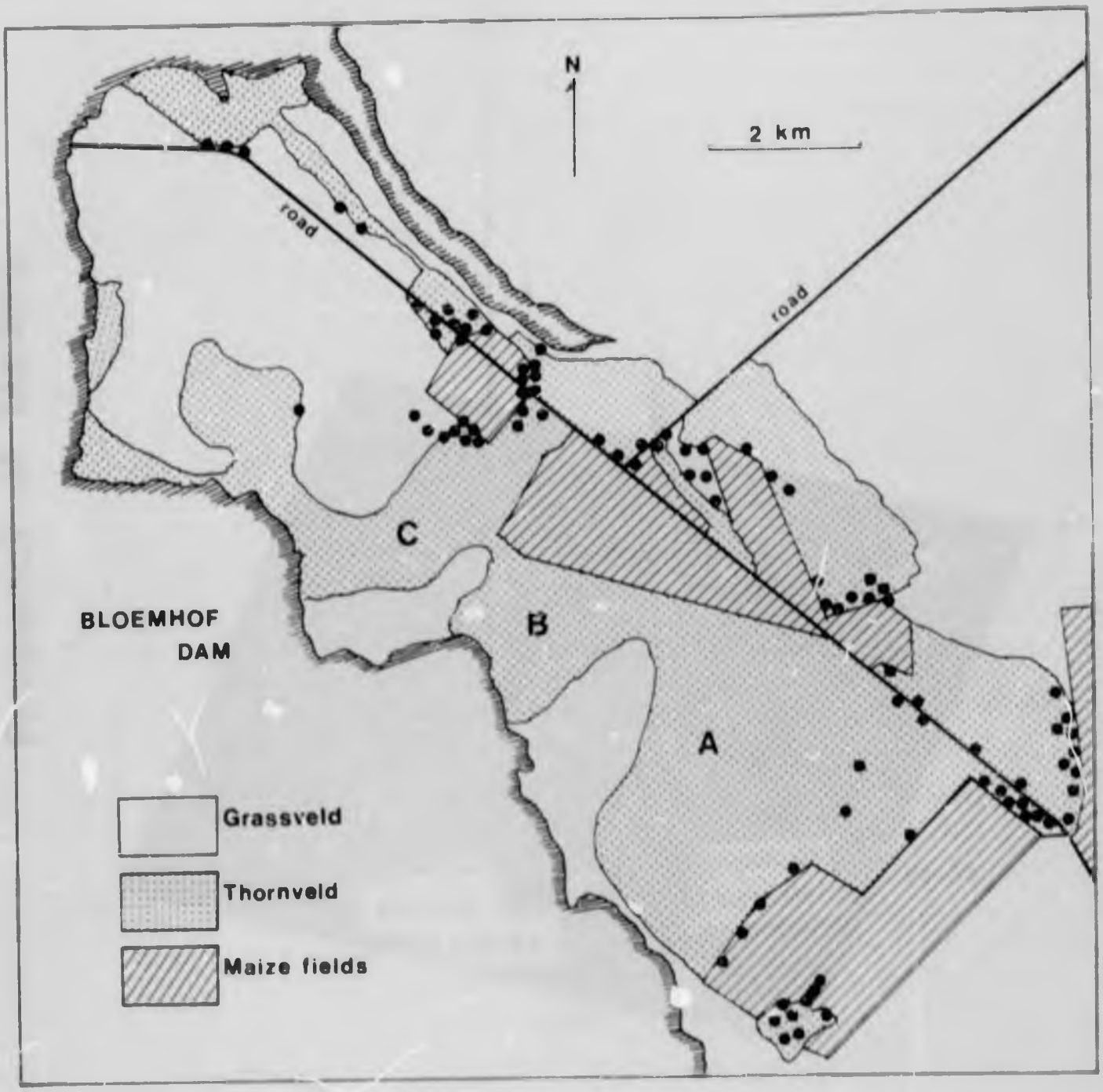

FIGURE 31. The locations of nest trees of 96 sparrow-weaver groups at Bloemhof (indicated by black dots) show that the birds prefer the margins of thornveld areas. Thornveld/Maize-land ecotones are much more intensively used compared to thornveld/grassland ecotones. The areas labelled A-C were searched intensively, but no sparrow-weaver nests were found.

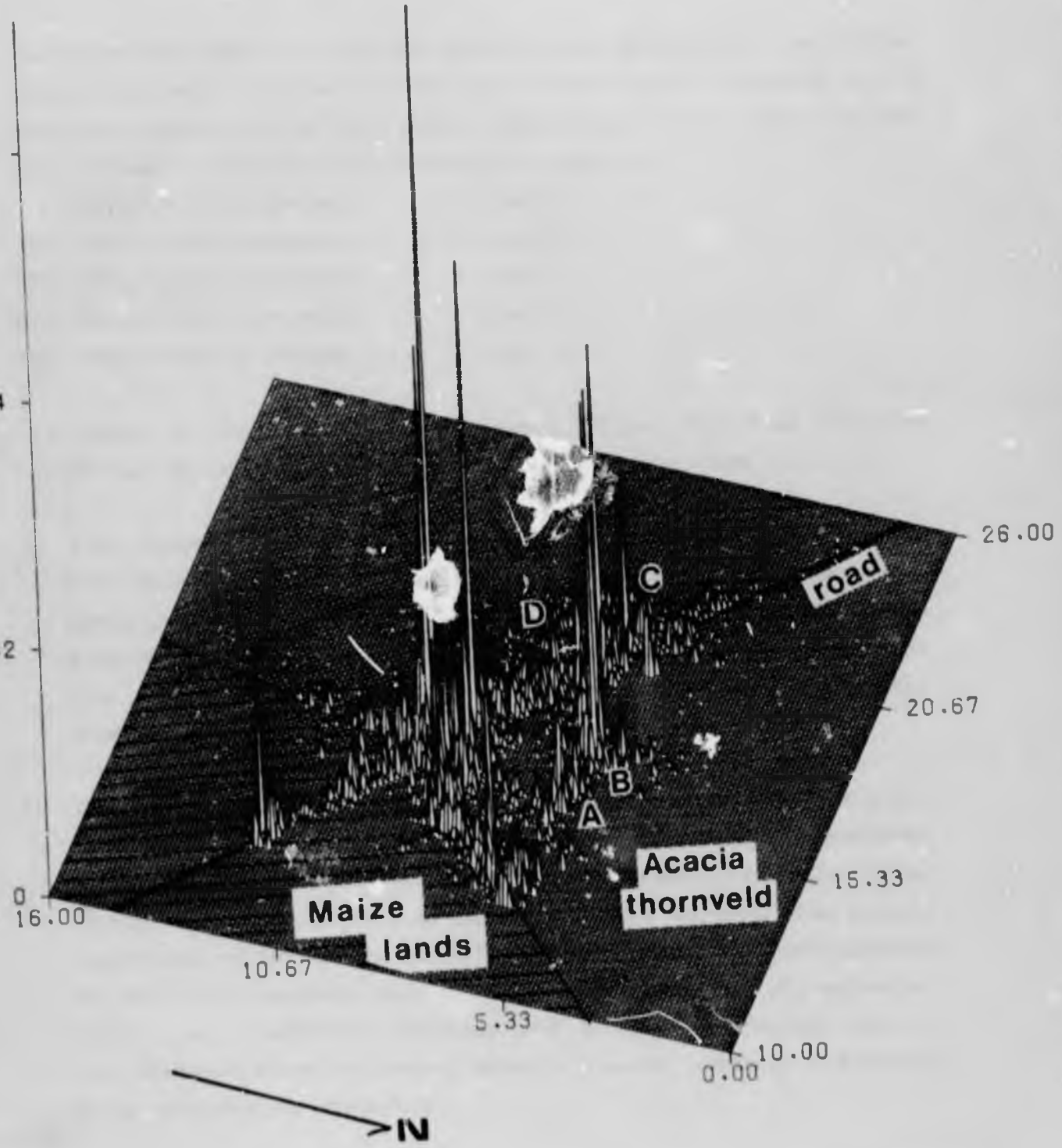

FIGURE 32. A three-dimensional representation of sparrow-weaver habitat utilisation at Bloemhof. The heights of peaks show the proportion of time spent feeding in various parts of the study area. Although this figure only shows the results for feeding behaviour, equivalent figures for other behaviour types look almost identical. Sparrow-weaver activity is concentrated in the ecotonal and open areas. The areas marked A - D inside the *Acacia* woodland have very sparse ground cover. Axis units are 100m.

placed in areas where the random sampling method seemed to leave large, unsampled areas. All plants within each releve were identified and a subjective assessment of the relative importance of the biomass of each species made according to the following convention:

1% - 6% of total phytomass	: class 1
7% -12% of total phytomass	: class 2
13% -25% of total phytomass	: class 3
26% -50% of total phytomass	: class 4
51% -100% of total phytomass	: class 5

The results of the Braun-Blanquet survey (Table 21) show that the habitat can be divided into three main floristic communities:

1. The *Acacia erioloba* thornveld community contains large *Acacia erioloba* trees, and is characterised by the shrubs *Felicia muricata, Barleria macrostegia, Acanthosycyos naudiniana* and the grass *Eragrostis curvula*. The grass *Tragus koelerioides* is also very common. This vegetation type matches Viljoen's (1979) description of the *Acacia erioloba - Stipagrostis uniplumis* community.

2. The *Nidorella resedifolia* community contains many *Acacia erioloba* shrubs, and is characterised by the shrubs *Nidorella resedifolia, Tephrosia lupinofolia, Helichrysum paronychioides* and the grass *Panicum kalaharense*. This community formed a marginal zone around the *Acacia erioloba* community. That part of the community situated on the south-western side of the road contained characteristic shrubs, e.g. *Indigofera daleoides* and *Kohautia lasiocarpa*, and a more detailed botanical survey than this would probably indicate it as an independent community.

3. The *Conyza bonariensis* community was found along the road and in the thornveld/maize land ecotone. It contained a number of characteristic shrubs, e.g. *Conyza bonariensis, C. floribunda* and *Oenothera indecora*. It is probably not a natural plant community in the area: releves in this community adjoining thornveld showed some similarity with the thornveld, as is evident from the presence of the grass *Anthephora pubescens* and the shrub *Chrysocoma obtusata*.

It is doubtful whether the *Conyza bonariensis* community may be considered a natural association since it is not found in undisturbed, natural areas at Bloemhof. Also, this "community" is likely to be very heterogeneous spatially and temporally. For the purpose of this study, however, its identification as a community facilitates description of the floristic and structural features of a habitat that is well-used by sparrow-weavers.

The broken line on Figure 33 indicates the boundary between the *Nidorella resedifolia* and the *Acacia erioloba* communities. Of the grasses that occurred in all the communities, some were especially common in only one community. *Cynodon dactylon* was very common in the *Conyza bonariensis* community, often forming a total cover of the area. Likewise, *Tragus koelerioides*, a grass with a similar structure to *Cynodon dactylon*, is very common only in the *Acacia erioloba* community. *Aristida stipitata* is very common in the *Nidorella resedifolia* community. The four plant species that formed the dominant component of the total biomass (excluding trees) in all the plant communities are *Eragrostis lehmanniana*, *Eragrostis tricophora*, *Aristida congesta* and *Stipagrostis uniplumis*.

When viewing sparrow-weaver habitat use as depicted in Figure 32, it is clear that the preferred habitat is the *Conyza bonariensis* community. The *Acacia erioloba* and *Nidorella resedifolia* communities were very little used, and no differential use of these habitats was observed, despite the floristic differences between them.

Structural characteristics of sparrow-weaver habitat

In an attempt to find the cause of the sparrow-weaver preference for the *Conyza bonariensis* association, it was necessary to determine the cover and biomass in each of the defined communities. In order to ascertain the ground cover of each plant species, a line-intercept survey (Canfield 1941), involving 12 transects of 50m each, was performed. In addition to the distances between plants on the transect line, the basal cover and crown cover of each plant on the line was measured. Each plant crossed by the transect line was identified. Five of the transects were situated in the *Acacia erioloba* community, three in the *Nidorella resedifollia* as-

FIGURE 33. An aerial photograph of the intensive study area at Bloemhof, showing the locations of the sample plots (releves) used during the Braun-Blanquet survey of herbaceous plants. The broken line demarcates the *Acacia erioloba* community from the *Nidorella resedifolia* community. The *Conyza bonariensis* community occurred along the edge of the maize land on the bottom right, and along the road that bisects the photograph.

TABLE 21

A differentiated Braun-Blanquet table of the results of the survey of herbaceous plants in the intensive study area at Bloemhof. Three plant communities are discernable:

1) the Nidorella resedifolia community.
2) the Acacia erioloba thornveld community.
3) the Conyza bonariensis ecotonal community.

The plant species encountered clearly indicate the arid affinities of the three plant communities. F=number of releves in which a particular plant species was encountered. Numbers in the table represent the relative biomass index for each species in a particular releve: 9 is the highest index.

Releve number: / Plant species.	F	344373333 701142369	33232222 80842569	11221414321012010010021000 37176312509653188943410752	4455545444 6821053794
Characteristic plants of the Nidorella resedifolia community:					
Tephrosia lupinofolia	4	1 2 11			
Indigofera daleoides	4	111 1			
Rohaytia lasiocarpa	3	1 1 1			
Cassia biennis	3	1 11			
Oxygonum dregeanianum	2	11			
Nidorella hottentottica	2	11			
Dichoma macrocarpa	2	1 1			
Nidorella resedifolia	11	111111 11	11	1	
Tephrosia sp.	8	11 11	11 1		1
Helichrysum paronicoides	7	12 1 1	1 1 1		
Rhynchosia confusa	6	1 1111	1		
Bergia pentheriana	6	1 11	1 1 1		
Panicum kalaharense	5	11	11 3		
Requienia sphaerosperma	2	11			
Plants common to both the Nidorella resodifolia and the Acacia erioloba communitie.					
Pogonarthria squarrosa	20	11 11111	1111111	22111 2	
Eragrostis pallens	16	1 112	1 1	2 1 22 131 1 2 1	
Tricholaena monachne	11	1 2 12	1111	1 1 1	
Nolletia ciliaris	7	1 1	1	1 111	
Cyperus margaretaceus	6	1		1 11 1 1	
Heteropogon contortus	4	11	1	1	
Characteristic plants of the Acacia erioloba community:					
Felicia muricata	6			1 1 1 1 1 1	
Barleria macrostegia	4			1 1 1 1	
Acanthosycyos naudinianus	4			1 1 1 1	
Eragrostis curvula	2			1 3	
Commelina ecklonians	2			1 1	
Portulaca kermesina	2			1 1	
Plants common to both the Acacia erioloba and the Conyza bonariensis communities:					
Anthephora pubescens	16			3 1 2 113 3 113 1	22 3 11
Chrysocoma obtusata	6			1 1 11	1 1
Liliaceae	6			1 1 1 1	1 1
Mariscus rehmannianus	5			1 111	1
Solanum supinum	5			111 1	1
Schmidtia pappophoroides	[illegible]			13 3 1	1
Characteristic plants of the Conyza bonariensis community:					
Conyza bonariensis •	6				11111 1
Conyza floribunda	4				111 1
Oenothera indecora	3				1 1 1
Bidens bipinnata	3				1 11
Gnaphalium oligandrum	3				1 1 1
Delosperma cooperi	2				11
Arctotis venustra	2				11
Chenopodium album	2				11
Plants that are common to all the plant communities:					
Eragrostis lehmanniana	49	23 111123	41111111	2313331 23331 333212314322	1131223111
Eragrostis trichophora	44	1 2 1 1	111 121	13211212112222322112112311	211 11221
Aristida congesta	43	11211111	11111 11	12111121 2211 112111 3131	11 1 11
Stipagrostis uniplumis	39	1341 1	113 1235	1211131 22321111231221 34	1 111
Walafrida densiflora	33	11 3 11	11213 12	21 13121 1 11 2 11	2111 1212
Hermannia tomentosa	31	11 11 111	11113111	11 1111 1 1111 11	11 1
Eragrostis superba	29	212111 21	21213	21222 21 1 14	22 112 1
Aristida stipitata	27	223153132	13112 31	22211 11 1	11 1
Trichoneura grandiglumis	23	232 11132	11211131	1 2 1 11 1	1
Cynodon dactylon	30	2112 114	11 121	2 14 1 2 323	4555551354
Tragus koelerioides	20	3 1		3 3 3 324333333 413 1	1 11
Brachiaria nigropedata	16	1 1	1 3	1 3 12 133	1 1122
Citrullus sp.	18	11 1 1	11 111 1	1 1	1111 11
Hibiscus microcarpus	15	111 111	1 1	1 11 1 1 1	1
Selago welwitschii	15	111 1 1	1 1 1	1 1 1 1 1 2	1
Shrub sp. (no. 127)	11	1 1 1 1	1 1	11	1 1 1
Plinthus sericeus	18	1 1	111	11111 1 1 1 1	1111
Sericorema remotiflora	12	1 1		1 111 1 1 11	11
Anthospermum rigidum	11		1 1	1 11 11 1	1 1 1
Acacia erioloba	11	1	1	1 11 1 11 1	1 1
Cleome rubella	7	1	1	1 1 1 1	1
Commelina sp.	7		1	1 1 1 1	1 1
Pollichia campestris	7	1		1 1	1 1 11
Elephantorrhiza sp.	5		1	1 1	1 1
Themeda triandra	4	1		1 1 1	
Lithospermum cinereum	3	1			1 1
Indigofera filipes	3	1	1	1	
Cassia sp.	3			1 1	1
Asparagus sp.	3			1 1	1
Lightfootia denticulata	3	1	11		
Ipomoea ommaneyi	2			1 1	
Trachyandra laxa	2			3	1
Hertia pallens	2		1		1
Aristida mollissima	2		4	1	
Limeum fenestratum	2		1 1		
Indigofera sp.	1	1			
Cyperus sphaerospermus	1	1			
Salsola kali	1				1
Convolvulus sagittatus	1				1
Asclepias sp	1				1
Stipagrostis sp.	1			1	
Hibiscus pusillus	1			1	
Setaria flabellata	1	1			
Rhyncholytrum repens	1	1			
Sida ovata	1	1			
Solanum panduraeforme	1		1		
Acrotome inflata	1			1	
Rhynchosia venulosa	1		1		
Brachiaria sp.	1			2	
Osteospermum muricatum	1				1
Kyllinga alba	1			1	
Senecio inaequidens	1			1	
Dichoma schinzii	1			1	
Elionurus muticus	1			5	
Amaranthus thunbergii	1				1
Helichrysum cerastioides	1			1	
Hermannia quartiniana	1			1	
Chenopodium carinatum	1				1
Lotononis calycina	1	1			
Tribulus sp.	1				1

sociation and four were situated in the *Conyza bonariensis* community (Figure 33).

The phytomass per unit area in the *Conyza bonariensis* community was compared with that of the two other communities, using the disc pasture meter described by Bransby & Tainton (1977). A wooden square, measuring 1m x 1m and weighing 6,06kg, was dropped onto the vegetation, and the height above ground of the four diagonal centerpoints on each side of the square was then measured, this being proportional to the amount of vegetation below the wooden square. Two hundred such measurements were made in the *Conyza bonariensis* community and a further 204 in the other two communities Calibration of the method was performed by removing the vegetation under the board and measuring the dry mass of 20 such calibration plots of one square meter each. There was a high correlation between the average height above ground of the board and the phytomass/m^2 (r=0,95; 95% confidence limits 0,88 and 0,98).

The aim of the survey decribed above was to compare the structural characteristics of the three plant communities. Any differences could possibly affect the visibility of insects on which sparrow-weavers feed, as well as the distance to which predators could approach sparrow-weavers on the ground. Two creeper grass species, *Tragus koelerioides* and *Cynodon dactylon*, formed a significant part of the ground cover in all these communities. Because these species formed a dense mat of vegetation on the surface, and did not impede visibility for sparrow-weavers, two separate sets of calculations were made, one including the data for the above two species and the other excluding that data (Table 22). The results that exclude the data for the creepers are considered more applicable to the sparrow-weaver situation. The basal cover in the *Acacia erioloba* community was highest when creepers were included, but when these grasses are excluded there are no drastic differences between the basal covers of the three plant communities. However, the total cover in the *Conyza bonariensis* community was much lower than in the other communities. The means of crown width, distances between plant crowns and distances between plant bases (Table 22) also indicate that the density of vegetation in the *Conyza bonariensis* community is much lower compared to the thornveld communities. The plant biomass in the thornveld communities was 803 g/m^2 (n=204) as compared

TABLE 22

A comparison of the structural characteristics of the three floristic communities in the central study area at Bloemhof, as reflected by a line transect survey consisting of 12 transects of 50m each. Two sets of calculations are given: A includes the data for Tragus koelerioides and Cynodon dactylon; B excludes these data.
Acacia = Acacia erioloba community.
Periph = Nidorella resedifolia community.
Ecoton = Conyza bonariensis community.

	A: including Tragus and Cynodon			B: excluding Tragus and Cynodon		
	Acacia	Periph	Ecoton	Acacia	Periph	Ecoton
No. transects	5	3	4	5	3	4
Basal cover (%)	19,1	9,1	7,2	5,1	8,4	4,6
Total cover (%)	88,1	63,3	57,1	72,7	60,4	35,5
Mean distance between plants on transect. (cm)	24,7	23,6	18,7	28,6	26,5	40,6
Mean distance between plant bases on transect (cm)	60,9	48,2	41,1	80,0	53,4	101,9
Mean crown cross-section (cm)	21,8	15,0	10,6	20,8	16,0	14,4
Mean basal cross-section (cm)	4,7	2,2	1,3	1,4	2,2	1,8

Basal cover denotes the percentage of ground surface occupied by grass- and shrub stems.

Total cover denotes the percentage of ground surface that are covered by canopies of plants.

TABLE 22

A comparison of the structural characteristics of the three floristic communities in the central study area at Bloemhof, as reflected by a line transect survey consisting of 12 transects of 50m each. Two sets of calculations are given: A includes the data for Tragus koeleroides and Cynodon dactylon; B excludes these data.
Acacia = Acacia erioloba community.
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	A: including Tragus and Cynodon			B: excluding Tragus and Cynodon		
	Acacia	Periph	Ecoton	Acacia	Periph	Ecoton
No. transects	5	3	4	5	3	4
Basal cover (%)	19,1	9,1	7,2	5,1	8,4	4,6
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Basal cover denotes the percentage of ground surface occupied by grass- and shrub stems.

Total cover denotes the percentage of ground surface that are covered by canopies of plants.

to an equivalent figure of 593 g/m² (n=200) in the *Conyza bonariensis* community; a significant difference (z=6,4; p<0,01) which provided additional evidence on the structural contrasts between the different plant communities.

Regarding the influences of these structural differences on sparrow-weaver biology, a number of factors may directly influence the feeding behaviour of these birds as well as the ease with which terrestrial predators can locate feeding sparrow-weavers.

1. The lower mean crown cross-section, combined with a larger inter-plant distance in the *Conyza bonariensis* community would cause visibility at ground level to be much better here than in the other communities.

2. The lower total cover in the *Conyza bonariensis* community causes a much larger proportion of open ground to be available to sparrow-weavers. If the birds feed mainly on open ground, the *Conyza bonariensis* areas may be advantageous.

3. The lower phytomass per unit area causes differences in the availability of plant food to phytophagous insects. This may cause differences in the insect species compositions of the plant communities.

Insect availability

The floristic and structural differences between the three plant communities at Bloemhof lead me to ask the following questions about insect availability:

- Are there any differences in the taxonomic composition of the insects between these plant communities?

- Are the insects that are taken characteristic of any physical feature of the habitat?

Pitfall traps (Southwood 1976) were used to collect terrestrial insects in the *Conyza bonariensis* and the *Acacia erioloba* communities. Two lines of ten traps were maintained during the period September 1982 to May 1983. Each trap (15cm in diameter, 18cm deep) was provided with a roof so that vertebrate predators could not remove the insects. Pits were placed 10m apart and adjacent ones were joined by a plastic barrier which was approximately 18cm high and 1mm thick. This barrier forced terrestrial insects which would have passed between two pits to move along the barrier to the proximity of the pits. Trap-lines were simultaneously laid in the ecotonal habitat and in the thornveld. Relative insect abundances were calculated in terms of trap-days. The number of active traps was greatly reduced by the activities of foxes, mongooses and shrews that attempted to dig out traps, fell into them or disturbed them in some other way.

Inadvertently, some of the pitfall material of the *Conyza bonariensis* and *Acacia erioloba* communities were combined. As a result, the data for only 224 trap nights in the *Conyza bonariensis* community and 468 trap nights in the *Acacia erioloba* community are available as separate results (Table 23). Even though the data are limited, it is clear that the pits in the *Conyza bonariensis* community yielded higher insect numbers in almost all the taxonomic groups that were caught. This tendency is dramatic in the case of the ants (Formicidae) and weevils (Curculionidae), which are two of the most important sparrow-weaver foods (Table 20).

The birds ignored tenebrionid beetles, which are probably the commonest terrestrial insect taxon in the area (Table 23). Although the sparrow-weavers ate large quantities of termites (Table 20), the traps failed to sample these insects.

TABLE 23

A comparison of the relative abundance of arthropods in the *Acacia erioloba* community with that of the *Conyza bonariensis* community in the Bloemhof central study area. The data below represent captures over 224 trap nights in the ecotonal community and 468 trap nights in the *Acacia erioloba* community from September 1982 to March 1983.
Aca = *Acacia erioloba* plant community.
Eco = *Conyza bonariensis* plant community.

TAXON	FREQUENCY (No. insects)		ABUNDANCE (Insects/trap night)	
	Aca	Eco	Aca	Eco
Coleoptera:				
Carabidae	89	165	0,19	0,74
Tenebrionidae	171	215	0,37	0,96
Curculionidae	26	119	0,06	0,53
Lampyridae	11	32	0,02	0,14
Scarabaeidae	19	5	0,04	0,02
Cerambycidae	1		0,002	
Cicindelidae	1		0,002	
Elateridae	2	5	0,004	0,02
Diverse		43		0,19
Orthoptera:				
Gryllidae	18	15	0,04	0,07
Tettigonidae	1		0,002	
Heteroptera:				
Pentatomidae		11		0,05
Reduviidae	1	2	0,002	0,01

(Continued on next page)

Table 23 (Continued)

Aca=*Acacia erioloba* plant community.
Eco=Ecotonal plant community.

TAXON	FREQUENCY (No. insects)		ABUNDANCE (Insects/trap night)	
	Aca	Eco	Aca	Eco
Hymenoptera:				
Formicidae	32	59	0,07	0,26
Dictyoptera:				
Blattidae		1		0,005
[illegible]optera		6		0,03
Le[illegible]ra	2	2	0,004	0,01
[illegible]		5		0,02

DISCUSSION

Why are sparrow-weavers restricted to thornveld?

Despite the preference for ecotonal or disturbed areas at Bloemhof, sparrow-weavers are commonly associated with *Acacia* spp. thorn trees. The Bloemhof area has relatively few tree species other than thorn trees. The fact that sparrow-weavers use thorn trees almost exclusively for nesting may, therefore, be an effect of the floristic composition of the area and little evidence from this study can be produced to indicate an actual preference. However, these trees are almost exclusively used for sparrow-weaver nesting in other parts of Africa (Mendelsohn 1968, Ferreira 1972, Burger & Gochveld 1978). Both Mitchell (1966) and Lewis (1982a) observed that sparrow-weavers in Zambia use thorn trees for nesting, even though there are many other tree species. Also, *Acacia* spp. trees are characteristic of the sparrow-weaver habitat in northern Kenya (Collias & Collias 1978). I propose that one of the main reasons for their association with thorn trees is related to the fact that sparrow-weavers build nests using dry grass stems which do not allow tight knotting of the nest to the branch of a tree, as is the case in the Ploceinae. It was shown in Chapter 4 that erosion by wind is probably the major factor causing the loss of sparrow-weaver nests. Thorn trees have two characteristics that ensure that a nest of dry grass stems does not come loose and fall when a strong wind blows:

1. The branches are rigid and they bend and move less in the wind than do trees with more flexible branches.

2. The thorns of these trees provide easy points of attachment on the tips of branches, without which it would be more difficult to attach a nest of dry grass stems (Figure 26).

In addition, the thorns on the branches of these trees probably restrict movements of predators that approach occupied nests.

Thorn trees are not a source of food for sparrow-weavers. No evidence could be found to indicate that the major food sources of sparrow-weavers are specifically associated with thorn trees, nor was there any suggestion that thorn trees play a role in sparrow-weaver signalling patterns.

I suggest that sparrow-weavers evolved in an environment in which *Acacia*-like trees were common and their present habits merely reflect a way of surviving in such an environment. The present preference for *Acacia* trees probably stems from adaptation to this habitat as a total unit (including its food sources and predators) and not only because these trees offer particularly good nesting sites. Thorn trees occur in the moister south-eastern parts of Africa (Acocks 1975) but sparrow-weavers do not: the presence of these trees is therefore not the only essential characteristic of sparrow-weaver preferred habitat.

The relation of diet to preferred habitat

The magnitude of the differences in terrestrial insect capture rates in the two sampled habitats suggests that they reflect real differences in insect abundances. However, several problems surround interpretation of the results from the pitfall traps. Firstly, the thornveld has a denser vegetation compared with the disturbed, ecotonal areas, and this exposes a larger plant surface area on which insects can crawl. It could be argued that because the pitfall trap lines had similar lengths in both habitat types, the probability that a crawling insect will be captured in a thornveld pit is lower (Southwood 1976). However, most of the common taxa that were captured are largely terrestrial, and thus not severely affected by the plant surface area. Among the captures, weevils was the only important insect taxon that usually crawls on plants.

The greater abundance of terrestrial insect taxa in the ecotonal area need not indicate that this area has a larger absolute insect abundance compared with the thornveld. Sweep net samples of insects that climb on to vegetation would have revealed a complimentary picture to indicate the absolute insect abundances in the two habitat types more accurately. However, since sparrow-weavers rarely forage on vegetation, I consid-

ered this unnecessary, and all I can suggest is that the ecotonal areas appear to have a greater abundance of the terrestrial insects eaten by sparrow-weavers.

The stomach content analyses usually did not allow the identification of insects down to generic level. However, the two weevil genera *Protostrophus* and *Brachycerus* formed 85% of the pit trap captured weevils and it is highly probable that the sparrow-weavers fed mainly on one or both of these genera. All the Curculionidae in Table 20 are typical of the sandy, arid parts of southern and central Africa and are common in disturbed or open areas (Gouwse 1977, Oberprieler *pers. comm.*). The other weevil genera caught in pitfalls, *Synthocos* and *Rhytirrhinus*, are terrestrial. Weevils of the genus *Brachycerus* have very hard exoskeletons which are likely to remain relatively undamaged in the stomachs. These were, however, not found; this suggests that the relatively soft-bodied *Protostrophus* species were the most important weevils in the sparrow-weaver diet. The termites eaten by sparrow weavers are also typical of the dryer habitats in Africa. *Hodotermes mossambicus* is not found in regions with more than 750mm annual precipitation (Coaton 1958), but occur in arid and semi-arid east, central and south-western Africa. The occurrence of these termites in moister areas is often the result of severe overgrazing or mismanagement of the veld (Gouwse pers. comm.). They are probably adapted to the arid parts of Africa and are characteristic of open ground and hard-pan soils (Buillon 1970). Apart from the occurrence of *Hodotermes* in Swaziland and Mocambique, the geographical distributions of white-browed sparrow-weavers and *Hodotermes* are largely similar. The genus *Hodotermes* has been claimed to be of Palaearctic origin, only appearing in Africa during the early Mesozoic (Buillon 1970).

The termite genus *Trinervitermes* is purported to have originated during the Miocene (Buillon 1970) and consists of several species inhabiting most of the Ethiopean region. *Trinervitermes* species are characteristic of savanna areas and are generally associated with sandy soils (Buillon 1970). Sands (1965) recognised 16 species in the genus, all of which have relatively restricted distributions. Two of these species, *T. bettonianus* and *T. trinervoides*, have a joint geographical distribution largely resembling that of white-browed sparrow-weavers. *T. trinervoides* occurs in southern and south-western Africa while *T. bettonianus* occurs in

central and eastern Africa (Sands 1965, Coaton & Sheasby 1973). I suspect that *T. bettonianus* is an important sparrow-weaver food source in East Africa.

The insect taxa eaten by sparrow-weavers show close affinities with arid and semi-arid habitats and are mostly characteristic of disturbed habitats in more mesic environments. An exact correspondence, however, between the sparrow-weaver geographical distribution and that of any of their insect foods does not exist, suggesting that sparrow-weavers are not dependent on any single insect taxon. The wide range of insects taken supports this point.

The vegetable food taken by sparrow-weavers also reflects the open, disturbed nature of the areas used for feeding at Bloemhof. Table 13 shows that cultivated crops are an important part of the vegetable component of the sparrow-weaver diet. Maize and wheat formed 22% of the identified vegetable food items. It is possible that the open structure of vegetation in cultivated fields presents a suitable habitat for sparrow-weaver feeding, and that the crops are taken opportunistically. The birds were often observed feeding in cultivated fields for long periods, during which much food was collected among the detritus below cultivated plants. Among the wild plants eaten, *Urochloa panicoides*, *Echinochloa crus-galli* and *Eleusine* spp. are all characteristic of open, disturbed areas (Henderson & Anderson 1966, Roberts & Fourie 1975) and not necessarily of sandy, arid areas. The only commonly eaten plant not characteristic of disturbed areas is the grass *Stipagrostis uniplumis* which was common in all the plant communities at Bloemhof and is characteristic of arid areas in southern Africa (Acocks 1975). I believe that sparrow-weavers have not evolved adaptations to feed on these specific plant species, but that the diet of these birds reflects the open vegetation which they prefer.

The sparrow-weaver preference for areas with sparse ground cover was commented upon by Lewis (1982a) and Vernon (1983) who observed these birds in *Colophospermum mopane* woodland. This vegetation type typically has a sparse ground cover (Acocks 1975). Vernon (1983) often found the birds in clearings in the mopane woodland. Although quantitative measurements were not taken, the herbaceous and grassy vegetation at Daan Viljoen was much more open than at Bloemhof (Figure 1). Daan Viljoen

is situated centrally within the geographical distribution of sparrow-weavers in southern Africa. At Bloemhof, which is near the moister, south-eastern boundary of the sparrow-weaver distribution, the vegetation is unlike the preferred sparrow-weaver habitat in that it is more dense than the arid, western parts of southern Africa. This causes the birds to feed in relatively small, open areas at Bloemhof which have been disturbed by man. In this respect, humans may be creating suitable sparrow-weaver habitats.

CONCLUSIONS

Sparrow-weavers are restricted to *Acacia* spp. veld. They seldomly nest in other tree species and the branches of the thorn trees provide suitable nesting sites. Therefore these trees limit the distribution of these birds. Sparrow-weavers are also dependent on sparsely vegetated areas for capturing terrestrial insects. At Bloemhof, sparrow-weavers inhabit open, disturbed grassland areas which may have a structural similarity to the sparsely vegetated habitat in more arid areas.

Sparrow-weavers feed on a wide variety of insects and seeds, many of which are typical of arid or disturbed areas. The food that is eaten by these birds does not appear to be very specific and except for the occurrence of termites, the distribution of the birds would probably not be influenced by the presence or absence of any individual food species.

This supports the contention that white-browed sparrow-weavers are not adapted to any single character of the habitat, but to a combination of characters that reflect the habitat in which they evolved. The preferred habitat of sparrow-weavers can best be typified as *Acacia* spp. thornveld with a relatively sparse ground cover. This study suggests that the following diverse characteristics of the arid thornveld affect the biology of sparrow-weavers.

First, the density of the herbaceous vegetation layer affects the amount of open ground which sparrow-weavers use for capturing terrestrial insects. High vegetation density is, therefore, disadvantageous. Second,

cold winter nights probably make roost nests essential. Third, soft green grass stems are often not available for nest building. This necessitates the construction of large, unwoven nests from dry grass stems. Fourth, the unwoven nests need secure sites to which they can be fastened. *Acacia* spp. trees appear to offer the only suitable sites. Fifth, the conspicuousness of sparrow-weaver nests causes them to be easily located by predators. The resulting predation on both full-grown birds and broods is alleviated by the construction of a large number of nests which again has ramifications for the social system of these birds.

One cannot rank any one of these environmental constraints as more important than any other. Animals are adapted to their preferred habitat as a unit and not to one or two specific aspects of that habitat. I assume that the factors influencing sparrow-weavers today were present when these birds evolved, and were important causative agents in their evolution.

CHAPTER 7: SOCIOBIOLOGY AND SPARROW-WEAVER SOCIALITY

INTRODUCTION

The following hypotheses have been proposed to explain altruism (Chapter 1):

A) The ecological model (Crook 1964, 1965). This constitutes the orthodox view that sociality and altruism arise in response to constraints imposed either by other animals or by the physical environment (Crook 1964:182). Being primarily interested in causes of flock formation and dispersion in ploceines, Crook concluded that ploceine dispersion (=the degree to which weavers occur in groups) is dependent mainly on two factors: a) the preferred food, its abundance and distribution in the environment, and b) nest site selection in relation to predator approach (Crook 1965:206). He envisaged natural selection shaping co-operation or altruism either through nest predation or increased chick survival (Crook 1965:212). He suggested that when sociality is the result of responses among individuals to overcome some ecological constraint, these relationships are, incidentally, co-operative. Crook did not investigate altruistic social behaviour in depth. In particular, he did not present detailed arguments for explaining the complex social behaviour of co-operatively breeding birds like the groove-billed ani *Crotophaga ani* (Davis 1942), and that of the eusocial insects.

B) The sociobiological explanations propose that co-operation and altruism can be explained in terms of the ways in which an individual can achieve maximum fitness. Because this approach emphasises relationships within a social unit, the level of explanation differs from that of Crook (1964,1965). These models assume that an individual can increase its fitness in indirect ways, dependent on the social and genetic relationships among individuals in a group. The sociobiological explanations of apparent altruism are based on three major models:

1. The kin selection model proposes that an individual can increases its individual fitness by altruism towards individuals with a similar

genotype (Hamilton 1964). This increased fitness is brought about through increased survival of individuals with similar genotypes.

2. The parental manipulation model suggests that parents can increase their individual reproductive success by manipulating their offspring to assist in the raising of siblings, instead of breeding themselves (Alexander 1974). A parent could produce more offspring if its offspring assisted in the raising of sibs.

3. The reciprocal altruism model suggests that an animal performs altruistic acts because of a high probability that these acts will be reciprocated by the beneficiary (Trivers 1971).

Because apparent altruism is a characteristic feature of sparrow-weaver society, I shall consider ways in which different age groups benefit from the observed social organisation and associated altruism. This will allow an evaluation of sparrow-weaver sociality in the light of the above theories.

Altruistic acts normally constitute only part of the total social system of animals: animals that perform helping often have many other aspects to their sociality, e.g. communal defence of territories and communal feeding. Field studies, however, have been interpreted as showing that, where altruism occurs, it usually lies at the centre of the broader repertoire of social behaviour; i.e. the forces shaping altruism also shaped the global social organisation, or at least yielded a particular social organisation as an incidental effect (e.g. Brown 1974, Ligon & Ligon 1978, Vehrencamp 1978). This chapter investigates the origin of altruism and sociality among sparrow-weavers. Two questions need to be answered:

1. Is any one of the above approaches more useful in explaining sociality and altruism among sparrow-weavers?

2. Are sparrow-weaver sociality and altruism adaptations for overcoming particular environmental constraints, or could either of these represent an incidental effect of unrelated evolutionary processes?

DISCUSSION

The interpretation of data in terms of sociobiological theory is usually based on estimates of decreased fitness of the altruist compared with the increased fitness of the beneficiary. In order to evaluate the possible role of kin selection (Hamilton 1964), parental manipulation (Alexander 1974) or reciprocal altruism (Trivers 1971) in shaping sparrow-weaver sociality, the advantages and sacrifices of the participating age/sex classes have to be evaluated.

Advantages to adults: The benefits that accrue to adults with non-breeders in the group, are derived from three sources:

1. The nest-building activity of immature sparrow-weavers enhances the breeding success of the adults. Each immature builds an average 7,3 nests/year (Table 13). Newly-established sparrow-weaver pairs with one immature have a high probability of having more than 10 nests at the start of breeding because of the nest-building activity of the three birds: this figure would be substantially less for single breeding pairs. Figure 28B shows that the breeding success of a group with 15 nests is 14% (i.e. 41%-27%) higher than that of a group with only five nests; i.e. 52% (i.e. 14%/28%) more chicks are likely to survive when compared with the situation when only 5 nests existed in the nest tree. An immature could therefore increase the brood survival by half, thus contributing a third of the surviving brood. In such a situation, the effective contribution of this immature towards the success of the breeding pair would be one third (0,6 chicks) of a surviving brood of two. This effect is, however, greatly reduced when the nest tree already has large numbers of nests (Figure 28).

2. Immatures could also increase the survival of broods through chick-feeding (i.e. "helping"). In 1-helper groups, helpers supplied about 20% (Table 15) to 35% (Lewis 1982a) of the food items brought to the nest, causing the adults to expend less energy in collecting food. In this study, breeding success did not appear to be influenced by the presence of helpers. This contrasts with the data of Lewis(1982a), which suggested that helpers increased breeding suc-

cess. However, he could not discriminate between the effects of helping and territory quality. In addition, he did not include the influence of nest building on survival. Lewis found a significant correlation between the number of helpers and the total feeding rate. This study, in contrast, indicates that the presence of one helper did not increase the total feeding rate significantly (Table 15). Therefore the relationship between number of helpers and breeding success may not be a simple one. The increased chick feeding rate as a result of helpers comes into effect only when a large number of helpers is present. Table 3 of Lewis(1982a) infers that, in the case of nests yielding a single fledgling, the feeding rate could be increased from about 5 feeds/h by about 0,9 feeds/h for every additional helper. This phenomenon would increase chick survival if food availability is limiting during the breeding season. Both the present study and that of Lewis (1982a) showed a decreased adult feeding rate in the presence of helpers; Lewis(1982a) reported that in the case of groups with three or more helpers, the proportion of feeding by the mother is halved. Because the adult female does most of the chick feeding, she benefits most from helpers. The reduction in adult feeding of chicks suggests that food supply is not an important limiting factor during breeding. In summary, the present study does not supply overwhelming evidence showing that helping increases brood survival. Chapter 5 presents an argument which discredits possibility that helping is an evolved adaptation that increases the survival of chicks during dry years. For ease of comparison during later arguments, I assume that enhancement of breeding success through helping does occur, and that it can be measured in terms of the proportion of food that chicks receive from helpers. If chick-feeding constitutes the most important activity during the raising of a brood, we could say that one helper normally raises 0,2 of the total brood which normally comprises two chicks; i.e. 0,4 chicks are raised through the feeding of the helper.

3. Immature sparrow-weavers perform a significant amount of vigilance behaviour (Figure 10) which allows the adults to spend more time feeding. Because adult males perform most of the vigilance behaviour, they benefit the most from vigilance by other age/sex classes. However, the abolute measurement of this benefit was not possible.

4. The nest building behaviour of immatures appears to enhance the survival of adults, presumably because nocturnal predators cannot locate adults that roost in a nest surrounded by many others. The survival of adults in large groups is higher than that of lone pairs (Figure 29).

Advantages to immatures: Since the immatures are altruistic and perform acts that apparently reduce their fitness, this is one of the key factors in elucidating the evolution of sparrow-weaver sociality. All the sociobiological models explaining altruism presuppose the maximisation of the inclusive fitness of immatures that remain in groups and do not disperse (e.g. Vehrencamp 1979; Emlen 1982a, 1982b, 1984). The benefits to immatures in large groups are as follows, some of which also apply to adults in large groups.

1. Adults perform the largest amount of vigilance behaviour. This would cause feeding immatures to be less exposed to predators. However, the low rate of interactions between predators and sparrow-weavers made the quantitative measurement of this protective effect impossible.

2. Large sparrow-weaver groups have more nest structures in their nest trees, and tend to have a larger nest/bird ratio (Figure 16). This presumably causes nocturnal predators to spend more time finding roosting birds. The annual survival of immatures was much lower than that of adults (Figures 29,30). This suggests that immatures are exposed to additional mortality factors which could involve diurnal ground-dwelling predators. Alternatively, immature sparrow-weavers could be less experienced in escaping from attacking predators. However, immatures of large sparrow-weaver groups survived about as well as lone sparrow-weaver pairs (Figure 29).

3. Immatures experience the opportunity of perfecting various behavioural patterns such as nest building, vigilance and chick feeding. These are crucial activities for successful reproduction during aculthood.

TABLE 24

Lifetime reproductive success of sparrow-weavers following different reproductive behaviours (See text). Annual survival figures were obtained from Figure 29, while probabilities of successful breeding originate from Figure 28B. Except in the case of a helper which contributes an effective brood size of 0,4 (20% of the care of 2 chicks), the normal clutch size at Bloemhof was two. Probabilities of survival up to age (y) were obtained by multiplying the annual survival figures up to age (y). Number of offspring raised per year was calculated by multiplying: (probability of survival) x (probability of successful breeding) x (brood size). Accumulated reproductive success represents the cumulative number of offspring raised over the life time of an individual following the indicated behavioural pattern.

SPARROW-WEAVER AGE(y)	ANNUAL SURVIVAL	PROBABILITY OF SURVIVAL TO AGE (y)	PROBABILITY OF SUCCESSFUL BREEDING	BROOD SIZE	NUMBER OF OFFSPRING RAISED	ACCUMULATED REPRODUCTIVE SUCCESS
BEHAVIOUR: Disperse just before 1st breeding season and breed without helpers every year.						
1	0,70	0,70	0,27	2	0,378	0,378
2	0,35	0.25	0,4	2	0,196	0,574
3	0,35	0.09	0,5	2	0,085	0,659
4	0,35	0.03	0,5	2	0,030	0,689
5	0,35	0.02	0,5	2	0,015	0,700
BEHAVIOUR: Breeds with the aid of helpers every year.						
1	0,70	0,70	0,5	2	0,700	0,700
2	0,70	0,49	0,5	2	0,490	1.190
3	0,70	0,34	0,5	2	0,343	1.530
4	0,70	0,24	0,5	2	0,240	1.771
5	0,70	0,17	0,5	2	0,169	1.942
BEHAVIOUR: Help for 1st breeding season; disperse before 2nd and breed with the aid of helpers each year.						
1	0,70	0,70	0,5	0,4	0,140	0,140
2	0,55	0,39	0,5	2	0,385	0,525
3	0,7	0,27	0,5	2	0,270	0,795
4	0,7	0,19	0,5	2	0,189	0,983
5	0,7	0,13	0,5	2	0,132	1,115

Vehrencamp (1979) suggested that the costs and benefits of altruistic behaviour should not be considered over a specific breeding attempt, but should be calculated for the total life span of each individual. Lifetime reproductive fitness is a more accurate reflection of the evolutionary forces shaping a population. Table 24 presents estimates of the lifetime reproductive potential of sparrow-weavers of different ages. Three estimates are presented, each based upon a different behavioural pattern. From the table it appears that the lifetime reproductive potential of lone sparrow-weaver pairs that establish new nest trees and territories, is very low, mainly because of low adult survival. Their initial breeding success would be low because the group would have a low nest/bird ratio in the absence of nest building by immatures. Sparrow-weaver pairs that breed with the aid of helpers throughout their lives could expect to produce 2,7 times the number of chicks produced by single pairs. It would appear that the advantage accruing to adults through helpers is substantial. The third (bottom) section of Table 24 represents the lifetime reproductive success of sparrow-weavers that help during their first breeding season, but disperse before their second season, to become breeding adults in groups assisted by immatures. The mean survival during their second year is slightly lowered because of the probability of them being joined by immatures only some months after establishing a territory. The effective brood size during the period of helping prior to dispersal is 0,4 (20% of two chicks). At an age of five years these birds have a reproductive potential half the equivalent value of birds with helpers throughout their lives, but higher than for birds that never have helpers. The biggest reproductive cost is incurred during the first year of helping but after three years of age, their reproductive potential is larger than that of birds that established new territories at the start of their first breeding season. This implies that the main advantage gained by immatures remaining in the natal group is the increased survival brought about by a large group size.

SPARROW-WEAVER SOCIALITY AND EMLEN'S MODEL

Emlen (1982a, 1982b, 1984) presented a model of sociality for immatures that are prevented to breed by some environmental constraint, e.g. a

skewed population sex ratio or an absence of suitable breeding territories. In contrast to Crook's ecological approach mentioned earlier, Emlen assumes that immatures in breeding groups strive to maximise their inclusive fitness. Immatures which are unable to breed therefore remain within larger breeding groups and act as altruists. The applicability of this argument is considered here.

In a situation where the suitable habitat has been filled with sparrow-weaver territories, one would expect immature dispersal to be reduced. The population at Bloemhof did not appear to be in this condition because three territories (PINK, YELLOW and WHITE) were vacant for the greater part of the study (Figure 3). From what is known about sparrow-weaver habitat requirements (Chapter 6), large amounts of suitable habitat appeared to be available at both Bloemhof and Daan Viljoen. Lewis (1982a:321) reported a case where the available habitat appeared to have been filled with sparrow-weaver territories: the few founder groups that he observed were all in suboptimal habitats and their success was low. The mean group size of 4,4 birds in Zambia was somewhat, but not statistically significantly, higher than the mean value of 3,5 birds per group at Bloemhof (Mann-Whitney U-test: N_1=33 N_2=27 U_1=565 U_2=326 $p<0.071$). The mean group sizes in the different study areas are remarkably similar (Table 6). Therefore, there is no compelling evidence to show that sparrow-weaver group size is influenced by the degree to which the preferred habitat has been saturated with territories. If food supply determines the availability of preferred habitat in arid and semi-arid areas where the annual rainfall is unpredictable, the saturation of preferred habitat would vary from year to year. This factor would oppose the establishment of a stable subpopulation of helpers unable to establish territories. The effect would be less noticeable in Zambia, where the annual rainfall is more constant than in northern Kenya and south-western Africa.

Sociality and altruism have often been related to an unequal sex ratio among full-grown birds (Rowley 1965, Fry 1972, Ridpath 1972, Tarboton 1979, Reyer 1980). Full-grown birds are supposedly retained within social groups because of a lack of potential mates. This was not the case in the Bloemhof area, where the sex ratio was 80 females to 84 males. Similar data from the other sparrow-weaver studies are not available.

Roughly a third of the total sparrow-weaver population at Bloemhof was involved annually in intergroup movements (Chapter 2). This suggests that these movements do not pose inordinately high risks. These data contrast with those of Lewis(1982b), who over 3 years observed 42 long-term intergroup movements in a population of about 100 birds (roughly 13% of the total population per annum). The ease with which Bloemhof juvenile and immature sparrow-weavers moved through territories adjacent to that of their native group, suggests that there are no social mechanisms to inhibit these animals from moving through foreign territories and temporarily joining such groups. Agonistic interactions are rare and occur mostly among adults of neighbouring territories (Chapter 3). Physical barriers obstructing dispersal were not noticed. These data suggest that dispersal does not entail prohibitive social or physical risks. High dispersal risks could thus not have been important in causing the retention of immatures within groups.

The probability of successful reproduction after dispersal appears to be low. None of the five founder colonies observed at Bloemhof between 1982 and 1984 were successful during their first breeding season. As discussed earlier, this low breeding success is probably related to the fact that founder groups did not have many nests.

Of the variables postulated by Emlen's model (1982a,1984) for explaining immature altruism, the only factor that would facilitate the retention of full-grown sparrow-weavers within groups is a high cost of reproduction following dispersal. If the possibility of becoming a dominant breeder within an established group were high, it would be advantageous for full-grown non-breeders to remain within their native groups. The crucial question regarding apparent sparrow-weaver altruism is whether it is an evolved adaptation or an incidental effect. If it were an evolved adaptation, Emlen's model should be seriously considered. This question is pursued after the usefulness of the sociobiological models of kinship, parental manipulation and reciprocal altruism has been considered.

SPARROW-WEAVER SOCIALITY AS A RESULT OF KIN SELECTION

A kin selectionist expectation that would apply in the circumstances like those of sparrow-weavers which forego breeding, is that when the right conditions prevail, an animal will increase the fitness of related individuals at the expense of its own fitness. The units of benefit to the recipient and of cost to the altruist can be measured either in terms of reproductive potential or in terms of indirect fitness (Hamilton 1964). Measurement of fitness must be directly related to the number of offspring that an animal produces. In the case of eusocial insects, the benefit accrued by the reproductive individuals can easily be measured in terms of the number of insects raised by workers that perform the whole task of brood rearing. Because sparrow-weaver helpers do not assume complete responsibility for the raising of chicks, their contribution towards the fitness of sibs cannot be measured in terms of discrete offspring. If helpers increased sibling survival, these additional surviving sibs could be considered as having been raised by the helpers. The present study points to two ways in which helpers increase the fitness of their sibs: a) by reduced predation on sibs as a result of nest building b) by helping with chick feeding (Figure 28, Table 15). Since these two factors are independent of each other, they would have separate, additive effects on the indirect fitness of helpers.

At Bloemhof, the most frequent clutch size was two, whereas Lewis(1982a) found a clutch size of one more common in Zambia. Taking the Bloemhof brood sizes as a standard, one helper could maximally contribute one third of a clutch or 0,6 chicks through its nest-building activity, as explained under "Advantages to adults". Helpers at Bloemhof performed about 20% of the total chick feeding: this feeding could contribute towards 20% of a brood, or 0,4 chicks. Summing the nest building and chick feeding effects, a single immature in a group with very few nests could thus contribute one sibling to the next generation without breeding itself. There are problems, however, in trying to attribute both of these advantages to a particular brood. Normally, helping occurs more than one year after the founding of a group: a founder pair has to breed successfully and the brood has to become old enough to assist in chick feeding. This allows ample time for the construction of many nests by adults at first, and then by their juvenile offspring before the first sib

feeding opportunity. At the stage at which helping appears within a group, the group is very likely to have more than 20 nests, thus minimising the effect of nest numbers on brood survival. Conversely, groups with few nests are breeding pairs that have just established a territory, making it unlikely that they will have offspring that could help with nest-building. If an immature helped with both the building of nests and with the feeding of chicks of a newly-established breeding pair, it would probably not be an offspring of this pair: arguments involving kin selection would thus not apply.

When combining the effects of nest building and chick-feeding, the number of offspring that a helper transmits into the next generation is thus unlikely to exceed 0,4 of the potential contribution of one chick. If the altruism of an immature results in the survival of 0,4 of a chick, one could say that the immature contributed 0,2 of the total investment necessary for successful fledging of a brood of two. This figure is much inflated because the calculation does not allow for the fact that incubation as well as the feeding of fledglings at Bloemhof is performed exclusively by adults: these activities are vital for altruist genes to be passed to the next generation.

In Table 25 the genetic contribution (in terms of its own genotype) that an altruist propagates into the next generation is contrasted with that of an immature that disperses to mate and breed separately. An altruist passes maximally about 0,1 gene copies into the next generation, compared with an equivalent figure of 0,27 for selfish sparrow-weavers that disperse. If altruism is to be maintained, the cost of independent breeding must be at least 2,7 times that of remaining within the parental group. Figure 29 suggests that the survival of single sparrow-weaver pairs is about the same as that of helpers in larger groups. No evidence can be offered suggesting a high mortality risk among dispersing immatures, compared with the mortality risks when remaining as an auxiliary within a group. It would therefore appear that helpers could contribute more offspring to the next generation by dispersing. When viewing sparrow-weaver altruism from the kin selection point of view, high pay-offs in terms of indirect fitness of helpers do not appear to be the rule.

TABLE 25

The potential gene contributions of sparrow-weaver helpers, compared with those of immatures that disperse to breed without help. Only breeding during one breeding season is considered. One gene contribution in this table represents the ability to transmit the equivalent of one copy of an animal's genotype into the next generation. The sources of the values n,f,p and s are respectively Chapter 5, Table 15, Figure 28B and Figure 29.

		Helpers	Independents
Beneficiaries:		Siblings	Offspring
Coefficient of relatedness to beneficiaries:	(r)	0,5	0,5
Brood size:	(n)	2	2
Fraction of total brood care performed:	(f)	0,2	1,0
Potential gene contribution to next generation:	(r.n.f)	0,2	1,0
Probability of successful reproduction:	(p)	0,50	0,27
Realised gene contribution to next generation if breeding takes place immediately after dispersal:	(r.n.f.p)	0,1	0,27
Probability of survival during the specific year:	(s)	0,37	0,33
Realised gene contriution to next generation if breeding occurs 1 year after dispersal:	(r.n.f.s.p)	0,037	0,089

SPARROW-WEAVER SOCIALITY AS A RESULT OF PARENTAL MANIPULATION

Adult sparrow-weavers are in an advantageous position when the group includes related immatures, because:

1. The survival of broods is enhanced as explained above and adults need to do less chick feeding.

2. The need to build nests for breeding or roosting is reduced because of the nest building activity of immatures.

3. The amount of time spent in vigilance behaviour is reduced because of immature vigilance.

The fact that parents reduce their chick feeding rate in response to chick feeding by helpers (Chapter 5), suggests that the parents could manipulate their offspring so that the parents themselves would need to invest less energy in breeding activities.

In the model of parental manipulation, altruists do not increase their own inclusive fitness, but the fitness of their parents. The manipulation of offspring by their parents has two aspects: 1) the parents may physically impose their will upon the altruists (often their offspring) via agonistic or other physical conflict interactions between parent and altruist. 2) The parents may bring about altruism by creating an environment that induces offspring to remain within the social group and perform altruistic acts (Alexander 1974). If the manipulated altruists are not descendants of the manipulators, parental manipulation cannot occur, but manipulation of some individuals by others in terms of 'arms races' (Dawkins 1982) could conceivably occur. The very low rate of agonistic interactions among sparrow-weaver group members (Chapter 3) suggests that the first of the above methods of parental manipulation is not present in sparrow-weaver society. A ritualised way in which regular conflict situations within the group are resolved, is a prerequisite if adults were to prevent altruists from either attaining breeding status (as occurs in e.g.wolves *Canis lupus* (Mech 1970)), or from increasing their fitness

at the cost of the parent. Such a mechanism does not exist for sparrow-weavers.

The second way of manipulating altruists, namely by luring them to remain within the group, would imply that the adults can do something that the altruists cannot do by themselves. Some arguments imply that adults actually perform apparently altruistic acts themselves in order to keep the altruists in the group. The behavioural and genetic mechanisms by which parental manipulation operates are not clear (Crozier 1982), so that little is known about the ways in which parents could induce offspring to remain within the social group. Chapter 3, however, pointed out that adult sparrow-weavers perform the greatest amount of vigilance behaviour: this behaviour could increase the survival of immature altruists to such an extent that they remain in a group because of the safety that this confers. Quantification of the increased survival that parental vigilance confers on the altruists is not easy to achieve. However, the mates of adult vigilant sparrow-weavers also benefit from vigilance behaviour, so that the advantages of vigilance are not restricted to immatures. The fact that adults take part in roost nest building could decrease nocturnal predation on altruists through the multitude of roost nests. This would benefit altruists compared with immatures that disperse and breed. The fact that immatures perform as much nest building as adults would confer an identical benefit to the adults, so that the adult behaviour could not be construed as functioning to induce the altruists to stay. A fundamental problem arises wnen, through acts that increase the fitness of their offspring, parents induce the offspring to take part in altruism. The fitness increase experienced by altruists as a result of soliciting by their parents, could be sufficient to turn the process into one of manipulation of parents by their offspring.

Several authors have investigated the conditions under which altruism can evolve as a result of either kin selection or parental manipulation (Charlesworth 1978, Craig 1979, Vehrencamp 1979). Both games theory and allele-frequency modelling predict that altruism will evolve through kin selection when the benefit to the recipient (b) exceeds the cost of altruism for the altruist (c). These parameters would normally be measured in term of changes in the fitness of the individuals involved (Charnov 1977).

Mathematically we can say that if altruism were to evolve in response to kin selection:

$$b/c = K > 1 \qquad \text{(Craig 1979)}$$

The constant K respresents the benefit/cost ratio of altruism. When $1>K>0,5$ parental manipulation can shape altruism and when $k>1$ both parental manipulation and/or kin selection could cause the evolution of altruism (Craig 1979), if an altruist helps its parent with the raising of sibs. From the parent's point of view, offspring of the altruist (= second generation offspring of the parent) contain half as much genetic material in common with the parent, when compared to direct offspring of the parent. The gene benefit to the parent would be the same if an altruist raised half as many siblings than it could by independent reproduction. Mathematically we can say that if parental manipulation were to cause altruism:

$$b/c = K > 0,5 \qquad \text{(Craig 1979)}$$

If K is less than 0,5 neither kin selection nor parental manipulation could cause altruism, and the offspring of a parent should behave selfishly (Craig 1979).

The K-value that applies to Bloemhof sparrow-weavers will now be estimated. Sparrow-weaver altruists do not perform the complete raising of siblings so that the cost of altruism (c) and the benefit to the beneficiary (b) could not be measured in terms of complete offspring. Instead we could use the realised gene contribution to the next generation, defined in Table 25, as a measure of cost and benefit. The figures in the first column in Table 25 represent the number of gene copies of a helper that are, on average, raised by itself. Both altruist and parents are related to the sibling chicks by 0,5. The realised gene contribution of a dispersing and reproducing immature is 0,27 (Table 25), and this can be used as c in the above equations, i.e. the sacrifice that an immature makes when forfeiting the opportunity to breed on its own. An altruist contributes 0,1 gene equivalents to the next generation, which could be taken as b in the above equations, i.e. the benefit received by the sibs. For an altruist sparrow-weaver $K = (0,1/0,27) = 0,37$. This low K-value suggests that neither kin selection nor parental manipulation are the

cause of sparrow-weaver altruism. The values of r and f for altruists in Table 25 are overestimates for reasons previously stated in this chapter, and would cause the value of K to be smaller than calculated.

The above figures are proportional to the cost and benefit in fitness involved over one breeding season, and disregards any benefit that breeders may have from the presence of immatures. In contrast to this approach, Vehrencamp (1979) proposed that the lifetime fitness of an altruist is selected, and not short-term fitness. The annual gene contribution of sparrow-weavers that disperse and reproduce could be expected to increase after the first breeding attempt because they might in turn receive help from immature altruists. The number of nests in the breeding tree of such a group is likely to increase rapidly, increasing the reproductive success of such animals. The long-term sacrifice of helpers is, therefore, likely to be more than 0,27 equivalent offspring/breeding season. The long-term c-value is, therefore, likely to be higher than that calculated, decreasing the value of K even more and making kin selection or parental manipulation even less likely.

The following formula was offered by Vehrencamp (1979) for determining the relative importance of kin selection, individual selection and parental manipulation in the evolution of communal breeding: the kin index I_k represents the fraction of the total change in inclusive fitness of an altruist due to the kin component, compared with the non-co-operative situation (Emlen 1984). As explained above, the kin index takes into account the lifetime fitness of an animal which is a more reliable value than fitness values taken over one breeding season:

$$L=(W_{ar}-W_a)R_{ay} \qquad (1)$$

$$N=(W_{ra}-W_r)R_{ary} \qquad (2)$$

$$I_k = N/(L+N) \qquad (3)$$

Let $(W_{ra} - W_r)$ be the change in lifetime reproductive success of the recipient R when aided by altruist A and $(W_{ar} - W_a)$ the change in lifetime reproductive success of the altruist A when providing aid to R. Let R_{ary} be the relatedness of A to the young of R and R_{ay} the relatedness of A

TABLE 26

Values for I_k applicable to sparrow-weavers with a longevity between two and five years (See text).

W_{ra} is the fitness of an adult that receives help throughout its life, obtained from Table 24 as the accumulated breeding success of birds that breed with the aid of helpers every year

W_{ar} is the fitness of a bird which initially acts as an altruist and which only breeds itself as from its second year of age. This figure was obtained from Table 24 as the accumulated breeding success of individuals that help for their first breeding season.

W_a is the fitness of a bird that breeds independently throughout its life, obtained from Table 24 as the accumulated reproductive success of birds that disperse before their first breeding season.

$R_{ay}=R_{ary}=0,5$ = coefficients of relatedness between parents and offspring; and between altruists and chicks being fed.

Longevity (v)	W_{ra}	W_{ar}	$W_a=W_r$	N	L	I_k
2	1,19	0,53	0,57	0,31	-0,03	1,08
3	1,53	0,79	0,66	0,44	-0,07	0,86
4	1,77	0.98	0,69	0,54	0,15	0,78
5	1,94	1,12	0,70	0,62	0,21	0,74

to its own young (Vehrencamp 1979, Emlen 1984). The change in fitness that an altruist experiences by not dispersing consists of two parts: a) the change in personal lifetime (direct) fitness (L; defined by (1) above) due to altruism ; and b) the change in indirect fitness (N; defined by (2) above) due to altruism.

The index has the property that if $I_k > 1$, pure kin selection is predicted whereas parental manipulation is predicted when $I_k < 0$. The values of N and L can readily be calculated from Table 24 and the values of I_k for lifetimes between two and five years are given in Table 26. The figures for I_k in the table suggest that neither kin selection nor parental manipulation alone operates on sparrow-weavers but that the total lifetime fitness of a helper bird consists of contributions from both kin selection (I_k = 0,86 to 0,74 for sparrow-weavers with a longevity of longer than two years) and an individual selection component ($1-I_k$ = 0,14 to 0,26 for sparrow-weavers older than two years). This would indicate that kin selection was important in the shaping of sparrow-weaver social organisation, even though individual selection also contributed towards this form of social organisation. The change in lifetime inclusive fitness (I_k; Vehrencamp 1979) of sparrow-weaver helpers contrasts with their yearly indirect fitness (K;Craig 1979): the former suggests that indirect fitness does indeed play an important role in the causation of sparrow-weaver sociality.

None of the above mathematical manipulations of fitness values indicated that parental manipulation is an important agent in sparrow-weaver sociality. In addition, no clear mechanism can be postulated through which parental manipulation in sparrow-weavers could operate. Parental manipulation as a causative factor in the formation of sparrow-weaver societies is thus rejected.

SPARROW-WEAVER SOCIAL ORGANISATION AS A RESULT OF RECIPROCAL ALTRUISM.

Trivers (1971) postulated that an animal may behave altruistically if this act is repaid to the initial altruist. Wiley & Rabenold (1981, quoted in

Krebs & Davies 1984) postulated that the repayment need not be made by the beneficiary, but may come from its offspring. Like parental manipulation, reciprocal altruism is essentially "selfish" in nature. It attempts to increase the altruistic individual's own fitness.

One of the main objections raised against reciprocal altruism theory is that it is seldomly demonstrated that the altruist can recognise the benefiting individual; a feat that is necessary to prevent "cheating" or non-repayment (e.g. West-Eberard 1975). In the case of sparrow-weavers it appears that adults can recognise other individuals. Unknown sparrow-weavers are immediately approached, and if they are adults, calling matches ensue immediately, or the strangers are chased. I postulate that a large part of this individual recognition takes place through calling (Chapter 3). The important point is that the requirement of individual recognition for reciprocal altruism is fulfilled in sparrow-weavers.

In addition, the opportunity for repayment of altruism does exist among sparrow-weavers. The annual mortality among adult sparrow-weavers is of the order of 30% (Chapter 5), so the probability that an immature helper will inherit the territory, is reasonably high. In such a case, younger siblings will probably help with the rearing of the heir's offspring. Some of the aspects of nest-building could also be implicated in arguments involving reciprocal altruism. If predation on roosting sparrow-weavers is an important ecological limitation, an immature is repaid immediately by being part of an established group that would normally have a larger nest/bird ratio: this confers better protection against nocturnal predators than in the case of an immature that established its own territory. Vigilance behaviour by adults is also a form of payback for altruism.

Observations on sparrow-weavers therefore suggest that reciprocal altruism may indeed explain how sociality arose in this species. Many authors involved in the study of co-operatively breeding birds have implicated reciprocal altruism in explaining the social organisation in the species they studied (e.g. Woodhoopoes: Ligon & Ligon 1978; Tasmanian hens: Ridpath 1972; acorn woodpeckers: Koenig 1981; bee-eaters: Emlen 1981).

In the case of sparrow-weavers, however, adult emigration and mortality are unrelated to the immediate presence of immatures within a group. The benefit that immatures get by remaining in a particular group is not because of a particular sacrifice on the part of an adult that disperses or dies. These events could thus not constitute repayment of immature altruism, and reciprocal altruism can, therefore, not be involved in the process.

Nest building by immature sparrow-weavers can not be considered solely as altruism because immatures themselves benefit from their own nest building activity. Nest building immatures thus do not necessarily incur a cost by taking part in nest building, which suggests that this activity is not a form of altruism. However, co-operative chick feeding and vigilance behaviour are aspects of sparrow-weaver sociality that potentially involve a cost to altruists. In these cases it is necessary to investigate critically the evolutionary role that such costs may play in the evolution of sociality, and this is assessed in the following section.

WHAT ARE THE COSTS OF SPARROW-WEAVER ALTRUISM?

In the above sections, several theories have been postulated for explaining sparrow-weaver sociality. However, one of the big problems encountered when attempting to assess the validity of some of the theories is that few means exist for choosing between alternative hypotheses. Apart from the mathematical methods employed above, no general, quantitative crucial tests have been set up. Other workers studying altruism, e.g. Sherman (1977), have encountered the same problem.

It is wrong to assume that apparent altruism - or any trait - *must* be adaptive. Williams (1966) and Gould & Lewontin (1979) argued cogently that many characters of animals are not adaptive but are effects of unrelated processes. Lewontin (1979) pointed out that sociobiology overestimates the adaptive characteristics of social behaviour. It is possible that some forms of altruism and of sociality are not adaptive *sensu* Williams (1966). This point of view necessitates a re-examination of the adaptive

value of sparrow-weaver sociality. One of the crucial aspects in such an assessment is the cost of altruism to individuals.

Sociobiological theory makes two assumptions. First, it assumes that an altruist does indeed make a sacrifice that lowers its individual fitness compared with that of a selfish individual. If, compared with selfish birds, sparrow-weaver altruists produced fewer offspring that survived to reproductive age, their fitness would be decreased. By extending the fitness concept to include the fitness of related individuals, sociobiology states that the above decrease in individual fitness of altruists is compensated for by indirect fitness effects, reciprocal acts or high parental fitness. Second, sociobiology assumes that the benefit accrued by the recipient of an altruistic act causes an increase in its fitness: either the number of offspring of the recipient surviving to adulthood is increased or the recipient itself is enabled to perform altruism. But the results of altruism is trivial unless it could eventually be translated into increased number of offspring of some recipients.

The fact that immature birds remain in their natal groups is not altruism in itself: altruism occurs through the performance of specific behavioural patterns, made possible by the existence of a group. As explained above, co-operative nest building by sparrow-weavers cannot be regarded as altruism: only vigilance behaviour and co-operative chick feeding are potential altruistic traits. The following paragraphs investigate the direct costs of these acts to altruists in terms of the physiological fitness of altruists or their beneficiaries. The fact that no birds are known to have died of disease or malnutrition during the period 1982 to 1984 does not support the view that the birds were in any physical or physiological stress during the study period (Chapter 5). Predation at the nest, a factor which is not directly related to the physical fitness of the birds, appears to have been the most important limiting factor (Chapter 5).

Vigilance behaviour: Clearly birds that feed on the ground benefit when a vigilant individual perches closeby. This would result in more offspring surviving to adulthood when compared with groups that do not include vigilant birds. Thus it appears that the beneficiaries do in fact receive an increase in fitness. It could be argued that the time invested in vigilance could cause such birds to spend less time in feeding, or in some other activity crucial for their physiological fitness. This is unlikely,

because vigilance appears to be integrated with territorial advertisement, nest building and pair maintenance behaviour. This implies that even though vigilance behaviour could indeed increase the physiological fitness of beneficiaries, it is unlikely to have an important effect on the fitness of vigilant "altruists".

Co-operative chick-feeding: The fact that chicks were fed by birds other than their parents did not necessarily involve any decrease in fitness for the apparent altruists, since food availability or physiological condition did not appear to be important limiting factors during the present study (Chapters 4 and 5) Chicks benefited very little by altruistic feeding behaviour: the effect of altruists on feeding rate, as measured in number of feeds/time unit for each chick, was negligible (Table 15). If food resources were in short supply and if co-operative feeding was an adaptation evolved to increase brood survival, one would expect helpers to affect breeding success and feeding rate/chick most in large broods, which have the largest food requirement. In contrast, Lewis (1982a) found that this effect of helpers was more pronounced in small broods than with large broods. Co-operative feeding clearly does not have a dramatic overall effect on the fitness of either the beneficiaries or the altruists.

The basic assumption made when examining altruism among vertebrates from the sociobiological point of view, is that every aspect of an organism's behaviour affects its fitness. This leads to the argument that the physiological fitnesses of the interacting individuals are affected by altruism. It is additionally assumed that the physiological fitness of an animal translates directly into reproductive fitness. These assumptions have not been verified. Such a long chain of events link the physiological fitness of an individual to its eventual reproductive fitness that the one form of fitness is unlikely to reflect the other directly.

Brown (1980) emphasised that altruism among vertebrates can often be described in terms of mutualism. He suggested that altruism often has a minimal cost in terms of fitness of the altruist. Energetic expenditure does not automatically imply change in fitness: "To assume that donor efforts always lower donor fitness merely because they expend energy or incur a risk is incorrect" (Brown 1980:119). This view is supported by the present study. Brown, however, assumed that altruism normally

is to the advantage of the beneficiary: this allows one to calculate so-called "fitness networks" which can explain the origin of altruistic traits. I believe that one should be cautious in assuming that altruism is advantageous to the recipient. This study suggests, for instance, that co-operative chick feeding does not necessarily increase the survival of chicks. It is possible that chick feeding responses are correlated with the avian maturation process. If non-breeding, full-grown sparrow-weavers encounter chicks, co-operative chick feeding could occur merely as an effect of adult hormone levels, which could be the result of unrelated maturation processes. Many other cases of altruism could also be fortuitous by-products of totally unrelated processes in which altruism could cause neither a significant fitness loss for the donor nor a significant fitness gain for the recipient. I do not suggest that the above applies to all cases of altruism: for instance, co-operative nest building among sparrow-weavers appears to be a perfect case of mutualism as suggested by Brown (1980).

AN HYPOTHESIS ON THE ORIGIN OF SPARROW-WEAVER SOCIALITY

The present study suggests the most important factor influencing sparrow-weaver fitness is the enhanced survival and breeding success of large groups, probably as a consequence of their large numbers of nest structures. Supporters of sociobiological theory would claim that sparrow-weaver altruism is a way of maximising indirect fitness within these constraints of low survival and high mortality. I believe that this view wrongly promotes a fortuitous effect to be seen as an evolved, adaptive mechanism. If apparent altruism in sparrow-weavers could be explained at a lower level *sensu* Williams (1966), the behaviour need not be viewed as an adaptation.

When considering the evolution of altruism, one of the fundamental issues relates to the time during the species' history at which altruistic traits evolved. It could be argued that some sociobiological arguments, e.g. kin selection theory, do not concern characters that arise at speciation but only the distribution of gene frequencies after a species arose. Kin selection theory suggests that gene frequencies for altruism will increase

within a population if this altruism enhances the fitness of individuals with similar genotypes. In this case gene frequencies for altruism increase at the expense of those genes that do not code for altruism. A change in population size because of this gene frequency change is not automatically implied. The more extreme views of Wilson (1975) and Dawkins (1978, 1979) interpret selection for altruistic genes as occurring from one generation to the next: selection *is* a continuous quest for maximum representation of genes during the next generation. I favour the opinion that modern social behaviour, if adaptive, arose relatively rapidly as a result of environmental stresses that reduced a population to near extinction (Eldredge & Gould 1972, Paterson 1980).

Roost nest requirements must have had an important influence in the evolution of sparrow-weaver sociality. The two entrances of sparrow-weaver roost nests are characteristic of this subfamily, and possibly constitute an adaptation against predation on roosting birds. It is therefore conceivable that roost nests could have evolved solely as an anti-predator adaptation, the energy-saving characteristics being a mere effect. This argument implies that the evolution of the sparrow-weaver social system went through two stages: 1) the acquisition of nest-building behaviour and 2) the retention of immatures within their natal groups. The importance of large nest numbers for predator evasion in the case of sparrow-weavers suggests that the nests of other colonial ploceids (e.g. the sociable weaver and the masked weaver) may have other functions than those often ascribed to them.

The fact that sparrow-weavers use roost nests throughout the year suggests that these structures may have a significance unrelated to energy saving during the winter, thus supporting the anti-predator function that has been ascribed to them.

It is, alternatively, also conceivable that roost nest use by sparrow-weavers throughout the year is an incidental effect of their roosting requirements during winter. If the summer use of roost nests did not lower the reproductive fitness of these birds there is no reason why the behaviour could not have persisted throughout the year, being neither advantageous nor disadvantageous. This alternative view implies that the roost nests are not only an adaptation against predation, but also for decreasing thermoregulatory energy expenditure during winter

(Chapter 4). It is possible that, initially, these nests were adaptations for the conservation of energy during cold nights which the sparrow-weaver ancestors encountered. If this were true it would mean that the birds roosted in nests regularly at least during part of the year, which implies that they must have performed nest building that was not directly related to breeding. This is in agreement with the arguments of White *et al* (1975) who found that the nest structures of sociable weavers, *Philetairus socius*, have the effect of reducing the energy requirements of roosting sociable weavers significantly during winter. The fact that all the plocepasserine species, except one, occur in arid areas which experience low winter temperatures, supports the suggestion that roost nests initially evolved solely for energy conservation. The fact that few or no green grass stems are available for nest building in arid areas would mean that the nests could not be woven as in the case of the Ploceinae, but that these structures had to be thatched using dry grass stems. Thatched nests are much larger than woven nests and are much more visible to predators, resulting in a high predation rate on birds that roost in them. I suggest that the characteristic of building many nests is a secondary adaptation against predation.

Assuming that roost nest building originally was an adaptation for heat conservation, it may be that their use results in higher predation during the summer season, compared with sparrow-weavers that roost in the foliage during summer. Accordingly, sparrow-weavers could be "locked" into an evolutionary trend that cannot be easily changed because of the complexity of the genetic change that would be needed for sparrow-weavers to use roost nests during winter, but to roost in the tree foliage during summer. At present, predation appears not to be such a severely limiting factor that results in the near-extinction of sparrow-weaver populations. In the modern context, sparrow-weaver roosting behaviour is a "working solution" in that it enables the birds to *survive*, and not to be optimally fit.

I suggest that the sparrow-weaver social system evolved at a time when the ancestors of the present species were under severe predation pressure because of their habit of nest roosting. Parents whose offspring fortuitously remained in the natal group would have been much more successful than parents whose offspring dispersed. The population would have been in a situation of environmental stress as envisaged by Crook

(1964,1965) and was reduced to a small remnant population. These animals survived because, fortuitously, a relatively large number of the immatures had the trait of not dispersing. Optimisation of genic contribution to the next generation would have been less important than the survival of individuals. Natural selection did not calculate the cost or benefit of altruism on inclusive fitness at that time: the traits that were selected for were those that merely allowed the birds to survive in the face of a harsh environment. If the theory of punctuated equilibrium is taken into account (Eldredge & Gould 1972), the rapid rate of genetic change would severely limit opportunities for optimisation. After the trait of retention of offspring had been fixed, survival and reproductive success would have been improved to such an extent that the population would increase rapidly in size, making fixation of new genes very difficult. The origin of sparrow-weaver sociality, as envisaged above, occurred during an all-or-none process (extinction and survival being the alternatives) during which the ancestral population was close to extinction. Group selectionist arguments are not implied in this argument, since group selection cannot act on a single, remnant population. If an engineer were to design sparrow-weavers for efficient survival in a harsh environment, better designs could be envisaged than those seen in modern sparrow-weavers. Natural selection, however, does not design; it only allows individuals with particular traits to survive and it is restricted by the genetic variation at speciation. Only preadaptations based on existing genetic variation could be acted upon by selection to produce necessary adaptations, causing sparrow-weavers not to go extinct. The result was a new, group-living sparrow-weaver species.

CHAPTER 8: THE EVOLUTIONARY HISTORY OF SPARROW-WEAVER SOCIALITY

This study investigated the relationship between sociality in sparrow-weavers, and mortality, breeding behaviour and roosting behaviour in the species. A high mortality rate (possibly in conjunction with cold nocturnal temperatures), vigilance behaviour and communal nest-building probably were the most important factors that interacted in shaping the observed social system (Chapters 5,3 and 4). Second, the most important characteristics of the white-browed sparrow-weavers' preferred habitat were described (Chapter 6): the aim was to identify environmental factors that could have contributed towards the evolution of sparrow-weaver sociality and to establish which parameters could be typical of the environment in which sparrow-weavers evolved. The function of this chapter is to place these characters and relationships into a broader perspective with respect to the plocepasserine subfamily, and with respect to palaeoclimatic events on the African continent.

The different aspects of an animal's biology, such as feeding, social behaviour, mortality and breeding, cannot be divided into discrete compartments. A change in any one aspect has repercussions on the others, especially as far as constraints on the expression of other characters are concerned. Adaptations dating from speciation are therefore likely to affect many aspects of an animal's life, e.g. a social system has implications for diverse aspects of sparrow-weaver biology such as mortality, feeding and signalling behaviour. Because such a complex set of traits must have arisen during a speciation event, this chapter investigates the palaeo-environmental conditions at speciation which resulted in the present plocepasserine social system. I propose to discuss this in the following manner:

1. Determine what the morphology and biology of present-day plocepasserines suggest about their evolutionary relationships, and whether ecological factors important to white-browed sparrow-weavers also apply to other plocepasserines.

2. Integrate palaeoclimatic data with the information on present-day plocepasserine ecology in order to estimate the time and place where the plocepasserines could have evolved.

The above approach involves assessing phylogenetic relationships within the plocepasserines. It is necessary to augment the existing morphological data with information regarding the behaviour and ecological relationships of these birds. Behavioural traits are probably less conservative than morphological characters. Stacey & Bock (1978), Macdonald (1979a, 1979b) and Kruuk (1972) showed that social organisation in acorn woodpeckers, golden jackals, red foxes and spotted hyaenas varies considerably from area to area, depending largely on ecological factors relating to predation, food procurement and breeding sites. The social behaviour of an animal in one area may, therefore, not be typical of the species as a whole, casting doubt on the utility of behavioural information in understanding the evolution of taxa. Behavioural traits seem to vary in a somewhat more qualitative way than does morphology. If, however, the complete range of expression of a particular behaviour type, e.g. social behaviour, is known for a species from most of its geographical distribution, there is no reason why the behavioural phenotype could not be used in a way analogous to morphological characteristics. This situation may be compared with that of a bird like the Cape white-eye (*Zosterops capensis*) which has three well-defined geographical races: a grey-bellied race in the eastern and south-western Cape province; a tawny-and-white race in the northern Cape province; and a yellow-bellied race in the Border, northwards to Natal and the Transvaal (Maclean 1985). If any one of these races was taken as typical of the species, an erroneous picture of the phenotypic expression of plumage colour would be obtained: all three of the colour variants must be examined for this to be avoided. Problems concerning behavioural phenotypes may, therefore, also be encountered in biochemical or morphological characteristics. Behavioural parameters are likely to change more rapidly during evolution compared with morphological characters, because behaviour is probably more immediately affected by ecological factors. Thus, behavioural data are often less useful in comparisons involving higher order taxa. When used with caution, however, their utility is clear. I will pay particular attention to behavioural characters that are common to most or all of the plocepasserines. The probability of the same behaviour evolving

convergently in all the species is small. I therefore assume that such characters were inherited from a common ancestor.

Evolutionary relationships of the plocepasserines

Sushkin (1927) compared morphological and skeletal characteristics of several ploceine genera, including the plocepasserines. His observations were purely qualitative and largely incomplete, making it difficult to judge the validity of his conclusions. He postulated that the four genera *Plocepasser, Pseudonigrita, Philetairus* and *Histurgops* form a relatively distinct group, intermediate in some characters between the buffalo weavers, *Bubalornis* (which are probably plesiomorphic) and the sparrows, *Passer* (which probably evolved recently). He also concluded that *Pseudonigrita* is the closest relative of *Plocepasser*. In a review, these statements were supported by Hall & Moreau (1970). The plocepasserines include eight species (Figure 34):

1) *Histurgops ruficauda*, the rufous-tailed weaver that occurs in Tanzania.

2) *Philetairus socius*, the sociable weaver which is endemic to arid southern Africa.

3) *Pseudonigrita arnaudi*, the grey-crowned social weaver of Ethiopia, Somalia, Kenya and Tanzania.

4) *Pseudonigrita cabanisi*, the black-capped social weaver with a geographic distribution resembling that of *P. arnaudi*.

5) *Plocepasser superciliosus*, the chestnut-crowned sparrow-weaver of central northern Africa, occurring immediately south of the Sahara between Mali and Kenya.

6) *Plocepasser donaldsoni*, Donaldson's sparrow-weaver of arid Kenya and Ethiopia.

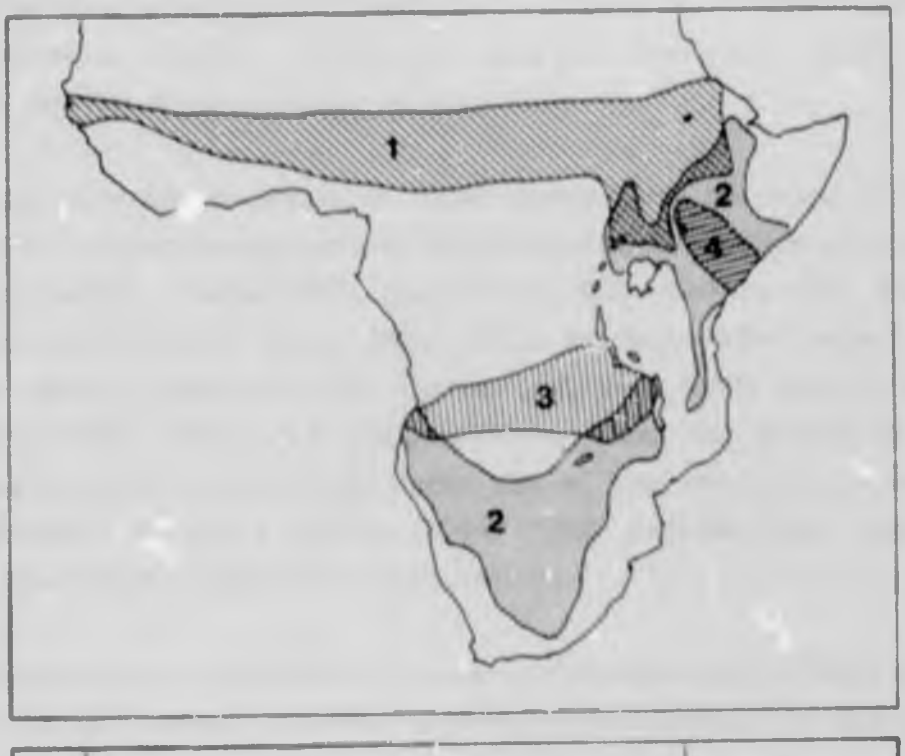

FIGURE 34. Maps showing the current distributions of the plocepasserines (adapted from Hall & Moreau 1970):

1=*Plocepasser superciliosus*
2=*Plocepasser mahali*
3=*Plocepasser superciliosus*
4=*Plocepasser donnoldsonii*
5=*Histurgops ruficauda*
6=*Pseudonigrita cabanisi*
7=*Pseudonigrita arnaudi*
8=*Philetairus socius*

7) *Plocepasser rufoscapulatus*, the red-mantled sparrow-weaver of Zambia, Zaire and Angola.

8) *Plocepasser mahali*, the white-browed sparrow-weaver which occurs over large parts of arid and semi-arid Africa, including Ethiopia, Somalia, Kenya, Tanzania, Zambia, Zimbabwe, Angola, Botswana, South West Africa and the Republic of South Africa.

More detailed distribution maps of these species can be found in Hall & Moreau (1970). The plocepasserines share the characteristics of sociality and ground feeding (Bates 1930, Bannerman 1953, Chapin 1954, Williams 1963, Mackworth-Praed & Grant 1953, 1973; Maclean 1973). Apart from *Philetairus socius* (Maclean 1973, Collias & Collias 1980) and *P. mahali* (Lewis 1982a, 1982b, 1983), very little is known about the ecology of these birds: general studies, like those listed above, are the only sources of such information. Collias & Collias (1964, 1980) provide some anecdotal observations on both species of *Pseudonigrita*.

Table 26 represents a comparison of several characteristics of this group. These characters reflect diverse aspects of the biology of the birds: factors related to preferred habitat and feeding behaviour, nesting behaviour, social and communicatory behaviour. The characters common to several species largely support Sushkin's (1927) view that *Pseudonigrita* and *Plocepasser* are closely related. In particular, the nesting behaviour and social systems in these two genera are very similar. The structure of the calls of *Pseudonigrita*, as judged from limited sonagraphic reproductions of *P. arnaudi* vocalisations, is similar to that of *Plocepasser* calls: they share tonality and a duration longer than one second (Chapter 3). In contrast, the calls of *Philetairus* have very broad instantaneous bandwidths and durations of less than 0,1 second, very similar to those of the ploceine weavers (Chapter 3). The nests of *Philetairus* and *Histurgops*, as well as their plumage markings (which presumably serve as visual signals) are totally different from those of *Plocepasser* and *Pseudonigrita*. Both *Plocepasser* and *Pseudonigrita* have a relatively high species diversity in Kenya, Ethiopia and Somalia; *Histurgops* and *Philetairus* occur outside these areas. Available evidence on plumage, nesting behaviour and distribution indicates that *Histurgops* and *Philetairus* are not closely related. The present behavioural data thus supports the view that the plocepasserines can be divided into three major

TABLE 27

A comparison of some behavioural characteristics among the Plocepasserines (see text for references). Species names are abbreviated as follows:

Phs=*Philetairus socius* Hir=*Histurgops ruficauda*
Psc=*Pseud nigrita cabanisi* Psa=*Pseudonigrita arnaudi*
Pls=*Plocepasser superciliosus* Pld=*Plocepasser donaldsoni*
Plr=*Plocepasser rufoscapulatus* Plm=*Plocepasser mahali*

KEY: x=Presence of trait; .=absence of trait; ?=Unknown quality.

	Phs	Hir	Psc	Psa	Pls	Pld	Plr	Plm
PREFERRED HABITAT:								
Association with Acacia	x	x	x	x	?	x	.	x
Association with arid areas	x	x	x	x	.	x	.	x
Feed on ground	x	x	x	x	x	x	x	x
Found in groups	x	x	x	x	x	x	x	x
NESTING BEHAVIOUR:								
Thatched nest	x	x	x	x	x	x	x	x
Build many nests in a tree	.	x	x	x	x	x	x	x
Nest with two entrances	.	.	x	x	x	x	x	x
COMMUNICATORY BEHAVIOUR:								
Calls:								
Tonal call structure	.	.	?	x	x	?	x	x
Visual signals:								
Moustachial stripe	.	.	.	.	x	.	x	x
Eyebrow	.	.	.	x	x	x	x	x
White bar on wing	.	.	.	.	x	.	x	x
Light rump	.	.	.	.	.	x	?	x

groups: 1) the *Plocepasser-Pseudonigrita* complex, 2) the genus *Histurgops* and 3) the genus *Philetairus* (Sushkin 1927, Hall & Moreau 1970).

The preferred habitat of sparrow-weavers

The sparrow-weaver preferred habitat has relatively large amounts of open ground where these terrestrial feeders find insects and seeds (Chapter 6). Throughout the geographic range of white-browed sparrow-weavers, (north-eastern and south-western Africa), this habitat is relatively uniform in terms of botanical structure and composition, as well as in insect composition. Some aspects of the geographical distribution of sparrow-weavers resemble those of some of their food plants. The seeds of the following shrub and grass genera are commonly eaten by sparrow-weavers (Table 26) and they occur both in arid north-east Africa as well as in south-western Africa: *Limeum, Commelina, Portulaca, Solanum* and *Ipomoea* (Verdcourt 1969). A plant genus eaten less frequently, *Sida*, has a similar distribution, and the genera *Schmidtia, Rhigozum, Tribulus, Dicoma* and *Tephrosia*, widespread within Africa, are common both in the Bloemhof area (Table 21) and in north-east Africa (Verdcourt 1969). All eleven of the above plant genera encountered at Bloemhof are represented in north-east Africa either by the same species or by close relatives, and these formed 20,8% of the non-cultivated vegetable food taken at Bloemhof. This demonstrates a close botanical similarity between the two areas (Verdcourt 1969) as far as sparrow-weaver food plants are concerned. The above comparison considers only herbaceous plants. The dominant trees in both areas are *Acacia* species. The preferred habitat of sparrow-weavers at Bloemhof is thus broadly similar to that of their conspecifics in Kenya and Ethiopia (Collias & Collias 1978). Because insects from sparrow-weaver stomachs could usually only be identified to family level, no precise comparisons could be made between the insect faunas of the two areas. Virtually all the families indicated in Table 20 occur in both north-eastern and southern Africa (Oberprieler pers. comm.). This is hardly surprising because these insect families are very large and widespread. The Curculionid genus *Protostrophus* is replaced by the genus *Sastates* in east Africa. The

distributions of the termite genera *Trinervitermes* and *Hodotermes* are very similar to that of white-browed sparrow-weavers.

Like *P. mahali*, most plocepasserines feed on the ground and occur in arid or semi-arid areas. Other plocepasserines thus have a number of features in common with white-browed sparrow-weavers with regard to their habitat preference. Information as to the history of plocepasserine habitats in general, and that of white-browed sparrow-weavers in particular, will now be assessed as an aid for understanding the radiation of the group.

The vegetational and climatological history of sparrow-weaver habitat

The Cretaceous and Tertiary periods: In discussing climatic and vegetational factors that might have influenced plocepasserines, the late Cretaceous, Tertiary and Quarternary periods are of importance. The Cretaceous period (roughly 135 m.y. to 70 m.y. before present) was characterised by relatively warm conditions, probably caused by increased solar radiation, surface albedo and cloudiness (Frakes 1979:179). Gondwanaland was still intact and most of the present African continent was covered by forest (Axelrod & Raven 1978). The only parts of Africa which were covered by arid or semi-arid vegetation, were isolated areas near the present Atlas Mountains (Figure 35)

The early Tertiary (roughly 70 m.y. BP) witnessed the major break up of Gondwanaland. This period was accompanied by a significant global cooling and the formation of the Antarctic ice-cap: this caused a decrease in sea level and an increase in land surface. This global drop in temperature was particularly marked at the end of the Eocene (about 38 m.y ago) and resulted in aridity on the continental areas (Frakes 1979:191). The continent of Africa, which lay 15° to 18° further south than at present, moved to its present position after the breakup of Gondwanaland, resulting in a southward movement of the tropical rain forest zone on the continent. The influence of the cold Atlantic sea currents, which arose after the separation of Africa from South America, and the establishment of the circum-Antarctic sea current, must also have

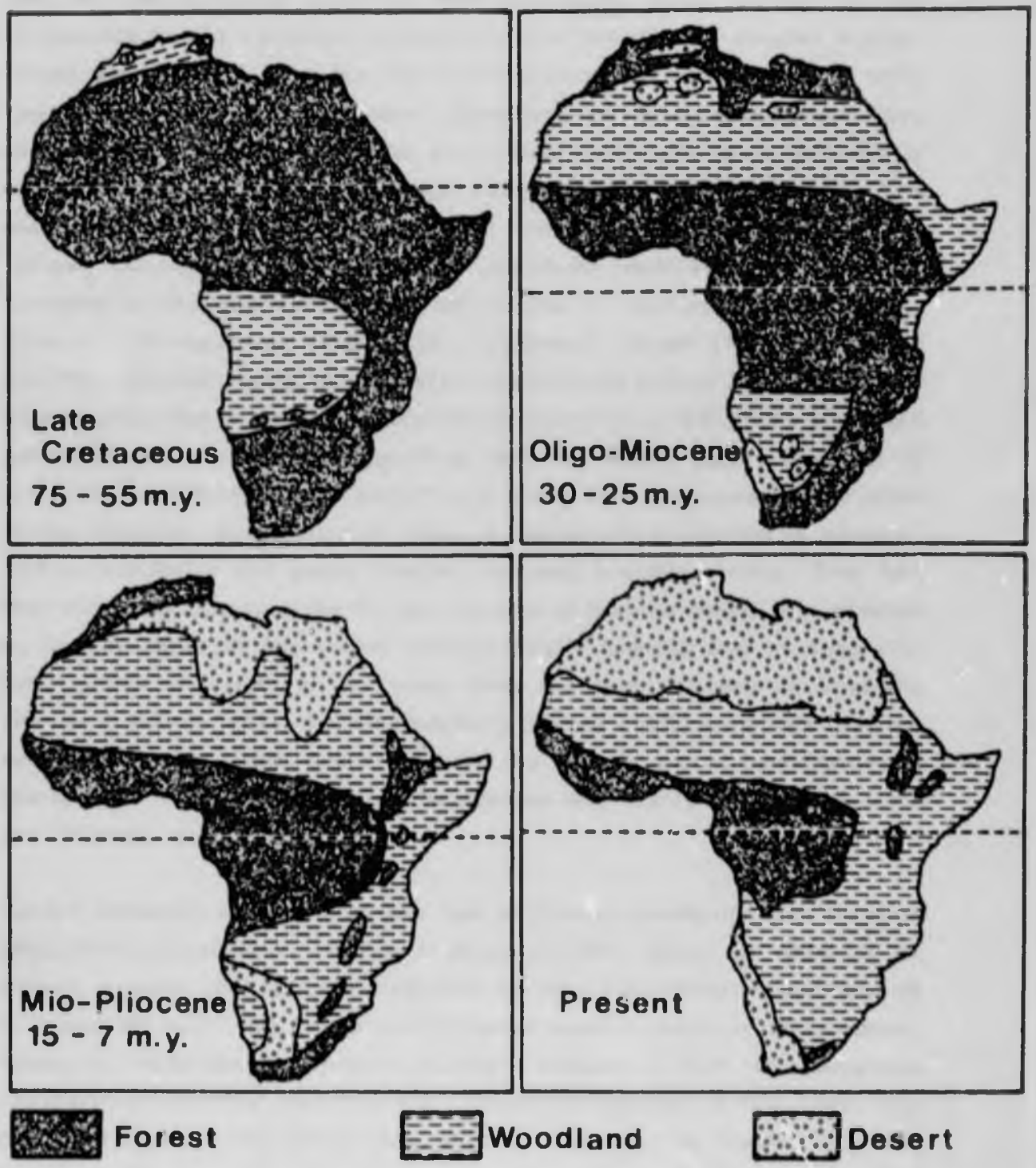

FIGURE 35. Maps showing how the widespread, Cretaceous, African forest disappeared and when arid areas originated (adapted from Livingstone 1975).

influenced the climate of Africa significantly. Palaeogeographic changes during the Miocene (about 20 m.y) and later, involved the destruction of the Tethys sea and significant uplifting of the rift zone in Africa (Frakes 1979). These geomorphological changes involved the uplifting of most of the highlands of south, east and north Africa during the late Cretaceous to mid Tertiary, followed by the formation of crustal arches. These were later to form the rift valley during the late Pliocene to early Pleistocene (King 1978). These alterations of topography must have caused major disruptions in the air currents over the continent, as is suggested by the formation of rain shadows west of the rift zone. The combined factors of decreased global temperatures, movement of the African continent, uplifting on the continent itself and new, cold sea currents on the west coast of Africa, caused a rapid aridification of the climate and vegetation (Figure 35). Axelrod & Raven (1978) suggested that the Kalahari-Namibian arid area was formed before Ethiopia-Somalia became arid, the latter being more recent than 7 m.y. BP. They also cited palaeobotanical evidence suggesting that the Namib desert is about 38 m.y. old, and that a major radiation in plant taxa occurred at the start of the Miocene, about 30 m.y. ago. It appears that legumes in general, and in particular the genus *Acacia*, followed a similar trend. The fact that the genus *Acacia* arose during the time of Gondwanaland is suggested by the presence of the genus both in South America and in Australia: fossil pollen of this taxon is known from the early Miocene of Australia (Raven & Polhill 1981). Polhill, Raven & Stirton (1981) proposed that the radiation of this genus occurred after the drop in global temperature at the end of the Eocene and that the process was highly accelerated since the Pliocene, some 7 m.y. BP.

Recent attempts to determine the age of African passerine taxa through DNA-DNA hybridisation (Sibley & Ahlquist 1980, Sibley & Ahlquist in press) suggest that a large radiation in bird taxa occurred between 40 m.y and 30 m.y. ago, when arid-adapted species such as larks arose. Sibley & Ahlquist (in press) further suggested that the sparrows (Passerinae) and the true weavers (Ploceinae) evolved at this time. The proposed ages of the above taxa should, however, be treated with extreme caution because the notions of constant rates of evolution and evolutionary clocks used by investigators employing DNA-DNA hybridisation to estimate the ages of taxa (Sibley & Ahlquist 1983), are controversial. The genetic distances calculated by means of these methods

are, however, useful for determining phylogenetic relationships. The available fossil material for African passerine birds is too sparse to allow for inferences about the origins of the weaver and sparrow taxa, so the results of DNA-DNA hybridisation remain the only clues to the relative ages of these groups.

The Quaternary period: The late Tertiary and Quaternary brought many periods of glaciation. Widespread, intense glaciations probably occurred at about 3 m.y., 1,5 m.y. 0,9 m.y., 0,5 m.y. and 90000 y. ago (Frakes 1979:236). In many areas it appears that at least some of the glacial stages were composite, displaying more than one advance of the ice (Livingstone 1975, Frakes 1979). More recent glaciation events on the African continent occurred about 16000 BP and about 6000 BP, and have been prominent in east Africa, as is evidenced by pollen and geological evidence on Mt Kenya and Ruwenzori (Livingstone 1975). During glaciation events, the continent became cold and dry, compared to the relatively hot, moist conditions that prevailed during interglacials. Northern and southern Africa were not affected to a large degree by glaciation during the Pleistocene (van Zinderen Bakker 1978). Fluctuations in climate during glacial cycles would have caused large shifts in the limits of both forest and arid areas on the continent, enhancing the formation of vegetational isolates, and the evolution of new species.

The history of arid and semi-arid areas in Africa

Although evidence shows that the arid areas in north-east and south-west Africa date back to before the Pliocene, the only relatively detailed information on arid areas in Africa comes from Pleistocene deposits. Although it is unlikely that the plocepasserines as a subfamily arose as recently as the Pleistocene, it is probable that some of the modern species evolved then. Information on Pleistocene arid areas is thus pertinent. Ethiopia/Somalia and the Namib have been arid constantly for at least the past 50000y (Moreau 1966:50, Verdcourt 1969). The palaeontological data, indicating climatological and vegetational conditions during the past 20000y, are far more complete than for earlier periods. Livingstone (1975) cited convincing evidence showing that Africa experienced two relatively

arid spells during the Quaternary period at 16000 and 7000 BP. The first of these two periods appears to have been very dry, and may have lasted from 22000y until 12000y BP. Core samples from Lake Victoria indicate that from at least 14700 until 12000 BP, central Africa was drier than present conditions: the lake level was remarkably low and its surface area was small. Pollen analyses of the other central African lakes also indicate that central Africa was open and dry at 13000 BP and that *Acacia* spp. trees were present (Livingstone 1975). It is generally agreed that the open vegetation at the time was not due to cold conditions, but to lack of moisture: central Africa was cold and dry (Livingstone 1975). Judging from the distribution of Kalahari sand deposits, the south-western arid areas once extended into the Congo Basin (Moreau 1966:51, Butzer 1971). In contrast, it appears that south-eastern Africa was relatively moist at the time. In addition, endemism among African forest mammals (Grubb 1982) and forest birds (Diamond & Hamilton 1980) indicate nuclei of endemic animals to the west and to the east of the central African lakes, suggesting that these foci are relatively ancient (Hamilton 1981).

The above evidence indicates that over the past 50000y the Ethiopian biogeographic region contained four relatively stable climatic and vegetational centres: arid areas in the north-east and south-west, and humid areas in the south-east and north-west. Because these areas are situated on diagonally opposing axes, one would expect the area surrounded by these four stable foci to have been affected substantially by the alternating climatic influences of glacial and interglacial periods. Cooke (1962) estimated that desert conditions extended as far north-east as Zambia about 10000y ago, with open and semi-arid vegetation crossing the continent. The pollen analyses carried out by van Zinderen Bakker (1962), Livingstone (1967) and Coetzee (1967) indicated that equatorial Africa experienced large changes in vegetation during the last 18000y, and that the area was dominated by grasses and herbs during the period 14700y to 12500 BP, as opposed to the forest conditions that prevailed during the interglacial periods. A number of publications speculate about the presence of a vegetational and climatic link between the Ethiopia/Somalia and the Namib arid areas during periods of aridity (van Zinderen Bakker 1966,1967,1969,1976,1978; Verdcourt 1969; Winterbottom 1967). There is agreement that the link must have been present for short periods: this view is supported by finds of fossil springbok (genus *Antidorcas*) - an antelope taxon typical of arid areas - at Kabwe (Broken

Hill) in Zambia (Clark 1959). The age of this material indicates that the link between the two arid areas in Africa is older than mid-Pleistocene.

Van Zinderen Bakker (1976) presented evidence that northward displacement of the trajectories of cyclones during glacial maxima caused arid conditions to prevail north of the 24th lattitude. He suggested that open *Acacia-Commiphora* savanna extended over most of Angola and Zambia during the glacial maxima, and that this vegetation extended into East Africa through a belt situated close to the present Lake Malawi. The interpretation of fossil pollen data is hindered by the meagre pollen production of mimosoids in general, and the genus *Acacia* in particular (Livingstone 1975, Guinet 1981). The matter is further aggravated by the fact that mimosoid pollen grains are very fragile and easily broken into smaller units which are difficult to recognise (Guinet 1981). This explains why *Acacia* pollen was found in a very sporadic pattern during the fossil pollen studies performed, for example, by Coetzee (1967) in eastern and central Africa. Pollen from this genus, estimated as nearly 30000y old, was found on Mt. Kenya by Coetzee (1967). In addition, this genus became more common during the dry, glacial period 15000y BP at the Sacred Lake, Mt. Kenya (Coetzee 1967). When examining some aspects of modern climatic parameters, the geographical connection between the Namib and the Ethiopia/Somalia arid areas is evident. Knoch & Schultze (1957) mapped the areas having at least three contiguous months with no measurable rainfall. Their map links Tanzania with Zambia, Zimbabwe and the Kalahari. Carter (1954) mapped the annual water deficiency (excess evaporation over precipitation) on the African continent and arrived at a map very similar to that of Knoch & Schultze. The distribution of white-browed sparrow-weavers in southern Africa is also closely approximated by the contour depicting 500mm of annual water deficiency (Schultze & McGee 1978). Summarising, it appears that large parts of central Africa were semi-arid during the Quaternary glaciations, and that the north-eastern and south-western arid foci were sometimes connected by an arid strip that stretched across the present Zambia and Kenya.

CONSIDERATIONS ABOUT SPARROW-WEAVER EVOLUTION

This section concerns possible speciation events within the plocepasserines. The typical situation thought to occur is that an established species is reduced to one or more small remnant populations by adverse environmental conditions. These small, isolated populations (if they survive) undergo speciation in allopatry, upon which they expand and become established over larger areas. Stasis is a characteristic of large, established populations: this allows one to make statements about the evolutionary past of organisms.

The origin of the plocepasserine subfamily

It is unlikely that extant plocepasserines evolved from a single, immediate ancestor. Of the four extant genera, at least *Plocepasser* and *Pseudonigrita* are sufficiently similar (within the genus), yet diverse to render it highly likely tha modern members of each genus had a separate, monophyletic origin. The constancy of characters among extant plocepasserines should, however, reveal something about the expression of that character in the plocepasserine ancestors. Therefore, the following paragraphs consider plesiomorphic (ancestral) and apomorphic (derived) characters of plocepasserines.

Plocepasserines are characteristic of *Acacia* spp. veld and it is tempting to speculate that these birds co-evolved with some species of *Acacia*. The modern genus *Acacia* is extremely diverse, with species restricted to environments as widely different as flood plains (e.g. *A. xanthophloa*) and arid plains (e.g. *A. erioloba*). Secondly, the genus is common in arid parts of Africa (e.g. Kenya, Somalia and Ethiopia) as well as in areas with a high annual rainfall (e.g. Mocambique). The genus is therefore not exclusively asscciated with arid or semi-arid areas, and may even not have evolvec' in an arid area. Coetzee (1967) showed that the genus was present in the open vege'ation types that characterised central Africa du ing glacial periods. I suggest that sparrow-weavers in particular, and plocepasserines in general, evolved in an area or areas where *Acacia* trees

were common. I also suggest that the occurrence of sparrow-weavers in woodland dominated by the tree *Collophospermum mopane* (like the Zambezi and Luangua valleys) is secondary for three reasons. First, mopane veld is not characteristic of the preferred habitat of white-browed sparrow-weavers throughout their geographical distribution; second, no other plocepasserine is found in mopane veld; and third, white-browed sparrow-weavers nest in *Acacia* trees, even when breeding in mopane woodland (Lewis 1982a). Mopane woodland has many of the physical and biotic characters of arid areas, so that many of the important ecological relationships of white-browed sparrow-weavers in mopane woodland are virtually identical to those of conspecifics in arid *Acacia* spp. savanna.

The association between *Plocepasser rufoscapulatus* and *Brachystegia-Jubernardia* spp. woodland is probably also secondary because it is the only plocepasserine species that occurs in this vegetation type: *P. rufoscapulatus* also has no geographic races, suggesting that it is a relatively recent species (Benson & Irwin 1966). The association between sparrow-weavers and *Acacia* spp. veld is probably a plesiomorphic character of the group.

All the species within the Plocepasserinae build nests by thatching dry grass stems. This suggests that the ancestors of these birds evolved in an environment which was dry for a large part of the year; perhaps even in an arid area. I suggest that the association between sparrow-weavers and a semi-arid or arid environment is a plesiomorphic character of the group. The fact that all the plocepasserines are terrestrial feeders is in agreement with this suggestion. This again implies that the association between *P. rufoscapulatus* and moister woodlands is an apomorphic character within the group.

The fact that *Plocepasser, Pseudonigrita* and *Histurgops* build excessive numbers of clumped nests suggests that high mortality due to predation is a primitive demographic character of plocepasserine populations. This contention is supported by the fact that both *Plocepasser* and *Pseudonigrita* (constituting six of the eight plocepasserines) build roost nests with two entrances. In addition, the plocepasserine ancestors might have lived in a cold environment, necessitating the use of roost nests in the first place.

Except for *Philetairus socius*, all the plocepasserines occur in East Africa, four of the eight species being endemic to that area. This suggests that the plocepasserines evolved in East Africa. The wide geographic ranges of plocepasserines in southern and western Africa suggests that the birds have occurred in the arid refugia outside east Africa since at least 16000 BP; i.e. the last major glaciation. The suggestion that the plocepasserines evolved in East Africa is supported by the fact that other taxa that have their origins there are adapted to open (arid?) plains; the large variety of antelopine ungulates found in that area (Dorst & Dandelot 1972) is remarkable. These antelope are all typical of open (and sometimes semi-arid: *Antidorcas*, *Litocranius*) plains (Vrba 1984a). Also, fossil material indicates that these species date back at least to early Pleistocene times (Vrba 1984b).

The large amount of geographic variation within the plocepasserines suggests that the subfamily is not very recent. Indeed, the birds in the subfamily differ so much that taxonomists have place them in four genera. Additionally, three species have differentiated into races: *P. mahali* has been divided into seven races (Clancey 1968), *P. superciliosus* into three races (Mackworth-Praed & Grant 1963) and *P. arnaudi* into two races (Mackworth-Praed & Grant 1963). It is, therefore, unlikely that the subfamily could have evolved during any of the last glaciations.

From this it appears that the plocepasserines evolved in *Acacia* savanna in east Africa during a dry, cold period. Also, the age of the subfamily is almost certainly greater than 30000 years and probably dates back to before the second last intense glaciation 0,5 m.y. ago. However, the subfamily is probably younger than 7 m.y., i.e. the estimated age of arid East Africa. The indication of a cold, dry environment suggests the subfamily evolved during a glacial period.

The origin of sparrow-weaver species

Plumage colour suggests that *P. rufoscapulatus* and *P. mahali* are very closely related. Indeed, Benson & Irwin (1966) considered them sibling species. The plumage of *P. donaldsoni* differs from the rest of the genus

in that it lacks the distinctive markings on the head. Its white rump and underparts show a closer resemblance to that of *P. mahali* than to *P. superciliosus*. I do not know of any firm evidence to support any further speculation on phylogenetic relationships. *P. mahali* probably evolved in East Africa and subsequently expanded its range to south-western Africa during an arid period when an arid vegetational corridor connected east Africa with the Kalahari area.

Benson & Irwin (1966) were probably correct when they suggested that *P. rufoscapulatus* evolved relatively recently from *P. mahali* when it became isolated in *Brachystegia-Jubernardia*-woodland in central-east Africa, and managed to adapt to the moist environment with denser vegetation. This event probably occurred during a wet period, i.e. an interglacial.

Since *P. donaldsoni* lacks the distinctive head markings of all the other sparrow-weavers, but shares the white parts of its plumage with *P. mahali*, it is possible that this species also evolved from either *P. mahali* or its immediate ancestor. *P. donaldsoni* has a closer resemblance to *P. mahali* than to *P. superciliosus* with respect to preferred habitat and geographical distribution. Donaldson's sparrow-weavers prefer a more arid habitat than white-browed sparrow-weavers (Britton 1980, Mackworth-Praed & Grant 1953) and therefore may have evolved during a very dry period (possibly a glacial period) when the parent population became trapped in a desert habitat.

Too little evidence is available for *Pseudonigrita* and *Histurgops* for allowing reliable estimates of their evolutionary history.

The phylogenetic relationships of *Philetairus socius* are obscure. In contrast to the other plocepasserines, sociable weavers might have evolved in southern Africa: this is suggested by their present distribution. Indeed, they differ so much from *Plocepasser* and *Pseudonigrita* in osteology (Sushkin 1927), signalling and nesting behaviour that they may be more closely related to other bird taxa, such as the Ploceinae (true weavers) or the Estrildinae (waxbills).

The origin of the sparrow-weaver communicatory system

As far as plocepasserine communication is concerned, the only quantitative evidence applies to *P. mahali* (Chapter 3). Calling is the most commonly used means of communication among white-browed sparrow-weavers, and observations by authors like Mackworth-Praed & Grant (1963), Bannerman (1953), Chapin (1954) and Bates (1930) suggest that this applies to all the sparrow-weavers. If sparrow-weavers evolved in open arid or semi-arid areas, why should auditory signals play such an important role in the communicatory behaviour of these birds? Visual signals have a long range in an open environment, a case in point being widow-bird displays (Andersson 1983). *A priori*, one would expect birds in open habitats to have a relatively strong visual component in their communication system. Any communicatory behaviour is, by definition, adaptive, i.e. it evolved for a particular purpose, and involves the ability of one animal to react to the behaviour of another. The mode of communication, however, need not be adaptive. As long as communication is efficient, there is no reason why the medium of communication should undergo evolutionary change.

It is conceivable that visual signals might be emitted with slightly less energy expenditure than auditory ones, but there is no need why optimisation should occur. The notion that bird song is generally structured for MAXIMUM propagation distance (Morton 1975, Cosens & Falls 1984) is a fallacy. Communicatory patterns are the result of phylogenetic constraints, as well as a combination of many ecological and behavioural factors and as long as efficient communication takes place, it would remain unchanged. As admitted by Morton (1975), it is nonsensical to postulate that close-range signals like sparrow-weaver mating calls would be selected for maximum propagation because these calls are only used when a male is in close proximity to a female.

The strongly auditory-based communication system, a character which sparrow-weavers share with most African passerines, may be an evolutionary legacy from their ancestors inhabiting the widespread forests that covered the continent of Africa 40 m.y. BP. These ancestors would have used vocal signals because visual ones would restrict communication in such dense vegetation. Several authors, e.g. Morton (1975), Marten &

Marler (1977) and Cosens & Falls (1984), have shown that the floral structure of avian habitats influences both frequency and modulation of bird calls. It is clear that open habitats have no characteristic that would make the use of auditory signals disadvantageous when compared to forest environments: in fact, the propagation of auditory signals is in many respects improve in open habitat (Marten & Marler 1977). The ploceine weaverbirds are atypical of the African passerines in having such a large visual component in their communicatory behaviour (Crook 1964). I believe that the visual signals of these birds evolved as a secondary adaptation for ensuring the location and recognition of mates among a multitude of calling males in a breeding colony. These signals have nothing to do with the structure of the habitat as such, but with the colonial breeding system of these birds.

The adaptive value of sociality for other plocepasserines

It is probable that a large proportion of the factors responsible for social cohesion in white-browed sparrow-weavers also operate in other plocepasserine species. Mortality of full-grown white-browed sparrow-weavers and on their broods is greatly influenced by group size, and one of the main findings of this study is that social organisation is an adaptation (*sensu* Williams 1966) to counter predation. One of the major ways in which a sparrow-weaver avoids predation is by 'hiding' its breeding or roost nest among many other unused nests so that a predator cannot easily find it. Judging from the descriptions of Bannerman (1953), Bates (1930), Chapin (1954), Collias & Collias (1978, 1980), Mackworth-Praed & Grant (1953, 1973) and Williams (1963) all species of Plocepasser, *Pseudonigrita* and *Histurgops* build large numbers of nests. Predation could therefore be a limiting factor on those species too.

Collias & Collias (1980) counted a mean of 13,3 *Pseudonigrita arnaudi* individuals belonging to three groups in Kenya. From 21 nest trees they estimated a mean of 12,3 nests/group. Their colonies had nest/bird ratios varying between 0,6 to 1 nest/bird. At night, more than one social weaver occupied a roost nest and about 66% of the nests were occupied. *Pseudonigrita arnaudi* does not seem to have the large nest/bird ratios

so characteristic of *Plocepasser*. Collias & Collias (1980) mentioned that the minimum nocturnal temperatures were 10 to 22°C in the areas where they studied social weavers; this is significantly warmer than those experienced by sparrow-weavers during this study. If use of roost nests is adaptive in *Pseudonigrita*, energy spent on temperature regulation must not have played a role in the evolution of this characteristic. The sociable weaver *Philetairus socius* is the only other plocepasserine for which quantitative data on nest numbers are available (Maclean 1973, Collias & Collias 1978, 1980). For sociable weavers, these sources indicate a lower nest/bird ratio than that observed for sparrow-weavers. They reported on four colonies, two of which were kept in captivity; a total of 63 birds and 35 nests. They also recorded three to five birds roosting in a nest. Regarding the function of roost nests in the groups of birds discussed above, it appears that the nest/bird ratio is so low in *Pseudonigrita* and *Philetairus* that any anti-predator adaptation of roosting, full-grown birds, analogous to that of roosting white-browed sparrow-weavers, can be disregarded. Second, if having many nests in the breeding tree is adaptive, the camouflage afforded by such a multitude of nests may be important for the survival of plocepasserines other than white-browed sparrow-weavers. In *Pseudonigrita*, neither predation on adult, roosting birds nor high costs of thermoregulation seem to be important, but reduced predation on broods (effected by the large number of roost nests closeby) could be important for survival. This possibility should also be investigated in the case of ploceine weavers, which often have many more nest structures in their nest trees than are used for breeding (Crook 1964). Third, it is clear that nest-building behaviour evolved in the ancestors of the plocepasserines, and, for that reason, the behaviour need not be adaptive in all the species derived from these ancestors.

As far as *Philetairus* is concerned, there is a possibility that the communal nesting could have evolved because of a shortage of nest sites. Nest site availability is a restriction in some areas, where virtually all the suitable thorn trees contain nests, while suitable nest trees are abundant in other areas (Maclean 1973:184). White *et al*. (1975) showed that sociable weaver nests have benefits in terms of thermoregulation, but as this factor may be a preadaptation or an effect, it need not necessarily be the adaptive reason for the nesting behaviour.

Sparrow-weavers *Plocepasser*, social weavers *Pseudonigrita* and sociable weavers *Philetairus* seem to lie along a continuum of increasing sociality (Collias & Collias 1980). *Plocepasser* is characterised by small groups which are almost invariably simple or expanded family groups (Lewis 1982a, 1982b; this study chapter 2). *Pseudonigrita* is, however, characterised by expanded groups, divided into subgroups, each apparently equivalent to a sparrow-weaver family unit (Collias & Collias 1930). In the case of *Philetairus*, the social organisation appears similar to that of *Pseudonigrita*, but with even more subgroups and more complex dominance relationships (Maclean 1973, Collias & Collias 1980). This gradient of increasing complexity of social organisation need not reflect a close phylogenetic relationship among the plocepasserine genera. *Philetairus* and *Plocepasser* might have evolved convergently because a) the nest structure of *Philetairus* is completely different from that of the other plocepasserines; b) its calls are totally different in structure from the sparrow-weavers (resembling more closely those of the ploceine weavers); and c) its geographical distribution is totally disjunct from the other plocepasserines (Figure 34), except *P. mahali*. When considering the expression of a particular character among a number of species, it is important not to assume that it is either adaptive or preadaptive in all these species. The adaptive nature of a trait for the ancestors of a species might have disappeared because of the change in preferred habitat that accompanies speciation events. A plesiomorphic that has lost its original adaptive value could even restrict the range of possibilities with which a population can overcome a new, peculiar environmental constraint. Regarding the social trait of the plocepasserines, insufficient data exists to make a valid comparison of the adaptive nature of sociality among these species. In white-browed sparrow-weavers, sociality is adaptive: it evolved to allow survival in a harsh, semi-arid environment.

CHAPTER 9: CONCLUSION

Dawkins (1982) compared biological research to the activities of a computer programmer who has lost the algorithm of a particular programme, and has to rewrite it by using a printout of the results produced by this programme. In this metaphor, the algorithm of the programme represents the rules that cause animals to behave the way they do, and the printout corresponds to the phenotypic traits being studied. I believe that the sociobiological approach assumes that a single, universal algorithm applies to the evolutionary process: maximisation of fitness. According to this view, behavioural study entails finding out how the algorithm is implemented (solved) in each particular animal species. In terms of Aristotelian metaphysics, the maximisation principle could be seen as a formal cause of evolution, while the actual ways in which maximisation is obtained are moving ("efficient") causes (see Grene 1983). Moving causes are the vehicles through which formal causes are realised. However, formal causes and final causes (*sensu* Aristotle) are inaccessable from within the limits of the scientific study of evolution and belong to the realms of metaphysics and religion. Formal and final causes, as seen by a particular person, emerge from his or her view of life, which in turn also affect the way in which this person approaches science. The concept of general evolutionary rules (evolutionary "algorithms" or formal causes) is thus intimately related to paradigms used by evolutionary biologists. Each scientist is therefore subject to the influences of culture and history (Kuhn 1962). The Western view of life that assumes a steady increase in our state of well-being (Baumer 1977:330) was probably antecedant to the concept of a continuous increase in the fitness of animals, and hence the optimisation principle.

Natural selection is environmentally-imposed differential survival. The reason why some animals survive while others fail to do so, cannot be ascribed to any universal "algorithm" or cause, but to the relationship between heritable phenotypic variation and environmental constraints for a particular population at a particular place and time. Although science strives to generalise, it is unlikely that we will discover general programmes describing the ways in which a particular animal adapts to any particular environmental constraint. The only general statement that

we can make relates to the constraints within which adaptation takes place ("the amount of computer memory available for running the programme"): adaptation is restricted to available heritable phenotypic variation. This defines the outer limits of the evolutionary arena, but no rules exist according to which the game inside the arena is played.

It would behove evolutionary biologists to take note of a fundamental principle used by historians. Someone that studies the actions of slave-owners during the time of the Roman empire cannot understand these deeds if he applies modern norms in his explanations. Since universal norms do not exist, such slave-owner actions can only be understood if the cultural and normative environment at the time is fully understood (Shafer 1974). The same applies to evolutionary problems: adaptations ("evolutionary actions") can only be understood within the context of the particular environmental constraints operative at the time when adaptation took place. Because adaptations were formed in the distant past, modern environmental and phenotypic parameters are only relevant to the extent that they may reflect the historical environment in which adaptation occurred. Any evolutionary biologist is of necessity an historian: the physical adaptations available for study are historical in nature.

The above argument explains why, in interpreting white-browed sparrow-weaver sociality, so much emphasis was placed on habitat characteristics (Chapter 6) and environmental constraints during past times (Chapter 8). It appears that the plocepasserine subfamily arose in East Africa some 20 m.y. BP, after large parts of the African continent had become semi-arid and devoid of forest (Figure 35). This placed the sparrow-weaver ancestors under severe environmental pressure, probably due to a high predation rate. White-browed sparrow-weavers probably originated in East Africa during a cold, dry glacial period during the Pleistocene when, despite heavy predation, social groups managed to survive. The well-developed vocal communicatory system of these birds (Chapter 3) may be an evolutionary remnant of the forest-dwelling ancestors of the plocepasserines. The use of the underlying concept of reciprocal altruism (Trivers 1971) appears attractive in explaining sparrow- weaver altruism, particularly if interpreted in terms of fitness networks in which the cost of altruism is negligible (Brown 1980). This approach, however, assumes that sparrow-weaver altruism is an adapta-

tion for maximising the fitness of altruists. I believe that an explanation in terms of the maximisation principle is less informative than one based on the environmental conditions that could have given rise to sparrow-weaver altruism. Explanations in terms of reciprocal altruism may also give an impression of universal (nonexistent, I believe) forces driving the evolutionary process.

The term "altruism" has been used fairly loosely in this work. In a strict sense, altruism involves behaviour that decreases the fitness of an altruist while increasing the fitness of another individual (Wilson 1975). In an evolutionary sense, only adaptations shaped by natural selection are worthy of special explanations. This also applies to altruism. At first glance, the occurence of communal chick-feeding, vigilance behaviour and of communal nest-building immediately evokes arguments used for explaining altruism. However, no evidence could be found to suggest that any of these sparrow-weaver traits decrease the fitness of the altruist while increasing the fitness of other sparrow-weavers (Chapter 7). White-browed sparrow-weavers therefore do not perform true altruism, but are engaged in "apparent altruism": group selectionist theories therefore can not explain sparrow-weaver sociality. The sociobiological approach emphasises that observed altruism is only apparent altruism that is actually aimed at maximising the fitness of a particular "altruist" (Wilson 1975). However, in contrast to the sociobiological view, this study suggests that cooperative chick-feeding is a fortuitous effect of the group-living characteristic of sparrow-weavers, and is not aimed at increasing the fitness of any individuals (Table 15 and Chapter 7). The same may apply to vigilance behaviour. Communal nest building is the only evolved adaptation with apparent altruistic qualities (Chapter 5). However, sociality in sparrow-weavers at Bloemhof can be explained in terms of increased fitness brought about by nest building (Figures 28 and 30). This explanation is at a lower level compared with that of the sociobiological approach because it is more direct and requires less assumptions. Explanation of sparrow-weaver sociality in terms of higher level theories is therefore unnecesary.

As explained in the introduction to this thesis, Darwin envisaged that eusociality might present a threat to his theory of natural selection. This threat turns out to be no threat at all. If one asks what benefit individual workers obtain from the social system within which they live, evolution

is approached from the wrong perspective. No reason exists why workers *have* to benefit from the social system; in fact they need *not* benefit at all. If the presence of workers enabled enough individuals to overcome some environmental crisis (thus causing enough individuals to survive), no reason exists why workers should be selected against, even if they do not gain individually. The same argument applies to sparrow-weavers. It is wrong to assume that helpers individually *have* to benefit from the social system within which they are found. If helping is an evolved adaptation, it should persist within a population (being essential for the survival of adult breeders), even though individual sparrow-weaver helpers do not attain the highest possible fitness.

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APPENDIX A

A summary of all the focal animal samples made on known sparrow-weaver individuals in the Bloemhof central study area. It was attempted to collect the data systematically through time: the number of observations on each individual reflects the length of time it was in the study area. Dates only reflect focal animal observations on each individual.

Sparrow-weaver: ID	Sex	Group	No. 2-min scans	Date of first observations	Date of last observations
BC	?	Black	45	84-01-20	84-01-23
BG	F	Black	694	82-10-09	84-02-22
BL	F	Black	629	83-02-02	84-02-22
BR	M	Black	279	82-07-20	83-01-17
BY	F	Black	332	82-08-06	83-10-03
GG	M	Green	351	83-10-31	84-02-22
GO	F	Green	723	82-12-09	84-02-22
GR	M	Green/Red	725	83-04-20	84-02-22
GW	M	Green	227	82-12-09	83-04-18
GY	M	Green	482	83-08-12	84-02-17
KG	F	Pink	303	82-12-11	83-06-06
KY	M	Pink/Black	1038	82-12-11	84-02-17
LV	F	Blue	67	83-11-11	84-01-30
LK	M	Blue	89	83-11-11	84-02-15
LR	M	Blue	737	83-03-11	84-02-20
LW	M	Purple	505	82-12-09	83-10-10
LY	F	Blue	631	82-11-29	84-02-22
NM	M	?	12	83-03-14	83-08-22
OB	M	Orange	38	82-07-19	82-08-04
OG	M	Orange	210	83-12-12	84-02-20
OL	F	Orange/Purple	105	83-11-11	84-02-22
OW	F	Orange	121	82-07-19	82-12-21
PC	?	Purple	15	83-11-02	83-11-02

Continued overleaf

Appendix A (continued)

Sparrow-weaver: ID	Sex	Group	No. 2-min scans	Date of first observations	Date of last observations
PG	M	Purple	97	82-12-09	83-01-12
PK	M	Purple	320	83-12-05	84-02-20
PO	M	Red	190	83-10-31	84-02-20
PR	M	Purple	1115	82-10-09	84-02-20
PW	F	Purple/Orange	459	82-10-09	83-09-05
PY	F	Purple	657	82-10-09	84-02-22
RB	M	Red/Orange	650	82-07-21	83-07-22
RE	F	Red (RV1)	98	82-07-22	82-08-10
RG	M	Red	857	82-11-27	84-02-17
RK	F	Red	141	83-10-31	84-02-22
RL	M	Red	105	84-01-06	84-01-20
RU	?	Red	8	82-07-23	82-08-04
RV	M	Red (RV2)	60	84-01-04	84-01-30
RW	M	Red	147	82-07-19	82-08-10
RY	F	Red	1034	82-07-19	84-02-22
UU	?	?	15	83-03-02	83-03-04
WG	M	White	270	83-12-09	84-02-20
WK	M	White/Orange	222	83-09-16	84-01-25
WV	M	White	218	83-09-16	83-12-21
XF	F	White	397	83-09-23	84-02-22
YL	F	Yellow	81	82-10-09	82-11-26
YW	M	Yellow/Blue	940	82-10-09	84-02-15

APPENDIX B

The dataset used to calculate disappearance rates of full-grown sparrow-weavers. The number of nests and group size for each group is given as measured at the beginning and end of the annual observation period (starting in July). The number of ringed birds in each group at these times is also shown, as is the number of ringed adults that disappeared. Immature loss is given as (no. immatures that disappeared)/(no. immatures ringed). Dots indicate that no immatures were present within a group.

GROUP:		NO. NESTS:		GROUP SIZE		RINGED:			
								ADULT	IMMATURE
ID	YEAR	Begin	End	Begin	End	Begin	End	LOSS	LOSS
30	82/3	22	15	2	3	2	1	1	.
32	82/3	31	23	4	2	2	0	2	.
33	82/3	21	27	2	2	2	0	2	.
34	82/3	58	62	4	3	3	3	0	0
35	82/3	50	18	2	4	2	2	0	.
36	82/3	28	26	2	3	2	2	0	.
3	83/4	8	19	4	4	4	3	0	1/2
4	83/4	49	11	6	4	5	3	1	1/3
7	83/4	16	38	4	5	3	2	1	0
8	83/4	6	20	2	0	2	0	2	.
13	83/4	25	33	5	5	5	3	0	2/3
14	83/4	22	0	4	0	3	0	2	1/1
16	83/4	22	19	4	5	4	1	1	2/2
17	83/4	13	23	5	0	5	0	2	3/3
27	83/4	3	11	2	2	2	2	0	.
30	83/4	15	13	3	0	3	0	2	1/1
31	83/4	9	19	3	0	3	0	2	1/1
1	83/4	42	37	6	3	5	2	0	3/3
2	83/4	39	25	4	4	4	2	0	2/2
10	83/4	19	37	3	4	2	2	0	.

Continued overleaf

Appendix B (continued)

GROUP:	NO. NESTS:		GROUP SIZE		RINGED:			
							ADULT	IMMATURE
ID	YEAR	Begin	End	Begin	End	Begin	End	LOSS	LOSS
11	83/4	53	60	6	6	5	2	1	2/2
15	83/4	23	15	2	2	1	0	2	.
18	83/4	17	29	3	4	2	2	0	.
19	83/4	20	34	4	4	4	2	0	1/1
21	83/4	43	38	5	4	3	1	1	1/1
23	83/4	6	18	2	2	2	2	0	.
24	83/4	15	18	3	2	2	1	1	.
33	83/4	27	36	4	3	4	3	0	1/1
35	83/4	18	41	4	5	4	4	0	0
36	83/4	26	29	5	4	5	3	1	1/3
5	83/4	77	54	6	4	3	1	1	1/1
6	83/4	35	38	5	2	5	1	1	3/3
9	83/4	40	40	4	3	3	2	0	1/1
12	83/4	71	58	4	5	2	1	1	.
20	83/4	55	42	5	3	4	2	0	2/2
22	83/4	29	34	3	3	3	3	0	0
32	83/4	23	23	2	2	2	2	0	.
34	83/4	62	48	3	3	3	2	1	0