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ECOLOGICAL SEPARATION OF SMALL CATHARTID VULTURES IN SOUTH AMERICA

A thesis submitted to the University of Glasgow for the degree of
Doctor of Philosophy
by
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"With leisurely, broad, swinging loops and circles they cover the shore-line and forest, or with abrupt turns shoot up the barrancos, always easily, always gracefully. The passage between my lookout and the forest is only twenty feet wide, but, facing the wind, they rush through at full speed in complete control of their movements and only rarely do they flap a wing. As though the function of flight were wholly automatic, their attention seems directed chiefly to that part of their surroundings over which they are passing. Now they look below, now to the right, again to the left. The movements of their heads seem independent of their body; one is impressed with the belief that nothing of interest escapes their attention, and where eyesight fails, experiment shows that sense of smell serves them."

Frank M. Chapman writing of Turkey Vultures on Barro Colorado island (*Life in an air castle - Nature Studies in the tropics 1938*).

CANDIDATES DECLARATION

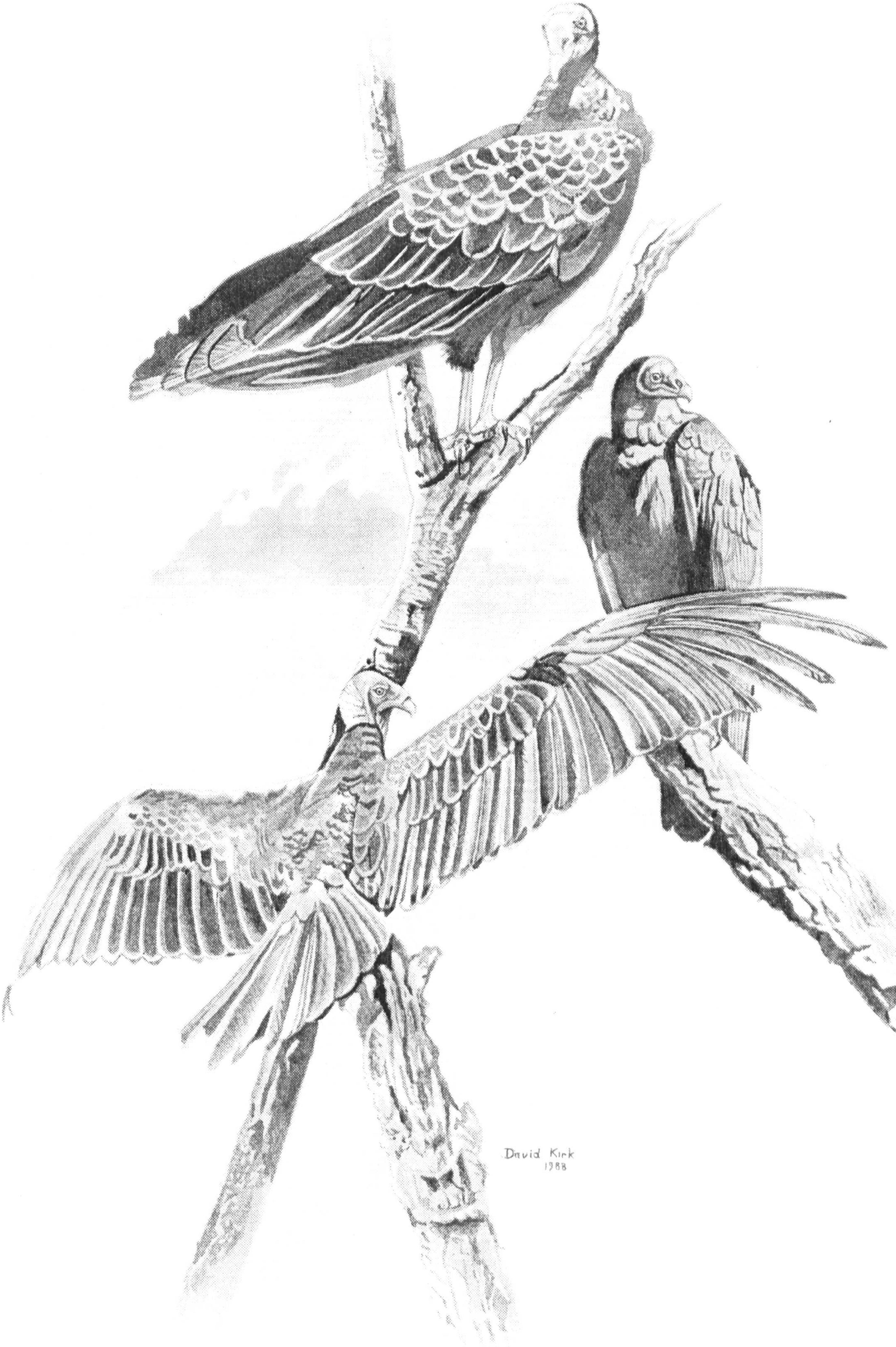
I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is of my own composition. No part of this work has been submitted for any other degree.

David A. Kirk

To my daughter, Genevieve

Top; Migrant Turkey Vulture
Cathartes aura meridionalis

Middle and lower; Resident Turkey Vulture
C. a. ruficollis


David Kirk
1988

Resident (left) and migrant (right) Turkey Vultures in the hand.

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ABSTRACT

During three field seasons, totalling 20 months between 1984-87, the ecological separation of four species of small Cathartid vultures was investigated at Hato Masaguaral in the flat savannas or Llanos of central Venezuela, South America. The focus of the study was an analysis of the role of migrant Turkey Vultures *Cathartes aura meridionalis*, in the scavenging guild of resident vultures, particularly in relation to a resident subspecies of Turkey Vulture *C. a. ruficollis*.

Ecological separation between different taxa was achieved by differential habitat use by foraging vultures, feeding on different types of carcases and at different times. Where mixed-species flocks fed at carrion, social dominance mediated competition; heavier taxa were not necessarily dominant. During the dry season, migrant Turkey, Lesser Yellow-headed *Cathartes burrovianus* and Black Vultures *Coragyps atratus* foraged at highest densities in open savanna habitats. By contrast, resident Turkey and King Vultures *Sarcor amphus papa* foraged almost entirely in closed gallery forest.

In the wet season, the numbers of *Cathartes* vultures declined by 6 fold in the absence of migrant Turkey Vultures which returned to North America. There was a distinct habitat shift in resident Turkey Vultures at the end of the dry season from gallery forest to open savanna habitats; conversely at the end of the wet season birds moved back into the gallery forest. Some residents may themselves have been migratory, moving into the ranch area at the end of the dry season, but this did not explain the decrease of *Cathartes* vulture density between seasons. The changes coincided with the departure of the majority of migrants in the spring and with the influx of migrants in the autumn, respectively. The core range areas used by radiotagged resident Turkey Vultures shifted seasonally from gallery forest to open savanna.

Most marked migrant Turkey Vultures were not resighted, suggesting that they passed through the study area on their way further south or that they had large home ranges. Compared to migrant Turkey Vultures a larger proportion of resident Turkey and Black Vultures were resighted.

Comparative observations at bait sites in gallery forest and open savanna showed that carcases were detected more quickly, group sizes of migrant Turkey Vultures were greater, and agonistic encounter rates were higher in the open. Both migrant and resident Turkey Vultures occurred at similar densities over the forest but most carcases were first located by residents. Migrants won almost all agonistic encounters initiated against resident Turkey Vultures. The feeding rate of resident Turkey Vultures was significantly and negatively affected by the numbers of migrant Turkey and King Vultures, but not by other residents present at carcases.

While the body condition of migrant Turkey Vultures was low after autumn migration from North America, the condition of birds trapped in subsequent months improved. However, the body condition of residents was below average throughout the dry season when migrants were present. By contrast, in the wet season when migrants were absent, the body condition of residents was above average.

The wing-loading of different taxa was related to their foraging strategies; low wing-loading enabled some taxa (eg. resident Turkey Vultures) to fly at low altitude over vegetation and forage using olfaction. Others, with higher wing-loading depended on sight for foraging (directly by observing carcases in the open or by watching the activities of other vultures) and on thermals to remain aloft (eg.

Black Vultures).

Results suggested that, although there may be seasonal changes in food supply which may explain wet season changes in foraging behaviour, resident Turkey Vultures were forced to forage in gallery forest during the dry season to reduce interference competition from migrants.

CONTENTS

CHAPTER 1 INTRODUCTION

CHAPTER 2 STUDY AREA AND GENERAL METHODS

2.1 STUDY AREA

2.2 GENERAL METHODS

CHAPTER 3 HABITAT SELECTION

3.2 METHODS

3.3 RESULTS

3.4 DISCUSSION

CHAPTER 4 RANGE BEHAVIOUR

4.2 METHODS

4.3 RESULTS

4.4 Radiotracking

4.5 DISCUSSION

4.5.1 Range behaviour of marked individuals

CHAPTER 5 FEEDING BEHAVIOUR

5.4 DISCUSSION

CHAPTER 6 BODY SIZE AND CONDITION OF VULTURES

6.2 METHODS

6.3 RESULTS

6.4 DISCUSSION

CHAPTER 7 MOULT

7.2 METHODS

Analysis of moult data

7.3 RESULTS

CHAPTER 8 GENERAL DISCUSSION

APPENDICES

CHAPTER 1 INTRODUCTION

Interactions between migrant and resident birds - general

Approximately one fifth of all breeding bird species in North America winter exclusively in the Neotropics (Cox 1985) and probably about half of these do so in South America (Terborgh 1980). Little was known about the New World migration system until recently (Cox 1985), but now wintering migrants are regarded as integral components of all tropical ecosystems (Keast 1980 a, Schwartz 1980, Stiles 1980, Lack 1983, Gochfield 1985) whereas previously they were seen as generalist invaders in ecologically complex communities (Willis 1966, Karr 1976). In some families, migrants have been shown to display greater ecological plasticity than residents (Keast 1980 c); Cox (1968) showed that bill morphology within the same family was less specialised in migrants than residents, which led to his theory on the importance of interspecific competition in the evolution of migration.

The behavioural ecology of birds resident year-round in the tropics suggests that there is strong competition for resources (see Skutch 1976) and this may be increased in the presence of migrants (Keast 1980 b). Although some migrants may exploit a seasonal abundance of food in their neotropical wintering range and occupy secondary habitats where there are fewer residents (Willis 1966, Karr 1976, Waide 1980), their integral role in all ecosystems (including forest-see Rappole *et al* 1983) suggests that competition probably occurs between closely related migrant and resident species. This is particularly likely where individuals of the same genera are sympatric (eg. Morton 1971, Smith 1971). However, resident breeding species which sometimes occupy niches vacated by migrants are not necessarily evidence of competition (Schwartz 1980).

In the Neotropics there have been few observations of interspecific interactions between migrants and residents, except in mixed-species flocks feeding at resource concentrations such as army ant swarms or fruiting trees (Willis 1966, Leck 1973, Karr 1976). Some studies have shown that migrants are subordinate to residents (Karr 1976, Keast 1980 a), but most interactions between flock foragers are intraspecific (eg. Chipley 1976). However, observations of interference competition are not the most important aspect of niche in these species since many migrant passerines are not typically flock foragers but occupy home ranges and show site fidelity (Rappole *et al* 1983). Most recent studies of resource partitioning between migrants and residents have been qualitative (eg. Barlow 1980, Johnson 1980) and only one involved experimental manipulation (Rappole & Warner 1980).

In the Palearctic-African migration system, large numbers of birds winter in the savannas and grasslands of the tropics (Moreau 1972). During this period many passerines (eg. shrikes, Laniidae) and non-passerines (eg. swallows, Hirundinidae) overlap with species of the same genera. Among raptors (eg. Black Kite *Milvus migrans*) there are a number of subspecies which are sympatric with their tropical counterparts. These also include the Palearctic Marsh Harrier *Circus a. aeruginosus* which overlaps and greatly outnumbers its tropical counterpart *C. a. ranivorus* south of Kenya (Moreau 1972).

In some cases there appears to be interspecific competition between Old World migrants and residents (eg. Wheatears *Oenanthe* spp.- see Sinclair 1978), but most species are either ecologically separated by habitat, foraging methods, or the period of overlap between migrants and residents coincides with an abundance of food. In relation to residents, migrant raptors possess several advantages. Because they are not restricted to a territory or nesting site, they can adopt an itinerant lifestyle exploiting temporarily abundant resources underutilised by residents (Brown 1970). Some migrant raptors in West Africa, for instance, follow rainbelts in response to fluctuating prey populations (Thiollay 1978).

Research on interactions between migrants and residents in the Nearctic-Neotropical migration system has concentrated on passerines (eg. Miller 1963, Morton 1971, Chipley 1976, Bennett 1980, Terborgh & Faaborg 1980) and has almost completely ignored large raptors and Cathartid vultures (see Smith 1980, 1985 a,b). Both Broad-winged Hawks *Buteo platypterus* and Turkey Vultures *Cathartes aura* have migratory subpopulations which breed in North America and resident semi-tropical or tropical ones. Turkey Vultures show differential migration, some individuals migrate long distances, while others move relatively short distances or remain sedentary. Thus, the study of interactions between migrant and resident vultures may indicate the importance of competition in the evolution of migration in this and other species (see Morton 1980, Ketterson & Nolan 1982).

Competition between migrants and residents

Although there may be some exceptions (Wiens 1977), the predominant role of competition in shaping ecological communities has been generally accepted (Diamond 1978, see Schoener 1982). However, the quantititave predictions of competition theory (see MacArthur & Levins 1972) have been of limited practical use because of the difficulties in assessing over which resources the competition occurs. Qualitative predictions are frequently used to collect circumstantial evidence of the importance of competition and this has been used in investigations of migrant and resident interactions (eg. Bennett

1980, see Greenberg 1986). These include variations in resource use or niche breadth by different species; when competition is high subdominant birds may adopt a more specialist lifestyle resulting in a narrowing of niche breadth (Smith *et al* 1982), while the reverse occurs when competition is low.

Resource partitioning between closely related species occurs by a number of avoidance mechanisms (Cody 1974). Among these are geographical or habitat separation, foraging in different altitudinal zones, or foraging on different resources (or at different times) or alternatively, maintaining low population densities by territoriality (Cody 1974). Competition between closely-related migrant and resident birds could be reduced by migrants being nomadic and exploiting areas of food abundance untapped by residents (eg. Yellow-rumped Warbler *Dendroica coronata*-Keast 1980 b). Some research has indicated that the breeding season of residents coincides with the absence of migrants, suggesting competition (eg. Miller 1963) but this has not been substantiated by the majority of studies (Karr 1976, refs. in Keast & Morton 1980).

Niche displacements, apparently in response to densities of migrants, have been suggested as evidence of competition in several species; for example, resident Ground Warblers *Microlegia palustris* occupy habitats where there are lower densities of migrants in the Greater Antilles (Terborgh 1980). In Jamaica, Yellow Warblers *Dendroica petechia* forage exclusively in mangroves in winter but begin to forage in shrub as soon as migrants depart in spring (Lack & Lack 1972). Willow Warblers *Phylloscopus trochilus*, (Palearctic migrants), may induce niche shifts in resident warblers in Kenya (Rabol 1987).

A criticism of these migrant-resident studies is that they do not adequately consider other plausible explanations for niche shift in residents. Arrival and departure of migrants may coincide with other factors such as seasonal changes in the food supply of residents (Gochfield 1985) or changes in their ecological requirements. A number of temperate, experimental studies have recently demonstrated a broadening of niche breadth (or niche shift) in resident passerines in the absence of a competitor (see Williams & Batzli 1979, Dhondt & Eyckerman 1980, Garcia 1983, Saether 1983, Alatalo 1982, 1987, Alatalo *et al* 1985, Gustafsson 1987). However, few experimental studies of migrant and resident systems have been carried out in the tropics, so evidence for niche shift remains circumstantial.

Cathartid vultures - General Background

The vultures of the New World belong to the family Cathartidae, are unrelated to the Old World, Accipitridine vultures and show close affinities to storks Ciconidae (Ligon 1967, Rea 1983). There are seven species of New World vultures; two Condors, the Andean *Vultur gryphus* and the extinct (in the wild) Californian *Gymnogyps californianus*- and five species of small Cathartids. Four of these occur in the study area in central Venezuela. In descending size order, the species are the King Vulture *Sarcorhamphus papa* (3.0 kg), Black Vulture *Coragyps atratus brasiliensis* (1.64), migrant Turkey Vulture *Cathartes aura meridionalis* (1.42), resident Turkey Vulture *Cathartes aura ruficollis* (1.22) and Lesser-Yellow headed Vulture *Cathartes burrovianus* (0.95). A fifth species, the Greater Yellow-headed Vulture *Cathartes melambrotus* occurs in rainforest areas elsewhere in South America (Blake 1977, Houston 1988).

Ecological separation of vultures

Assuming resources are limiting, vultures might avoid competition by a number of different strategies. In the New World Cathartid vultures, to some extent taxa are geographically separated (eg. the

Andean race of Turkey Vultures from the lowland race, or Lesser Yellow-headed from Greater Yellow-headed Vultures) though there is clearly much overlap. Habitat separation may be important, but there is no quantititave information on densities of vulture species in different vegetation types (Wilbur *et al* 1983).

In a study of African vultures, Kruuk (1967) showed that the morphological characteristics of different species were suited to feeding on particular parts of carcases, they avoided each other by feeding at different times and dominance hierarchies reduced conflict. In their feeding ecology, New World vultures are remarkably convergent to Old World ones; recently Wallace and Temple (1986) found that social dominance and differential feeding times reduced competition at feeding sites in a guild of scavengers in Peru.

In Venezuela, Houston (1988) compared bill morphology between different vultures and suggested that these were related to feeding niches. For example, King Vultures have powerful bills enabling them to tear the skin of large mammals although they have a much smaller gape than Black Vultures which are able to swallow large amounts of soft material (Houston 1988). There were also differences in group sizes of different vulture species feeding on carcases of different weight; Black Vulture numbers were correlated with increased carcase weight in the latter study, while there was a much lower correlation for Turkey Vultures (Houston 1988).

Migrant and resident taxa

There are six races of Turkey Vulture, (three which breed in North America, and three year-round residents in Central and South America), three races of Black Vulture (two in South America) and two races of Lesser Yellow-headed Vultures (a southern and northern race in Central and South America-Blake 1977). King Vultures are confined to Central and South America. Races of Black and Turkey Vultures from North America are considerably larger than those occurring in the study area. Within migratory subpopulations of *Cathartes aura* individuals from the north are larger than southern birds.

The North American western race of the Turkey Vulture *C.a. meridionalis* is highly migratory (Brown & Amadon 1968, Blake 1977). Its summer range extends from southern Canada to northern Mexico. Some subpopulations winter from California and Nebraska southward, while others migrate considerably further to Central and South America. A smaller subspecies *C.a. aura* spends the non-breeding season south to Panama, but has not been recorded in Venezuela (Blake 1977). The remaining north American subspecies *C. a. septentrionalis* winters as far as southern Florida (by wing-tagging, Gaby (1982) showed that individuals wintering in Florida were from Ontario and the eastern third of the United States). Turkey Vultures have a leap-frog migration (Salmonsen 1955, Stewart 1977), larger northern individuals migrating further south than the smaller southern birds, a pattern found in many migratory raptor populations (Newton 1979).

In South America, one race of Turkey Vulture occurs in the Andes, the other in the Falkland Islands, while the third *C. a. ruficollis* inhabits the lowlands (Brown & Amadon 1968). Black Vultures were thought to be partial migrants in Central America by Eisenmann (1963) and Skutch (1969) but these observations are not now accepted as true migrations (see Jackson 1988). The southern race of Lesser Yellow-headed Vulture may migrate to northern South America during the wet season (April-October; Blake 1977, Koester 1982).

Social behaviour

Small Cathartid vultures differ considerably in their social systems. Black Vultures show strong associations between family members at all times of year, both between mates and dependent or independent young and between neighbouring families (Rabenold 1983 a, b, c, 1986, 1987). These associations include defending family members from unrelated birds at feeding sites, allopreening and meeting family members at nest sites prior to roosting. In addition, there is indirect evidence for the use of communal roosts as information centers. Rabenold (1983 a c, 1986, 1987) proposed that because feeding sources usually contain sufficient food for several birds, it would benefit successful foragers to recruit related birds from a roost to cooperatively search for and defend large carcases. Black Vultures have complex dominance hierarchies and these are established not just over food or roost sites, but often on the ground below roosts and may serve to mediate competition for food resources (Rabenold 1983 a).

By contrast, *Cathartes* Vultures do not seem to have a complex social system. Associations between related birds have not been demonstrated, though there is evidence that in Turkey Vultures, unsuccessful foragers may follow successful birds from roosts (Rabenold 1983 c). However, because Turkey Vultures generally feed on smaller carcases than Black Vultures (Stewart 1978, Houston 1988), there appear to be few selective advantages for group foraging. This is because at small carcases there are usually few feeding sites and these can be defended by individual birds.

King Vultures live in small family groups, consisting of adults and young of different ages (Koester & Koester-Stowesand 1978, Houston 1988). This species does not attain adult plumage until six years old (Brown & Amadon 1968), when first breeding probably occurs. Little is known about the duration of parent-offspring ties.

Foraging ecology of vultures

The use of olfactory foraging in the Turkey Vulture (Bang 1964, Stager 1964) may explain why New World, but not Old World vultures, play an important role as forest scavengers (Houston 1985, 1986 a). Houston (1986 b) found that vultures removed over 90% of carrion from a forest in Panama. In many tropical forests, there is almost complete canopy cover making it impossible for vultures to locate carrion efficiently using vision alone (Houston 1986 b). In addition to Turkey Vultures, other members of the *Cathartes* genus (eg. Lesser Yellow headed Vulture) also probably use olfaction (Houston 1984).

Neither the Black or King Vulture has highly developed olfaction (Stager 1964, Houston 1984) but they watch the activities of *Cathartes* Vultures flying below and follow these birds to find carrion (Koester & Koester-Stowesand 1978). The ability to detect carcases by smell is important in ecological separation since it often enables *Cathartes* Vultures (some of which have low interspecific ranking) to find hidden food before other species arrive. Vultures which use olfaction to locate carcases are also able to forage in large areas of forest where Black Vultures are often absent (Houston 1985).

Introduction to the study

The present study is an investigation of ecological separation between five taxa within the guild of small Cathartid vultures, sympatric in the northern Neotropics of Venezuela (see Blake 1977). Little is known about the habitat selection or feeding ecology of these vultures in natural habitats (Wilbur *et al* 1983). This study focuses on the role played by migrant Turkey Vultures in the ecology of resident vultures and in particular focuses on the interactions between migrants and a resident subspecies. By studying resource partitioning and interference competition at feeding sites the aims of this project are to contribute to current knowledge of the relationships between migrants and residents. There is almost no information about the role of competition in other gregarious migrant species, partly due to the absence of studies involving individually marked birds, but also the nomadic nature of many migrant species (Greenberg 1986) .

In autumn, large numbers (eg. 958,634 in 1972) of migratory Turkey Vultures *Cathartes aura meridionalis* fly south through Panama (Smith 1980) and spend the dry season (November to April) in South America when food supplies are probably most abundant due to high animal mortality (see Ojasti 1973, 1978). Migrants considerably outnumber resident Turkey Vultures *C. a. ruficollis* by about seven to one in South America and are significantly heavier, thus dominating residents at feeding sites (Koester 1982). Counts of *Cathartes* Vultures made in Colombia led Koester (1982) to suggest that the influx of migratory Turkey Vultures from North America may result in changes in the foraging behaviour of residents.

For nomadic avian scavengers with large populations, experimental removals are not practical. However, if there is no change in food supply, the arrival and departure of migrant vultures effectively simulates the experimental introduction and removal, respectively, of competitors. In the presence of more dominant migrants, resident Turkey Vultures may be forced to forage in habitats with low food availability. Conversely, when migrants depart, residents may show 'competitive release' (niche expansion in the absence of a competitor- Schoener 1965). However, such natural 'experiments' are often unreliable and we must be cautious of drawing conclusions based solely on them (Newton 1980). Therefore, comparative studies of resource use by other species within the guild is also examined.

Aims and lay-out of the thesis

To assess resource use by different vulture taxa, the main objectives were the following;

(1) To investigate the dispersion of vultures over different habitats and examine any seasonality in habitat use.

(2) To individually mark large numbers of vultures and investigate seasonal changes in foraging movements, and site fidelity of migrant and resident vultures. A further aim was to use radiotelemetry to demonstrate any possible habitat shifts by resident Turkey Vultures.

(3) To assess the relative importance of avoidance mechanisms at feeding sites in mediating potential competition.

Chapter 2 is an introduction to the study area, including a description of the main vegetation types, its suitablity for research on vultures, and other scientific research. Chapter 3 presents the results from census counts carried out in different habitat types and discusses dispersion of foraging vultures in relation to habitat type and competition. Seasonal changes in the density of vultures in different habitats and the effects of migrant emigration on habitat selection in the resident race of Turkey Vulture are discussed.

In Chapter 4, the movements and habitat selection of marked vultures are described, including a short radiotracking study of resident Turkey Vultures. Resource partitioning at feeding sites and how this is achieved, is discussed in Chapter 5. This Chapter focuses on detailed interactions between vultures in gallery forest, where there is least human influence on food sources. The relationships between foraging strategies and morphology, body size and social dominance are discussed in Chapter 6. This Chapter also includes a comparison of body condition of vultures in different months in order to indicate the importance of seasonal changes in food supply or competition levels. Chapter 7 investigates moult and compares moulting strategy between migrant and resident vultures. Finally, Chapter 8 is a general synthesis of the results and a discussion of the evolution of migration in Turkey Vultures, including a comparison between the present study and other studies of the relationships between migrant and resident birds.

CHAPTER 2. STUDY AREA AND GENERAL METHODS

2.1 Study Area

2.1.1 Description of the Llanos

The northern savannas or Llanos of South America cover an area of about 200,000 km.^{2} They are bordered in the south and east by the River Orinoco and in the north and west by the Andes and coastal mountains (Sarmiento & Monasterio 1975). The study site, Hato Masaguaral is located in the middle Llanos, in Venezuela (Figures 2.1 and 2.2), intermediate in altitude between the low Llanos south of San Fernando de Apure (which flood more deeply) and the high Llanos north of Calabozo, Guarico State. Topography is almost flat, the highest elevation being only 60 - 75 m above sea level.

There is a marked seasonality in climate with a pronounced dry season for four months of the year (December to March), a wet season from May to October. April and November are transitional months. The average rainfall was 1400-1500 mm annually over a 20 year period- (Troth 1979). However, the onset of the rainy season and the annual rainfall total are highly variable. For example, in 1969 the wet season began in February whereas in 1988, rains had not begun by July. Daytime temperatures are similar throughout the year, but greatest changes occur in the dry season; the annual temperature variation at Masaguaral is only 24-37^{o}C. In the Estacion Biologica de los llanos, near Calabozo the maximum temperature over a 10 year period was 40^{o}C (February 1978), and minimum 17^{o}C (December 1975). Winds are often strong in the dry season with east, north-eastly prevailing, sometimes shifting to the east (Troth 1979). In the wet season there is no change in wind direction but a large reduction in velocity occurs.

Masaguaral is bisected by a highway running from Calabozo to San Fernando (Figure 2.3). On the east side of the highway there is a

Figure 2.1 Map of Venezuela showing location of study site

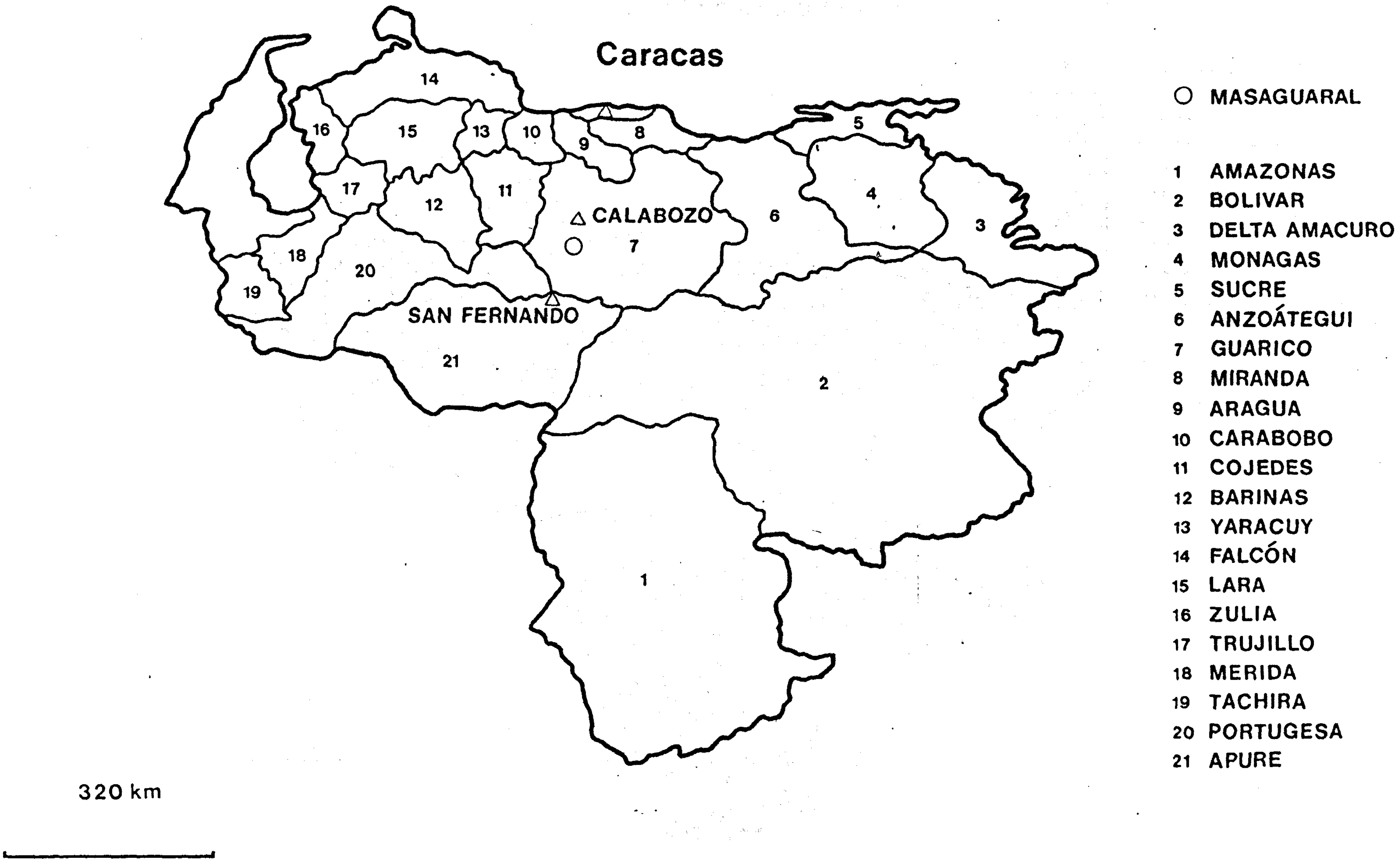
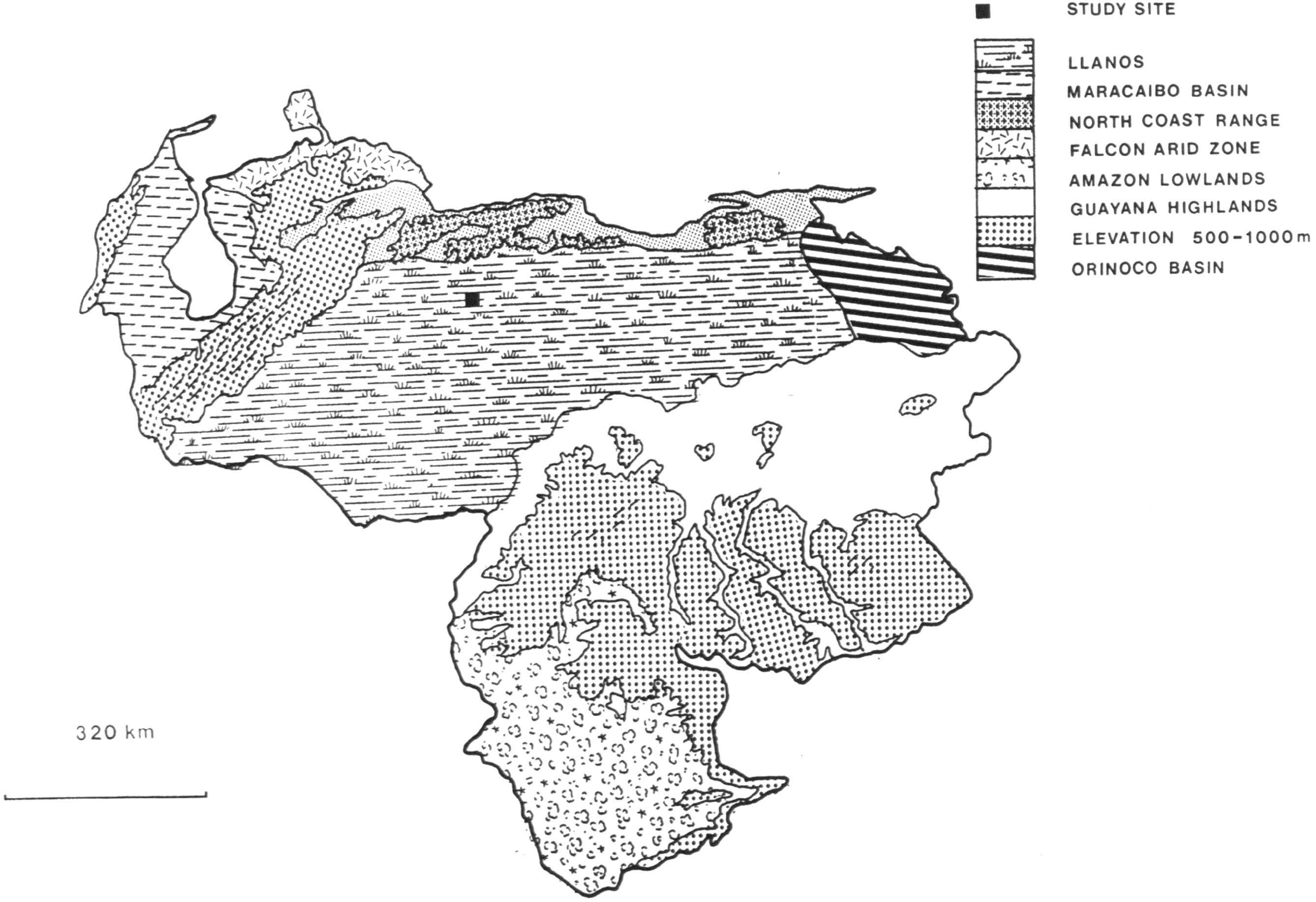


Figure 2.2 Map of Venezuela showing main geographical areas and location of study site



relict area of gallery forest bordering the Rio Guarico and its tributary the Caño Caracol (Figure 2.4). The gallery forest is a semi-deciduous dry tropical forest covering an area within the ranch of 4.5 km east-west by 2.5 km north-south (Troth 1979). This vegetation type, which is only found along permanent water courses, contrasts with habitats in the west of the study area which are generally much more open savanna vegetation, comprising open grassland with scattered palms *Copernicia tectorum* and matas, or clumps of trees (Troth 1979). The ranch vegetation is classified as dry tropical forest (Ewel & Madriz 1968) under the Holdridge system.

2.1.2 History of the research base

Hato Masaguaral lies 45 km south of the town of Calabozo, located at 8 34 ′ N, 67 35′ W. In 1972/73, Señ. Tomàs Blohm (who is the owner and a dedicated wildlife conservationist), J. Eisenberg and R. Thorington of the Smithsonian Institute, intitiated the first studies at the ranch and set up the research base. The ranch is listed as an internationally important wetland (Scott & Carbonell 1986) and the diversity and richness of wildlife is evident from the following account of past and current projects. This research also provided important information on the food supply of vultures in the study area. Early studies concentrated on the Red Howler monkey *Aloutta seniculus* (see Rudran 1979, Crockett & Eisenberg 1987, Pope in prep) and later the Wedge-capped Capuchin monkey *Cebus nigrivattus* (Robinson 1979, 1987, Robinson *et al* 1987), Giant anteater *Mymecophaga tridactyla* and Lesser anteater *Tamandua tetradactyla* (Montgomery & Lubin 1977), Possums *Didelphis marsupialis* and Crab-eating foxes *Cerdocyon thous* (Brady 1979).

Other ongoing long-term studies include those on Spectacled Caiman *Caiman crocodylis* and the endangered Orinoco crocodile

Crocodilus intermedius by J. Thorbjarnsson; cooperative breeding studies in Stripe-backed and Bicoloured wrens *Campylorhynchus* species (see Rabenold 1984, Austad & Rabenold 1985, 1986); Snail Kite *Rostrhamus sociabilis sociabilis* foraging (Beissinger in prep) and the Hoatzin *Opisthocomus hoazin* (Strahl 1988). A number of botanical studies have also been undertaken on the ranch including work on phytosociology by Troth (1979).

2.1.3 Study site decription

The ranch habitats comprise four physiographic savanna units (numbers) and seven main vegetation types (letters):

1)**Bancos** (Non - flooded low ridges)

a Lines of old water courses, often of the Rio Guarico with savanna type vegetation; shrubs and palms.

2)**Bajio** (moderately flooded lowlands)

b Discrete mata savanna (trees shrubs and palms with herbaceous layer).

c Palm savanna (all palms, shallow water in the wet season).

d Shrub woodland (almost closed canopy, palms often abundant).

3)**Estero** (deeply flooded lowlands)

e Flooded savanna (deeply flooded savanna - in the wet season, isolated palms).

4)**Medano** (non-flooded high ground)

f Sandhill (grassland and shrubby grassland).

5)**Gallery forest** (tree heights ranging from 10-20 m, maximum 42 m, near to Rio Guarico) (Troth 1979).

In terms of contribution to overall area the Bajio physiographic

Figure 2.3 Location of census count sites and ranch houses

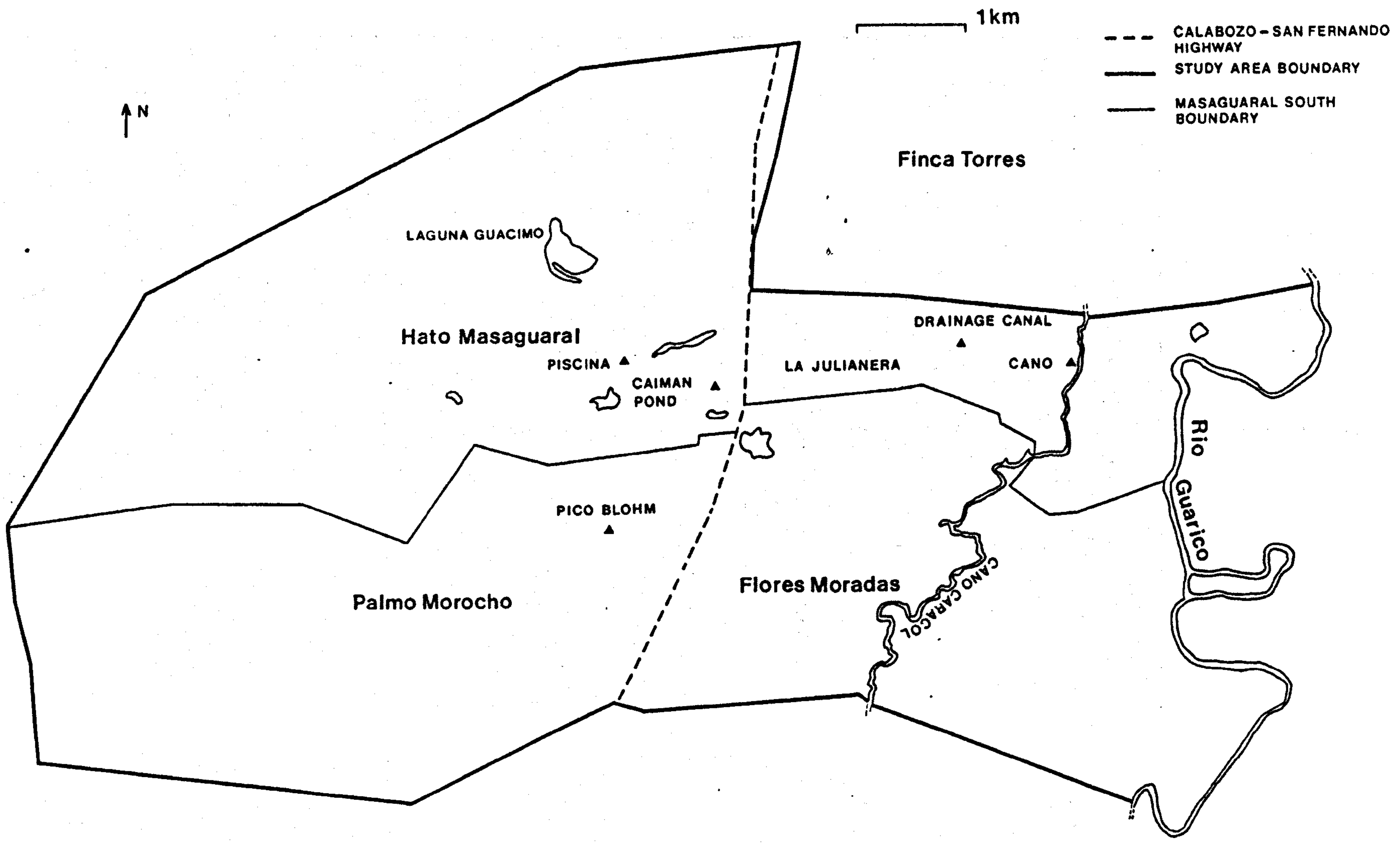
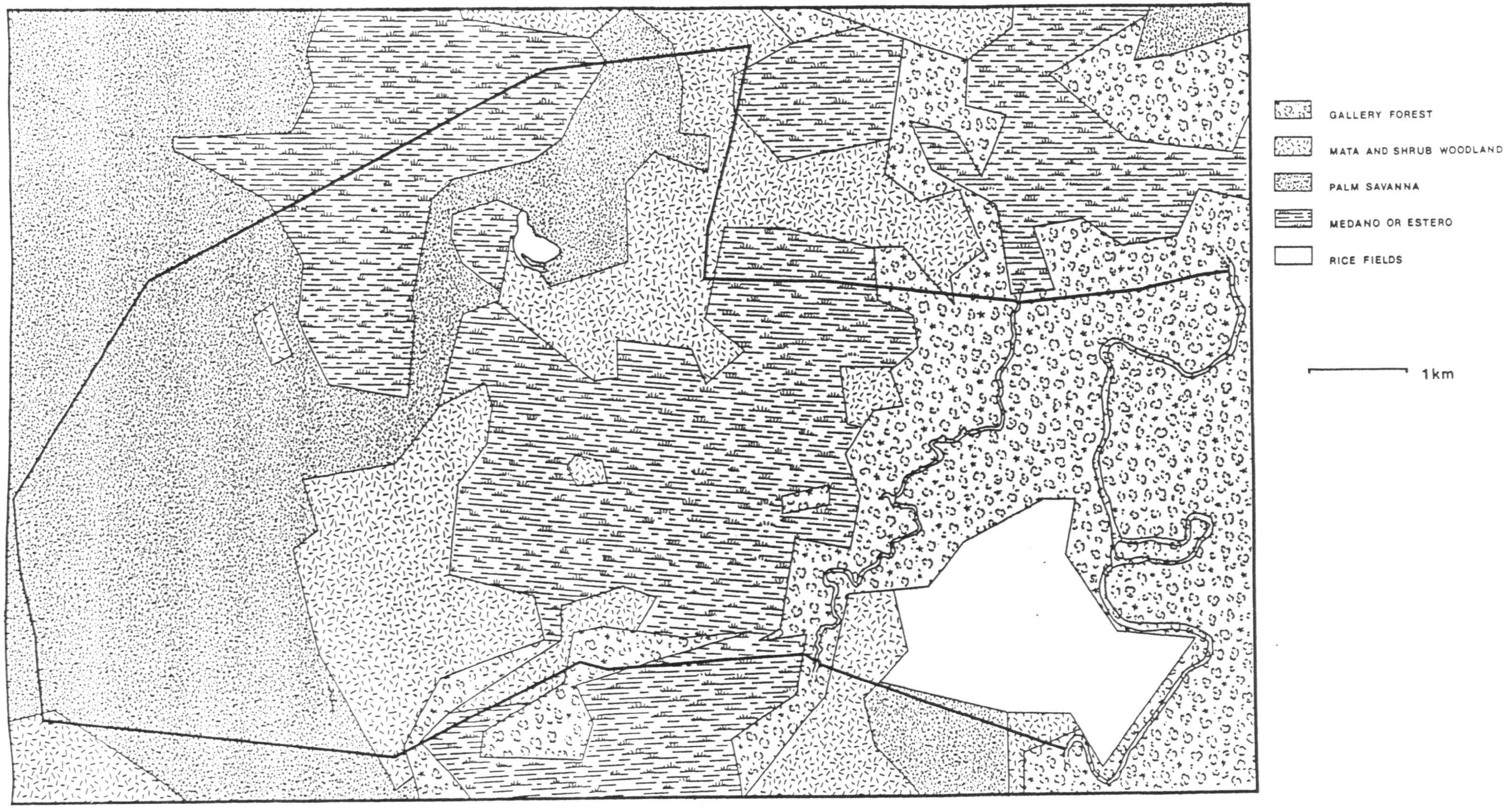


Figure 2.4 Map of study area with main vegetation types



unit is most common, followed by Estero, Medano, Gallery forest and Banco. Figure 2.4 shows the relative areas of different habitat types (simplified).

The nature reserve was initially established by Señ. Blohm to demonstrate that a working cattle ranch need not destroy areas of important wildlife interest. Although large numbers of domestic livestock have some impact on both the structure and composition of vegetation (especially regeneration), the ranch, which is 7500 hectares in extent, provides an important refuge for typical llanos fauna and flora. Three lagoons and adjacent marshes are flooded during the dry season by diesel-driven pumps and these areas provide a refuge for large numbers of waterbirds (eg. White-faced Whistling Duck *Dendrocygna viduata*, Black-bellied Whistling Duck *Dendrocygna autumnalis* and Scarlet Ibis *Eudocimus ruber*).

The importance of the gallery forest area at Masaguaral has increased in recent years because of the extensive habitat destruction on neighbouring ranches for the establishment of rice fields. There are already suggestions that as the area of gallery forest declines, populations of certain species may no longer be viable (eg. Robinson unpublished, has modelled the effect of reduction in forest area on the Wedge-Capped Capuchin *Cebus nigrivattus* population). Additionally, forest and savanna fire have affected the vegetation structure with the result that much of the area bordering the Rio Guarico is secondary forest (Putz pers. comm.). The construction of a dam on the upper reaches of the Guarico, north of Calabozo has increased the extent of discrete mata woodland at the expense of more open habitats due to a rise in the water table.

The lowland forests and savannas of the neotropics provide an ideal situation in which to examine resource partitioning in Cathartid vultures. Firstly, there are four sympatric species of vultures in the region (including two races of Turkey Vulture). Secondly, the mosaic of different habitat types (riverine gallery forest, patches of woodland, palm savanna and seasonally flooded grassland (Eisenberg 1979, Troth 1979) allow detailed comparison of habitat use between different vulture taxa. Furthermore, because of the almost flat terrain, differences in flying conditions at low altitude (where *Cathartes* Vultures forage) are likely to be related to vegetation cover rather than to physiographical features (see Houston 1988). In Africa, vultures selectively forage over mountains where there is increased lift to facilitate soaring (Houston 1974, 1976).

2.2 GENERAL METHODS

A total of 20 months was spent in Venezuela on three separate visits. The first was from 17 November 1984 to 10 July 1985, the second, 28 November 1985 to 21 June 1986 and the third, 6 October 1986 to 26 March 1987 inclusive.

2.2.1 Catching Vultures

To provide data on movements, biometrics and moult sequence, large numbers of vultures were trapped and marked with patagial wing-tags (Wallace *et al* 1980). Vultures were trapped using several different methods. The most effective was a walk-in funnel trap design which has been used extensively in the United States (Rabenold 1983 b). Cages were initially constructed of wire netting (3 cm.) and bamboo but because birds damaged themselves on these (they cut their unfeathered heads on the wire) new traps were built. The latter traps were constructed of weldmesh and 5 x 2 cm timber (dimensions 2 m x 2m by 2m). A trap was built 5m long x 1.2m high x 2m wide to catch King Vultures. However this had to be supervised continuously and, as populations of King and Lesser Yellow-headed Vultures were comparatively small it was decided that insufficient time was available during the present study to catch these species. Five traps were built so that birds could be caught at a number of locations simultaneously.

Walk-in traps were extremely effective for Black and Turkey Vultures but not for Lesser Yellow-headed or King Vultures. A small number of birds were also caught using a clap net, but birds were generally wary of this design. A large variety of carcases were used to bait traps and different baits were used depending on the target species of vulture. For Black and migrant Turkey Vultures, most success was achieved using cows, pigs or caiman. Most resident Turkey Vultures were trapped using possums and foxes.

2.2.2 Marking

Cathartid Vultures practice urohydrosis, defaecating on their legs to facilitate cooling (Hatch 1970). This means they cannot be colour-ringed (banded) which is the commonest method used to identify individuals of many species. Ringing results in the accumulation of uric acid over and inside rings and this contricts the legs of birds and can result in serious deformities, lesions or even loss of feet (Henckel 1976, Wallace *et al* 1980, and Sweeney *et al* 1984). Banding of Cathartid vultures is no longer permitted in the United States.

An alternative and reliable method of permanently marking vultures is to use patagial wing-tags. The use of Allflex cattle tags for this purpose has been well documented (Wallace *et al* 1980, Sweeney *et al* 1984). Initially, in the present study, yellow darvic wing-tags were used with an engraved letter / number code, attached by stainless steel wire with a loop on each side of the patagium and nylon washers to minimise abrasion. However, a small percentage of birds could remove these tags and patagial skin irritations were caused. The tagging system was therefore changed to the yellow, numbered Allflex cattle-tags which are attached with an applicator. This considerably increased the speed and ease with which birds could be handled.

2.2.3 Biometrics

Biometric measurements were taken to permit investigation of individual variation within and between species. The aim was to relate body size to dominance at carcases and develop body condition indices for vultures. During the first field season 11 different measurements were made on all species (Chapter 6). When a large sample of Black Vultures had been obtained (100 birds) Pearsons correlation matrices showed 3 measurements (flat wing cord, tarsus, bill length) were good predictors of body size. The number of measurements was also reduced for practical reasons to minimise handling time for birds and increase the number of birds which could be marked. However, as the focus of the study was a detailed comparison between the two races of Turkey Vulture, all measurements were continued on these races - only 67 resident Turkey Vultures were caught. The measurements made are described in Chapter 6 (Body size and condition of vultures).

Sequence of moult and the position of growing feathers were also recorded as this is related to the energetic requirements and the ecology of vultures. The timing of moult in migratory Turkey Vultures was important in relation to when birds departed from the ranch heading northwards; generally migrant birds complete an energy demanding moult before their long spring migration. The stage of moult could also be used as an indication of the stability of vulture populations within the study area.

2.2.4 Statistical techniques

Most data were analysed using a computer package (SPSSx, McGraw Book Company 1986) which was essential for the handling of the large quantities of data. Biometric data were analysed using Minitab (see Ryan *et al* 1985). For statistical analyses, non-parametric statistics were used (Kruskal-Wallis one-way ANOVA, Mann Whitney U Test, Chi-squared, Wilcoxons Matched pairs rank sign Test, Spearman Rank Correlation - Siegel 1956, Fowler & Cohen 1987) when data were not found to be normally distributed even after log-transformations, or where sample sizes were small. Range data, vulture counts and focal animal sampling feeding behaviour (peck rates) data did normalise with log-transformation and were therefore analysed with parametric techniques; (One and two-way ANOVA, Covariance Analysis, unpaired T-tests, Linear and Multiple regression - Sokal & Rohlf, 1981). Throughout the thesis the following symbols represent probability levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; N. S. not significant.

CHAPTER 3 HABITAT SELECTION

3.1 INTRODUCTION

Differential habitat selection is an important mechanism by which many closely related species are ecologically separated (Partridge 1978, Schoener 1982). Habitat selection may take the form of preferences within the same habitat (eg. differences in feeding niche) or between different habitats (Cody 1985). Both morphology and behaviour affect habitat choice and preferences may be based upon physiographical features which provide suitable breeding or foraging sites. Thus, breeding requirements may account for seasonal changes in habitat use (Cody 1985). Migrant birds may experience very different habitat types in their 'winter' range compared to those on the breeding grounds, so specialised morphology which may have evolved in response to habitat features (eg. bill width in Great Tits *Parus major* - Ulfstrand *et al* 1981, Gosler 1987) may not be an advantage (see Cody 1985).

Many small passerine birds discriminate between habitats on the basis of vegetational structure and composition (eg. Catchpole 1973, Gochfield 1978, Cody 1985, Alatalo *et al* 1985). Recent experimental work has demonstrated that there are many examples of mutual avoidance by differential habitat selection between species (eg. Williams & Batzli 1979). There is evidence that these species exploit different resources or habitats to minimise direct interspecific competition (eg. Alatalo 1982, Garcia 1983) and this is also indicated by species distributions on islands (eg. Diamond 1973). Habitat shifts may be attributed to the presence or absence of congeneric species. For example, Common Nighthawks *Chordeiles minor* occupy a wide range of habitats in the northern United States, but are excluded from desert areas in the south by Lesser Nighthawks *C. acutipennis* (Caccamise 1974).

In large birds like raptors, ecological segregation may be achieved by selecting different macrohabitats or environments in which to forage (eg. in South African Accipiters, Simmons 1985, and races of American Kestrel *Falco sparvius*, Bohall-wood & Collopy 1986). Schmutz *et al* (1980) found that in the same area, Ferruginous Hawks *Buteo regalis* inhabited open habitats while Red-tailed Hawks *B. jamaicensis* foraged in woodland and Swainson's Hawks *B. swainsoni* were found in intermediate habitats. Vegetative cover is probably an important consideration in habitat selection by raptors because of its effect on hunting success (Southern & Lowe 1968, Wakeley 1978, 1979, Bechard 1985). In Cathartid vultures, vegetative cover affects the speed at which carcases are located and group composition at feeding sites (Chapter 5). Carcases hidden in dense vegetation must be located by *Cathartes* vultures using olfaction (see Stager 1964, Houston 1985), whereas those at open sites are visible to other vulture species.

The habitat preferences of vultures may also be related to their wing-loading. Species with low wing-loading are able to fly at low altitude and use relatively weak lift caused by air turbulence over irregularities in vegetation, while those with higher wing-loading depend on high altitude thermals over savanna (see Houston 1988).

The structural diversity of vegetation in the Llanos results in considerable differences in mammalian biomass or species-richness and therefore abundance of carcases (Eisenberg 1979), so one might expect spatial differences in vulture density. The foraging strategies of vultures would be likely to reflect the patchy and unpredictable nature of food sources and also the behaviour and social status of birds. The best quality habitats may be occupied by dominant individuals making only poorer habitats available to subordinate individuals or species (see MacArthur 1972). Little is known about habitat selection in New World vultures (Wilbur *et al* 1983). This chapter investigates the importance of habitat selection as one mechanism for resource partitioning in closely related vultures. Specifically the objectives were to;

i) Compare relative densities of vulture species and races in different habitats on the ranch to see if vultures selected different habitats in which to forage.

ii) To investigate any seasonal variation in habitat selection.

iii) Determine the variation in numbers of migrants throughout the dry season because this affects the level of competition for food resources in the area.

iv) Assess the role of habitat selection in potential competition between resident and migrant Turkey Vultures.

3.2 METHODS

The population sizes (approximate estimates in parenthesis) of vultures using the study area during the dry season, in order of abundance were as follows; Black Vulture (600), migrant Turkey Vulture (500), resident Turkey Vulture (80), Lesser Yellow-headed Vulture (30) and King Vulture (15).

3.2.1 Time periods of census counts.

Preliminary counts were made in different habitats to determine the most suitable time periods to record activity. Cathartid vultures do not generally forage before 0900 hr or after about 1600 hr (pers. obs.) but this depends on many factors, including wind speeds and whether vultures located food sources the previous day (Black Vultures were sometimes seen flying directly to carcases at dawn). In the tropics, higher temperatures may permit soaring earlier in the day than in temperate regions (vultures flew earlier in the study area than in North America, K. Rabenold pers. comm.)

Counts were made from dawn until dusk on four days in three vegetation types. They were made in different habitats because vegetative cover could affect air currents and therefore the suitability of conditions for flying. Marked habitat differences in vulture density were likely, so the counting strategy was designed to detect these rather than other factors affecting vulture numbers. Counts were made on several days to account for variability in numbers of birds resulting from local enhancement (the presence of a large carcase in the vicinity of count sites could temporarily attract vultures from a wide area.)

No attempt was made to differentiate between the *Cathartes* taxa (resident Turkey, migrant Turkey and Lesser Yellow-headed Vultures) during the preliminary activity counts because these taxa could only be identified at close range (less than 200m). Counts of flying vultures were made at hourly intervals throughout the day at three sites on four dates (9th, 16th, 22nd (counts made at two sites) and 29th December, 1985)). These included three counts at open sites (Caiman pond), one in gallery forest (Cano Caracol) and one at the forest edge (Canal).

The data gathered from preliminary activity counts of vultures were used to fix time periods when there was least fluctuation in the numbers of flying birds. Results of these counts (presented later- Figures 3.2-3.6) showed a variable peak in flying vultures at 0900 hrs, a quiescent period around mid-day and significantly lower counts in the afternoon compared to the morning (see Table 3.2). The periods 0930-1130 and 1330-1530 were therefore selected to avoid the early morning peak and mid-day lull.

3.2.2. Selection of census count sites

Roadside transect counts are commonly used to count New World vultures and raptors (eg. Koester 1982, Ellis *et al* 1983, Hubbard 1983). Point counts were used in this study, because they overcame many of the problems of transect counts such as variations in visibility (see Fuller 1973, Fuller & Langslow 1978, Jarvinen 1978, Dawson 1981 a, b for a discussion of point counts). Vantage points were selected representing areas of each of the seven main vegetation types described by Troth (1979) (see Chapter 2, Section 2.1.3). These were:

Bajio sites (west of the highway - Figure 2.3)

(1) Piscina tower (this included habitats mata, shrub woodland, estero and medano).

(2) Caiman (Baba) pond (mainly medano, estero and mata).

(3) Pico Blohm (predominantly medano, estero and palm savanna).

Julianera sites (east of the highway-Figure 2.3)

(4) Drainage canal (shrub woodland, estero, medano and gallery forest).

(5) Cano Caracol (gallery forest).

To enable coverage of the main vegetation types within a fixed time period, five sites were chosen which could be visited in a linear sequence using a motorcycle. Three of the sample points (1, 4 and 5) were tall towers c.20 metres high erected by S. Strahl for Hoatzin *Opisthocomus hoazin* studies (Strahl 1988). These were ideal sites from which to count vultures and provided extensive views over surrounding habitats for up to 4 km. The remaining two sites were located in medano areas where a tower was unnecessary because these sites were of higher elevation than the surroundings, providing a vantage point. It was not possible to find a site of suitably elevated vantage point to view over palm or mata vegetation types at close enough distances to be able to identify *Cathartes* races (Section 3.2.2).

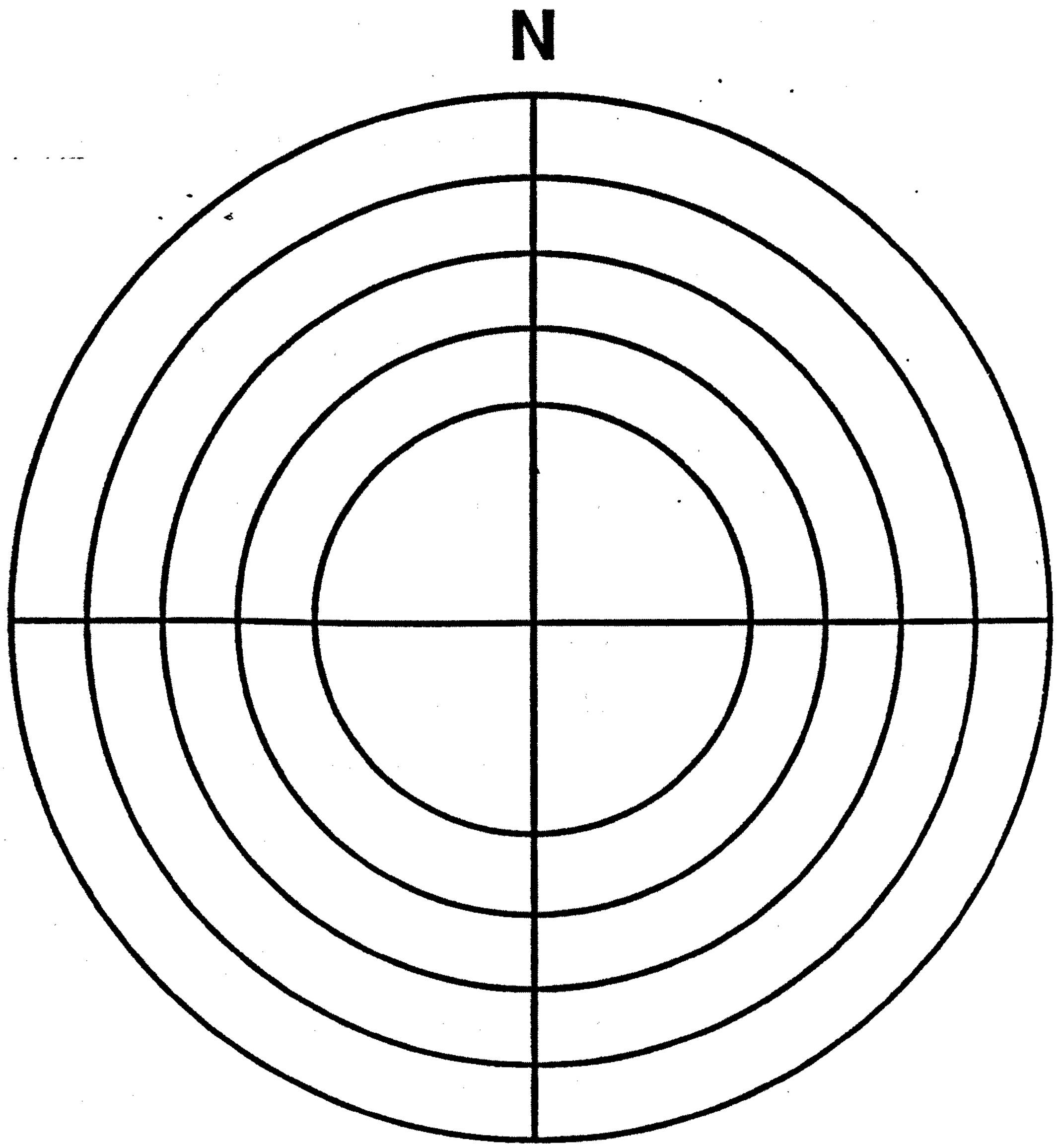
3.2.3 Weekly census counts

Weekly counts were made at each site. It was important to count all sites on the same day because variations in weather conditions and location of food sources could bias results if different sites were counted on different days. Weather conditions had a pronounced effect on the numbers of airborne vultures, so censuses were made on dry days with low cloud cover (in the dry season, conditions were always suitable but counts were regularly postponed in the wet season because of poor weather conditions).

The order in which the sites were visited within each two-hour period (0900-1130 and 1330-1530 on each count day) was determined using random numbers, but sites east and west of the highway were treated separately. Otherwise, the furthest sites would have been too distant to visit within the two-hour period.

At the start of each field season my estimated distances were compared with actual distance by using a cut-out, life-size silhouette of a flying Turkey Vulture and a range finder. Flying vultures were counted in a clockwise direction from a fixed point using 10x40 binoculars and information was recorded on a microcassette. Vultures were recorded in 90^{o} sectors at each location and the birds counted in distance categories at 200 m. intervals up to 1 km. within these sectors (see Figure 3.1). This method enabled the habitat type over which vultures were flying to be determined at a later date (from aerial photographs)-this would have been difficult to do directly in the field. Vulture densities from the first 200m arc (called small area counts) were considered separately from the densities in the remaining arcs from 200-1000m (called large area counts) because at the former distance it was possible to identify different species and

Figure 3.1 Method of counting vultures at census sites (birds were counted within each 200m arc up to 1000m in each 90° sector of the circle).



races of *Cathartes* vultures. Data from arcs greater than 200m were combined to obtain a density estimate of Black Vultures, *Cathartes* taxa and King Vultures.

Although identification of *Cathartes* Vultures was often possible at distances greater than 200 m, it was necessary to standardise this distance to ensure that identification could be made even in bad light conditions. Resident Turkey Vultures *Cathartes aura ruficollis* have a very distinctive yellow or cream-coloured nape enabling them to be distinguished from migrants at close range. At 200m, *Cathartes* species and races were distinguished by the field characteristics referred to by Blake (1977) and De Schaunsee (1978). Black and King Vultures, however, could be identified confidently at distances of up to 4 km. Vulture counts at greater distances were discarded because of differences in visibility between sites and difficulties arising from intense heat shimmer.

3.2.4 Densities of vultures foraging over different vegetation types

The area of each of the seven vegetation types in each of the distance arcs within each sector (four 90° sectors at each count site-Figure 3.1) was determined by tracing them from aerial photographs of Hato Masaguaral, and then weighing them. Each arc was then classified according to its habitat composition using a hierarchical Cluster analysis (Ward's method) because several different savanna habitats occurred in each arc. The cluster analysis classified arcs into one of eight vegetation groups (1) Estero/Medano; 2) Mata and palm savanna/Medano; 3) Medano/Estero; 4) Shrub woodland/Estero/Medano; 5) Shrub woodland; 6) Palm/Estero; 7) Gallery forest and 8) Gallery forest/Medano/Shrub woodland.

Since the relative cover of vegetation was most important for foraging vultures, the eight classes were combined into three habitat groupings based on their similarity using the cluster dendrogram. These were 1) Forest - groups 7 and 8; 2) Semi-open - groups 2,5,6 and 3) Open - 1,2,3. Vulture densities over different arcs could then be calculated for each of these three vegetation types.

Of the total area in the large area arcs (200-1000m), forest comprised 29%, semi-open 18% and open habitats 53%. In the small area arcs (0-200m) forest comprised 35%, semi-open 16% and open 49%. However, these proportions did not reflect the availability of these habitats over the whole study area (Chapter 2, Section 2.1.3).

Counts of vultures were not normally distributed, so they were log-transformed. A two-way ANOVA was then performed for large area counts (1 km radius) comparing vulture densities between habitats for each month and to account for weekly variations in the numbers of vultures. However, sample sizes were too small in the 200 metre arc counts to carry out a two-way ANOVA, since only a few vultures were seen in each habitat type for each month. For comparisons of vulture density between habitats for these small areas a X^2 Goodness of fit test was carried out, based on the null hypothesis that the number of vulture counts in each habitat was proportional to habitat area. Densities of *Cathartes* Vultures were compared between months using a one-way ANOVA. As well as calculating mean counts including zero values, the percentage of zero counts and average positive vulture densities were calculated (see Appendices Tables 1.1-1.12).

3.3 RESULTS

Between 26th January and 9th June 1986, 23 censuses were made and a further 20 censuses from 12th October 1986 and 28th February 1987. Counts therefore covered the dry season (November to April) and during the wet season counts were made in June, July and October.

3.3.1 Annual and diurnal differences in counts

Diurnal

The preliminary activity counts (N=5 days) reflect the following; (1) Large differences in densities of *Cathartes* vultures occurred between open (savanna) and closed (forest) vegetation types (Figures 3.2-3.6). Hourly counts were significantly different between a gallery forest site and three counts in an open habitat (Table 3.1). No significant differences were found between three replicate counts at the same open site on different days but differences were significant between a forest edge (which overlapped slightly with the savanna site) and forest site (Table 3.1). Hourly counts of Black Vultures were highly variable and there were no consistent habitat differences (Table 3.1). For example, on one count day in the open, significantly more Black Vultures were counted than a repeat count a week later at the same site (Caiman pond, Table 3.1, Figures 3.2 and 3.4).

(2) The general pattern was a distinct morning peak and on some days an afternoon peak in each habitat type, although there was some variation between species and habitats (Figures 3.2-3.6).

(3) Figures 3.2-3.6 show that there was an earlier morning peak in numbers of flying vultures at open sites (Caiman pond) than at the Cano Caracol, a gallery forest location, but this observation was only based on one gallery forest count day (the other site was at the forest edge - Figure 3.5) and three open site days. A larger sample size would be needed to establish this.

(4) Table 3.2 shows that during the period 0900-1200 hrs, counts were higher and there was less variability than afternoon counts (1300-1600). There was also greater variability in the counts of Black Vultures than *Cathartes* vultures (Table 3.2).

Table 3.1 Hourly counts of vultures at three sites on five separate days between the period 0700-1800 (median and range in parentheses, N = number of hourly counts)

Species	Open 1 N = 12	 2 Caiman Pond N = 12	 3 N = 11	Forest 4 Canal N = 12	 5 Cano Caracol N = 12
Cathartes	28 (0-41)	24 (0-68)	26 (0-118)	14 (0-69)	9 (1-21)
Black	4 (0-49)	21 (0-75)	12 (0-53)	10 (0-37)	4 (0-36)

Differences (Wilcoxon's test for matched pairs) in hourly vulture counts between forest and non-forest sites on four days (Figures 3.1-3.6).

		Cathartes Vultures			Black Vultures		
Cano vs Caiman pond	1	T = 3,	N = 12,	**	T = 22,	N = 9,	N.S.
	2	T = 3,	N = 10,	**	T = 7.5,	N = 10,	*
	3	T = 0,	N = 9,	**	T = 12.5,	N = 9,	N.S.
Caiman pond	1 vs 2	T = 7,	N = 7,	N.S.	T = 4.5,	N = 10,	**
	2 vs 3	T = 16,	N = 10,	N.S.	T = 9,	N = 8,	N.S.
	1 vs 3	T = 24.5,	N = 12,	N.S.	T = 19.5,	N = 10,	N.S.
Canal vs Cano		T = 8,	N = 11,	*	T = 6.5,	N = 9,	N.S.

Table 3.2 Variation in hourly counts on 3 days in open, 1 in forest edge and 1 forest sites within count periods used for weekly census counts (Median counts with range below, N = number of hourly counts in period).

Species	Morning (0900-1200) Open N=12	 Semi-open N=4	 Forest N=4	Afternoon (1300-1600) Open N=11	 Semi-open N=4	 Forest N=4
Cathartes	39 (18-118)	59 (53-69)	21 (17-22)	27 (11-42)	14 (0-40)	9 (3-13)
Black	18 (1-75)	19 (16-37)	10 (3-36)	13 (1-74)	8 (0-34)	7 (1-22)

Figure 3.2 Counts of flying vultures from dawn until dusk on 15/12/86 at Caiman Pond

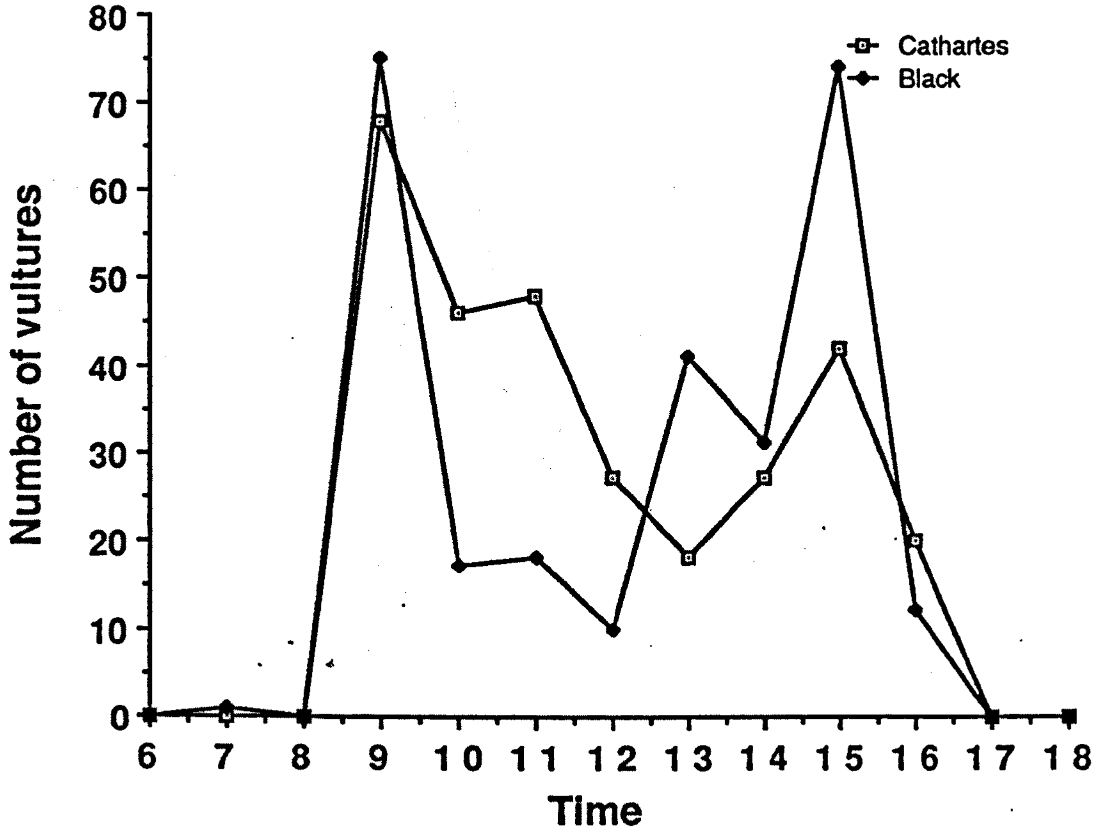


Figure 3.3 Counts of flying vultures from dawn until dusk on 9/12/86 at Caiman Pond

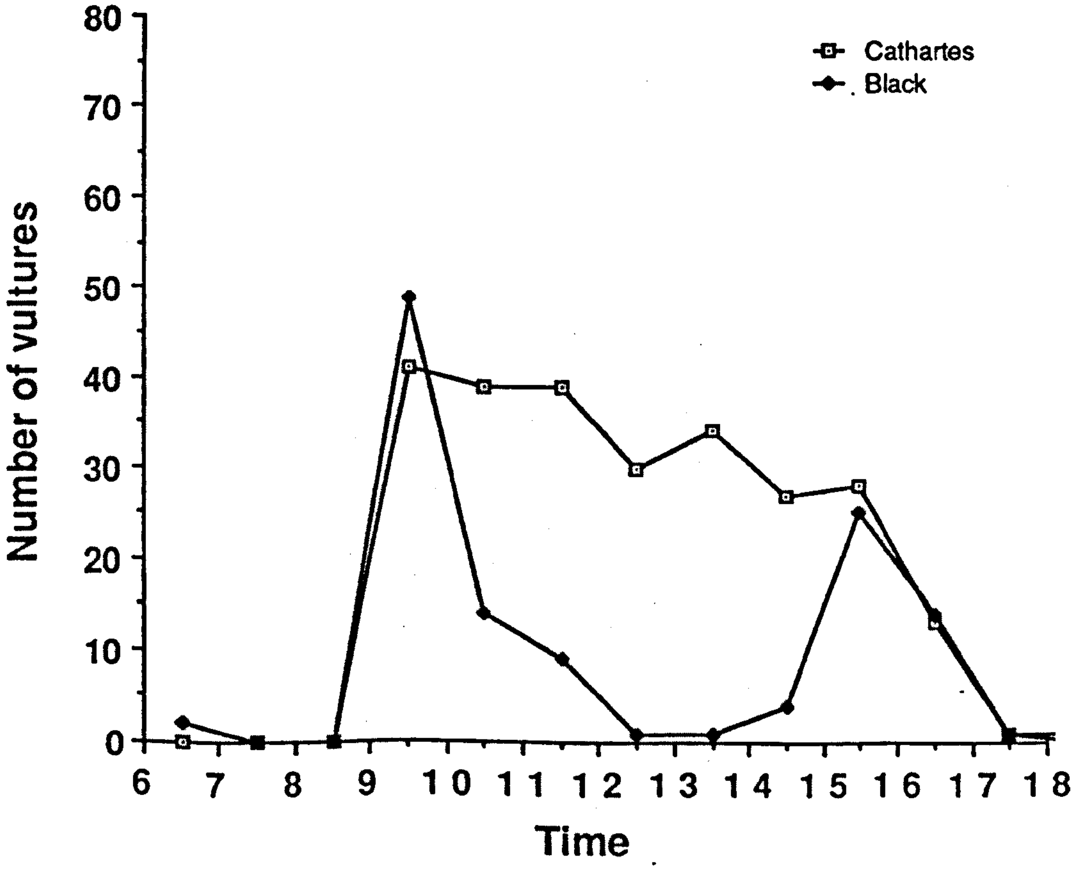


Figure 3.4 Counts of flying vultures from dawn until dusk on 22/12/86 at Caiman Pond

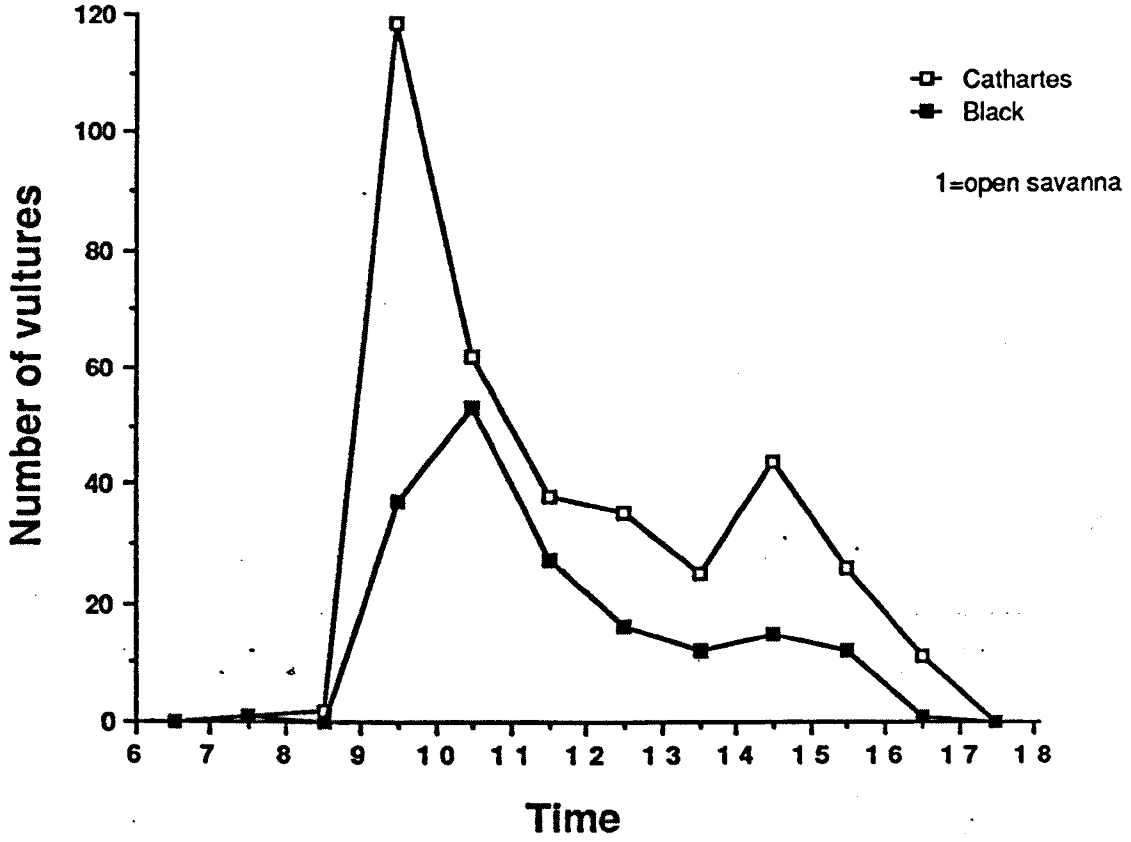


Figure 3.5 Counts of flying vultures from dawn until dusk on 22/12/86 at drainage canal

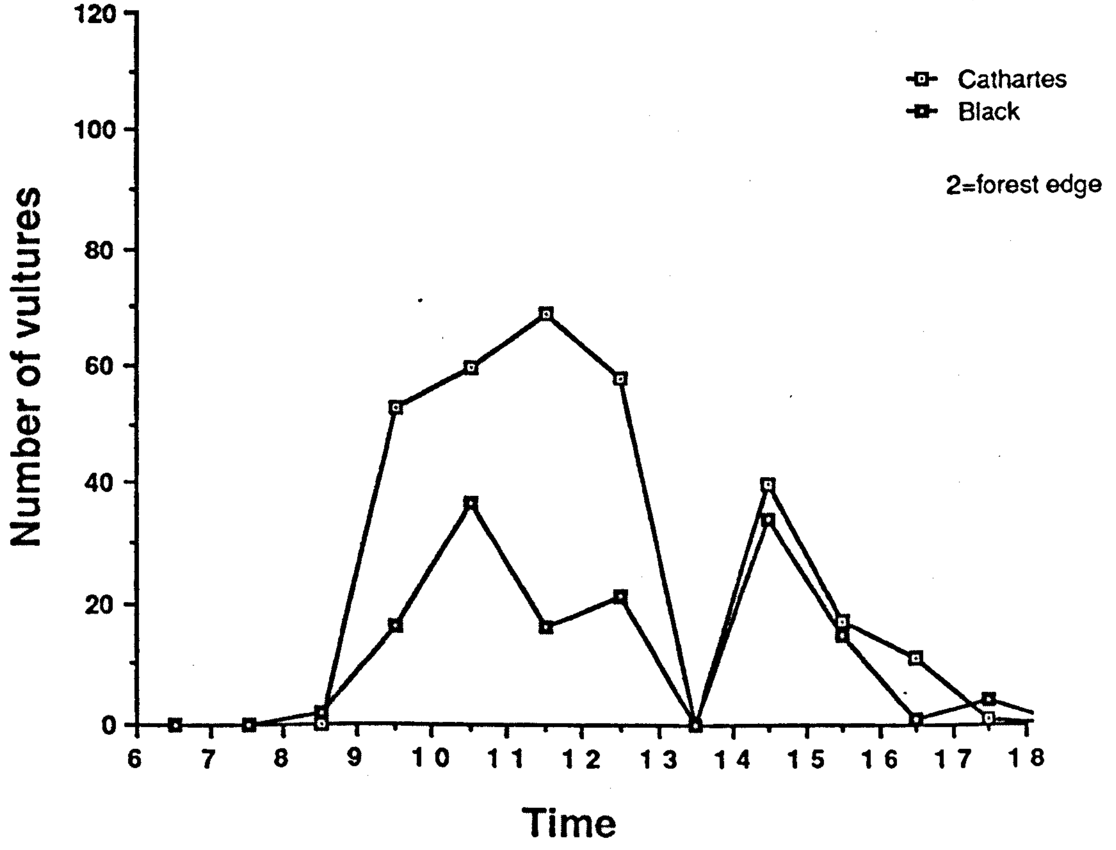
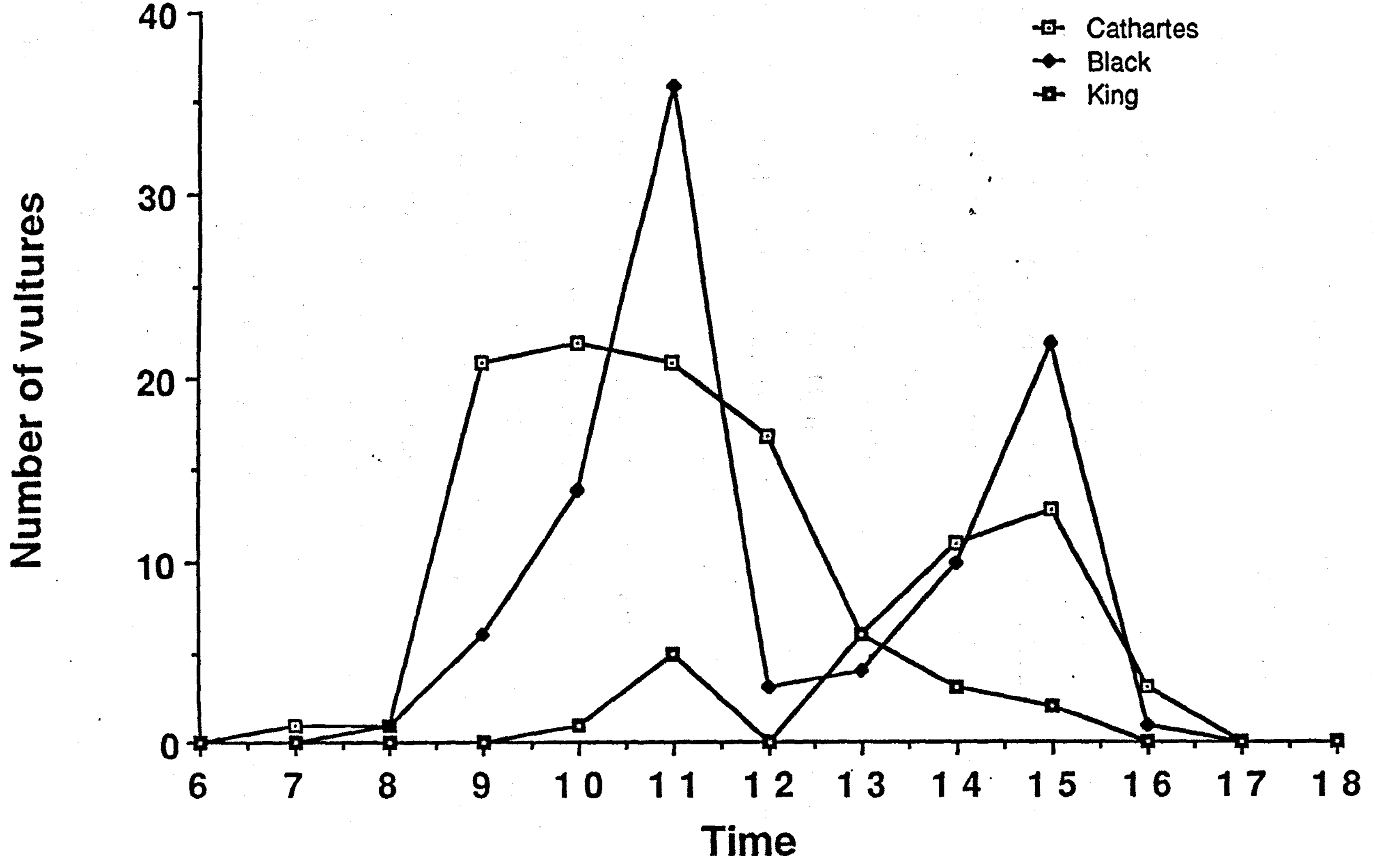


Figure 3.6 Counts of flying vultures from dawn until dusk on 29/12/86 at Cano Caracol



Annual

Only a small overlap in months occurred between census counts made in the two separate years during February. For the purposes of analysis, therefore, data were analysed together for the two years. The two-way ANOVA comparing densities in different habitat types took into account monthly variations and therefore any possible year-to-year differences.

3.3.2 Comparisons of morning and afternoon counts

Counts of vultures were significantly higher in the morning than in the afternoon when monthly variations in numbers were taken into account for both Black Vultures (two-way ANOVA $F_{8,4631} = 2.5$, $P = 0.01$) and *Cathartes* Vultures ($F_{8,13911} = 2.04$, $P < 0.05$). Morning counts were therefore used throughout the analyses because this was the period when most vultures were flying and thus likely to show any differences in density between habitats. They were also subject to less variability than afternoon counts (see Section 3.3.1)

3.3.3 Monthly variations in the number of *Cathartes* vultures

Overall, there was a significant difference between densities of *Cathartes* vultures in different months during the dry season (Table 3.3). The general pattern was for migrants to arrive in large numbers over a period of several weeks in November/December, but the reverse migration in March/April was staggered over a longer period. However, because these data were collected over two field seasons (spring migration 1986, autumn migration 1986), this might be due to annual changes in numbers of migrating vultures. Figure 3.7 shows that highest densities were counted in late November and early December. Densities of *Cathartes* Vultures remained at a level above a mean of 0.20 birds km^2 from mid-November until mid-February after which there

Table 3.3 Monthly variations in density (birds/km^2) of *Cathartes* Vultures (mean with 95% Confidence limits, N = number of arc counts, data log-transformed).

Month	mean	95% CL	N	% zero counts
1 October	0.04	0.03-0.05	720	92.8
2 November	0.16	0.13-0.20	960	80.3
3 December	0.18	0.15-0.22	1200	79.0
4 January	0.16	0.14-0.20	1200	80.0
5 February	0.13	0.11-0.15	1632	82.3
6 March	0.07	0.04-0.07	960	89.6
7 April	0.02	0.01-0.03	720	95.1
8 May	0.01	0.008-0.02	912	96.3
9 June	0.02	0.01-0.03	480	95.2

Comparison between densities of *Cathartes* Vultures in different months during the dry season (one-way ANOVA)

$F_{5,7338} = 59.1$, $P < 0.0001$
* denotes pairs of groups significantly different at $P < 0.05$ (Tukey test)

Order of increasing density during the dry season

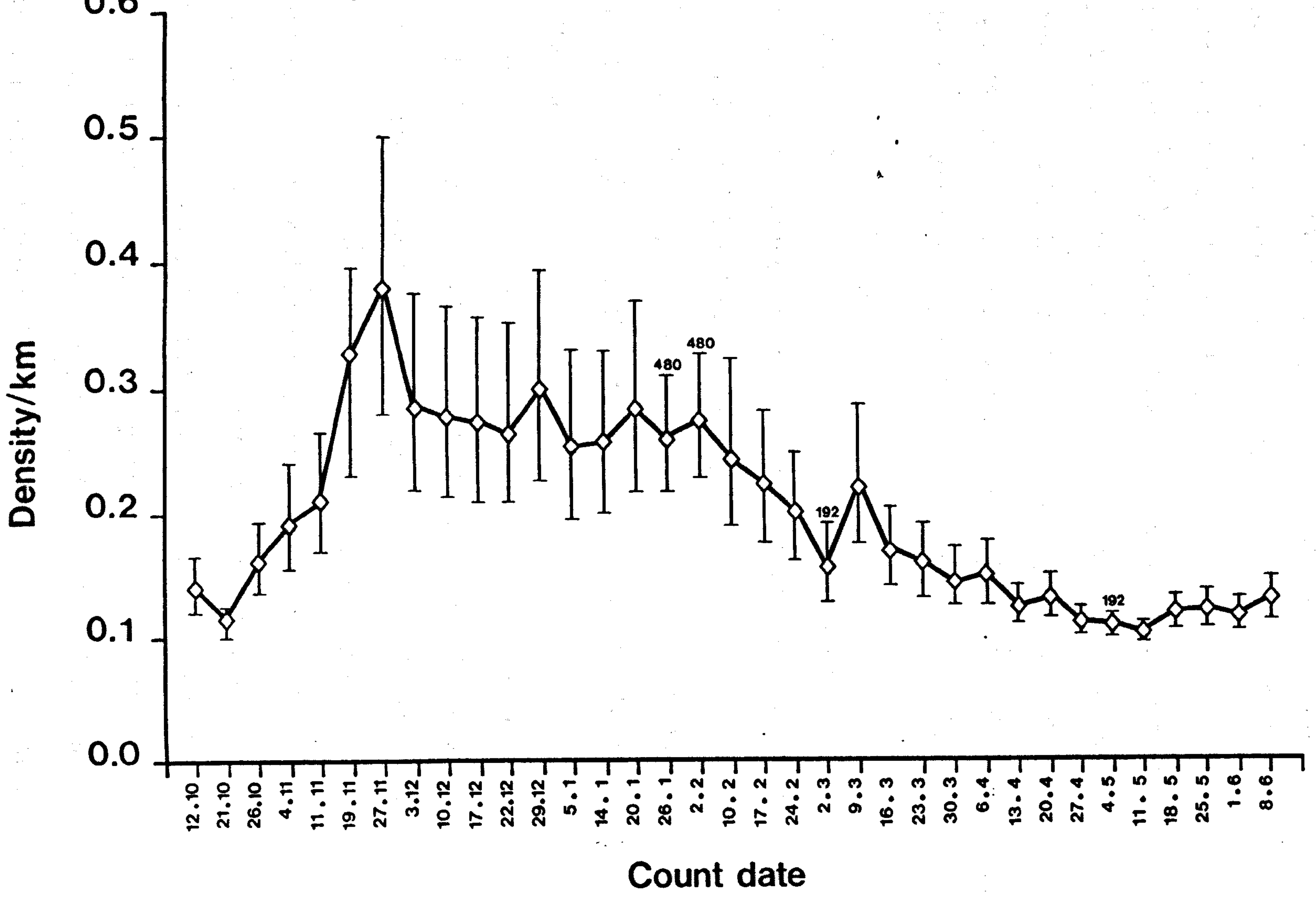
		7	6	5	2	4	3
April	7						
March	6						
February	5	*	*				
November	2	*	*				
January	4	*	*				
December	3	*	*	*			

Table 3.4 Median numbers of resident and migrant Turkey Vultures counted weekly at a roost close to the San Fernando - Calabozo highway showing wet/dry season and dry/wet season transition.

Month	Migrant Turkey	Range	N	Resident Turkey	Range	N
October	40	9-166	9	23	12-33	9
November	239	104-345	5	6	2-11	5
December	131	52-306	5	1	0-3	5
January *	166	153-195	4	-	-	4
**	85	70-124	4	-	-	4
February*	97	72-160	3	-	-	3
**	71	53-98	4	-	-	4
March	44	39-53	3	-	-	3
April	55	0-62	3	-	-	3
May	-	-	4	5	1-13	3
June	-	-	4	15	7-20	4

* 1987 ** 1986

Figure 3.7 Densities of Cathartes vultures on each count day at 5 sites (mean with 95% confidence limits, No. of arcs = 240/count day unless indicated otherwise)



was a decrease (Figure 3.7). Variability in densities between the five sites on each count day was high during the dry season, in marked contrast to the wet season (Figure 3.7). Thus, the differences in density betwen the five sites was greatest in the dry season. The departure of migrants resulted in very low densities of *Cathartes* vultures in the wet season (Figures 3.7).

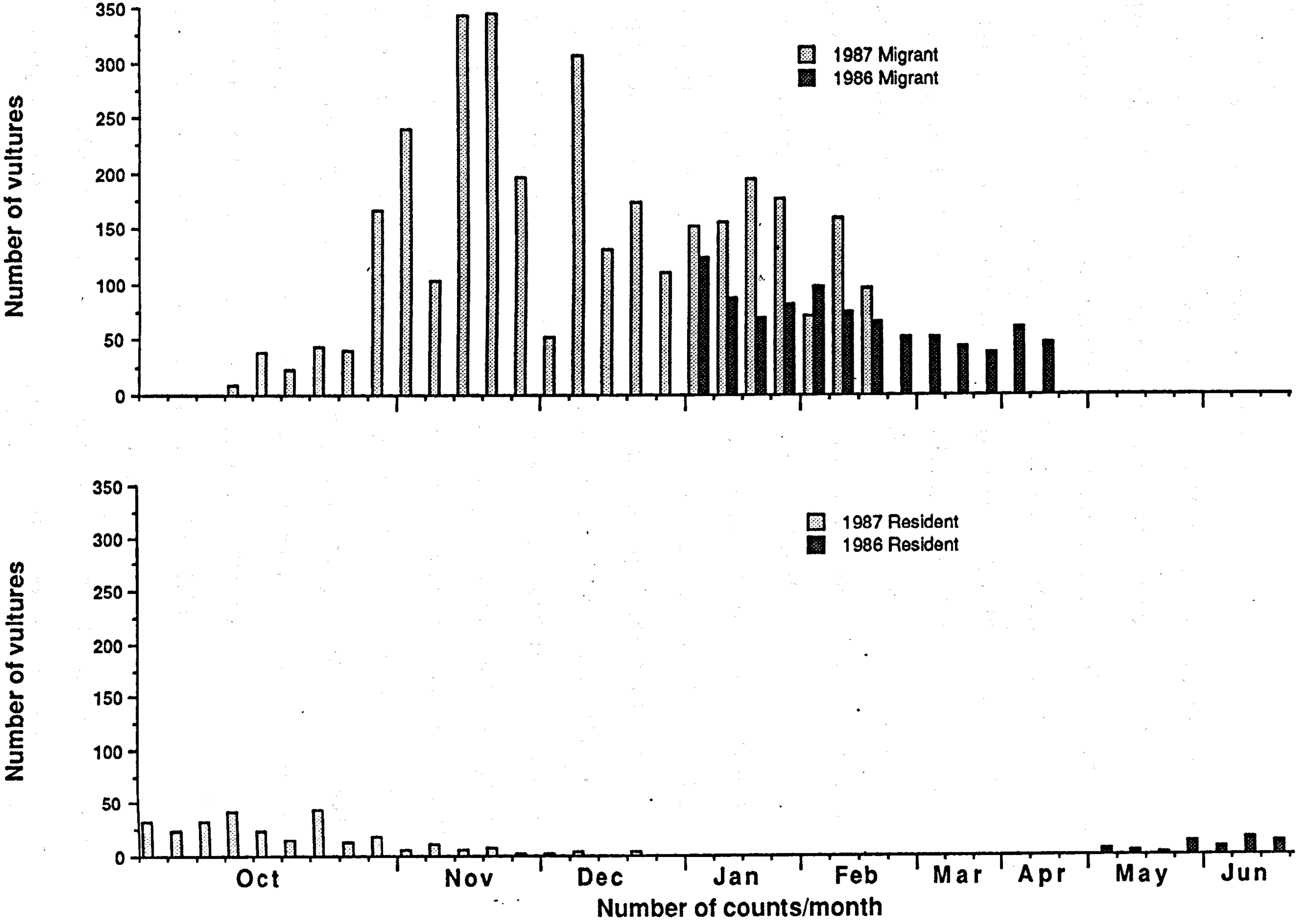
This trend was also substantiated by counts of a roost which were made weekly at a communications tower located at the north border of Masagural along the main Calabozo-San Fernando highway (Table 3.4, Figure 3.8). Roost counts were made for the months October to June in two separate years (January-June 1986 and October-February 1986/87) and show;

1) After migrants had departed (at the end of April) the numbers of resident Turkey Vultures using the highway roost increased (Median 5 in May, to 15 in June - Table 3.4, see Figure 3.8).

2) During most of October, before migrants had arrived, residents occupied the tower and surrounding dead trees in relatively large numbers (median 23 birds).

3) Although there was very little overlap there was some indication that counts of migrants were higher in 1987 than 1986 (Table 3.4). Increased use of the tower by migrants arriving in early November forced the subordinate residents to occupy lower roosts and dead trees in the vicinity. The number of residents occupying the tower roost and neighbouring trees was negatively correlated with the number of migrants ($R_S = -0.55$, $N = 15$, $P < 0.05$), when counts were compared on days when both races were present. By the end of December, no residents were roosting on or near the tower (see Table 3.4). Although a few individual resident Turkey Vultures roosted at the tower after migrants had arrived in large numbers (maximum count 345 birds in November), these birds almost certainly foraged in gallery forest

Figure 3.8 Counts of Turkey Vultures at a communications tower roost on Calabozo-San Fernando highway



nearby (over 2 km away).

3.3.5 Habitat use in the dry season

Habitat type had a significant effect on densities of Black Vultures but there were also significant differences due to the effect of monthly variations in counts (Figure 3.9). The combined effect of these two variables resulted in no significant difference in densities of Black Vultures between habitats (Figure 3.9). This was due to the large variability in counts in the different habitat types caused by locally high concentrations of vultures (see Appendix: Table 1.1. Appendix Tables 1.2 and 1.3 show densities calculated from positive counts and proportions of zero counts respectively).

However, for *Cathartes* vultures, the effect of both habitat type and month combined was significant (Figure 3.10). Thus, despite monthly variations in counts there was a significant difference in densities of *Cathartes* vultures between the three habitats. During five months (November-April) of the dry season, densities in open and semi-open habitats were significantly higher than those in gallery forest (Figure 3.10). Migrants outnumbered resident Turkey Vultures and Lesser Yellow-headed Vultures by at least 6 fold (calculated by subtracting dry from wet season densities), hence the results indicated that much higher densities of migrants foraged in open savanna habitats than gallery forest. King Vultures were seen only in the gallery forest during census counts (Table 3.5)

Results from the small area counts showed that there were striking differences between the occurrence (presence/absence data) of different *Cathartes* species/races in the three habitats. Migrant Turkey Vultures occurred significantly more often than expected in open habitats and significantly less often than expected in the gallery forest (Table 3.6). By contrast, significantly more resident data log-transformed

Comparison between densities in different habitat types for each season (two-way ANOVA)

Dry season November to April;

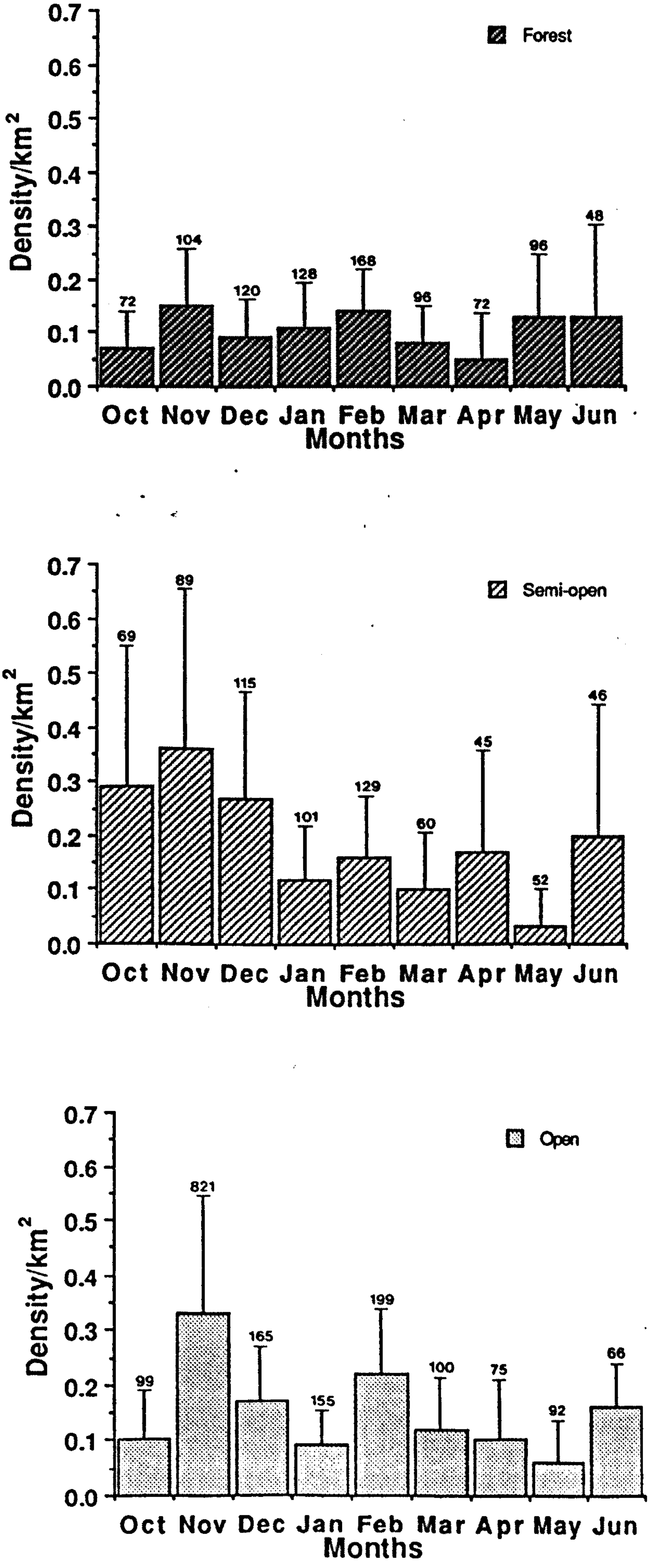
Habitat effect $F_{2,2030} = 4.99$ **
Month effect $F_5 = 4.97$ ***
Habitat x month $F_{10} = 0.89$ NS

Wet season October, May, June

Habitat effect $F_{2,631} = 1.26$ NS
Month effect $F_2 = 0.31$ NS
Habitat x month $F_4 = 3.41$ **

see Appendices Tables 1.1, 1.2, 1.3

Figure 3.9 Densities of Black Vultures in three habitats in different months (mean with 95% confidence limits)



data log-transformed

Comparison between densities in different habitat types for each season (two-way ANOVA)

Dry season November to April;

Habitat effect $F_{2,6126}$ = 29.60 $**$
Month effect F_5 = 26.65 $***$
Habitat x month F_{10} = 2.49 $**$

Wet season October, May, June

Habitat effect $F_{2,1911}$ = 5.95 $**$
Month effect F_2 = 5.83 $**$
Habitat x month F_4 = 0.64 NS

see Appendices Tables 1.4, 1.5, 1.6

Figure 3.10 Densities of Cathartes in three habitats in different months (mean with 95% confidence limits)

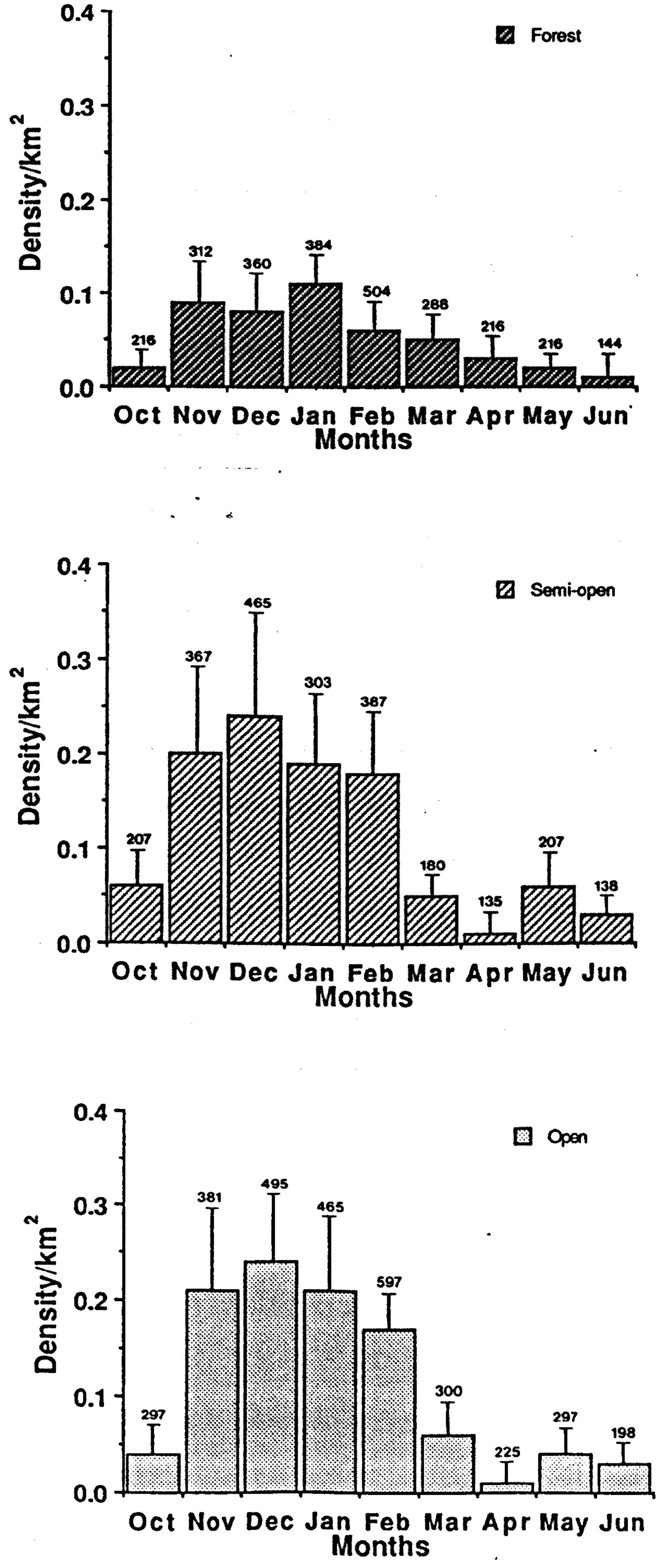


Table 3.5 Densities of vultures in different habitat types (large arcs) in dry and wet season (mean density/km^2 in each habitat with 95% Confidence limits in parenthesis, N = number of arc counts in each habitat)

			Vegetation type				
Species	Season	Forest	N	Open	N	Semi-open	N
Black Vulture	Dry	0.11 (0.08-0.14)	688	0.17 (0.13-0.21)	821	0.19 (0.15-0.25)	539
	Wet	0.11 (0.07-0.17)	216	0.09 (0.06-0.14)	257	0.16 (0.09-0.24)	167
Cathartes Vultures	Dry	0.07 (0.06-0.08)	2064	0.16 (0.14-0.21)	2463	0.15 (0.13-0.18)	1617
	Wet	0.01 (0.01-0.02)	648	0.03 (0.02-0.04)	771	0.04 (0.03-0.05)	501
King Vulture	Dry	0.02 (0.01-0.03)	688	-		-	
	Wet	0.01 (0.002-0.02)	216	-		-	

(see Appendices Tables 1.7, 1.8, 1.9, 1.10)

Comparison between dry and wet season counts in different habitats (two-way ANOVA);

Black Vultures; Habitat effect $F_{2,2661}$ = 5.36, **
Season effect F_1 = 3.60, N.S.
Habitat x Season F_2 = 1.47, N.S.

Cathartes vultures; Habitat effect $F_{2,8637}$ = 38.6, ***
Season effect F_1 = 180, ***
Habitat x Season F_2 = 3.81, *

Table 3.6 Densities of vultures in different habitat types (200m arc) in the dry season (mean densities of vultures/km^2 in each habitat with 95% Confidence limits, N = total arc counts including zero values).

Taxa	Forest (N = 200)	Vegetation type Open (N = 301)	Semi-open (N = 55)
Black	0.08 (0.04-0.13)	0.30 (0.19-0.44)	0.39 (0.13-0.88)
Migrant Turkey	0.09 (0.05-0.15)	0.62 (0.41-0.91)	0.30 (0.09-0.71)
Resident Turkey	0.08 (0.04-0.13)	-	0.04 (0.01-0.06)
Yellow-headed	0.01 (0.009-0.02)	0.02 (0.01-0.02)	0.01 (0.01-0.04)
King	0.04 (0.01-0.07)	-	-

Comparison between forest and non-forest habitats (using presence/absence data, with expected values calculated from the percentage of each habitat at the count sites, 34.6% forest, 65.4% non-forest in 200m arc).

Black Vulture $X^2 = 10.6$, df 1, ***
Migrant Turkey Vulture $X^2 = 17.2$, df 1, ***
Resident Turkey Vulture $X^2 = 25.2$, df 1, ***
Lesser Yellow-headed Vulture $X^2 = 0.76$, df 1, N.S.

(see Appendices Tables 1.11 and 1.12)

Turkey Vultures occurred in the gallery forest than expected (they were recorded on only four occasions in open or semi-open habitats - Table 3.6, Appendices Tables 1.11, 1.12). However, Table 3.6 shows that the occurrence of Lesser Yellow-headed Vultures did not differ significantly between habitats from that expected (based on the null hypothesis that counts of vultures in each habitat would be proportional to habitat area). Black Vultures occurred significantly more than expected in open habitats (Table 3.6).

3.3.6 Habitat use in the wet season

In the wet season, neither habitat or month had an effect on densities of Black Vultures but the combined effect of the two variables was significant (Figure 3.9). This indicated high variability between months and habitat densities and that the effect of these variables on density varied in parallel. Thus, there was a significant difference between densities of Black Vultures in different habitats but this difference was not consistent (no apparent selection of particular habitats).

Although the effects of habitat and month were significant separately, there was no significant difference in the combined effect of the variables on densities of *Cathartes* vultures (Figure 3.10). Thus, the monthly variations in density estimates in different habitats showed no pattern of habitat selection by *Cathartes* vultures. This was in marked contrast to findings in the dry season. Since in the wet season the *Cathartes* group was mostly comprised of resident Turkey Vultures (residents probably outnumbered Lesser Yellow-headed Vultures by approximately 2 fold) this indicated a distinct shift in use of habitats by these vultures. Sample sizes were too small in the 200m arc counts to compare densities between habitats (only 5 occurrences of resident Turkey Vultures, 3 in gallery forest, 2 in the open and 4 Lesser Yellow-headed Vultures, all in semi-open habitats). However, presence/absence data in the large area counts showed that *Cathartes* vultures occurred significantly more often in open habitats than expected ($X^2 = 5.9$, df 1, $P < 0.05$).

3.3.7 Seasonal differences in densities of vultures in different habitats

Overall, regardless of habitat type, there was no significant difference in mean densities of Black Vultures between wet and dry seasons. The combined effects of season and habitat had no significant effect on densities of Black Vultures (Table 3.5). Thus, no significant change was detected in habitat use by Black Vultures between seasons.

By contrast, the density of *Cathartes* vultures declined 6 fold in the wet season after migrants left the study area in April (Figure 3.7). Seasonal differences in density of *Cathartes* vultures were therefore very large, resulting in a highly significant effect (Table 3.5). However, the combined effects of habitat and season were also significant, indicating that, despite large seasonal changes in densities of *Cathartes* vultures, differences were significant between the three habitats (Table 3.5). Higher densities occurred in open and semi-open habitats than gallery forest (Table 3.5). This analysis did not take into account monthly variations in density counts between habitats dealt with in Section 3.3.6, which may explain why results differed. Both, however, confirmed a shift away from gallery forest areas by resident Turkey Vultures.

There was some evidence of an increase in densities of Lesser Yellow-headed Vultures in the wet season suggesting an influx of migrants. This could not be confirmed because of low counts in the small area arcs.

3.4 DISCUSSION

3.4.1 Relationship between foraging strategy and wing-loading

Old World vultures have been shown to selectively forage over areas which have more suitable conditions for soaring such as mountains (Houston 1974, 1976). Although there is little physiographic variation in the mid-Llanos of the Neotropics, there are probably considerable spatial differences in air currents related to irregularties in vegetation. The wing-loading of different vultures may preadapt them to forage over different habitat types. Resident Turkey Vultures have a lower wing-loading than migrants (Chapter 6) which may give them greater manouverability over the uneven forest canopy. In the open savannas, wind velocities may be higher, creating more suitable conditions for migrant Turkey Vultures (they could fly more efficiently due to their higher wing-loading). Lesser Yellow-headed Vultures have the lowest wing-loading of small Cathartid vultures and also forage in the open, but they do so using very low level flight (see Houston 1988), unlike migrant Turkey Vultures. This foraging strategy may enable them to feed on small items of carrion (see Chapter 6).

Conditions for flying in the wet season were much less suitable than the dry because of lack of thermal uplift and decrease in wind velocity, associated increased cloud cover and high humidity. The effects of weather conditions were probably most accentuated in Black and King Vultures which have high wing-loading (Chapter 6) and soar at high altitiudes (Fisher 1949, Houston 1988). As a result, fewer vultures may be flying at any time and by reducing count variability this could affect comparisons of vulture density between habitats in the wet season.

Decision-making by individual vultures about where to forage is a trade-off between foraging optimally in areas of highest density of food and foraging in places where there is likely to be least interference competition (see Stephens & Krebs 1987). The relative importance of these factors varies between vulture species, races or individuals depending on their ranking in inter- or intraspecific dominance hierarchies, and the extent of ecological separation by other parameters (such as the type of carcases on which vultures feed).

3.4.2 Differences in densities of vulture taxa in different habitats

There were striking differences in the use of forest, semi-open and open habitats by different vulture taxa. Lowest densities of foraging vultures were found over gallery forest and highest over more open savanna habitats. However, this general rule differed between vulture taxa, and the variability in vulture densities was high. Thus, in the dry season although overall mean densities of Black Vultures were higher in the open than in the gallery forest, the variability in densities on a week by week basis was so large that habitat differences were not significant overall. This was due to the large aggregations of Black Vultures at carcases of domestic livestock, resulting in high densities in some locations (arcs) but no birds in others.

Despite variability in weekly counts of *Cathartes* vultures due to migrants moving through the study area, there was a significant difference in densities between habitats. Based on the occurrence of different taxa in small arcs (200m) during the dry season, the approximate ratio of the different taxa comprising the *Cathartes* genus in the study area was 80% migrants, 15% resident Turkey and 5% Lesser Yellow-headed Vultures. Thus, the significantly higher densities in open and semi-open habitats can be attributed almost entirely to migrant Turkey Vultures.

Counts showed that in the dry season, resident Turkey Vultures foraged almost entirely in gallery forest or adjacent shrub woodland. Gallery forest comprised a relatively small area of count sites (34% of the small arc, 29% of large ones) and overall only 15% of the study area was gallery forest. This demonstrated strong selection by resident Turkey Vultures in the dry season. The gallery forest on Masaguaral extends along the river Guarico to the south-east and north-west (Figure 2.4) so it seems likely that resident Turkey Vultures foraged along the river during the dry season. A few individuals foraged in an area of shrub woodland or relict gallery forest at the extreme south end of the ranch (west of the highway) until November when large numbers of migrants arrived, but residents were never observed at open sites during mid-dry season (ie. December-February) censuses.

By contrast, migrant Turkey Vultures used open habitats more than expected from the proportion of open savanna at each count site. During the dry season, densities of migrant and resident Turkey Vultures in the gallery forest were not significantly different, despite the considerable differences in population sizes of the two races. This indicated that open habitats were selected by migrants in preference to gallery forest. Although sample sizes were small, Lesser Yellow-headed Vultures did not appear to show any selection between the three habitats. King Vultures were only seen in gallery forest during census counts. However, on other occasions they were often observed feeding at carcases outside the gallery forest (Chapter 5).

3.4.3 Seasonal differences in habitat usage

During the wet season when migrants were absent, there was a 6 fold reduction in density of *Cathartes* vultures from 0.12 *Cathartes* vultures/km^2 to 0.02/km^2 (mean densities of five sites, all habitats combined). This compares well with the order of magnitude of seasonal change (dry season 0.28 km^2 (SD ± 0.12), wet season 0.04/km^2 (SD ± 0.01) observed by Koester (1982). However, *Cathartes* vulture densities were probably lower in the present study because counts were made over a longer period and Koester's roadside counts (which may include biases due to the presence of carrion), were made in coastal Colombia close to where many migrants first arrived on their way south from the isthmus of Panama.

Even allowing for some possible changes in the density of *Cathartes* vultures attributable to a wet season influx of Lesser Yellow-headed Vultures (*C. burrovianus urubutinga* is a migratory race wintering in northern South America from April to October - Blake 1977, Koester 1982) results showed that resident Turkey Vultures shifted their foraging ranges outside the gallery forest in the wet season. In the late dry season and late wet season (ie. March - April and October - November respectively) only four birds were counted in semi-open habitats outside the forest. However, in the wet season *Cathartes* vultures were found in both gallery forest and savanna habitats and this is evidence for a distinct seasonal habitat shift in resident Turkey Vultures.

Sample sizes from small arc counts were too small to make statistically meaningful comparisons between relative densities of resident Turkey Vultures and Lesser Yellow-headed Vultures because of the 200m limit of their distinguishability.

3.4.4 Habitat shift in resident Turkey Vultures

The observed niche shift in resident Turkey Vultures from foraging in gallery forest sites to open sites coincided with the departure of migrants and the onset of the wet season. These data support the hypothesis that resident Turkey Vultures foraged in gallery forest to reduce competition from high densities of migrants present at the ranch in the mid-dry season. The departure of migrants in the early wet season could have produced the 'release effect' observed in residents. However, other factors (such as seasonal changes in food supply) could influence habitat shift by resident Turkey Vultures (see Chapter 4). In the wet season, canopy cover in the forest was almost complete, making it more difficult for vultures to locate carcases by olfaction, because of reduced air movements from the forest floor (Chapter 5).

The low ranking status of resident Turkey Vultures (Chapter 5) may require them to search more actively for carcases which have not been found by migrants. The chances of resident Turkey Vultures first locating carcases was highest in the gallery forest where there were low densities of migrants. The relatively low wing-loading of resident compared to migrant Turkey Vultures (Chapter 6) may enable birds to fly closer to the forest canopy and this could increase their efficiency in locating food by olfaction.

3.4.5 The effect of food supply on dispersion of foraging vultures

Vultures depend to a great extent on medium to large-sized mammal carcases (Houston 1985). Therefore, mammalian biomass and mortality rates are probably the ultimate factors affecting their food supply. Detailed work by Eisenberg *et al* (1979) has shown that there are large spatial differences in native mammalian biomass at Masaguaral because of structural variations in different vegetation types. In addition, the densities of livestock are much higher in open habitats than gallery forest, where there is little food for herbivorous grazers. Eisenberg *et al* (1979) found an ecological biomass (biomass corrected for area of suitable habitat) of 9,604 kg/km^2 (90% domestic livestock) on the west side of Masaguaral compared with 12,560 kg/km^2 (86% domestic livestock) on the east side of the highway (including the gallery forest).

The dispersion of foraging vultures is determined by the availability and density of dead animals; on Barro Colorado this has been calculated as an average of one 4.1 kg. animal dying every two days per km^2 (Houston 1985). However, the composition of the mammalian fauna is very different in the Llanos, where grazing and browsing herbivores predominate, in contrast to arboreal species at Barro Colorado (Eisenberg & Thorington 1973). While Sloths (*Bradypus infuscatus* and *Choloepus hoffmanni*) comprise most of the mammalian biomass at Barro Colorado (Montgomery & Sunquist 1973), Capybaras are the most important contributor to biomass in the Llanos (Eisenberg *et al* 1979). This has important implications for vulture populations and the habitats over which they forage.

Species with low mortality rates such as the Edentates (Sloths and Anteaters) or primates (eg. Howler Monkeys *Aloutas seniculus*) are less important for vultures with large populations (Black Vultures and migrant Turkey Vultures) than r-selected species like Capybara which have high mortality rates and extremely high productivity. Most of the browsers and grazers at Masaguaral occur in open habitats outside the gallery forest, with the exception of White-lipped Peccary *Tayassu tajacu*. In gallery forest there were few domestic livestock. In addition, native mammals which occur in the forest have far lower mortality rates and lower densities than Capybara and deer which occur in open habitats. These two factors combined result in a greater food supply for scavengers in the open habitats on the west side of the ranch.

Mammalian mortality in the Llanos is strongly seasonal. A number of long-term studies of individual species have shown an increase in mortality during the dry season when conditions are particularly severe (eg. Capybara, Ojasti 1973, 1978). In addition, carrion lasts longer in the dry season in the absence of bacterial activity associated with moisture (Cornaby 1974). However, flooding reduces the faunal carrying capacity of savannas (Eisenberg 1979) and may increase mortality in some species because of changes in behaviour (ie. vulnerability to predation - Eisenberg pers. comm.). Counts of road casualties along the Calabozo - San Fernando highway showed differences in mortality in the most common species (Possums and Caiman) between dry and wet season months (see Appendix Figure 1.1). However, overall, food is probably more abundant in the dry season. Seasonal shifts in habitat use observed in resident Turkey Vultures could therefore be related to changes in food availability at the beginning of the wet season. This, however, does not explain why vultures selected to forage in gallery forest during the dry season.

The possibility that the resident Turkey Vulture population was also composed of migratory and resident components was also considered. Apparently seasonal shifts in foraging behaviour could then be accounted for by an influx of migratory residents from elsewhere in Venezuela (gallery forest birds being resident all year). This explanation appears unlikely in view of the very low densities of *Cathartes* vultures in the gallery forest in the wet season; at least some of these birds must move into more open habitats.

3.4.6 Potential problems in assessing habitat use by vultures

There are several possible sources of error in using an estimate of vulture densities to examine habitat selection. Perhaps the largest is the affect of local enhancement (Crook 1965) due to human activities (see Chapter 4). For example, large numbers of Black Vultures frequented the ranch compound which contained garbage sites and where cattle or pigs were slaughtered. The three sites on the west side of the highway were not equidistant from ranch houses so this may have introduced some biases. Variability in the days when animals were slaughtered at the ranch could also affect counts. To reduce these errors, whenever possible counts were made on Sunday when there was least human activity. However, one of the tower sites was located close to a pig pen where food was frequently available for vultures.

Both seasonal changes in mortality of domestic livestock and the production of young could affect counts and result in large variations in density. For instance, up to 189 Black Vultures were observed at a horse carcase on one day during the dry season (Chapter 5) and usually concentrations of domestic livestock at watering places (where there was a higher likelihood of vultures finding food - eg. afterbirths, sick calves) attracted large numbers of vultures. Biases associated with human activities were largest for Black and migrant Turkey Vultures. Resident Turkey, Lesser Yellow-headed and King Vultures generally foraged away from human dwellings.

The presence of a highway and availability of road-killed animals could affect vulture density and this reflects the biases of relying on roadside transect counts used to estimate numbers of vultures (eg. Koester 1982, Santana *et al* 1983). In the present study, carcases were usually removed from the road in the early morning before counts took place. Most of the small arc counts did not include highway birds or those attracted to ranch houses. In Colombia, Koester (1982) found that resident Turkey Vultures fed at road-killed animals but this was never observed at Masaguaral. In the present study, any habitat shifts observed in resident Turkey Vultures were therefore probably unrelated to human activities.

In the case of Black and migrant Turkey Vultures, it is difficult to exclude human effects on habitat selection. The role of humans and the ecology of vulture populations is inextricably linked as shown by the dependence of Black Vultures on human garbage and refuse in the tropics (Smith in *pers. comm.* to Houston 1985) and domestic livestock in North America (Wilbur 1983). The range extension of Turkey Vultures into more northerly parts of North America may at least in part be due to the expansion of the White-tailed deer population following the clearance of large forest areas by humans (Bagg & Parker 1951).

Many flying vultures were probably not searching for undiscovered food but were attracted by the activities of other individuals (see Koester & Koester-Stowesand 1978). Thus, birds could be counted flying towards a food source where other vultures were gathering and therefore the habitat type over which they were flying bore no relation to any habitat preferences. This was especially likely in group foraging species like Black Vultures, but also when individual *Cathartes* vultures followed other birds which had already located a carcase.

During census counts birds could theoretically be counted twice, because of the way counts were conducted, but this probably resulted in small errors. Biases associated with multiple counts of the same individuals, while small, were most accentuated on the west side of the ranch where there was a high density of birds. The altitude at which vultures flew may also have affected counts. For instance, no

King Vultures were counted during censuses on the west of the highway. This may have been because birds flew at much higher altitudes over open habitats and so were not detected in counts.

In conclusion, there were marked differences in habitat use by different vulture taxa. Black and migrant Turkey Vultures foraged to a large extent close to ranch houses where they fed on dead livestock and domestic offal. The relatively high density of carrion in open savanna (compared to gallery forest) probably accounted for the high densities of the latter two species in this habitat. Resident Turkey Vultures selectively foraged in gallery forest during the period when migrants were present and it was suggested that this may have been due to the low densities of migrant competitors in this habitat.

SUMMARY

1) On five dawn-to-dusk counts of vultures, activity was highest in the morning between 0930 and 1130 hrs. On some days there was a lower peak of activity in the afternoon, generally between 1330 and 1530, although this was very variable between species and habitats. Usually, *Cathartes* Vultures were seen flying earliest in the day because they were less dependent on thermals than Black Vultures and King Vultures which flew later. Trial counts in different habitats showed that densities of *Cathartes* Vultures were significantly higher in open and semi-open habitats than gallery forest.

2) Weekly counts over the study period showed that although there were significantly higher densities of Black vultures in open and semi-open habitats overall in the dry season, week-to-week variations were so large that there were no significant difference in densities when the combined effects were considered. However, in the small area arcs significantly fewer counts of Black vultures were made in gallery forest than expected from the proportion of this habitat in the count

areas. By contrast, despite week-to-week variations in densities of *Cathartes* Vultures due to fluctuations in the numbers of migrants in the study area, significantly higher densities occurred in open and semi-open habitats than gallery forest. More than 80% of the *Cathartes* group consisted of migrants in the dry season, suggesting that migrants foraged in open savanna where food was more abundant.

3) Analyses of the small area counts showed that in the dry season resident Turkey Vultures were seen almost entirely foraging over the gallery forest and used this area significantly more than expected. However, migrants were seen less than expected in the forest assuming a random dispersion of vultures over all habitats. King Vultures were only counted in the gallery forest and there was no significant difference in use of different habitats by Lesser Yellow-headed Vultures.

4) In the wet season there were some striking differences in habitat use. There was a 6 fold reduction in densities of *Cathartes* Vultures after all migrant Turkey Vultures had departed. No significant difference was found between densities of *Cathartes* Vultures in different habitats when weekly variations in counts were considered. However, when the combined effect of season and habitat type were considered, significantly more *Cathartes* Vultures occurred in open habitats than forest despite the dramatic decline in density due to the absence of migrants in the wet season. Thus, there was a distinct shift in habitat use by *Cathartes* Vultures (composed mostly of resident Turkey Vultures) during the wet season. In the absence of large numbers of competing migrants in semi-open and open habitats, resident Turkey Vultures foraged outside the gallery forest.

5) Resident Turkey Vultures appeared to 'fill' the niche space temporarily vacated by migrants and this suggested either that

competition occurred between the races and / or there were changes in food supply coinciding with departure of migrants. An influx of 'migratory' residents from elsewhere within Venezuela may have occurred to some extent and coincided with departure of migrants.

CHAPTER 4 RANGE BEHAVIOUR

4.1 INTRODUCTION AND AIMS

The range size of birds is highly variable and depends on species, sex, social status of individuals as well as habitat quality, food supply and ecological requirements at different times of year. To measure dispersion and range behaviour it is essential to mark and track individual birds (Newton 1979). Thus, by wing-tagging a large number of birds, Village (1982) was able to measure home range size of Kestrels *Falco tinnunculus* and relate range size to changes in prey abundance, breeding and intraspecific competition. An extension of marking birds is the use of radiotelemetry and this has been widely used to assess sexual (Koplin 1973, Marquiss & Newton 1981, 1982) and to a lesser extent, species differences in habitat use (Fuller 1979) in addition to investigations of secretive birds such as Sparrowhawks *Accipiter nisus* or Goshawks *Accipiter gentilis* (Gray 1987, Kenward 1977, 1982) or nocturnal ones like Tawny Owls *Strix aluco* (Nilsson 1978) or Barred Owls *Strix varia* (Nicholls & Warner 1972).

The dispersion of foraging vultures over savanna habitats is partly related to food supply, which varies according to vegetation type and human-induced factors. Seasonal changes, both in food supply and density of vultures affect foraging movements. Although Cathartid vultures are not known to be territorial, probably because of the nature of their food supplies, interspecific and intraspecific competition could determine their foraging behaviour. Subordinate vultures may be forced to forage in less profitable habitats or over larger distances and this has been shown for young adult Black Vultures *Coragyps atratus* (Rabenold 1983 b, 1986).

Chapter 3 showed that during the dry season resident Turkey Vultures were only seen in gallery forest, while in the wet season they were seen in all habitats. The aim of the present chapter was to investigate aspects of range behaviour, especially those which could reduce potential competition between resident and migrant Turkey Vultures. This was achieved by;

i) examining any general patterns of seasonal change in range behaviour by marked vultures.

ii) examining the movements and habitat use of uniquely marked or radiotagged resident Turkey Vultures when migrants and residents were sympatric and the same individuals in the absence of migrants to investigate whether niche shift occurs in resident birds.

ii) individually marking migrant Turkey Vultures during the dry season to establish the stability of the population in the area.

4.2 METHODS

4.2.1 Movements of marked birds

The range behaviour of individually marked vultures was investigated by; (i) plotting the distribution of resightings and measuring the distances between consecutive sightings ('intersite distance'); (ii) calculating the distance between trapping sites and positions where vultures were subsequently resighted and (iii) calculating the total area or 'home range' used by vultures using the Maximum Convex Polygon method (Kenward 1987). A total of 382 vultures was caught and marked using yellow, numbered cattle-tags attached to the patagium as described in Chapter 2.

All subsequent sightings of individual birds were recorded together with dates of sighting, location and habitat type. Sightings were recorded; (i) on weekly transects between point count sites in different habitat types (Chapter 3) (ii) while actively searching for carcases and (iii) on days when behavioural observations were made at carcases (Chapter 5).

There were a number of potential biases in some of these techniques and for some methods coverage of the ranch was not uniform. Areas near to the ranch houses were visited most often when searching for carcases and these areas also attracted large numbers of Black Vultures because of slaughter offal and refuse, making these vultures more likely to be sighted. Another factor was visibility, which was generally good in open habitats, but very restricted in forest areas. Hence, few marked birds were sighted in forest areas during transects between census point counts or while generally searching for carcases. To assess the effects of these factors, not only were the pooled data from all three sampling methods analysed, but also from sightings made at carcases which had been placed out for behavioural observations, because these data were not subject to these two potential sources of bias.

Intersite distances were used as a measure of range behaviour for wing-tagged vultures because too few resightings were obtained to calculate home range areas for more than a few individuals. Resightings from three field seasons were nested to maximise sample sizes. Thus, resightings for one individual may have been made over a three year period, although there were a number of potential biases associated with this: (i) Range behaviour of vultures may differ year-to-year because of fluctuations in food supply (ii), changes in status due to age effects and (iii) the ecological requirements of birds may change at different times of the year. In addition, measures of range behaviour such as distance from trapping site would be affected if vultures had seasonal range shifts, thus altering the relative position of traps within the range (see Discussion). Intersite distances or distances from trapping sites were not found to be normally distributed so they were log-transformed and analysed using parametric statistics.

4.2.2 Comparison of distances moved by different species by season

The effect of seasonal changes on vulture movements was investigated by comparing the mean intersite distances moved by vultures in different seasons using data from all sampling strategies.

4.2.3 Habitats in which vultures were sighted

All vulture sightings were plotted on a habitat map of the study area to investigate seasonal and species differences in habitat use.

4.2.4 Home ranges of wing-tagged birds

Ranges were calculated using Maximum Convex Polygons (MAPs), and probability polygons of 90%, 70% and 50% (areas which contained 90%, 70% and 50% of sightings respectively) were plotted within this area using a computer program (Kenward 1987). Sample sizes were too small and resightings of individuals too infrequent to use more sophisticated range analyses.

4.2.5 Radiotelemetry study of resident Turkey Vultures

The timing of radiotelemetry work on resident Turkey Vultures was based on the departure and arrivals of migrants: (i) In late March/early April (end of the dry season) when migrants were leaving the ranch in large numbers (Chapter 3), residents were fitted with radiotransmitters to investigate changes in their range behaviour.
(ii) In late October/early November (start of the wet season) the effect of returning migrants on the range behaviour of different resident vultures was investigated.

Radiotransmitters were attached to five resident Turkey Vultures during period (i) at the end of the dry season (4.3.86, 9.3.86, two on 31.3.86 and 4.4.86) and to six different vultures in period (ii) (19.10.86, three on 20.10.86, 21.10.86 and 27.10.86). Thus, movements of residents were followed 2-6 weeks around the time that migrants departed during period (i). Radiotransmitters fitted to birds during period (ii), 2-3 weeks before migrants arrived, produced no results because of radio failure or because vultures left the area and were out of receiver range.

Radiotransmitters were tail-mounted. Vultures have long, stiff tail feathers suitable for carrying 1-3% of their body weight (Kenward pers. comm.). Tail-mounts also have the lowest impact on behaviour of subjects (Kenward 1978) and have been used successfully in several raptors (eg. Marquiss & Newton 1982, for review see Kenward 1980, 1985). Each radiotransmitter was attached dorsally to the base of the central tail feathers in the manner described in Kenward (1978), which allows tail feathers to be moulted independently. Pushing the needle through the centre of the tail shaft was considerably eased by using a very small drill to make a hole.

Initially radiotransmitters were fixed to the 2 central tail feathers but as Kenward (1985) pointed out these are the first to moult in many raptors, so later the second, third or all four central feathers were used to delay radio loss. (more play then had to be allowed in the threads so that the tail feathers could spread in flight).

The two-stage radiotransmitters used each weighed 14 grams (less than 1% of the average weight of the birds). Those attached to vultures during period (i) had a theoretical life of 3 months, those in period (ii) 8 months. In practice, most birds lost tail feathers and attached radiotransmitters well before batteries had expired. An AVM receiver (Model LA 12) was used to follow radio-tagged vultures and signals were detected using a 3-element yagi antenna.

Birds were radiotracked between 0830 and 1800 hrs (when most vultures were known to forage - see Chapter 3, Section 3.3.1). Whenever possible, observation towers (20 m high) erected for studies of the Hoatzin *Opisthocomus hoazin* (Strahl 1988) were used to increase range of reception. Windpumps were also useful to obtain better signals while tracking. Signal direction was recorded using a compass, while activity was monitored by strength or nature (alternating signals indicated that vultures were flying, steady signals that they were perched - Kenward 1987). Bearings were taken from two points close to 90° from the vulture to obtain the most accurate fix possible. Positions were then calculated using triangulation, though it was recognised there were some inaccuracies in this technique (see Springer *et al* 1979). When the time interval between bearings was greater than one hour, fixes were discarded since birds were capable of moving large distances in such a period. The foraging flight of Turkey Vultures means that they do not usually travel far within a short period of time as do Black Vultures.

During a test of radio strength it was found that a transmitter at a height of about 20m (approximately the height at which resident Turkey Vultures usually forage above the tree canopy) could be detected from at least 12 km. Thus, when vultures were soaring, signals were probably received at even greater distances. However, vultures on the ground could hardly ever be detected because of the dampening effect of vegetation. Radio-tagged birds could be detected while perched on the telecommunications tower by the highway from at least 4 km but birds roosting in trees in the gallery forest could rarely be detected even from close range, again because of signal attenuation. (Roost fixes were not used in the analysis.)

After three weeks of radiotracking during the second period (October/November), none of the birds carrying radiotransmitters could be found. Therefore a search was made for these vultures by light aircraft. To ensure adequate coverage of the area, transects were flown for 140 km to the south, from the town of Calabozo to San Fernando de Apure (see Figure 2.1). Two transects were flown at a distance of 2 km apart, one to the south and the other to the north so that at least 40 km in either direction was scanned for birds carrying radiotransmitters, on each flight path. This was repeated at a distance of 10 km to the west of the first transects.

4.2.6 Radiotelemetry analysis

To assess seasonal changes (dry - March-April, wet - May-June) in ranging behaviour of radio-tagged residents, distances between fixes (intersite distances) were compared for each season, both for individual birds (if sample size permitted) and all birds combined. Intersite distances were log-transformed, as for resighting data because they were found to have a skewed distribution (means are therefore derived means and log-transformation gave a normal distribution). Sizes of home ranges and intensity of use were investigated using a hierarchical cluster analysis (Don & Reynolls 1983) modified by R. E. Kenward, a technique which treats clusters of fixes separately and so avoids some of the problems associated with isolines not matching fix distribution in Harmonic mean contouring (Kenward 1987). To reduce errors of overestimating total range size due to outlying fixes, 90% and 50% (core range area) polygons were used.

Activity of birds was determined by whether they could or could not be detected. If birds were known to be in the study area but could not be detected they were assumed to be feeding on the ground. (This assumes that birds did not forage out of receiver range during the day and then fly back within range in a short period.)

4.2.7 Habitat use within home range

Insufficient fixes were obtained for vultures to compare seasonal habitat use by all individuals, thus a plot was made of total fixes of all individuals on a habitat map of the study area. Habitats were recorded at each fix location in the dry and wet season and the expected frequencies (assuming random use) in each habitat were derived from random coordinates (generated by a computer). To overcome the problem of small areas of habitats resulting in expected values of less than five, fixes for analyses using individual birds, vegetation types were combined into forest and non-forest categories, rather than the three categories described in Chapter 3. In the case of ranges with greater than 20 fixes, expected frequencies of fixes in each habitat were calculated as a proportion of the area of the habitat in the total range and comparisons made for individual birds.

A small percentage of fixes were located outside the study area so it was not possible to identify the habitat type at these locations. However, the 50% polygon fell within the mapped area. The distribution of fixes in different habitats for each range in proportion to habitat area was calculated using the 100% polygon for fixes within the mapped area (see later Figures 4.9-4.10).

4.3 RESULTS

4.3.1 Resightings of marked vultures

A total of 382 vultures were marked (Table 4.1). There were large differences in numbers of resightings as a percentage of birds marked between the taxa. Only 16% of marked migrant Turkey Vultures were resighted (Table 4.1) and this confirmed findings in Chapter 3 (see Section 3.33) which showed that there were large weekly variations in counts of migrants. In the early dry season (November/December, first arrival 12th October) migrants moved through the ranch in considerable

Table 4.1 Numbers of birds resighted and total numbers of resightings for each species in relation to number marked.

Species	Total marked	No of individuals resighted	% resighted of marked *	Total resights of all birds	Median sightings per individual
Black	178	74	41.6 (44.0)	406	3
Migrant TV	133	21	15.8 (16.2)	88	3
Resident TV	67	24	35.8	73	2
Yellow-headed	4	1	25.0	26	
Total	382	120		593	

*correction for tag loss

Comparison between the proportions of vultures resighted between taxa.

MTV vs BV X^2 = 23.85, 1 df, ***
MTV vs RTV X^2 = 10.25, 1 df, **
RTV vs BV X^2 = 0.45 1 df, N.S.

MTV = migrant Turkey Vulture RTV = resident Turkey Vulture
BV = Black Vulture

Table 4.2 The number of resightings of individual marked birds

Species	1-4	5-10	11-15	>15	Range
Black	47	9	13	5	1-21
Migrant TV	15	5	-	1	1-26
Resident TV	18	6	-	-	1-10

numbers, heading north again in the late dry season (March/April, last sighting 19th April) - this accounts for the low resighting rate. Table 4.1 shows that there was a significant difference between the proportions of resightings obtained for different species; significantly more Black and resident Turkey Vultures were resighted than migrants. However, there was no significant difference between the proportions of resighted Black and resident Turkey Vultures (Table 4.1).

Table 4.2 shows that numbers of resightings for individual marked vultures were low, particularly in the case of migrant and resident Turkey Vultures. Three migrant Turkey Vulture individuals were resighted in different years in the same localities.

A small number of birds (8) which were tagged in both wings were known to lose darvic tags. At the beginning of the study, 21 Black and 16 Turkey Vultures were marked with only one wing-tag, so that tag loss must be assumed to be 11% and 8% respectively, since there was no way of knowing if birds had lost the tag (Table 4.1). No birds were found to be able to remove cattle-tags.

4.3.2 Movements by marked vultures

Intersite distances were highly significantly different between taxa in the dry season period (oneway ANOVA, $F_{2,273} = 9.62$, $P < 0.001$ excluding Yellow-headed Vulture - Table 4.3) During the dry season, both Black Vultures and resident Turkey Vultures moved significantly larger intersite distances than migrant Turkey Vultures (Table 4.3). However, there was no significant difference between intersite distances of Black and resident Turkey Vultures in either the dry or wet season (Table 4.3).

Table 4.3 Intersite distance (m) moved by marked vultures in different seasons with derived means and 95% Confidence limits.

Taxa	DRY Mean intersite distance (m)	N	95% CL	WET Mean intersite distance (m)	N	95% CL
Black	1292	177	1090-1531	1747	151	1456-2096
Migrant TV	705	67	534-930	-	-	-
Resident TV	1843	32	1173-2896	2442	20	1359-4387
Yellow-headed	1694	14	971-2953	3001	11	1988-4531

Comparison between intersite distances moved by different vultures.

	Dry season	Wet season
MTV vs BV	$t_{242} = 3.72$, ***	-
MTV vs RTV	$t_{97} = 3.77$, ***	-
RTV vs BV	$t_{169} = -1.23$, N.S.	$t_{207} = -1.60$, N.S.

Differences in intersite distances between dry and wet seasons ('Student' t test).

Black Vulture	$t_{326} = -2.42$, *
Resident Turkey Vulture	$t_{50} = -0.75$, N.S.
Lesser Yellow-headed Vulture	$t_{23} = -1.58$, N.S.

Table 4.4 Intersite distances (m) moved by marked vultures in both seasons on behavioural observation days only, with derived means and 95% Confidence limits.

Species	DRY Mean intersite distance (m)	N	95% CL	WET Mean intersite distance (m)	N	95% CL
Black	2039	23	1532-2714	2395	38	1688-3399
Migrant	1424	12	874-2320	-	-	-
Resident	2329	12	1494-3631	3773	9	2349-6061

4.3.3 Movements by marked vultures estimated from resightings on behavioural observation days only

On behavioural observation days, 96 marked birds were resighted at least once. Table 4.4 shows the relative numbers of each taxa seen on these days. Out of the total number of sightings for each taxa, 18.7% of Black Vulture, 17.9% of migrant Turkey Vulture, and 40.4% of resident Turkey Vulture sightings were made on behavioural observation days. There was no significant difference in the intersite distances moved by different taxa in the dry season when these sightings were treated separately ($F_{2,44} = 1.42$, $P > 0.1$ - Table 4.4).

4.3.4 Comparison of intersite distances moved by vultures using all data and behavioural observation days separately

Intersite distances were compared between sightings made on behavioural observation days and all other resightings. Table 4.5 shows that the former were generally significantly larger except for resident Turkey Vultures. Thus, sample strategies excluding behavioural observation days may underestimate movements of vultures. However, the absence of significant differences between taxa is almost certainly due to small sample sizes; relatively few vultures were resighted on behavioural observation days, except in the case of resident Turkey Vultures.

4.3.5 Seasonal changes in movements

In Black Vultures, intersite distances were significantly different between seasons, birds moving much larger distances between sightings in the wet season (Table 4.3). Distances moved by Black Vultures from trapping sites were also greater in the wet season than the dry season (Table 4.3). No seasonal difference was found between mean intersite distances in resident Turkey Vultures (Table 4.3),

Table 4.5 Comparison of mean distances (m) moved by vultures using all data (A) and behavioural observation days only (B). (t = 'Student' t test).

Taxa	A			B					
	Mean	95% CL	N	Mean	95% CL	N	t	df	P
Dry season									
Black	1207	(998-1459)	154	2039	(1531-2714)	23	2.09	175	*
Migrant TV	604	(444-822)	55	1424	(874-2319)	12	2.45	65	*
Resident TV	1601	(816-3142)	20	2329	(1494-3631)	12	0.80	30	N.S
Wet season									
Black	1571	(1273-1938)	113	2395	(1688-3399)	38	2.03	149	*
Resident TV	1710	(652-4483)	11	3773	(2349-6061)	9	1.37	18	N.S

Table 4.6 Mean distances (m) moved by vultures from trap sites in different species, with 95% Confidence limits

Species	DRY			WET		
	Mean distance from trap site	95% CL	N	Mean distance from trap site	95% CL	N
Black	1725	1517-1960	217	2074	1829-2353	184
Migrant	1582	1298-1928	88	-	-	-
Resident	1792	1365-2352	52	3235	2475-3699	24
Yellow-headed	1464	1059-2024	14	1883	1262-2809	12

Comparison between distances from traps moved by vultures in different seasons

Dry season
Black Vulture $t_{399} = 2.04$, *
Resident Turkey Vulture $t_{74} = 2.68$, **
Yellow-headed Vulture $t_{24} = 0.99$, N.S.

indicating that changes in habitat use in the wet season did not affect distances between sightings. However, there was a significant difference between mean distances from trapping sites and resighting locations between dry and wet seasons (Table 4.6). In the wet season, resident Turkey Vultures moved significantly further from trapping sites than in the dry season. Migrant Turkey Vultures were not present in the wet season.

4.3.6 Home range areas of marked birds

Sample sizes were too small to compare seasonal differences in the range of different vulture species from marked individuals. When Maximum area polygon was plotted against number of fixes on which the MAP estimate was based for radio-tagged resident Turkey Vultures, the values and standard deviation increased with sample size until about 20 fixes had been obtained when MAP levelled (Figure 4.2 and 4.3). The range sizes of three vulture taxa, for individuals for which about 20 fixes were obtained are shown in Table 4.7. However, because these Maximum polygons were based only on individual birds, they cannot be used to compare between vulture taxa and any conclusions must be tentative.

4.3.7 Habitat use by marked birds

During different seasons the habitat type at sighting was compared for each vulture taxa (Table 4.8). Assuming that gallery forest covered approximately 15% of the total area at Masaguaral, the expected numbers of sightings were calculated in forest and non-forest habitat, based on the null hypothesis that if vultures showed no habitat selection, the number of sightings would be proportional to the area of habitat. Vegetation types were placed in these two categories because of the difficulty of determining areas of open and semi-open habitats in the field within the study area (due to habitat

Table 4.7 Home range polygons (ha.) for 3 vulture species

Species	Identity	Maximum area	90%	70%	50%	N
Black	N6	1470	1003	195	68	17
Black	08	2207	733	115	14	21
Migrant TV	J3	296	103	61	14	26
Yellow-headed	V1	2533	813	536	134	26

Table 4.8 Seasonal changes in proportions of sightings of vultures in different habitats; Number of sightings (expected frequency). X^2 Goodness of Fit test to compare proportions of sightings in different habitats.

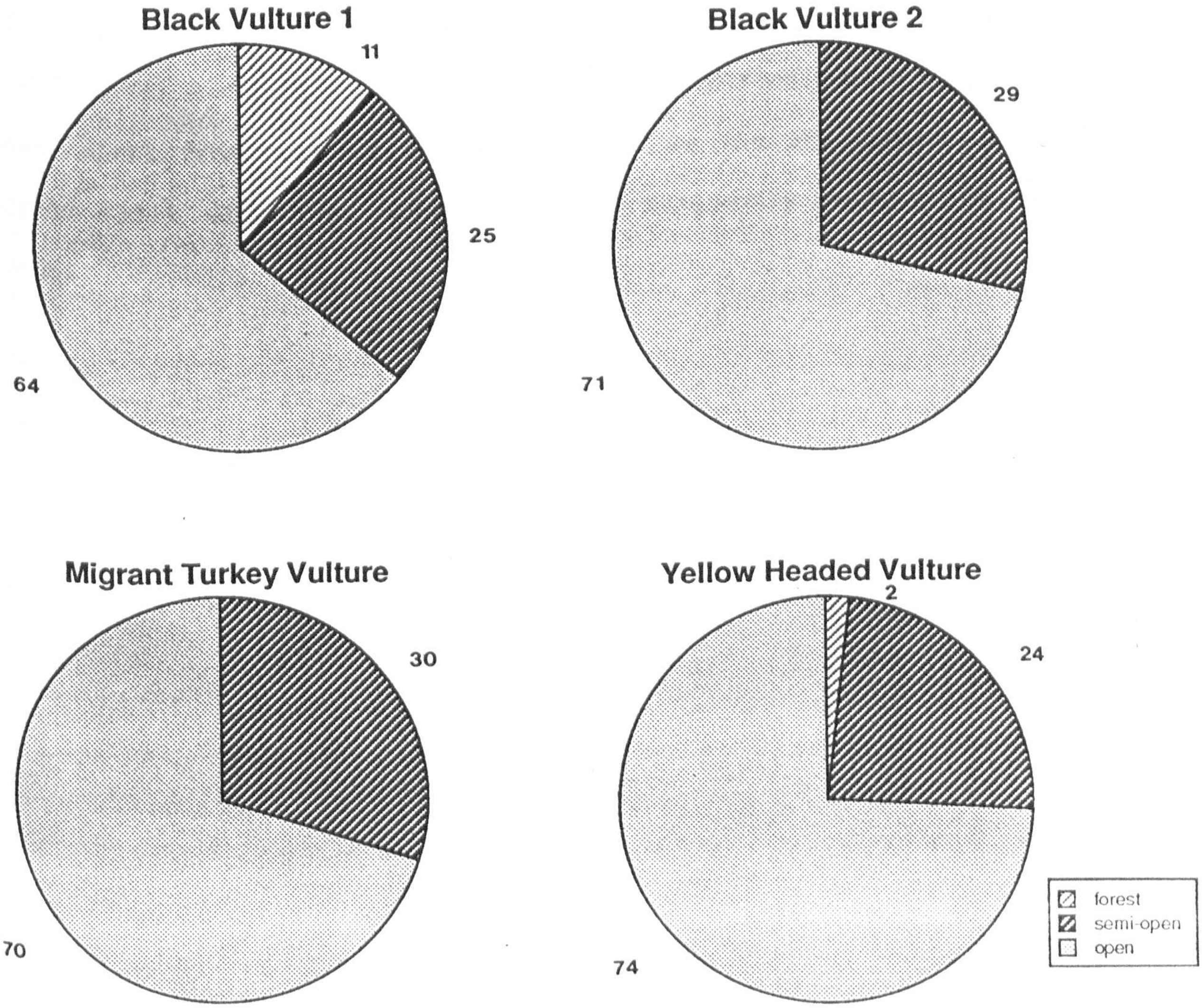
	Dry				Wet			
Taxa	Forest	Non-forest	X^2	P	Forest	Non-forest	X^2	P
Black	13 (31)	194 (155)	20.3	***	4 (27)	178 (137)	31.9	***
Migrant TV	7 (13)	81 (66)	6.2	*	-	-	-	
Resident TV	33 (8)	19 (39)	88.4	***	8 (4)	17 (19)	4.2	*

patchiness) and the fact that the possible shift which occurs in resident Turkey Vultures is from gallery forest to savanna. Table 4.8 shows that, in the dry season there were significantly more sightings of residents in gallery forest than expected. However, there were fewer Black or migrant Turkey Vultures sighted in the forest than expected and this confirmed findings elsewhere (Chapter 3, Section 3.3.5) that very low densities of both these species occur in the gallery forest. Differences in the proportion of resightings in the two habitats for migrants and residents was highly significant (X^2 = 49.4, df 1, $P < 0.001$).

For resident Turkey Vulture sightings during the wet season the pattern was somewhat different (Table 4.8). Slightly more sightings than expected were still in gallery forest ($P < 0.05$). When the proportion of sightings in the two habitat classes were compared there was a significant difference between dry and wet season (X^2 = 6.7, df 1, $P < 0.01$), indicating a distinct seasonal change in habitat use by residents. As in the dry season, in the case of Black Vultures there were significantly fewer sightings in forest during the wet season than expected (Table 4.8).

To substantiate observations from habitat usage for all marked vultures, a more detailed analysis was carried out using marked Black, migrant Turkey and Lesser Yellow-headed Vulture for which > 17 sightings were obtained. Figure 4.1 shows the relative proportion of different habitats in the ranges of these birds. All ranges contained a low proportion of forest. The expected number of sightings in each habitat (based on the null hypothesis that the frequency of sightings in each habitat was related to its proportional area within the range) was compared with the observed distribution. For both the migrant

Figure 4.1 Percentage of different habitats in home ranges (M.A.P.S.) of wing-tagged vultures



Turkey and one Black Vulture there were significantly more fixes than expected in semi-open habitats than open ones (X^2 = 15.4, df 1, $P < 0.001$ and X^2 = 15.6, df 1, $P < 0.001$ respectively). However, for the remaining individual Black Vulture there was no significant difference in the frequency of sightings in different habitats (X^2 = 0.3, df 1, $P > 0.1$). The Lesser Yellow-headed Vulture was seen significantly more often than expected in open habitats and less so in semi-open ones (X^2 = 7.3, df 1, $P < 0.01$). These data substantiate findings in Chapter 3 that, apart from resident Turkey Vultures in the dry season, other marked small Cathartids were seen most frequently outside gallery forest.

4.4 RADIOTRACKING

During three months of radiotracking, between March and June 1986, 162 fixes were obtained from 5 resident Turkey Vultures (Table 4.9). Individuals 24 and 60 provided most dry season data, and individuals 24 and 58 most wet season data (Table 4.9). Few wet season fixes were obtained for individual 60 because its radio was dropped in early May, and a radio was not attached to individual 58 until after it began foraging in more open habitats. Neither individual 101 or 102 provided sufficient data for either season because radios were attached late in the dry season and birds moulted them early in the wet season (Table 4.9). Overall, during the three months (March to June, 1986) 25 whole days were spent radiotracking and 35 part days (less than 4 hours tracking). Often in the wet season tracking was curtailed because of rain in the late afternoon - usually then birds returned to a roost and remained inactive for the rest of the day.

Radiotracking during the second period (October-November) was not successful, probably because of radio-transmitter failure. After tracking 6 birds for 3 weeks none could be detected on the ranch, and only one vulture was found, during aerial radiotracking close to Calabozo (about 30 km. from the study area).

4.4.1 Activity of radio-tagged resident Turkey Vultures

Table 4.10 shows that during the period over which vultures were radiotracked, they spent most time flying. There were no significant seasonal differences between the relative frequencies of flying compared to non-flying activities in any individual. However there were significant differences in proportions of time spent flying in different individuals (Table 4.10).

Table 4.9 Date of radio attachment, estimated radio loss date, and number of days spent radiotracking.

Identity	Date of capture	Date of radio loss	No. of tracking days Dry	Wet
24	4.3.86	*	35	24
58	4.4.86	*	13	24
60	9.3.86	11.5.86	29	5
101	31.3.86	20.5.86	15	11
102	31.3.86	27.4.86	15	-

* Radio carried by vulture from capture date to end of field season (21st June 1986).

Table 4.10 Activity (% of individuals detected, flying and undetected, non-flying during radiotracking) of resident Turkey Vultures during wet and dry season.

Identity	DRY			WET				
	Flying	Non-flying	N	Flying	Non-flying	N	X^2	P
24	91.4	8.6	151	90.8	9.2	120	0.1	N.S
60	90.1	9.9	131	100.0	0	25	2.7	N.S
101	78.8	21.2	66	80.8	13.5	52	0.1	N.S
102	86.4	13.6	66	-	-	-		
58	70.6	29.4	68	87.6	12.4	105	1.1	N.S

Comparison between proportions of time spent flying and non-flying between individuals;

Dry season $X^2 = 21.3$, 4 df, $P < 0.01$
Wet season $X^2 = 11.9$, 4 df, $P < 0.05$

4.4.2 Preliminary examination of range data

When Maximum area polygons (MAPs) were plotted against number of fixes, the values and standard deviation increased until about 20 fixes had been obtained and then levelled off (Figures 4.2 and Figure 4.3 show separate plots for dry and wet season for two individuals in each season). The increase in range size shown in Figure 4.3 after about 25 fixes was due to expansion in range as birds began to forage outside gallery forest in the late dry season. It was therefore not possible to obtain a reliable estimate of dry season range sizes, because ranges were expanding during the period when vultures were tracked. Ranges with fewer than 20 fixes were discarded from area and habitat analyses. A small proportion of fixes occurred outside the study area (Table 4.11).

4.4.3 Range sizes of three resident Turkey Vultures during dry and wet season in three months of radiotracking

Range sizes were calculated using a multinuclear cluster analysis technique (Don & Reynolls 1983, Kenward 1987). There was great variability in range size. Table 4.12 shows the polygon areas for individual resident Turkey Vultures in the dry and wet season. Despite small sample sizes, a comparison of range behaviour in different seasons was undertaken.

4.4.4 Comparison of seasonal movements by radiotagged resident Turkey Vultures.

Overall, there was no significant difference between distances moved in different seasons when data were combined for all individuals, either from fixes within the study area (Table 4.13) or for all fixes (Table 4.14), including those outside the ranch. Even when individuals for which small sample sizes were obtained (less than

Figure 4.2 Relationship between number of fixes and area of home range of resident Turkey Vultures during the dry season (n=2 birds, mean with SD)

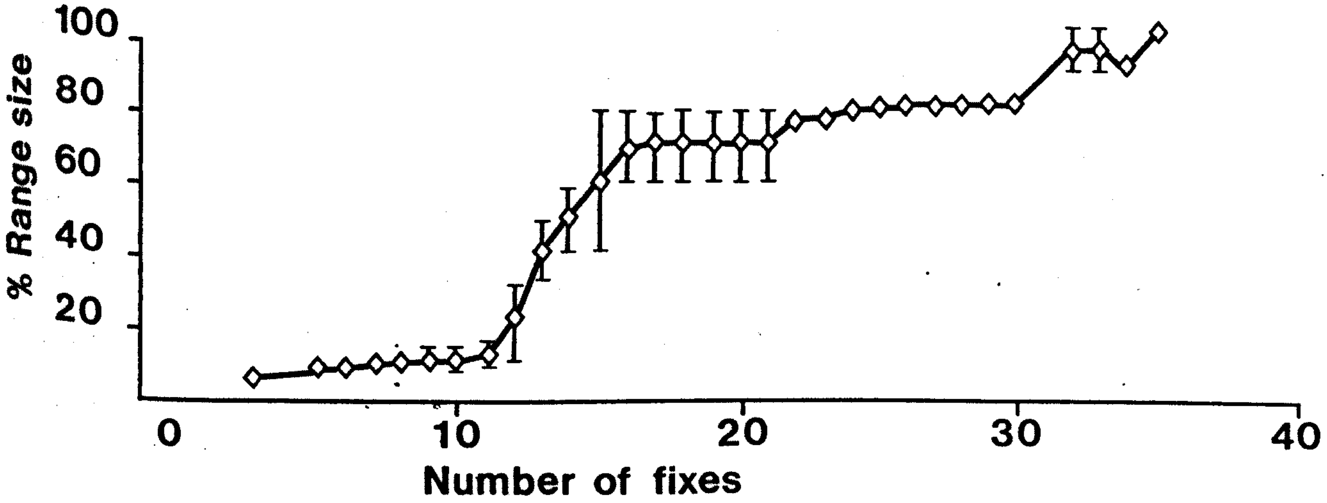


Figure 4.3 Relationship between number of fixes and area of home range of resident Turkey Vultures during the wet season (n=2 birds, mean with SD)

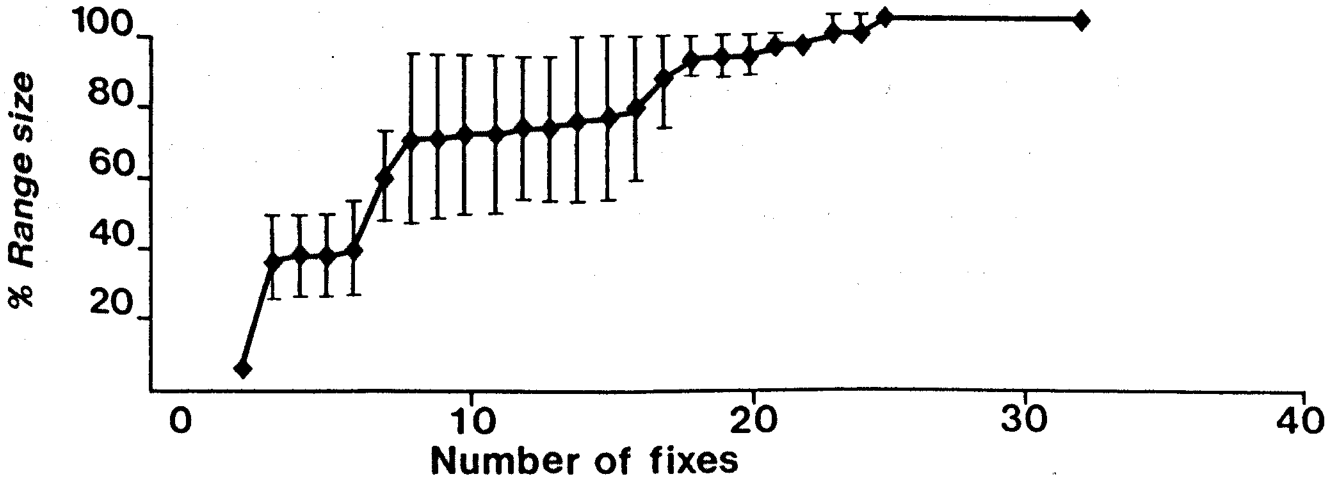


Table 4.11 Numbers of fixes obtained in dry and wet season from 5 resident Turkey Vultures showing percentage inside and outside study area.

Identity	DRY			WET		
	Inside	Outside	%	Inside	Outside	%
24	32	2	0.6	29	6	17.1
58	10	1	10.0	26	1	3.8
60	28	8	22.2	5	2	28.6
101	11	1	8.3	10	2	20.0
102	11	2	18.2	-	-	-
Total	92	14	15.2	70	11	15.7

Table 4.12 Range size (ha.) using fixes for each season in three resident Turkey Vultures (% of total range).

Identity		Maximum area	90%	70%	50%	N
24	Dry	4314 (100)	2326 (53.9)	518 (12.0)	86 (2.0)	34
	Wet	6736 (100)	3498 (51.9)	1574 (23.4)	296 (4.4)	33
58	Wet	2243 (100)	1380 (61.5)	124 (5.5)	51 (2.3)	29
60	Dry	2294 (100)	1160 (26.0)	286 (6.4)	141 (3.2)	36

10 fixes in each season) were discarded there was no significant seasonal difference in movements. Combined data from all birds supported the findings from sightings of marked resident Turkey Vultures that there was no significant seasonal difference in movements.

There was a significant difference between seasons in intersite distances of individual 24, when fixes outside the ranch were included (Table 4.14). This was probably due to exploratory forays outside the usual range of this bird in the late dry season after migrants had departed. For individual 24 there was an increase in distances between fixes during a transition period when the bird was shifting its range and subsequent wet season movements when range size had approximately stablised.

4.4.5 Seasonal changes in habitat use by resident Turkey Vultures

Results of plotting fixes from all radiotagged individuals (Figures 4.4 and 4.5) showed clear seasonal habitat differences. In the dry season (Figure 4.4), significantly more fixes were located in the gallery forest area than in open or semi-open habitats (X^2 = 31.8, df 2, $P < 0.001$) based on the null hypothesis that the numbers of fixes in each habitat was proportional to the area available on the ranch to the vultures. By contrast, in the wet season (Figure 4.5) significantly more fixes were located in semi-open habitats and significantly fewer than expected in gallery forest (X^2 = 20.68, df 2, $P < 0.001$). Thus, in the wet season, radiotagged resident Turkey Vultures foraged outside the gallery forest but preferred semi-open to open habitats.

Table 4.13 Mean (derived) distances (m) moved within study area between fixes in Confidence limits).

Identity	Dry Distance		N	Wet Distance		N
24	1746	(1312-2323)	31	2263	(1763-2905)	28
58	2819	(1884-4219)	9	1879	(1280-2759)	27
60	1397	(1046-1867)	27	4226	-	4
101	1818	(716-4614)	8	1421	(367-5501)	7
102	1331	(475-3729)	10	-	-	
Combined intersite distances	1654	(1341-2038)	84	2073	(1735-2632)	66

Comparison of combined intersite distances between seasons t = 1.43, ,df 148, N.S.
Individual No 24 t = 1.35, df 57, N.S.

Table 4.14 Mean intersite distances (m) of resident Turkey Vultures including fixes outside main study area (95% CL).

Identity	DRY Distance		N	WET Distance		N
24	1742	(1328-2285)	35	2961	(2161-4056)	32
58	2994	(2044-4386)	10	2082	(1377-3149)	28
60	2751	(2016-3754)	34	5779	(3561-9378)	6
101	2070	(875-4896)	9	2137	(723-6313)	9
Combined intersite distances	2284	(1878-2779)	101	2633	(2053-3377)	75

Comparison of combined intersite distances between seasons t = 0.91, df 174, N.S. Individual No 24 t = 2.56, df 65, *

Figure 4.4 Plot of fixes obtained from five radio-tagged resident Turkey Vultures in different habitats during dry season

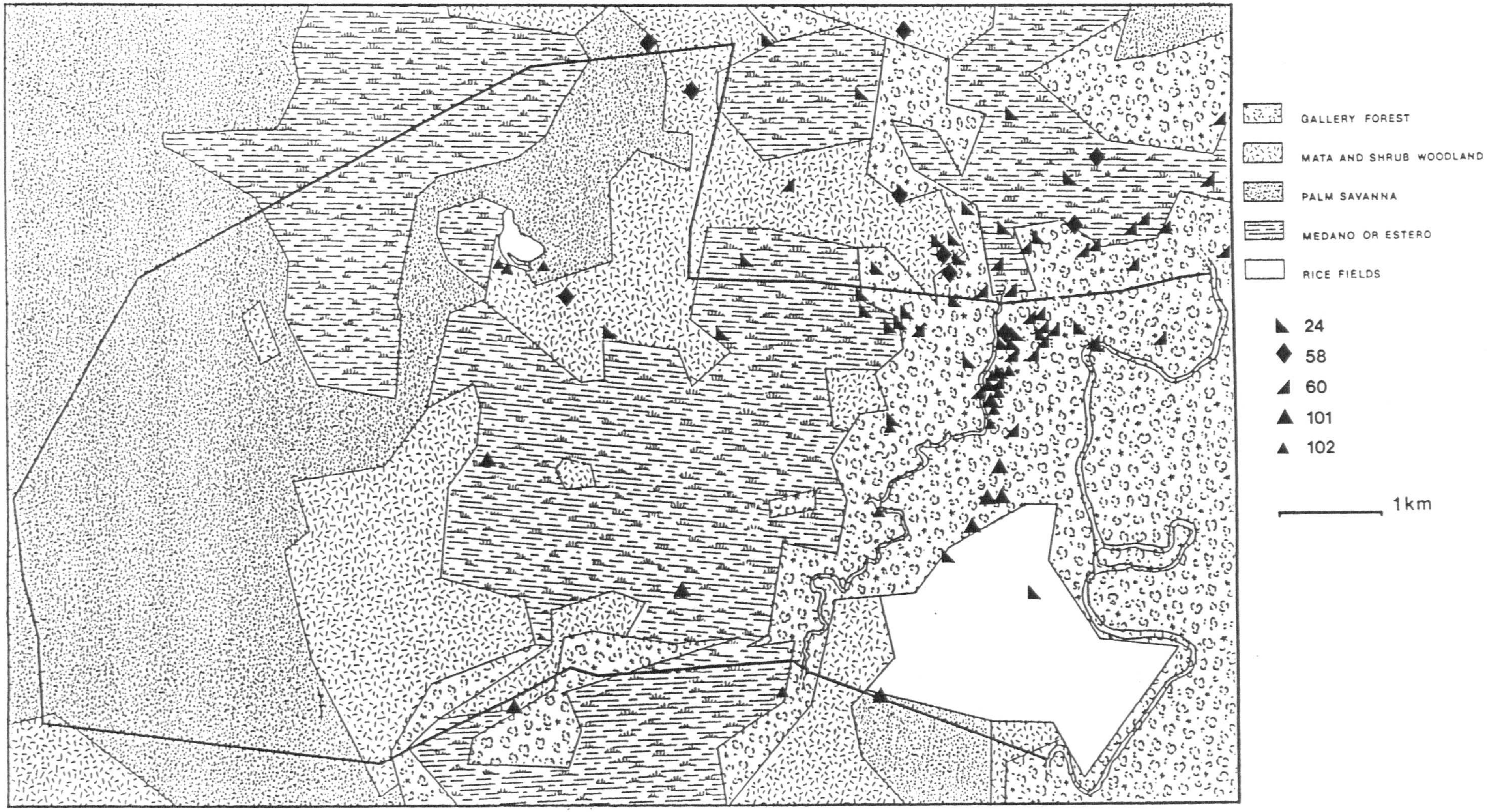
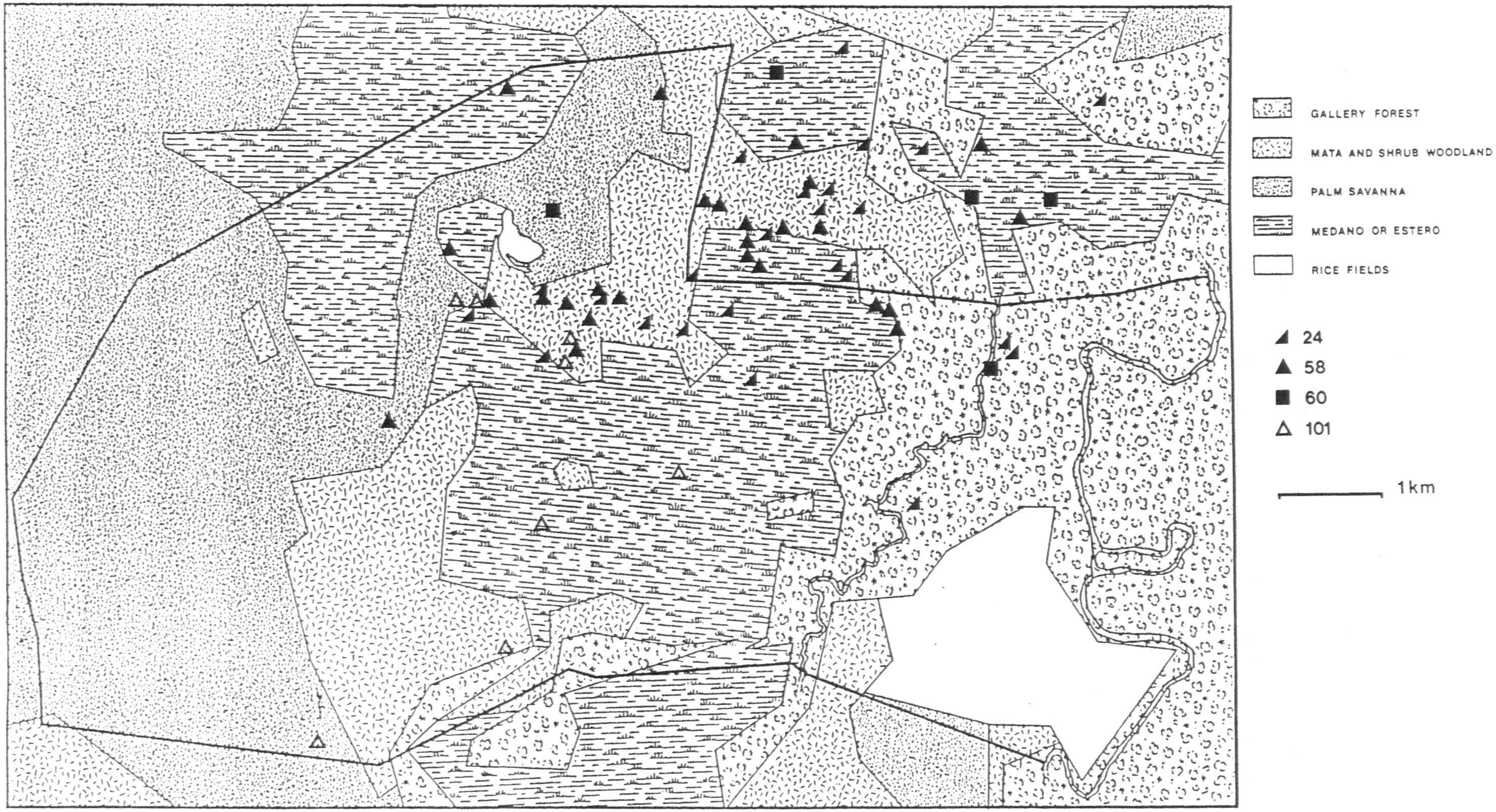


Figure 4.5 Plot of fixes obtained from four radio-tagged resident Turkey Vultures in different habitats during wet season



4.4.6 Habitat content and use within ranges

Despite small sample sizes some obvious trends are apparent in habitat usage by vultures. For four ranges (for individuals for which more than 20 fixes were obtained - two birds in the dry and two in the wet season) 50 % probability polygons were plotted, including fixes outside the mapped area. Habitat analyses of these areas were more likely to accurately reveal seasonal changes in foraging behaviour, because they were based on the core range of vultures. In the dry season, gallery forest contributed a much higher percentage of the core range (50% polygon) than in the wet season for all individuals (Table 4.15, Figure 4.6). During the dry season, forest comprised 76 or 83 % (individuals 24 and 60) of ranges compared with no forest and 3 % (individuals 24 and 58 respectively) of wet season ranges (Figure 4.6). In the case of individual 24, semi-open habitats increase as a component of range from 6% in the dry season to 85% in the wet season (Figures 4.6, 4.7 and 4.8).

The 50% polygon areas show that in the dry season activity was concentrated in the gallery forest (Figure 4.7) whereas in the wet season there was a distinct shift to open savanna habitats (Figure 4.8). Dry season ranges contained habitats other than forest (where most fixes occur - Figure 4.7) because they include forays outside the range which occur prior to birds shifting to more open habitats.

Intensity of habitat use within home ranges (100% polygons plotted within study area) by individual birds (Tables 4.16, 4.17, Figures 4.9 and 4.10) show a similar pattern. More fixes than expected were located in gallery forest in the dry season and fewer in more open habitats (eg. individual 24-see Table 4.16). However, in the wet season no significant preference for any of the habitats was shown and fixes were distributed randomly within the each individual's range (Table 4.17 Figure 4.10). Overall, when data were combined for birds,

Figure 4.6 Percentage of different habitats in core areas (50% polygons) of ranges in resident Turkey Vultures during dry and wet seasons

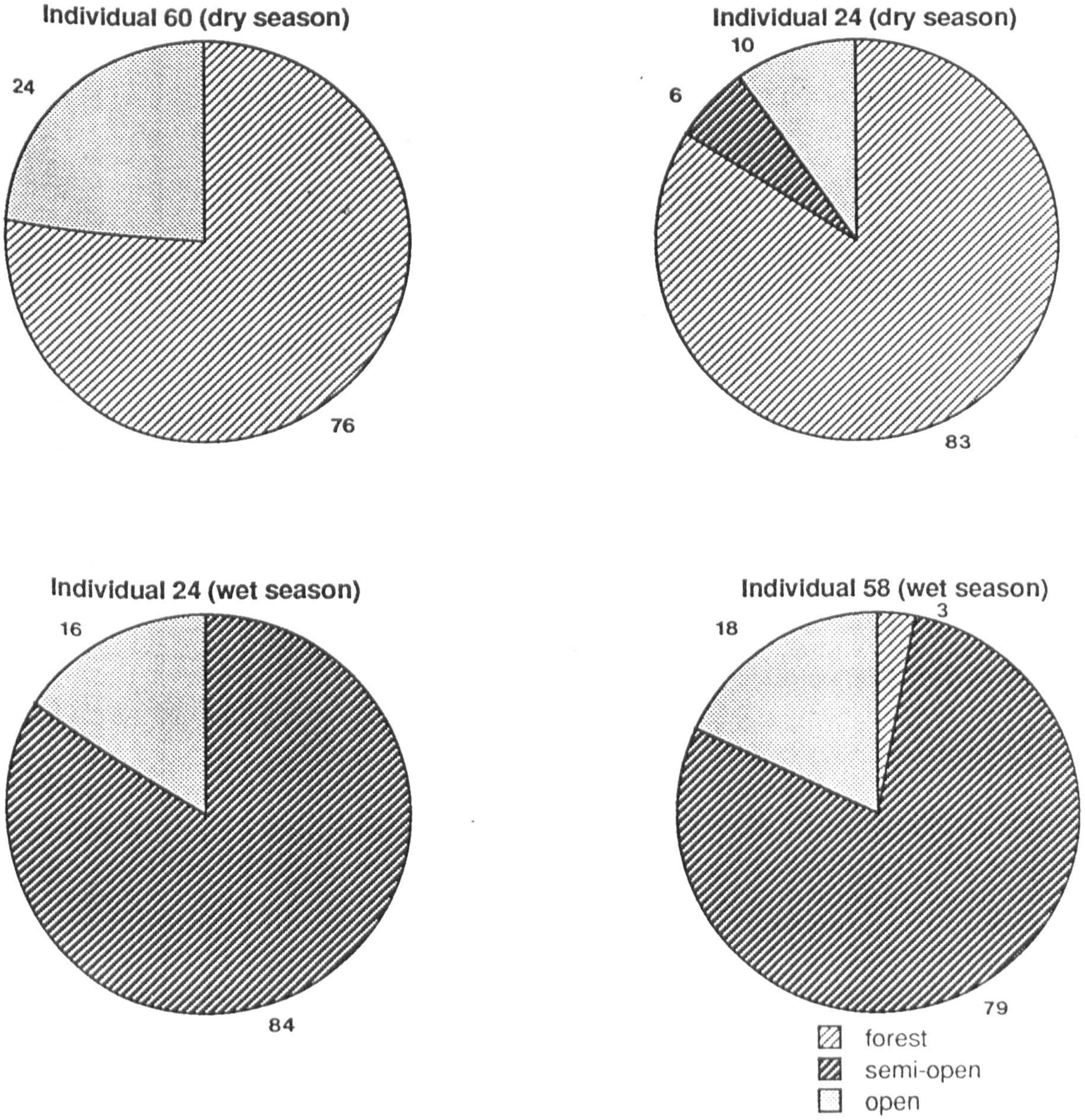


Figure 4.7 Location of core range (50% polygon) of individuals 24 and 60 during dry season in relation to forest habitat

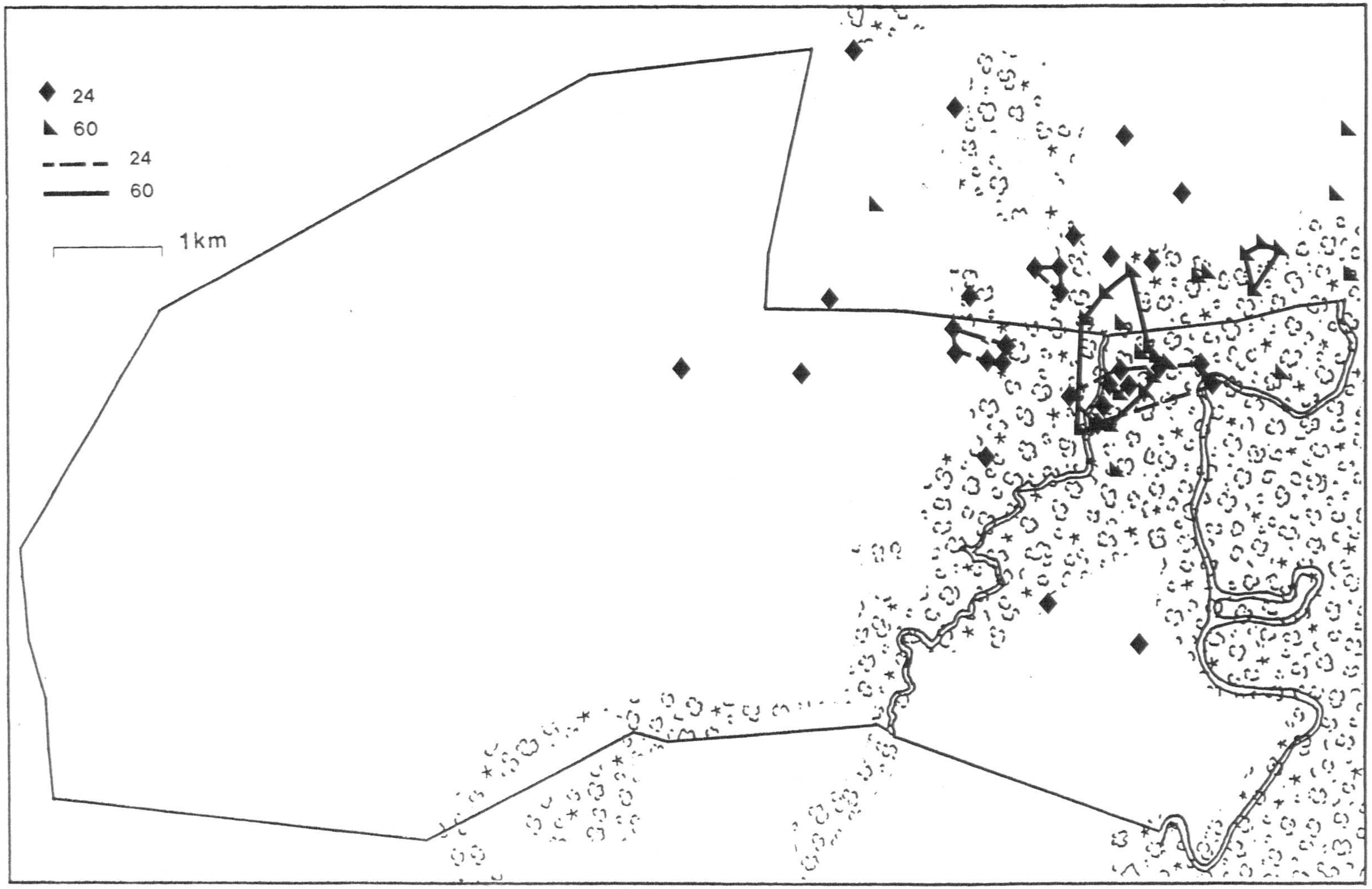


Figure 4.8 Location of core range (50% polygon) of individuals 24 and 58 during wet season in relation to forest habitat

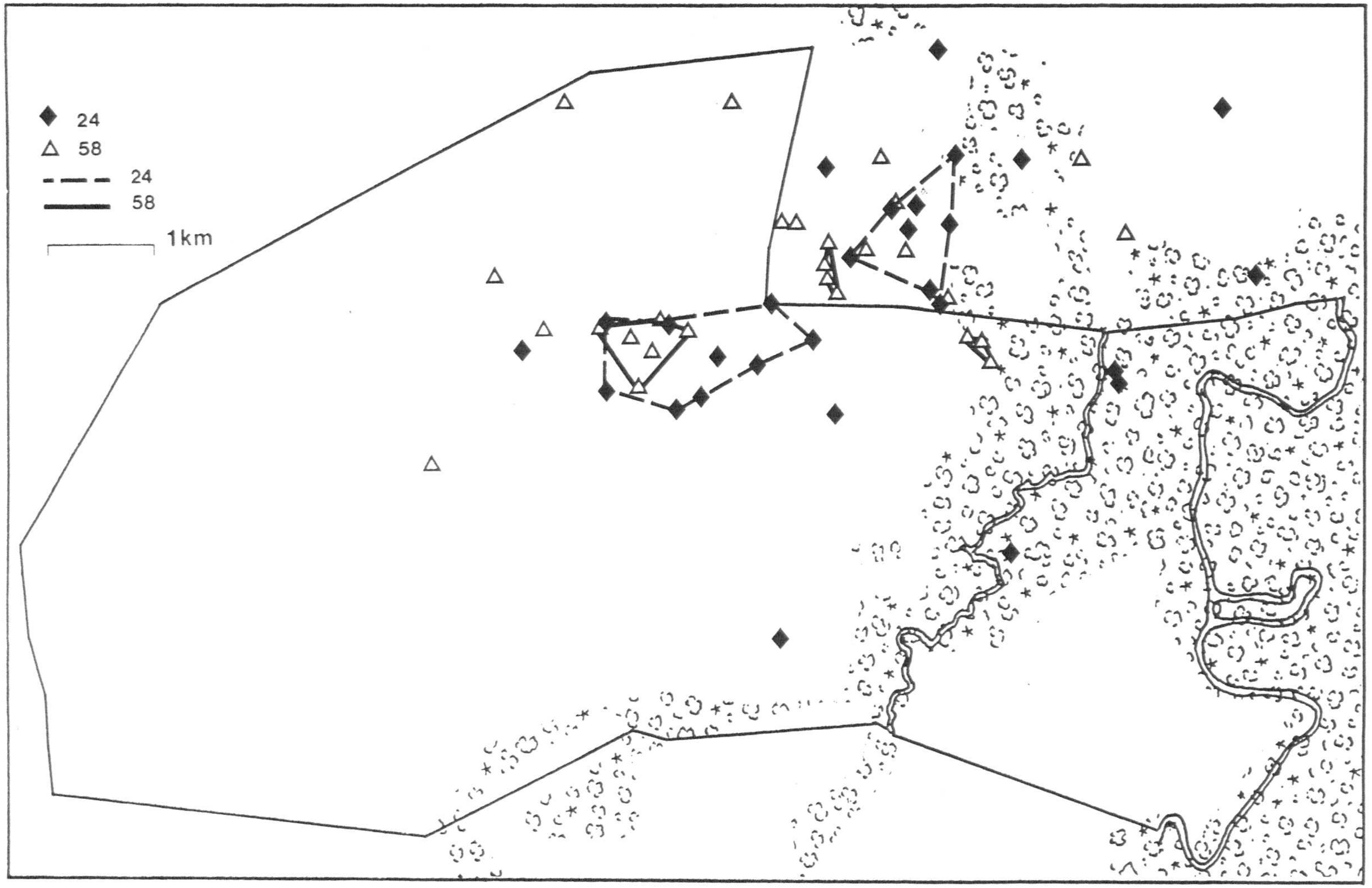


Table 4.15 Habitat content of core ranges (area in ha) during the dry and wet season (%)

Habitat	Season	Bird Identity 24		58		60	
Forest	Dry	72.2	(84.2)	-		108.7	(77.0)
	Wet	0	-	1.6	(3.0)	-	
Semi-open	Dry	5.4	(6.3)	-		0	
	Wet	250.1	(84.6)	40.4	(78.8)	-	
Open	Dry	8.9	(10.4)	-		34.0	(24.1)
	Wet	47.1	(15.9)	9.3	(18.2)	-	

Table 4.16 Observed (O) and Expected (E) numbers of fixes in gallery forest and non - forest areas in the dry season (100% polygons within study area)

Identity		Habitat type Forest	Non-forest	Chi-squared	df	N	P
24	0	18	14	3.8	1	32	**
	E	12.6	19.4				
60	0	21	7	3.9	1	28	*
	E	15.8	12.2				
Total	0	56	34	31.4	1	91	***
	E	31	60				

Table 4.17 Observed (O) and expected (E) numbers of fixes in gallery forest and non - forest areas in the wet season (100% polygons within study area)

Identity		Habitat type		Chi-squared	df	N	P
		Forest	Non-forest				
24	O	5	24	0.6	1	29	N.S.
	E	6.8	22.2				
58	O	2	24	0.3	1	26	N.S.
	E	1.4	24.6				
Total	O	9	59	11.4	1	68	**
	E	22	46				

Table 4.18 Percentage overlap using 90% polygons, between four ranges in dry and wet season (50% in parentheses)

			Overlapper			
			Dry	Wet	Wet	Dry
			24	24	58	60
Overlapped	Dry	24	-	-	23.5 (4.2)	18.0 (35.0)
	Wet	24	-	-	34.4 (15.1)	11.2 (0)
	Wet	58	40.1 (7.6)	85.3 (75.8)	-	0
	Dry	60	34.7 (21.4)	33.3 (0)	0	-

Figure 4.9 Location of 100% polygon of individuals 24 and 60 during dry season in relation to forest habitat

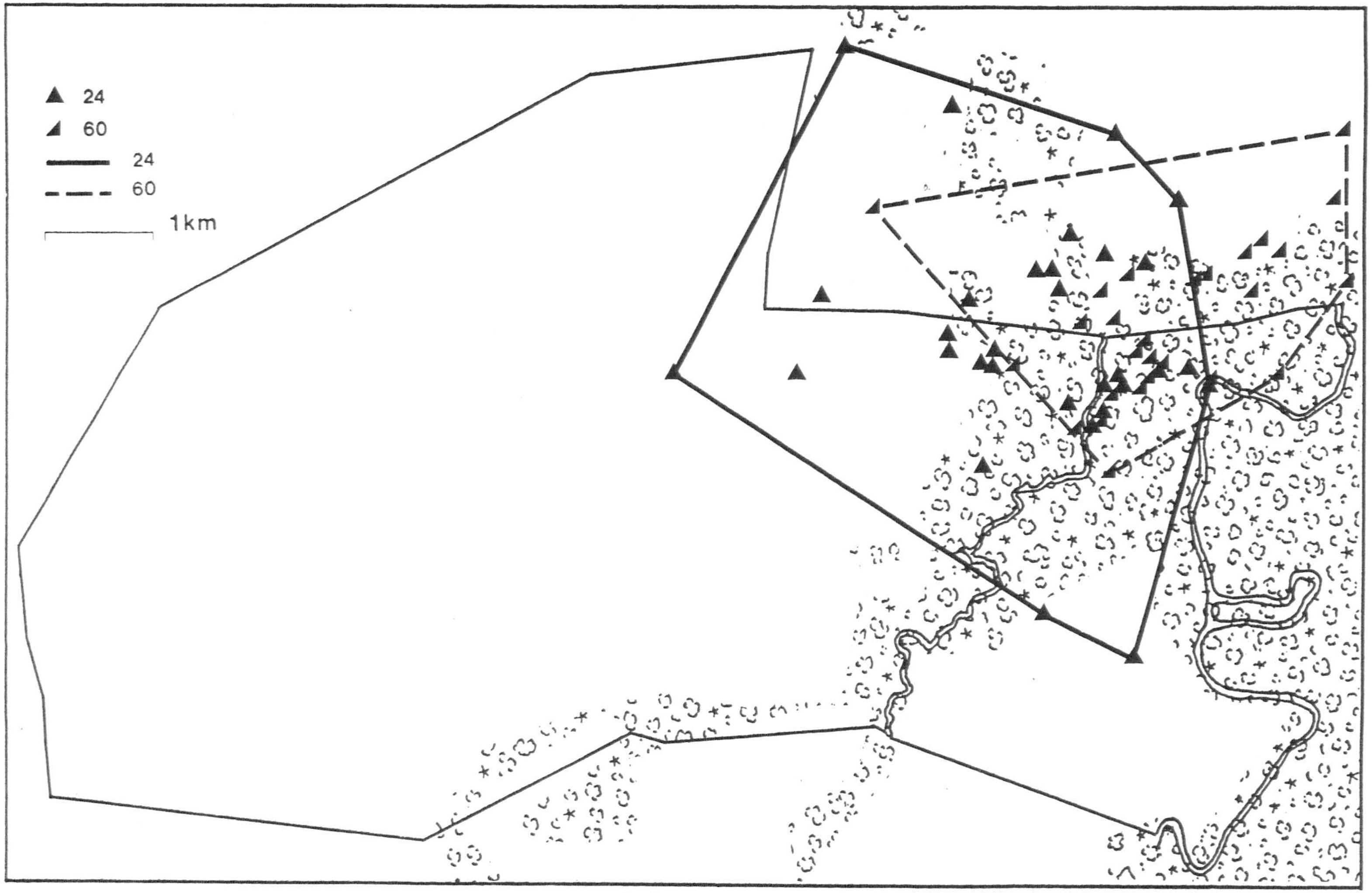
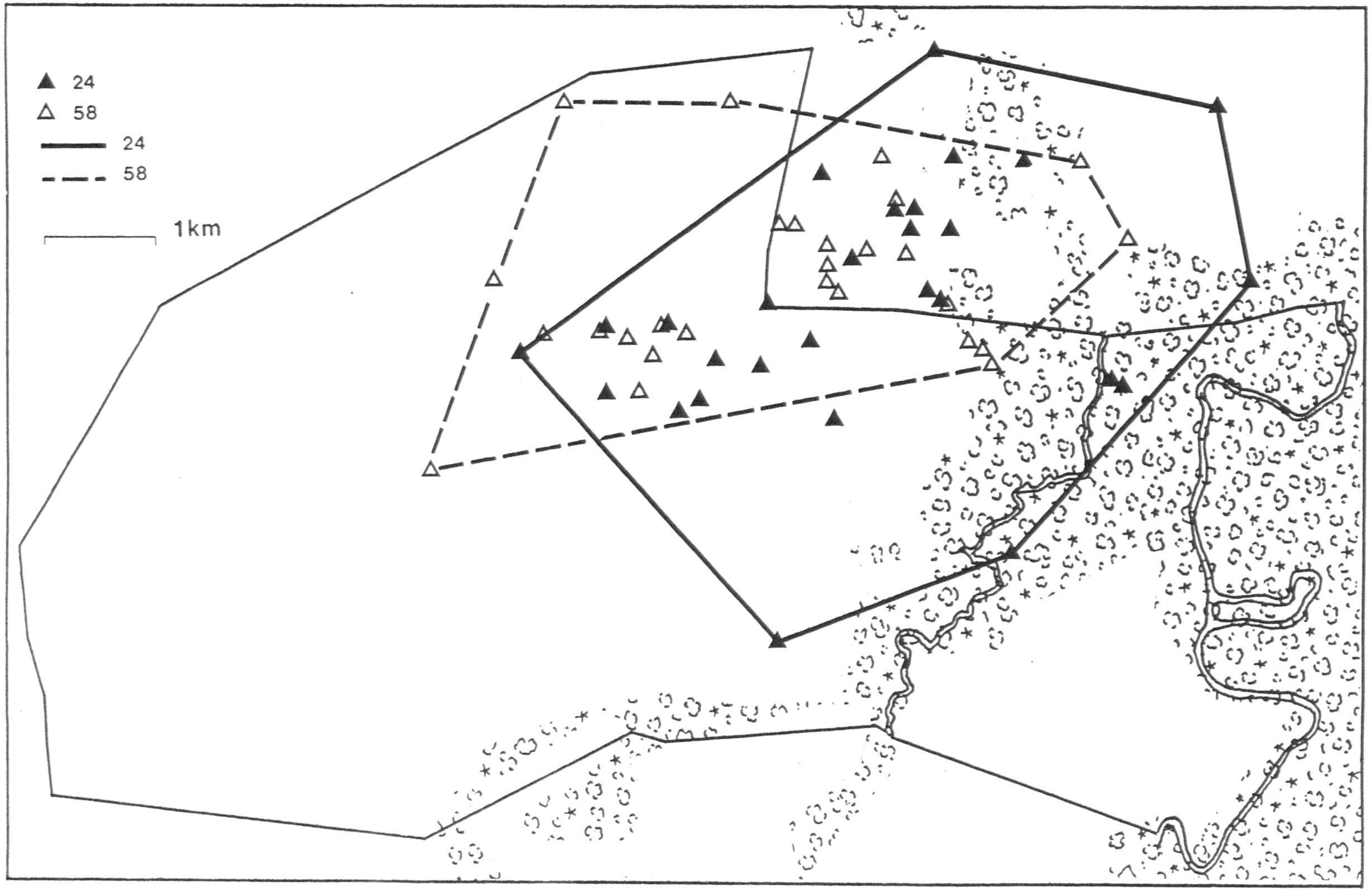


Figure 4.10 Location of 100% polygon of individuals 24 and 58 during wet season in relation to forest habitat



in the wet season fewer fixes were located in gallery forest than expected and more in open habitats (Table 4.17).

4.4.8 Seasonal overlap of ranges

The degree of overlap between ranges was assessed for the four ranges presented in Table 4.18 using 90% polygons. There was a relationship between the extent of range overlap between different individuals on a seasonal basis. Greater overlap occurred between dry season than wet season ranges indicating that in the former season the activity of birds was more concentrated in the small area of gallery forest. This trend is more marked in 50% core range overlap (Table 4.18), because this is where activity of birds is concentrated. Wet season ranges also overlapped (Figure 4.8) and these findings suggest that vultures foraged in similar areas outside the gallery forest (mainly semi-open areas).

4.5 DISCUSSION

4.5.1 Range behaviour of marked individuals

Resighting rate

The probability of sighting marked vultures was affected by many factors, including the habitat preferences of the different species and some observer bias. Marked Black Vultures feeding at large carcases were very conspicuous, and this may have influenced the frequency with which they were resighted. At least during the dry season, the majority of resident Turkey Vultures were sighted on behavioural observation days in the gallery forest, where, because of low visibility few birds were sighted using other sampling strategies.

A high resighting rate for Black Vultures was attributed to their site fidelity and close association with domestic livestock. For instance, large carcases such as horses or cows attracted Black Vultures from a wide area (up to 189 Black Vultures were counted at one carcase - Chapter 5, Table 5.23).

Some marked Black Vultures probably bred in the area and this would restrict adult's foraging movements. Although Parmalee & Parmalee (1967) showed that lifetime foraging ranges of Black Vultures in the eastern United States was 160-320 kilometres, Rabenold (1983 a, b) suggests that breeding birds concentrate their foraging movements within a radius of 20 kilometres. Of 344 Black Vultures marked by Rabenold in North Carolina, 100 were resighted at least 10 times (the maximum number of resights for one individual was 61). Rabenold's study was carried out over a longer time period and this probably accounts for the difference in numbers of resightings compared to the present study.

By contrast, few migrant Turkey Vultures were resighted as a proportion of the numbers marked. Generally, migrant Turkey Vultures were more evenly dispersed and visited smaller carcases in only small numbers (Chapter 5) so fewer marked birds were sighted in relation to observer search time than Black Vultures.

Despite the fact that a small number of birds showed high site fidelity (a number of birds returned to the same area of the ranch in different years, a phenomenon not uncommon among raptors - Newton, 1979) most wing-tagged migrant Turkey Vultures were never resighted. The majority of vultures were therefore probably part of a nomadic group, or used the ranch as a staging post on their way to more southerly destinations (*C. a. meridionalis* winters as far south as Argentina - Blake 1977). Migrant Turkey Vultures caught in late October/November or in late March/April were likely to be transient in the study area as was suggested by large weekly fluctuations in densities of birds (Chapter 3). By adopting a nomadic habit, migrants could reduce interspecific and intraspecific competition for food resources and move to areas where there was a temporary abundance of carrion. This strategy has been observed in many other migrant species (eg. those following rain belts - Sinclair 1978, Thiollay 1978). The resighting rate for resident Turkey Vultures was relatively high (36%) indicating that, compared to migrants, more birds remained in the ranch area. In the dry season, some birds may have moved to other areas of gallery forest along the river Guarico (Figure 2.4), to reduce intraspecific competition.

Age-related differences in movements may have contributed to variation in resighting rate within taxa. In Black Vultures, young adults, which have undeveloped food-finding skills and competitive ability, range over a wider area than adults and may follow successful foragers in different groups over a very large area. By contrast, breeding adults show high site fidelity and are experienced finders of food (Rabenold 1983a). Thus, the age composition of the sample of marked birds would affect resighting rate.

4.5.2 Differences between species and seasonal differences in movements

In Black Vultures, seasonal differences in movements were best explained by the lower incidence of livestock mortality in the wet season, when birds were forced to forage further away from ranch houses. However, movements of Black Vultures could also be affected in the wet season by the decline in density of *Cathartes* vultures, which they depend on to find concealed food (Koester & Koester-Stowesand 1978). A lower density of searching *Cathartes* vultures, in addition to greater leaf cover in the wet season (making carcases more difficult to find), may mean that Black Vultures must search over a wider area to locate food.

The significantly smaller intersite distances moved by migrants in comparison to resident Turkey Vultures was probably due to the fact that migrants which remained on the ranch for sufficiently long to be resighted showed high site fidelity. For itinerant vultures which did not stay in the study area for long periods, opportunistic foraging close to ranch houses may have been the best foraging strategy to adopt. Foraging in the more remote gallery forest area may have been more difficult (Chapter 6, Section 6.4.2) and migrants would perhaps be at a disadvantage to resident Turkey Vultures in this habitat.

A sampling bias related to resightings of vultures was that no account was taken of vultures which may have foraged over a much larger area outside the ranch. Although differences in movements between migrants and residents could have been due to sampling strategy (most migrants were seen on transect counts or by searching for tags at feeding sites, most residents were seen on behavioural observation days) the results fit the hypothesis that the majority of migrants were transients with the exception of a few individuals which had high site fidelity.

Residents, on the other hand, had comparatively large mean intersite distances during the dry season and, unlike migrants, avoided ranch houses, associated human activity and larger carcases. The density of carcases in the gallery forest was probably lower than elsewhere because of the lower mammalian biomass (mainly due to lower livestock and Capybara densities - Eisenberg *et al* 1979). Although there was no significant seasonal difference in mean intersite distances for resident Turkey Vultures, at the end of the dry season and during the wet season, marked individuals were seen on the west side of the highway (in open habitats) whereas in the main dry season period they were only seen on the east side, in or close to, the gallery forest. This was reflected in the ratio of birds trapped on each side of the highway; in the dry season only one resident Turkey Vulture was caught on the west side of the highway, in the wet season all birds (N=15) were trapped in open habitats. In the dry season, most residents were caught at the edge of, or inside, the gallery forest on the east side.

4.5.3 Distance from trapping sites as a measure of movement

Resident Turkey Vultures had significantly larger mean distances between their original trapping sites and resighting location in the wet than the dry season. This was because most birds in the dry season were trapped on the east side of the highway and were subsequently sighted in the adjacent gallery forest. By contrast, in the wet season, resident Turkey vultures were seen in all habitats (Chapter 3, Section 3.3.6) including those on the west side of the highway (Figure 2.4) which were much further away from the gallery forest. Black Vultures were resighted at significantly larger mean distances from where they were trapped in the wet season than the dry season. However, the fact that a large number of trapping sites (21) were used, in different parts of the ranch, means that these distances would be biased toward marked vultures which were trapped close to the ranch and frequently foraged in this area.

4.5.4 Seasonal differences in habitat use of marked vultures

In relation to the areas of habitats available to vultures there were striking differences between taxa in habitat use by marked birds. The most important finding was that marked resident Turkey Vultures were seen significantly more than expected in the gallery forest in the dry season. Seasonal differences in the proportions of sightings in different habitats were significant, supporting evidence of niche shift in resident Turkey Vultures described in Chapter 3 (Section 3.3.4). There was some evidence that marked resident Turkey Vultures foraged on the west side of the highway before the start of the wet season but this was based on a very small number of trapped birds. By contrast, both marked Black and Turkey Vultures were seen significantly less frequently than expected in the gallery forest. Although the habitat content of ranges in only a few marked individuals was examined in detail, these results also indicated that the proportion of gallery forest was very low.

4.5.5 Range behaviour by radiotagged resident Turkey Vultures

The use of resighting observations alone was insufficient to demonstrate seasonal changes in range behaviour by resident Turkey Vultures because too few resightings were made of marked birds and because generally, sighting data was likely to underestimate movements (eg. Village 1983). Despite small sample sizes, findings from the radiotracking study were consistent with the view that seasonal niche shift occurs in resident Turkey vultures. There was some evidence to suggest that a migratory subpopulation of resident birds may have departed from the ranch after migrants arrived (the disappearance of radiotagged birds at the end of the wet season).

4.5.6 Range movements

There was no significant difference in mean intersite distances moved by radiotagged resident Turkey Vultures between seasons. However, such a comparison necessitates an arbritrary dividing point between seasons (30 April) and resident Turkey Vultures foraged outside the forest before this date (when most migrants had left). Thus, increased movements during range expansion may be included in dry season or wet season data which could clearly affect conclusions. Comparison between these different periods for one individual with sufficient data showed that movements during the transitional stage were not significantly different to either dry season or wet season movements. However, there was a significant difference between dry and wet season intersite distances. In the absence of competition from migrants, resident Turkey Vultures may have foraged over larger distances in savanna habitats (constituting approximately 85% of the total ranch) unavailable to them in the dry season.

4.5.7 Habitat use within home ranges.

Vultures began to forage consistently outside the forest (Figure 4.4 and 4.5) on different dates (around the middle of March) before the first rains (when changes in animal mortality were most likely to occur) and coincided with the departure of migrants (March-April). The exact timing of niche shift and density of migrants in open habitats may be correlated but insufficient data from individual birds were available to determine this.

Other undetected factors could contribute to niche shift in resident Turkey Vultures. Changes in the ecological requirements of birds, particularly during breeding can affect their energetic demands and foraging strategy. For example, in male Sparrowhawks range size contracts while birds are establishing a nesting territory but subsequently expands when birds must supply food to dependent young (Marquiss & Newton 1981). The breeding season of resident Turkey Vultures was not established in the present study, but in Panama Smith (1980) has recorded egg-laying between February and April. Judging from information on length of breeding collected by Davis (1983a) for *C.a. septentrionalis,* resident Turkey Vultures would have well grown young by the late dry or early wet season (April/May). This would be when migrants were absent or at least numbers were declining as vultures moved northward. Thus, the increased demand for food at this time of year could mean that birds had to forage over a larger range area outside the gallery forest.

While this could partly explain range shift in the wet season it does not explain why residents foraged almost entirely in the gallery forest during the dry season. It seems unlikely that changes in the food supply of vultures occurs before the first rain, so this does not account for late dry season niche shifts in radiotagged resident Turkey Vultures.

The habitat analysis using fixes from all radiotracked vultures circumvented the statistical problems associated with small fix sample sizes and enabled use of data from all individuals. The findings clearly showed that in the dry season, use of gallery forest was much greater than expected assuming random habitat use according to area (approximately equivalent to the combined area of all ranges), whereas in the wet season semi-open habitats were used more than expected and few fixes occurred in forest. Results from individual birds showed the same general pattern except that in the wet season there was no significant difference in usage between habitats. Large areas of open palm savanna and estero were not visited by radiotagged residents suggesting that areas with higher structural diversity were preferred in the wet season, probably because they contained higher densities of carcases.

During the dry season some individuals were located outside the forest (Figure 4.4) and these appeared to be forays outside the core area frequented by the birds. Observations at bait sites also indicated that occasionally resident Turkey Vultures visited carcases in more open habitats, close to the forest (see Chapter 3). Niche shift in resident Turkey Vultures occurred gradually. The radiotracking study usefully identified the time periods over which it would be necessary to follow resident Turkey Vultures to investigate changes in habitat use.

There were a number of problems associated with assessing changes in habitat selection by radiotagged birds in the present study. A small proportion of fixes were excluded from the habitat analyses because they were outside the mapped area. In addition, while there were potential biases of vultures ranging over a larger area than the ranch, outside receiver range, it must be assumed that birds would behave in a similar way when foraging outside the study area.

SUMMARY

1) There were significant differences in the number of resighted marked birds as a percentage of those marked between taxa. Significantly more Black and resident Turkey Vultures were resighted than migrant Turkey Vultures. Most migrant Turkey Vultures caught on the ranch were probably itinerant individuals, or birds on their way south or north during the migration period, which accounted for the low rate of sightings. Some marked individuals showed high site fidelity and returned to the same part of the study area in different years.

2) During the dry season resident Turkey and Black Vultures had significantly larger mean intersite distances than migrant Turkey Vultures. However, there was no significant difference between distances moved by Black and resident Turkey Vultures either in the dry or the wet season. A separate analysis for behavioural observation days alone showed no significant difference between taxa but this may have been due to small sample size. It was not possible to use resightings from transect counts alone because sample sizes were too small.

3) Seasonal differences in mean intersite distances were significant for Black but not for resident Turkey Vultures. Increased movement during the wet season in Black Vultures may have been because of seasonal changes in the level of livestock mortality or human-induced factors. There were significant seasonal differences in the mean distances between trapping sites and sighting location for both species, but the use of this measure in assessing movements was complicated by trap location in relation to where birds spend most time (a large number of trap locations were used). Despite this,

results suggested that residents, mostly caught on the east side (in gallery forest) moved larger distances from trap sites in the wet season than the dry season. This supported the hypothesis of a niche shift in residents during the wet season.

4) Results from sightings of marked vultures showed that both migrant and Black Vultures were sighted more frequently than expected in open savanna habitats than in the forest during the dry season. However, by contrast, resident Turkey Vultures were sighted in gallery forest significantly more than expected. This indicated that residents selectively foraged in the gallery forest in the dry season, while Black and migrant Turkey Vultures showed no such preferrence and used forest less than expected.

5) Radiotracked resident Turkey Vultures showed a significant preference for gallery forest (despite its small contribution to overall area within the ranch) in the dry season when all fixes were plotted on a map of the study area, but showed no preference for forest in the wet season. Results were similar for individual birds except that fixes occurred more frequently than expected in semi-open habitats in the wet season. No significant differences were detected between mean intersite distances in dry and wet seasons. Changes in foraging behaviour of residents occurred when most migrants had left the study area by late March/early April and prior to the first rain.

CHAPTER 5 FEEDING BEHAVIOUR

5.1 INTRODUCTION and AIMS

The potential for competitive interactions between animals increases greatly where mixed-species flocks feed on patchily distributed food resources and there are many avian examples of this amongst waders Charadriidae (Goss-Custard 1980, Thompson & Barnard 1983), gulls Laridae (Monaghan 1980, Greig *et al* 1983) and vultures, both Accipitridae (Kruuk 1967, Houston 1974, 1983, Anderson & Horwitz 1986) and Cathartidae (Wallace & Temple 1986). The mechanisms by which food resources are partitioned in such foraging groups have been the subject of much study.

By reducing the costs of engaging in agonistic interactions, social dominance may be a behavioural means of mediating competition (Huntingford & Turner 1987). For instance, the partitioning of resources at refuse tips in three gull species is achieved by the use of different feeding methods and interspecific and intraspecific hierarchies (Greig *et al* 1986). Wallace & Temple (1986) have recently shown that among Cathartid vultures interspecific competition is reduced by arrival sequence and dominance hierarchies based on body size; intraspecific dominance was related to age of individuals. In addition, morphological adaptations enable different vultures to feed on specific parts of carcases (Houston 1988). Ecological separation may also occur by carcase type; Turkey Vultures feed on small or medium-sized carcases, whereas Black Vultures prefer large carcases such as domestic livestock (Davis 1974, 1979, Stewart 1978).

There are a number of advantages to animals feeding in groups (Bertram 1978) (eg. group size varies according to the maximium net energy gain for each individual (Pulliam & Caraco 1984)). Groups of Lions *Panthera leo* or Hyenas *Crocuta crocuta* can take larger prey than can individuals (Schaller 1972, Kruuk 1972). Increased foraging group size increases the rate at which food is discovered (eg. in Great Tits *Parus major* - Krebs *et al* 1976). By foraging in groups, animals may overcome the higher resource-holding potential of despotic individuals (see Barash 1974).

At large carcases, where Black Vultures predominate, the mechanical activity of the group is advantageous in dismembering the carcase, cooperative defence allows subdominant family members to feed (Rabenold 1983a, 1986) and few Turkey Vultures can compete for feeding sites. High-ranking species like King Vultures do not need group cooperation to defend large carcases because they can dominate other species at carcases. Turkey Vultures cannot defend such carcases against large numbers of Black Vultures. On smaller carcases, individual Turkey Vultures are able to defend the food resource available; thus, few Black Vultures feed on such carcases. With large group sizes and finite food resources subordinate individuals (and species) are likely to be affected most (Pulliam & Caraco 1984), being denied access to food and having to forage elsewhere (eg. immature Herring gulls *Larus argentatus*; Monaghan 1980).

This chapter investigates the feeding ecology of vultures at carcases and focuses on the interactions between resident and migrant Turkey Vultures in gallery forest. Some comparisons were made between savanna and forest bait sites, but the feeding behaviour of Black Vultures is not considered here in detail because when visiting forest sites they rarely fed or interacted with other vultures. A number of detailed studies have been conducted on Black Vulture feeding behaviour in the United States (see Rabenold 1983 a b). One aim was to determine how residents obtain their food supply in the dry season and how they coexist with more dominant taxa which forage in the forest by investigating interactions between migrant and resident Turkey Vultures at feeding sites. To investigate ecological separation in vultures and to determine why resident Turkey Vultures foraged almost exclusively in gallery forest in the dry season it was necessary to;

i) Record the sequence of arrival at carcases in forest and savanna habitats to test the hypothesis that residents arrived at different times to migrants to avoid interference competition.

ii) Compare numbers and arrival rates of vultures on similar carcases at forest and non-forest sites.

iii) Compare feeding behaviour (specifically encounter and peck rates) in forest and savanna habitats between taxa.

iii) Investigate the carcase preferences of different vultures.

5.2 METHODS

5.2.1 Baiting

Dead animals were placed at a distance of 5-30 m (depending on the density of vegetation) from an observation hide. In dense woodland within gallery forest, particularly in the wet season, observations could only be made at short distances. Occasionally, because of reduced visibility in forest it was sometimes necessary to stake baits to prevent their being dragged by vultures to locations out of view.

Baits were put out as early in the day as possible but this time was variable because of the difficulty of finding fresh carcases. The time at which carcases are laid out affects arrival sequences, since throughout the day the numbers of flying vultures fluctuates considerably, so this had to be taken into account when interpreting results (see Chapter 3 - Section 3.3.1). Additionally, the later in the day baits are laid out, the higher the likelihood of birds locating an alternative food source. It was important to use fresh carcases (animals which had been killed the previous night) since vultures foraging by olfaction could locate an older carcase much more quickly, increase the rate at which vultures arrived at a carcase and therefore alter the sequence of arrival (birds would follow me, King Vultures would be attracted to the area and would discourage other species from alighting at carcases). When carcases were carried to a bait site there was also the possibility that birds would follow me if the carcase was more than one day old. Where possible unruptured carcases were used. An approximate estimate was made of the percentage canopy cover immediately above the observation site (for a radius of c. 25 m) and the vegetation type recorded (using the classification of Troth 1979).

Most carcases were collected from the Calabozo - San Fernando highway (which bisects the ranch) where Crab-eating Foxes, *Cerdocyon thous*, Possums, *Didelphis marsupialis*, and Caiman, *Caiman crocodylis* were frequently killed at night. Dead animals were collected at dawn each day before they decomposed or were removed by scavengers.

Vultures were also observed feeding on domestic livestock (cattle, horses and pigs) which had died as a result of disease or snake-bite. Baits were observed until vultures had finished feeding and the carcase was consumed, or up till an hour before sunset. The remains were weighed (to 0.01 kg accuracy) to obtain an index of the rate at which carcases were consumed, in relation to the number and species of scavenging vultures. Data were pooled separately for medium-sized (less than or equal to 6 kg) and large (between 40-120 kg) carcases on focal sampling days.

5.2.2 General (Ad libitum) observations

After carcases had been positioned, the start time of observations was recorded as were the arrival and departure times of vultures. Aggressive interactions between individuals were recorded as they occurred, determining the aggressor, recipient and winner of each conflict, (see Altmann 1974, Greig *et al* 1984, Anderson & Horwitz 1986, Wallace & Temple 1986).

The aggressor was the bird which initiated an interaction (usually but not always the feeding bird) and the recipient the bird at which aggression was directed. The outcome of conflicts was apparent from subsequent behaviour. If a feeding bird directed an attack at a conspecific and then returned to its feeding position then this bird was considered to have won the interaction. This was very obvious in species such as the Turkey Vulture because often only one bird fed at a carcase at any one time, until satiated. Aggressive interactions were categorised according to their intensity; 1. Low - Intention movement 2. Medium - Pecks, Shoulder pushing (undertaken only by Black Vultures) or chases. 3. High - flapping or Kick-fighting (see Davis 1979, Rabenold 1983 a).

A number of problems were associated with these more general observations: more subtle interactions may have been overlooked. In other instances, such as the example of large numbers of Black Vultures on a small carcase, it was impossible to record all the interactions that occurred, because feeding was chaotic.

5.2.3 Focal animal sampling

Focal animal sampling (Altmann 1974) was used in the second and third field seasons because this allowed random sampling of subjects. Individuals were selected by choosing the third bird from the left in my field of view and recording interactions and peck rates for a 60-

second period. In small groups there was a frequent shift in position of birds but in large groups of vultures at large carcases the latter procedure would bias focal birds towards edge individuals which remained in the same position for long periods. Therefore, in large feeding groups focal subjects were selected using random number tables.

Agonistic interactions were categorised in the same way as for the general observations. The peck rate of subjects was recorded to enable inter-species comparisons and assess how fast carcases were depleted. It was not possible to always define a peck as an instance when a vulture raised its head above an angle perpendicular to the carcase because species like migrant Turkey Vultures did not do this, but often swallowed without lifting the head up. Vultures also made pecks without swallows and these were not counted. Periodically, during observational periods the numbers of vultures and proportions of different species were recorded to see if this had any effect on the peck and interaction rate of focal birds. Counts were made when flock size and composition changed.

For King, resident Turkey and migrant Turkey Vultures, pecks and associated swallows were easily counted. However, at carcases of domestic animals in the open (where most observations of Black Vultures were made), it was difficult to count peck rates for two reasons. Firstly, there were usually large numbers of vultures on such carcases, which meant that when vultures fed it was often impossible to obtain an unrestricted view of focal birds and secondly, few Black Vultures fed on smaller mammalian carcases. When large numbers of Black Vultures were feeding on a large carcase (eg. horses or cows), focal samples of 15 seconds were made because birds could not be followed for 60 seconds. Black Vultures visited carcases infrequently in the gallery forest so the small sample size of peck rates for Black Vultures does not affect any conclusions from analysis of feeding rates in other taxa.

5.2.4 Analysis of results

The rates at which vultures arrived at carcases per 15 minute period were compared within the same vegetation types and on similar baits between pairs of taxa. A comparison was also made of intraspecific arrival rate between vegetation types. The total number of arrivals at carcases clearly depends on the density of vultures in the area, overall population sizes of different species and size of carcase.

Data from peck rate counts were log-transformed to normalise them, so means presented are derived means with 95% Confidence limits (±). In addition, multivariate analyses were carried out for focal animal data to test the effect of group sizes of different taxa on feeding rates. Non-parametric tests were used for analysis of general observations and encounters in focal observations because log-transformation did not normalise these data.

Complete carcases had only two feeding sites (mouth and anus) where vultures could feed (though later on more sites became available as carcases were depleted). If several carcases were used for observations (as in the first two field seasons) this increased the number of feeding sites initially available to birds. Although this reduced competition for each site, some feeding individuals attempted to defend all of the sites, thus increasing the number of agonistic encounters. Therefore, separate analyses were carried out for days when only single carcases were used and compared with the large data set from all bait sites.

5.3 RESULTS

A total of 405 hours of observations of vultures at baits was made on 96 separate days. Twenty-one different animal species were used as baits; 2 Horses, 8 Cows, 3 Pigs, 4 Capybara *Hydrochaeris hydrochaeris*, 5 Spectacled Caiman *Caiman crocodilus*, 21 Crab-eating Foxes *Cerdocyon thous*, 48 Possums *Didelphis marsupialis*, and 3 Lesser Anteaters *Tamandua tetradactyla*; as well as Jaguarundi *Felis yagouaroundi*, Grison *Grison vittatus*, Tayra *Eira barbara*, Agouti *Dasyprocta aguti*, Howler Monkey *Aloutta seniculus*, Racoon *Procyon cancrivorus*, Armadillo *Dasypus novemcinctus*; 38 domestic hens, 3 bird species (Boat-billed Heron *Cochlearius cochlearius*, Black-bellied Whistling Duck *Dendrocygna autumnalis* and Rufous-vented Chacalaca *Ortalis ruficauda*) Iguana *Iguana iguana* and Boa Constrictor *Boa constrictor*.

5.3.1 Time taken to locate carcases

In this analysis days when vultures did not locate carcases on the day of observations were excluded because on a few occasions it took vultures more than one day to find carcases and there was no way of controlling for other variables (eg. changes in food availabilty in the immediate area). Only fresh carcases were used in these observations (see Methods 5.2.1). In the dry season, vultures (all taxa combined) located baits significantly faster in semi-open or open sites than in closed gallery forest (Table 5.1). Baits were located significantly faster in open savanna in the dry season than in the wet season (Mann Whitney U test, U = 156, 32, 18, $P < 0.01$ - Table 5.1). The sample size for forest bait sites in the wet season was too small to make meaningful comparisons but from census count results (Chapter 3, Sections 3.3.5 and 3.3.6) it would be predicted that it would take vultures longer to find carcases in gallery forest because of the

Table 5.1 Time (minutes) taken for vultures to locate baits in three vegetation types for dry and wet seasons (r = range, n = number of days)

Habitat type	Dry season			Wet season		
	m	r	n	m	r	n
Forest	102.6	33-243	12	84.1	84-326	3
Semi-open	25.3	6-190	20	79.3	17-207	9
Open	35.5	6-74	12	76.2	10-111	9

Comparison between habitats (Mann Whitney U test)
Forest vs Semi-open U = 29, *
Forest vs Open U = 17, *
Semi-open vs Open U = 110, N.S.

Table 5.2 Number of times different species arrived first at carcases in different vegetation types in the dry season

Species	Vegetation type					
	Semi-open			Open		Forest
	Palm	Mata	Shrub	Estero	Medano	Gallery
Black	-	3	-	1	1	-
Migrant	4	4	2	3	4	2
Resident	-	2	-	-	-	11
Caracara	2	2	1	2	8	-
Total	6	11	3	6	13	13

Comparison between proportions of migrant and resident Turkey Vultures arriving first in forest and combined non-forest habitat; $X^2 = 17.6$, df 1, ** lower densities of vultures (compared to savanna) and the effect of increased vegetation cover.

5.3.2 Arrivals of vultures at carcases

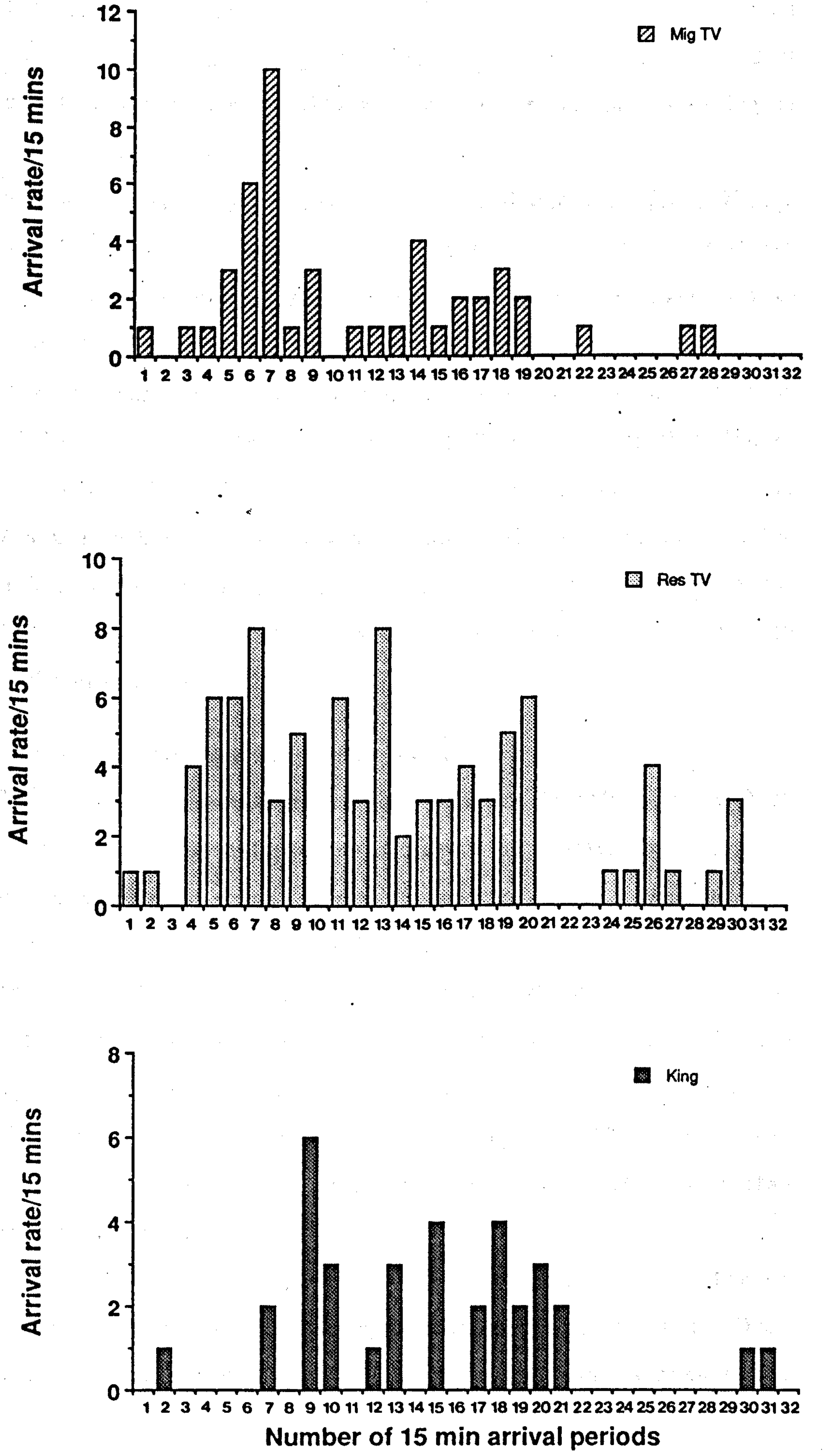
Table 5.2 shows that in the dry season Black Vultures arrived first at 15% of the carcases in semi-open sites compared with 11% in open sites and on no occasions in gallery forest sites. Migrant Turkey Vultures were first to arrive at 58% of open sites, 50% of semi-open but only 17% of forest sites. On the few occasions resident Turkey Vultures visited semi-open sites (close to the forest edge and towards the end of the dry season when most migrants had left) they arrived first on only 10% of occasions. However, at baits in forest sites in the dry season, resident Turkey Vultures were first to arrive on 83% of occasions. Census counts showed that gallery forest held equal densities of migrant and resident Turkey Vultures and both races foraged solitarily. The null hypothesis was therefore that there was an equal chance of either race locating baits first. However, significantly more resident than migrant Turkey Vultures arrived first at food sites ($X^2 = 6.23$, df 1, $P < 0.05$, with Yate's correction factor - Table 5.2).

The arrival rates of different vulture species were compared using Wilcoxon's test for matched pairs, by comparing numbers of vultures arriving in each 15 minute period throughout the total arrival sequence. In gallery forest sites (on 8 days), where there were equal densities of foraging migrant and resident Turkey Vultures, a significant difference was found between arrival rates of the two subspecies with larger numbers of residents arriving than migrants (Figure 5.1). There were no significant differences between arrival rates of migrant Turkey Vultures and Black Vultures or between migrant Turkey and King Vultures. However, in comparison to King Vultures

Comparison between taxa (Wilcoxon's test for matched pairs)

MTV	vs	RTV	Z = 2.48	N = 17	*
MTV	vs	BV	Z =-1.35	N = 7	NS
MTV	vs	KV	Z = 0.67	N = 8	NS
RTV	vs	KV	Z = 2.19	N = 11	*

Figure 5.1 Numbers of vultures arriving in each 15 min period at carcases in Gallery Forest



significantly more resident Turkey Vultures arrived at forest bait sites in the dry season (Figure 5.1). This indicated that resident Turkey Vultures were numerically the most important taxa arriving at forest carcases on these days.

At open sites (7 days) with medium-sized carcases (less than 6 kg.) significantly more migrant Turkey Vultures than Black Vultures arrived at baits (Figure 5.2). A direct comparison was made on five days using the same carcase types and similar observation periods in both open savanna sites and forest of the arrival rates of different taxa; Table 5.3 shows that both migrant Turkey and Black Vultures arrived in significantly larger numbers at savanna bait sites. This reflects the much higher densities of these vultures foraging in the open (Chapter 3). Comparisons between other vulture species were not possible because only small numbers visited carcases in the open during the dry season.

5.3.3 Numbers of carcases visited by vultures

Table 5.4 shows the numbers of all carcases (mainly weighing less than 6 kg.) visited by vultures in different vegetation types in each season. At almost all forest sites in the dry season, carcases used were either possums or foxes (all less than 6 kg, range of carcase weights 1.37-6.00 kg); at open savanna sites in the dry season a wider range of carcases were used (74% were less than 6 kg, range 0.55-c.120 kg). In the wet season, domestic hens were used most (81% of baits were less than 6 kg, range of carcase weights 1.12-120 kg). The following is a general summary of relative numbers of carcases visited by different vultures.

During the dry season, King Vultures visited 68% of forest sites, but only 19% of those in open savanna, in contrast to Black Vultures which visited 47% and 86% of forest and savanna sites

Comparison between taxa (Wilcoxon's test for matched pairs)

MTV vs BV $Z = -2.52$ $N = 8$ * *

Figure 5.2 Numbers of vultures arriving in each 15 min period at carcases in open savanna (n=7 days)

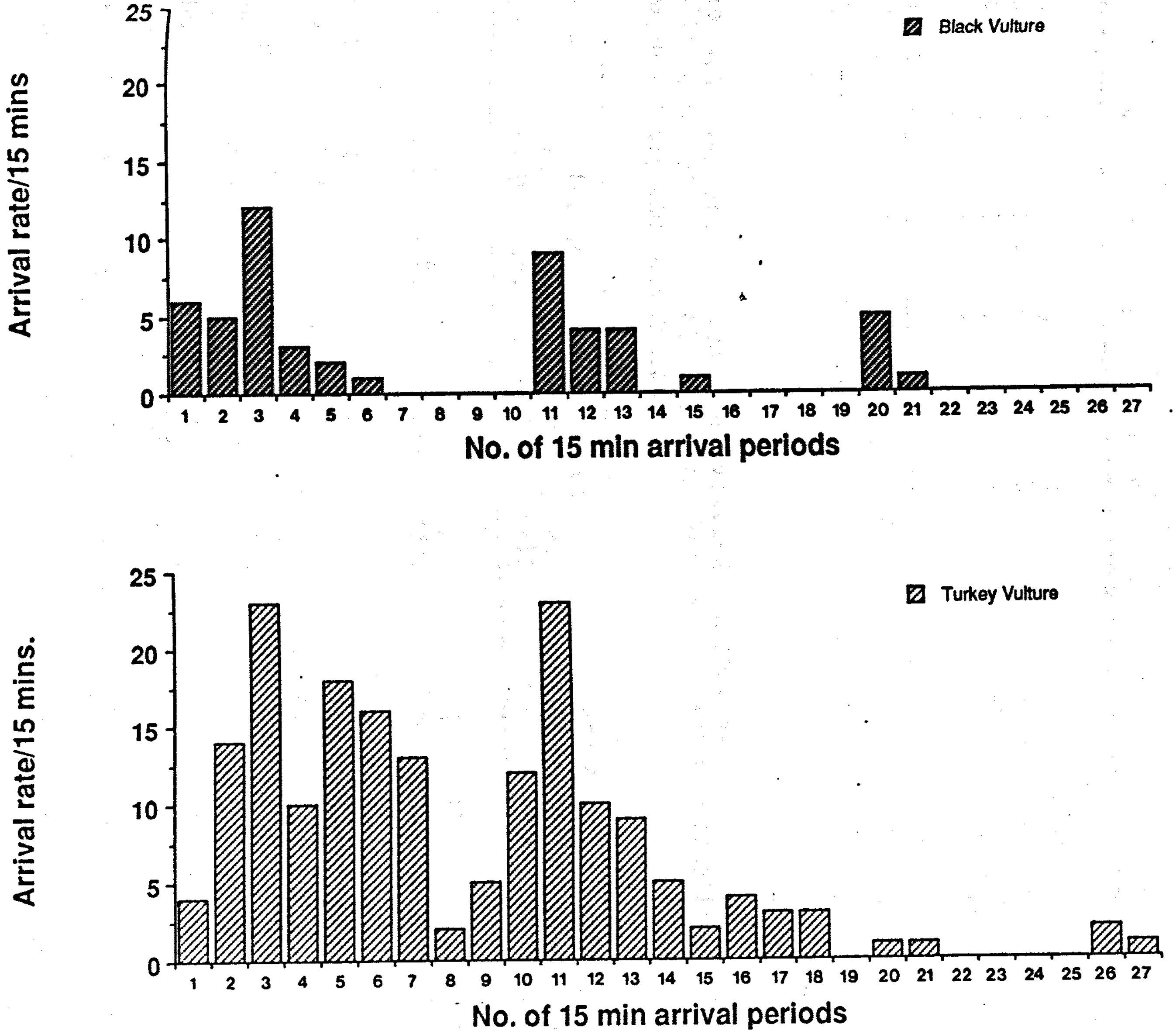


Table 5.3 Arrival rates of vultures at medium-sized carcases at five gallery forest and five open savanna sites (median arrival rate/15 minutes, r = range, n = total number of 15 minute arrival periods).

Taxa	Vegetation type							
	Forest			Open savanna				
	m	r	n	m	r	n	U	P
Black	1	1-5	9	4	1-12	12	27.0	*
Migrant	1	1-6	18	5	1-22	23	80.5	**
Resident	3	1-3	21	1		1		
King	2	1-6	12	1	1-2	5	14.0	N.S

Table 5.4 Numbers of carcases visited in general and focal sampling observations by different vulture taxa in three vegetation types in the dry and wet season (%).

Taxa	Forest		Open		Semi-open	
	Dry n=19	Wet n=3	Dry n=15	Wet n=11	Dry n=28	Wet n=12
Black	9 (47)	2 (67)	15 (100)	8 (73)	22 (79)	11 (92)
Migrant Turkey	17 (89)	-	13 (87)	-	24 (86)	-
Resident Turkey	17 (89)	2 (67)	2 (13)	4 (36)	6 (21)	5 (42)
Yellow-headed	-	-	2 (14)	5 (45)	1 (4)	6 (50)
King	13 (68)	1 (33)	3 (20)	1 (8)	5 (18)	3 (25)

Comparison between proportions of visits in each habitat in the dry season

Black Vulture X^2 = 7.32, df 2, *
Resident Turkey Vulture X^2 = 27.76, df 2, ***
Migrant Turkey Vulture X^2 = 0.15, df 2, N.S.
King Vulture X^2 = 14.60, df 2, ***
Resident vs Migrant
Forest X_2 = 0, df 1, N.S.
Open X_2 = 16.10, df 1, ***

respectively (Table 5.4). Migrant Turkey Vultures visited a similar proportion of baits in all habitats. Resident Turkey Vultures visited significantly more forest (89%) than open savanna sites (19%-Table 5.4). Most of the baits visited by residents were in savanna and close to the gallery forest edge, but on a few occasions residents visited carcases in the open, on the west side of the highway. During the dry season, there was a significant difference in the proportions of baits visited by migrant and resident Turkey Vultures in the three habitats (Table 5.4). In contrast to residents, migrants visited open or semi-open sites and forest in equal proportions (Table 5.4).

The proportion of resident Turkey Vultures which visited forest sites compared to open or semi-open ones was significantly different between dry and wet seasons; savanna baits were visited on 41% of occasions in the wet season (Table 5.4), usually west of the highway. However, no such seasonal difference between proportions of sites visited was found in the case of Black Vultures (Table 5.4). Although sample sizes were too small for statistically meaningful comparisons, relatively more savanna sites were visited by Lesser Yellow-headed Vultures in the wet season than the dry season.

Feeding behaviour

5.3.4 Residence times at bait sites

There was a significant negative correlation between the proportion of time spent by residents at baits on each day and that spent by both migrant Turkey and King Vultures (Table 5.5, Figure 5.3). Thus, resident Turkey Vultures stayed longer at baits on days when migrants and King Vultures spent least time. However, there was no correlation between the proportion of time spent by migrant Turkey Vultures and King Vultures at carcases (Table 5.5). The proportion of each day spent by migrants at carcases was correlated with that spent by Black Vultures, but there was no correlation between resident Turkey Vultures and Black Vultures.

5.3.5 Proportion of time feeding

During focal sampling observations in the dry season gallery forest (total number of 60 second observations = 1096), King Vultures fed on 89%, resident Turkey Vultures on 65% and migrant Turkey Vultures on 59% of focal samples (Table 5.6). On days when only single baits were used (number of focal samples = 642), King Vultures fed on 90%, resident Turkey Vultures on 79% and migrant Turkey Vultures on 54% of occasions and the differences between taxa were significantly different (Table 5.7).

Resident Turkey Vultures fed more during focal samples than migrants because most peck rates for residents were obtained when they arrived first, or when group sizes were small. Migrants arrived later and spent less time feeding and more time interacting with conspecifics or standing by. There was a highly significant difference between vultures in the proportion of time spent standing still (ie. loafing or preening - Table 5.6 and 5.7), King Vultures standing still

Table 5.5 Proportion of total observation time spent by different vulture taxa at gallery forest sites in the dry season (%).

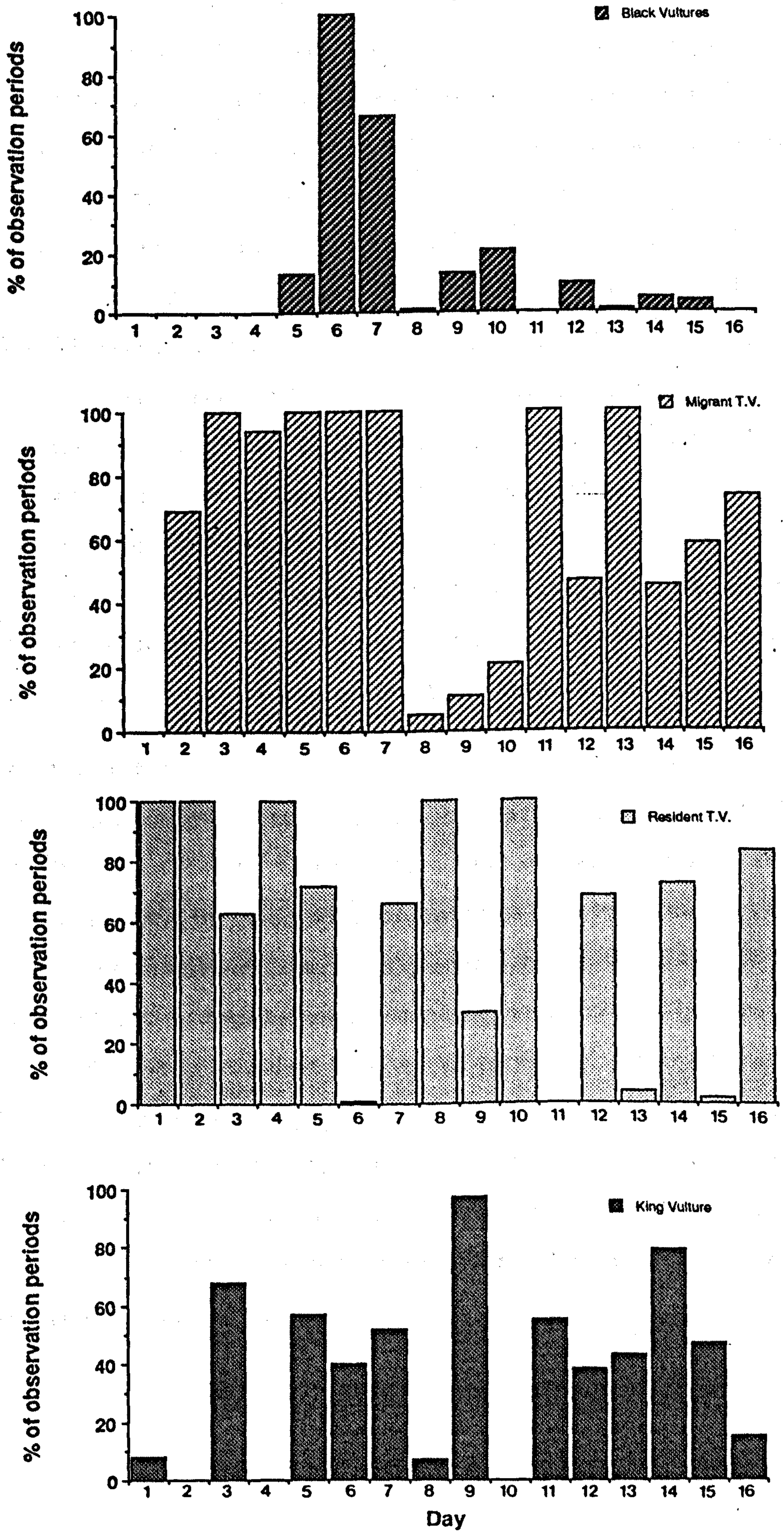
Day	Total observation time (min)	Black Vulture	Migrant Turkey Vulture	Resident Turkey Vulture	King Vulture
1	133	-	-	133 (100)	11 (8)
2	110	-	76 (69)	110 (100)	-
3	98	-	98 (100)	62 (63)	67 (68)
4	215	-	203 (94)	215 (100)	-
5	192	26 (13)	192 (100)	138 (72)	109 (57)
6	309	309 (100)	309 (100)	2 (1)	123 (40)
7	248	163 (66)	248 (100)	163 (66)	130 (52)
8	276	2 (1)	14 (5)	276 (100)	20 (7)
9	202	27 (13)	22 (11)	61 (30)	196 (97)
10	183	39. (21)	39 (21)	183 (100)	-
11	172	-	172 (100)	-	94 (55)
12	213	22 (10)	101 (47)	144 (68)	80 (38)
13	235	2 (1)	235 (100)	10 (4)	101 (43)
14	249	12 (5)	111 (45)	179 (72)	197 (79)
15	440	18 (4)	256 (58)	11 (2)	209 (47)
16	342	-	249 (73)	279 (82)	52 (15)
Median		2.5	71	70	41.5

Relationship between proportion of time spent by different taxa at carcases (Spearman Rank Correlation Coefficient)

RTV vs MTV r_s =-0.394, N=14, *** RTV vs BV r_s =-0.147, N=10, N.S.
RTV vs KV r_s =-0.432, N=12, *** MTV vs BV r_s = 0.308, N=10, **
MTV vs KV r_s = 0.076, N=11, N.S.

(see Figure 5.3)

Figure 5.3 Proportion of observation periods in which different vulture taxa were present at Gallery Forest sites in dry season



on average for only about 25% of the time of migrants. Compared to residents, migrants spent significantly more time standing still (Table 5.6 and 5.7). Resident Turkey Vultures fed significantly more often than migrants during focal samples because they arrived earlier when there were fewer competitors (Tables 5.6 and 5.7).

At open savanna sites, (822 focal samples), migrant Turkey Vultures fed on 53% of samples (on all carcase types, including domestic livestock). During 15 second samples of Black vultures feeding on domestic livestock (weighing more than 40 kg), birds fed on only 15% of occasions (339 focal samples). However, these observations were not comparable with those on other species which were made at much smaller carcases: Black Vultures feed selectively at large carcases, where they congregate in large groups, and therefore a high proportion of individuals do not feed at any one time. There were also some biases in the feeding observations (see discussion).

5.3.6 Feeding rates

Peck rates varied greatly between the different taxa. Table 5.8 shows feeding behaviour of three vulture taxa at gallery forest sites in the dry season. In this guild of vultures (pooled data for days when several or single carcases used), there was a highly significant difference in peck rates between the three most frequently recorded taxa, King Vultures, resident Turkey Vultures and migrant Turkey Vultures (one-way ANOVA, $F_{2,700} = 49.8$, $P < 0.0001$) and results were similar for single carcase days ($F_{2,461} = 41.0$, $P < 0.0001$). Peck rates of migrant Turkey Vultures were higher than King Vultures and peck rates of residents were higher than for either migrants or King Vultures (Tables 5.8 and 5.9).

Table 5.6 Frequencies of different activities (presence/absence) in 3 forest vulture species during 1052 focal samples on all carcases (%).

		Activity				
Species	N	Total Feeding	Total Interactions	Feeding with no intera-	Interacting not feeding	Stand -ing still
MTV	447	265 (59.3)	138 (30.9)	164 (36.7)	37 (8.3)	145 (32.4)
RTV	337	220 (65.3)	97 (28.8)	162 (48.1)	40 (11.9)	77 (22.8)
KV	268	238 (88.8)	65 (24.3)	178 (66.4)	5 (1.9)	26 (9.7)

Total feeding - Incidence of feeding in 60 second samples.

Total interactions - Incidence of agonistic interactions recorded in samples.

Feeding with no interactions - Incidence of feeding in samples when vultures had no agonistic encounters.

Interacting, not feeding - Incidence of agonistic encounters in samples when focal bird did not feed.

Standing still - No feeding or agonistic encounters observed during sample.

Differences in frequency of activities in 3 vulture taxa

Activity	X^2	df	P
Feeding	70.68	2	***
Interacting	3.62	2	N.S.
Standing still	48.20	2	***
Feeding/no interactions	59.34	2	***
Interacting/no feeding	40.46	2	***

MTV vs RTV	X^2	df	P
Feeding	2.93	1	N.S.
Interacting	0.40	1	N.S.
Standing still	8.71	1	***
Feeding/no interactions	10.25	1	***
Interacting/no feeding	14.16	1	***

Table 5.7 Frequencies of different activities (presence/absence) in 3 forest vultures during 613 focal observations on single carcases (%).

Species	N	Activity Total Feeding	Total Interactions	Feeding with no intera--ctions	Interacting not feeding	Stand-ing still
MTV	195	106 (54.4)	60 (30.8)	70 (35.9)	24 (12.3)	65 (33.3)
RTV	213	168 (78.9)	58 (27.2)	128 (60.1)	19 (8.9)	26 (12.2)
KV	205	184 (89.8)	51 (24.9)	136 (66.3)	4 (2.0)	18 (8.8)

Differences in occurrences of activities in 3 vulture taxa

Activity	X^2	df	P
Feeding	69.30	2	***
Interacting	1.76	2	N.S.
Standing still	48.20	2	***
Feeding/no interacting	41.49	2	***
Interacting/no feeding	15.87	2	***

MTV vs RTV	X^2	df	P
Feeding	27.70	1	***
Interacting	0.62	1	N.S.
Standing still	26.20	1	***
Feeding/no interactions	23.86	1	N.S.
Interacting/no feeding	1.24	1	N.S.

Table 5.8 Peck rates of 3 vulture taxa in 60 second focal samples in dry season gallery forest on all days; mean, n = sample size, 95% confidence limits in parenthesis, other activities = % of samples when no feeding observed.

	Migrant Turkey	n	Resident Turkey	n	King	n
Pecks/60 secs.	10.6 (9.5-11.7)	252	13.3 (12.1-14.6)	216	6.9 (6.3-7.5)	235
Other activities % of all samples	32.4	145	22.9	77	9.7	26
Total No. 60 sec. samples		447		337		268

Comparison of peck rates between taxa ('Student' t test, log-transformed data)

MTV vs.RTV t_{466} =-3.33, ***
MTV vs.KV t_{485} = 6.45, ***
RTV vs.KV t_{449} = 10.63, ***

Table 5.9 Peck rates of three vulture taxa in 60 second focal samples on single carcase days (mean , n = sample size, 95% confidence limits in parenthesis, other activities = % of samples when no incidence of feeding.

	Migrant Turkey	n	Resident Turkey	n	King	n
Pecks/60 secs.	10.2 (8.7-12.1)	115	13.8 (12.6-15.2)	166	7.1 (6.4-7.8)	183
Other activities % of all samples	33.3	65	12.2	26	8.8	18
Total No. of 60 sec samples		195		213		205

Comparison of peck rates between taxa ('Student' t test, log-transformed data)

MTV vs RTV t_{270} = -3.37, **
MTV vs KV t_{287} = 4.17, ***
RTV vs KV t_{347} = 9.95, ***

5.3.7 Effect of vegetation type

There was a highly significant difference in peck rates of migrant Turkey Vultures, on similar, medium-sized baits (foxes and possums), between open vegetation types and forest for single carcase days. Peck rates were higher in open (savanna) than in the forest on similar carcase types (savanna; mean 14.4, 95% CL 13.5-14.4; $t_{585} = 5.02$, $P < 0.01$). This was because in the open, migrants often arrived first and more feeding rates were obtained when smaller group sizes were present, early in the arrival sequence. Resident Turkey Vultures briefly visited open carcases at a distance from the gallery forest on only a few occasions (Table 5.4) so that comparisons were not possible between vegetation types. Sample sizes were too small for other species to permit statistical comparisons between vegetation types.

5.3.8 Effect of group size

The effect of group size on peck rates in the three taxa was significantly different (slopes significantly different; Covariance analysis, $F_{2,694} = 7.4$, $P < 0.01$). For migrant and resident Turkey Vultures there was no difference in the effect of group size (slopes not significantly different) on peck rate (peck rate declined by 40% with an increase of 1 in total group size). There was a significant difference between the peck rates of the two races when group size was taken into account (elevation significantly different; Covariance analysis, $F_{1,466} = 11.1$, $P < 0.01$).

Peck rates in taxa feeding at carcases were still highly significantly different (one-way ANOVA, $F_{2,147} = 26.7$, $P < 0.0001$) when there was no interference competition (ie. group size of 1). The differences were due to the significantly lower peck rates of King Vultures compared to both migrants and residents (Table 5.10).

Table 5.10 Feeding rates of vultures when different group sizes (A = 1, B = greater than 1 but less than 3, C greater than 3) were present at carcases on all days (mean peck rate with 95% confidence limits in parenthesis).

	Group size							
Taxa	A	n	B	n	C	n	F	P
MTV	14.1 (12.2-16.2)	43	11.2 (8.9-14.0)	62	9.5 (8.3-10.9)	147	4.3	*
RTV	14.6 (13.0-16.3)	85	15.2 (13.5-17.1)	82	9.2 (7.0-12.0)	46	10.6	***
KV	6.5 (5.0-8.4)	28	6.8 (6.1-7.7)	95	7.0 (6.2-8.0)	124		N.S.

(Log-transformed data)

Differences in peck rate between taxa at carcases with different attendant group sizes (Student 't' tests).

	Group size		
	A	B	C
MTV vs RTV	N.S	$t_{142} = -2.56$ *	N.S
MTV vs KV	$t_{69} = 5.65$ ***	$t_{155} = 4.27$ ***	$t_{259} = 3.29$ ***
RTV vs KV	$t_{111} = 6.52$ ***	$t_{175} = 9.64$ ***	$t_{155} = 2.37$ *

Differences in peck rate within taxa at carcases with various group sizes.

MTV A vs C $t_{188} = 2.97$, **
RTV B vs C $t_{129} = 3.89$, ***
A vs C $t_{132} = 3.64$, ***

However, there was no significant difference in peck rate between migrant and resident Turkey Vultures when the group size was only one. Thus, the overall comparison of peck rates between migrants and residents reflects the fact that 39% of peck counts in feeding residents were made when group size was only 1, in comparison to only 15% in the case of migrants.

For both migrants and residents, there was a significant difference in intraspecific peck rate when group sizes of one (a), one to three (b) and greater than three (c) were compared (Table 5.10). However, differences were highly significant for residents. In migrants, peck rates were only significantly different between (a) and (c). Peck rate in residents was significantly different between (b) and (c) and between (a) and (c) (Table 5.10). Thus, residents were not able to maintain their average feeding rates when group sizes were larger than three. Migrants had highest feeding rates when they fed alone, but when joined by other vultures, could maintain their average feeding rate regardless of group size (unless King Vultures arrived - see results of Stepwise Multiple Regression analysis, Section 5.3.4).

Of the 220 occasions when residents fed during focal samples, on 74% of occasions they fed in the absence of migrants (19% were when one migrant was present, only 5% when two or three migrants were present and 2% when there were more than three migrants). Residents spent more time standing still when there were more migrants present but when time spent standing was compared as a proportion of all samples, for different group sizes of migrants, no significant difference was found. When migrant group size was greater than three, residents usually left the bait sites. Numbers of resident Turkey Vultures were negatively correlated with group size (excluding residents) at carcases $r_{206} = -0.14$, $P < 0.05$), but there was no correlation with numbers of migrants.

5.3.9 Multivariate analyses

Table 5.11 shows the results of the Stepwise Multiple regression analysis. A separate analysis was performed for each focal taxa because of the known differences in peck rates between species and the effect of dominance status on feeding shown in the earlier one-way ANOVAs. The results of this analysis (Table 5.11) showed that both King and migrant Turkey Vulture group size significantly reduced average peck rate in focal resident Turkey Vultures (Table 5.11). For 1 standard deviation increase in migrant group size, peck rate of residents declined by 52% (Table 5.11).

Although group size of King Vultures was the most important factor affecting peck rate in resident Turkey Vultures (peck rate of residents declined by 75% with an increase of one standard deviation increase in group size of King Vultures), the length of time King Vultures stayed at carcases was comparatively short compared to resident Turkey Vultures (median 42% of total observation time compared to 70% in migrants - Table 5.5, Figure 5.3). King Vultures also usually arrived late in the sequence. A positive correlation was found between group size of Black Vultures and peck rate in resident Turkey Vultures (Table 5.11) which could be due to several factors (see Discussion, Section 5.4.8). Strikingly, there was no significant relationship between the numbers of resident Turkey Vultures present at carcases and the peck rate of other residents.

The peck rate of migrant Turkey Vultures in gallery forest was negatively correlated with increased numbers of King Vultures present at carcases (Table 5.11) but there was no significant relationship

Table 5.11 Results of the Stepwise Multiple Regression showing the effect of group size and composition on peck rate in 3 vulture taxa in dry season gallery forest and savanna (for migrant Turkey Vultures only); separate analyses were carried out for different focal species, using peck rate as the dependent variable and group size, numbers of migrant Turkey, resident Turkey Black and King Vultures as the independent variables.

Taxa	Independent variable	Multiple r-square	SE	N	Change in peck rate resulting from increase of 1 in independent variable	SE	t	P
Resident	King	0.344	0.655	336	-0.75	0.17	-4.30	***
	Migrant	0.426	0.633		-0.52	0.11	-4.56	***
	Black	0.461	0.622		0.34	0.14	2.69	**
Migrant (forest)	King	0.313	0.769	447	-0.62	0.12	-5.20	***
Migrant (savanna)	Migrant	0.210	0.622	599	-0.28	0.07	-3.92	***
King	Resident	0.156	0.631	268	0.25	0.16	2.39	*

(Log-transformed data)

between peck rates of migrant Turkey Vultures and the numbers of any other taxa (Table 5.11). However, on similar carcases in open savanna there was a striking difference: peck rate of migrant Turkey Vultures decreased significantly with group size of migrants (Table 5.11) but there was no relationship with numbers of any other species. Peck rate in King Vultures did not decline in response to numbers of any taxa, but was correlated with numbers of residents (Table 5.11).

Agonistic Behaviour

5.4.1 Factors affecting the frequency of agonistic interactions at carcases.

Encounter rate was defined as the number of agonistic interactions per 60 second focal sample, and included attack rate by focal birds and the rate at which they were attacked by other birds. A small percentage of attacks by the three main taxa were directed at Black Vultures, but this species was rarely present in the forest (see Section 5.3.4 - Residence times). A detailed analysis of the number of submissions and wins between each taxa is presented later in Section 5.3.6.

There was a significant difference between the encounter rates of King Vultures, migrant Turkey and resident Turkey Vultures in the dry season gallery forest using pooled data (Table 5.12) and for single carcase days treated separately (Table 5.13). Focal migrant Turkey Vultures had the highest encounter rates, followed by King Vultures and resident Turkey Vultures (Tables 5.12 and 5.13). On all carcases, focal migrant Turkey Vultures had more interactions than residents or King Vultures (Table 5.12). No significant difference was found in encounter rates between King and resident Turkey Vultures (Table

Table 5.12 Frequency of agonistic encounters among 3 vulture taxa in dry season gallery forest sites on all days (mean and range in parenthesis).

	Migrant Turkey	n	Resident Turkey	n	King	n
Encounters/ 60 secs.	1.89 (1-6)	138	1.70 (1-9)	97	1.45 (1-5)	65
Attack rate/ 60 secs.	1.80 (1-6)	84	1.63 (1-9)	49	1.49 (1-5)	49
No. attacks received/60 secs.	1.38 (1-4)	79	1.43 (1-7)	60	1.17 (1-2)	18
Total no. of 60 sec samples		447		337		268

Differences (Mann Whitney U test) in attack rate and rate of being attacked in 3 vulture species (including encounters with other species).

	Attacks	No. of attacks received /60 secs.
MTV vs RTV	N.S.	N.S.
MTV vs KV	U = 1715, N = 133, N.S.	N.S.
RTV vs KV	N.S.	N.S.
	Encounters	
MTV vs RTV	U = 5952, N = 235, **	
MTV vs KV	U = 3607, N = 162, **	
RTV vs KV	N.S.	
	Kruskal-Wallis ANOVA	
Encounters	H = 7.19, N = 300, *	
Attacks	H = 4.40, N = 182 N.S.	
No. of attacks received/60 secs.	N.S.	

Table 5.13 Frequency of agonistic encounters in 3 vulture species in dry season gallery forest sites on single carcases (mean with range).

	Migrant Turkey	n	Resident Turkey	n	King	n
Encounters/ 60 secs.	1.75 (1-4)	60	1.36 (1-7)	58	1.41 (1-4)	51
Attack rate/ 60 secs.	1.65 (1-3)	31	1.20 (1-4)	30	1.47 (1-4)	36
No. of attacks received/60 secs.	1.35 (1-7)	37	1.47 (1-2)	30	1.19 (1-2)	16
Total no. of 60 sec samples		195		213		205

Differences (Mann Whitney U - test) in rates of attacking and being attacked between focal birds of 3 species (including encounters with all species).

	Attack rate	No. of attacks received/ 60 secs.
MTV vs RTV	U = 341, N = 61 *	N.S.
MTV vs KV	N.S.	N.S.
RTV vs KV	N.S.	N.S.
	Encounters	
MTV vs RTV	N.S.	
MTV vs KV	N.S.	
RTV vs KV	N.S.	

Encounters: Kruskal-Wallis ANOVA, H = 6.85, N = 169, $P < 0.05$
Attacks: N.S.
Being attacked: N.S.

5.12).

On single carcase days, there was no significant difference between numbers of encounters in which the two subspecies were involved (Table 5.13). Therefore, there were more encounters on days when several baits were provided and this increased the encounter rate between resident and migrant Turkey Vultures, probably because dominant migrants tried to defend several feeding sites on different carcases simultaneously.

Attack rates within the three species (Tables 5.12 and 5.13) were highest in migrant Turkey Vultures and King Vultures. Migrant Turkey Vultures attacked other vultures at a significantly higher rate than King Vultures, using the larger data set. On single bait days, migrants attacked other vultures at a significantly higher rate than did residents (Table 5.13). Analyses of attack rates using only interactions between the three main taxa (excluding a small number of encounters with Black Vultures or Crested Caracaras) were similar, except that attack rates of migrant Turkey Vultures and King Vultures were significantly different ($U = 1392$, $N = 80, 44$, $P < 0.05$). There was no significant difference in the rate at which focal vultures were attacked between any of the taxa pair combinations.

5.4.2 Effect of vegetation type

On medium-sized carcases (Foxes or Possums) there was no significant difference in the overall rate of agonistic encounters by focal migrant Turkey Vultures between gallery forest and savanna habitats (Table 5.14). No significant difference was found between forest and non-forest food sites in attack rate or rate of being attacked in observations of migrants. However, there were striking differences in overall encounter rates (all taxa) between forest and savanna. Total encounter rates were higher in savanna than in forest habitats (Table 5.15). The majority (80%) of these agonistic encounters in the open were due to migrant Turkey Vultures (compare sample sizes in Tables 5.14 and 5.15). Thus, the presence of King Vultures and resident Turkey Vultures in the forest resulted in a lower encounter rate than in the open where migrant Turkey Vultures predominated (see later).

5.4.3 Effect of group size

There was a significant positive correlation between group size and frequency of encounters in both resident and migrant Turkey Vultures for all observation days (Table 5.16). The encounter rate in migrants was correlated with increased numbers of residents but was not significantly affected by numbers of other migrants or King Vultures (Table 5.16). For resident Turkey Vultures, there was a highly significant positive correlation between encounter rates and numbers of migrants but this was not affected by numbers of residents or King Vultures (Table 5.16). There was no correlation between encounter rates in King Vultures and the numbers of birds present at carcases (Table 5.16).

Results were different when single carcase days were analysed separately. There was no significant relationship between encounter

Table 5.14 Comparison between rate of agonistic encounters in migrant Turkey Vultures between open savanna and gallery forest habitats on single, medium-sized carcases (m = mean, r = range, n = number of samples, U = Mann Whitney U test).

	Forest			Savanna				
	m	r	n	m	r	n	U	P
Encounters/ 60 secs.	1.75	1-4	60	2.01	1-9	105	2935	N.S
Attack rate/ 60 secs.	1.65	1-4	31	2.09	1-8	73	2857	N.S
No. of attacks received/60 secs.	1.35	1-4	37	1.41	1-4	39	2804	N.S

Table 5.15 Comparison of rate of agonistic encounters (all vultures combined) between open savanna habitats and gallery forest habitats on single carcase observation days (m = mean, r = range, n = number of samples, U = Mann Whitney U test).

	Forest			Open savanna				
	m	r	n	m	r	n	U	P
Total Encounters/ 60 secs.	1.54	1-7	176	1.87	1-9	131	10128	*
Attack rate/ 60 secs.	1.43	1-2	99	2.08	1-8	77	2857	**
No. of attacks received/ 60 secs.	1.43	1-7	91	1.37	1-4	62	2804	N.S

Table 5.16 Relationship between group size and encounter rate at dry season gallery forest sites on all days combined (figures are for Spearman Rank Correlation Coefficient, R_s).

Encounter rate of	Total group	Number of birds Migrant	Resident	King
Migrant Turkey	0.28 ** (N = 138)	N.S.	0.39 *** (N = 91)	N.S.
Resident Turkey	0.28 ** (N = 97)	0.88 *** (N = 138)	N.S.	N.S.
King	N.S.	N.S.	N.S.	N.S.

rates of resident Turkey Vultures and group size or numbers of any taxa alone. When only one carcase was present, resident Turkey Vultures usually stood at the periphery of the feeding site and were less likely to interact with other birds. However, on days when several carcases were provided, residents had higher encounter rates, indicating increased competition. The encounter rate of migrant Turkey Vultures was positively correlated with numbers of migrants present ($r_s = 0.25$, $N = 60$, $P < 0.05$) showing that birds attacked conspecifics more often when defending a single food site. Encounter rate in King Vultures was positively correlated with group size of migrants ($r_s = 0.31$, $N = 60$, $P < 0.01$), when single carcases were provided.

5.4.4 Interactions in the gallery forest in the dry season

In the gallery forest, the order of dominance between different vultures was the following; King Vulture, migrant Turkey Vulture, resident Turkey Vulture and Black Vulture. Black Vultures attended carcases infrequently in the forest (Tables 5.4 and 5.5) but when they did they had lowest dominance ranking. During focal and general observations, vultures which initiated attacks almost invariably won the conflict, except when Turkey Vultures of either race made intention movements against King Vultures (Tables 5.17 and 5.18). Most intitiators of attacks were feeding birds. The incidence of agonistic interactions was highest between taxa most similar in dominance status. However, there were large variations in group size and composition during observations, so this does not in itself provide information about selective attacks. The following is a summary of all observed interactions between species on all days.

During continuous observations, more attacks by migrants were made against residents than against other migrant Turkey Vultures, but

Table 5.17 Number of interactions between 4 vulture taxa during general observations in dry season forest observations (%).

Aggressor	Recipient Black n	 Migrant TV n	 Resident TV n	 King n	 Total
Black	19 (48)	6 (15)	14 (35)	1 (2)	40
Migrant TV	115 (15)	281 (36)	374 (49)	1 (0.1)	771
Resident TV	34 (9)	49 (12)	313 (79)	1 (0.3)	397
King	98 (34)	100 (35)	42 (15)	46 (16)	286
Totals	266	436	743	49	1494

Outcome of aggressive attacks by different taxa.

Aggressor focal bird		Recipient	Focal bird won	Focal bird lost
BV	vs	MTV	3	3
BV	vs	RTV	13	1
BV	vs	KV	-	1
MTV	vs	BV	115	-
MTV	vs	RTV	373	1
MTV	vs	KV	1	1
RTV	vs	BV	34	-
RTV	vs	MTV	48	1
RTV	vs	KV	-	1
KV	vs	BV	98	-
KV	vs	MTV	99	1
KV	vs	RTV	42	-

this reflected the larger numbers of residents present at forest carcases (Table 5.17). During both continuous observation days and focal sampling days, the majority of attacks by residents were directed against other residents (Tables 5.17 and 5.18).

On occasions when residents initiated attacks against migrants during general observations, 48 out of 49 conflicts were won (Table 5.17). (Twenty percent of these attacks by residents were against juvenile migrants.) However, 69% of these conflicts occurred during one observation day (N=11 days), when at any one time only one migrant was present, but from 1-5 residents, and this indicated that the migrants involved may have been immature birds; residents won only 2 encounters of the 6 they initiated against migrants on focal observation days (Table 5.18). Resident Turkey Vultures won all attacks initiated against Black Vultures (Tables 5.17 and 5.18).

Migrant Turkey Vultures won all but one interaction which they intitiated on focal sample days (ie. all interactions against other migrants and against residents). Most attacks by King Vultures were against migrant Turkey Vultures, while the remainder were against other King Vultures and a small proportion against resident Turkey Vultures. King Vultures won all interactions against other species (Tables 5.17 and 5.18). However, the outcome of interactions in which Black Vultures initiated agonistic encounters varied and showed that sometimes Black Vultures were dominant to resident Turkey Vultures (Table 5.17).

To test the hypothesis that attacks were not random between taxa, the expected frequency of attacks was calculated using the relative numbers of different taxa present at carcases on focal sampling days (see Table 5.19). The null hypothesis was that the expected number of encounters between each taxa was proportional to the number of each

Table 5.18 Number of interactions between 4 vulture taxa during focal sampling observations (%).

	Recipient				
Aggressor	Black n	Migrant TV n	Resident TV n	King n	Total
Black	5 (71)	1 (14)	1 (14)	-	7
Migrant TV	24 (9)	153 (56)	97 (35)	1 (0.4)	275
Resident TV	11 (11)	6 (6)	85 (83)	-	102
King	13 (10)	63 (47)	14 (10)	45 (33)	135
Totals	53	223	197	46	519

Outcome of aggressive attacks by different taxa.

Aggressor focal bird		Recipient	Focal bird won	Focal bird lost
BV	vs	MTV	-	1
BV	vs	RTV	-	1
MTV	vs	BV	24	-
MTV	vs	RTV	250	-
MTV	vs	KV	-	1
RTV	vs	BV	11	-
RTV	vs	MTV	4	2
KV	vs	BV	13	-
KV	vs	MTV	63	-
KV	vs	RTV	14	-

Table 5.19 Comparison of numbers of agonisitic interactions (between aggressor and recipient) between resident and migrant Turkey Vultures (expected values).

		Recipient MTV	RTV	Total	X^2	P
Aggressor	MTV	57 (74.2)	97 (79.8)	154	7.7	**
	RTV	4 (24.8)	44 (24.2)	48	33.6	***

Expected values were calcuated from the ratio of different races present at carcases in the following way; if there were 3 migrants and 2 residents and a total of 10 interactions when migrants were initiators of attacks, the expected number of interactions between migrants and migrants was 5. If residents were the aggressors, the expected number of attacks between each race would be 10/4 = 2.5 for attacks against other residents and 10/4 x 3 = 7.5 for those against migrants.

taxa present. The number of attacks by migrant Turkey Vultures against residents was significantly higher than expected from the expected value based on attacks ratios relative to group sizes of residents and migrant Turkey Vultures (Table 5.19). Migrants were, therefore, more likely to attack residents than other migrants. Residents were far less likely to be initiators of attacks against migrants than expected due to chance and and were more likely to attack other residents (Table 5.19). Thus, there was strong interference competition at feeding sites between migrant and resident Turkey Vultures.

To some extent, residents avoided attacks from migrants by feeding on small scraps or waited for their turn to feed at some distance from the carcase while migrants were feeding. Resident Turkey Vultures also often waited in trees above the carcase until feeding migrants were satiated. A comparison between numbers of attacks by King Vultures against other King Vultures, migrant Turkey and resident Turkey Vultures showed there was no sigificant difference in the frequency with which each taxa was attacked when expected values were calculated from the proportion of each taxa present (X^2 = 5.8, df 2, P > 0.1).

5.4.5 Interaction intensity on focal sampling days

In both migrant and resident Turkey Vultures, the commonest type of intraspecific interaction was (medium intensity) pecking or chasing (49% and 63% of all interaction types respectively), but in King Vultures most interactions were of low intensity (60% - Table 5.20). The proportions of different types of interactions were compared for aggressor individuals in each taxa (Table 5.20). Compared to migrant Turkey Vultures, aggressor King Vultures had a sigificantly higher proportion of low intensity interactions and fewer medium and

Table 5.20 Frequency of different types of agonistic interactions between three vulture taxa at dry season gallery forest sites when focal vulture is aggressor (i = interaction type, n = number of interactions).

	Aggressor								
	Migrant Turkey			Resident Turkey			King		
Recipient	i	n	%	i	n	%	i	n	%
Migrant	1	58	38	1	3	50	1	43	68
	2	75	49	2	2	33	2	18	29
	3	20	13	3	1	17	3	2	3
Resident	1	26	27	1	13	15	1	9	64
	2	49	51	2	55	65	2	4	29
	3	22	23	3	17	20	3	1	7
King	1	1		1	-		1	21	47
	2	-		2	-		2	18	40
	3	-		3	-		3	6	13

1 = low - intention movements
2 = medium - peck or chase
3 = high - wing-flapping, kick-flapping).

Table 5.21 Numbers of different types of interactions in three Cathartid vulture taxa at dry season forest sites when focal species is aggressor (%).

	Interaction types			
Taxa	1	2	3	TOTAL
MTV	85	124	42	251
	(34)	(49)	(17)	
RTV	16	57	18	91
	(18)	(63)	(20)	
KV	73	40	9	122
	(60)	(33)	(7)	
TOTAL	174	221	69	464

Comparison of frequency of different interaction types between species

MTV vs RTV X^2 = 8.6, df 2, *
MTV vs KV X^2 = 23.5, df 2, **
RTV vs KV X^2 = 38.8, df 2, **

high intensity interactions (Table 5.20). The difference was less significant between migrant and resident Turkey Vultures; when residents initiated attacks they mostly pecked, whereas in attacking migrants there was a higher frequency of low level intention movements. However, there was a highly significant difference between resident Turkey Vultures and King Vultures (Table 5.20). Thus, migrant and resident Turkey Vultures had significantly more high intensity encounters as a proportion of all interactions than King Vultures, but the difference was less significant between migrants and residents.

Most interactions (51%) involving aggressor migrants and recipient residents were of medium intensity and few conflicts developed into high intensity flapping or kick-fights (Table 5.21). The relative proportions of each type of interaction were significantly different between migrants attacking conspecifics and residents attacking conspecifics ($X^2 = 13.5$, df 2, $P < 0.001$ - Table 5.21). This indicated that interactions of higher intensity occurred between residents than between migrants. No significant difference was found between intensity of intraspecific interactions between King Vultures and migrant Turkey Vultures (migrants interacting with other migrants). However, the difference between resident Turkey and King Vultures was significant ($X^2 = 15.1$, df 2, $P < 0.0001$). These findings indicated that relatively more medium intensity (compared to low intensity) interactions occurred between residents than between either migrants or King Vultures.

5.4.6 Group sizes of vultures on carcases of different weight

Table 5.22 shows a breakdown of the mean numbers of different vulture species recorded during focal observations on carcases of different sizes during the dry season. The largest groups of Black

Table 5.22 Group sizes of vultures counted throughout observation periods in gallery forest and open habitats on large (40-120 kg) and medium (<= 6 kg) mammal carcases (mean with 95% Confidence limits, N = number of counts with range below).

	Medium-sized carcases		Large carcases
	Forest	Open	Open
Black	2.1 (1.9-2.2) N = 61 r = 0-4	2.5 (2.3-2.7) N = 45 r = 0-9	7.2 (6.6-9.0) N = 130 r = 0-74
Migrant Turkey	2.5 (2.4-2.6) N = 166 r = 0-6	3.6 (3.4-3.7) N = 184 r = 0-11	2.2 (2.1-2.3) N = 89 r = 0-8
Resident Turkey	2.6 (2.5-2.7) N = 149 r = 0-5	-	-
King Vulture	2.2 (2.1-2.3) N = 152 r = 0-5	1.7 (1.4-2.0) N = 4 r = 0-2	-
Total group size	3.8 (3.7-4.0) N = 274 r = 0-10	4.3 (4.2-4.4) N = 190 r = 0-15	8.8 (8.1-9.6) N = 143 r = 0-74

Comparison between mean group size on medium-sized and large carcases in Black and migrant Turkey Vultures at open sites ('Student' t test);

MTV t_{271} = -7.43, ***
BV t_{176} = 7.62, ***

Comparison between mean group sizes on medium carcases in open and forest habitats;

MTV t_{348} = 6.91, ***
BV t_{104} = 2.09, *

Relationship between carcase weight and group size.

	Open		Forest
Group	r_{401} = 0.44, ***	Group	r_{285} = 0.07, N.S.
Black	r_{203} = 0.50, ***		
Migrant	r_{386} =-0.25, **	Migrant	r_{176} = 0.11, N.S.
		Resident	r_{173} =-0.09, N.S.
		King	r_{165} = 0.19, *

Table 5.23 Counts of groups of Black Vultures on different carcase types in wet and dry season (median with range).

	Wet	N	Dry	N
Horse	37 (23-60)	5	44 (4-100)	10
Cow	89 (38-189)	15	28 (6-150)	6
Calf	26 (9-70)	6	21 (8-40)	3
Pig	47 (6-123)	5	36 (1-121)	20
Capybara	-		18 (1-50)	8

Vultures were recorded on domestic livestock (Table 5.23 shows counts at carcases made over the study period). During focal sampling at baits, average group sizes of Black Vultures were significantly higher on domestic livestock (large baits) than medium-sized carcases. However, group sizes of migrant Turkey Vultures were significantly higher on medium-sized than large carcases (Table 5.22).

Overall group size of scavengers at carcases was significantly positively correlated with carcase weight in open habitats, but not with carcases weight in the forest (Table 5.22), partly because only a small range of carcase weights were provided in the forest but also because scavenging groups were much smaller there. The number of migrant Turkey Vultures recorded at similar-sized carcases was significantly higher in open savanna than forest habitats (Table 5.22).

There was also a highly significant correlation between numbers of Black Vultures and carcase weight in open habitats (Table 5.22). However, by contrast, group size of migrant Turkey Vultures was negatively correlated with carcase weight in the open (Table 5.22). Despite the small range of bait sizes used in the gallery forest the group size of King Vultures was correlated with increased carcase weight. Resident Turkey Vulture numbers showed no correlation with carcase weight. During focal sampling observations no Lesser Yellow-headed Vultures visited carcases, therefore it was not possible to compare numbers of this species with carcase weight. However, general observations made during the wet season were all at domestic hen carcases. Other observations suggested that Lesser Yellow-headed Vultures fed selectively at small (snake, amphibian and avian) carcases.

Table 5.24 Rate of removal of carcases by vultures in gallery forest and non-forest habitats in the dry season (Carcase type indicated in parentheses; where more than one bait provided weights summed. F = Fox, P = Possum, C = Caiman, B = Boa Constrictor, T = Tayra, D = Pig)

Date	Habitat	Median group size (Range)	N	Carcase weight (kg)	Amount removed (kg)	Time taken (min)	Rate of removal (kg/hr)
10/01/86	Gallery forest	3 (0-6)	42	4.36 (F)	2.18	284	0.46
11/02/86		8 (1-13)	16	5.04 (P,T)	4.07	205	1.19
18/02/86		5 (4-7)	16	4.52 (C,P)	4.14	331	0.75
21/02/86		2 (0-9)	9	4.12 (F)	1.94	276	0.42
07/03/86		8 (1-11)	25	5.18 (F,P)	4.40	352	0.75
18/03/86		3 (1-7)	17	1.63 (P)	1.48	183	0.49
21/03/86		4 (1-7)	11	3.72 (P,P)	2.30	182	0.76
12/12/86		3 (0-7)	50	6.00 (F)	2.50	249	0.60
03/01/87		4 (1-9)	69	5.58 (F)	4.50	439	0.61
16/01/87		4 (0-10)	30	2.35 (P)	1.40	213	0.39
15/02/87		2 (1-4)	7	1.40 (P)	1.01	171	0.35
13/03/86	Open	3 (2-3)	3	1.60 (P)	0.88	98	0.54
21/11/86		3 (0-12)	43	4.50 (B)	3.10	428	0.43
23/11/86*		5 (2-38)	28	6.00 (D)	5.57	133	2.51
28/11/86		2 (1-5)	12	1.29 (P)	0.89	236	0.23
08/12/86		5 (0-11)	64	2.80 (F)	1.81	334	0.32
18/01/87		3 (0-8)	14	2.62 (P)	1.67	193	0.52
23/01/87		1 (0-3)	11	4.48 (F)	3.62	219	0.99
28/02/87		4 (0-5)	59	4.78 (F)	2.35	360	0.41

Comparison of rate of removal between forest and non-forest sites; Mann Whitney U Test, U = 25, 11, 7, N.S. (* excluded from analyses because one day old).

5.4.7 Rate of removal of medium-sized carcases in forest and open savanna during the dry season

In gallery forest the rate at which carcases were depleted was significantly correlated with group size (Table 5.24 - $r_s = 0.79$, $N = 11$, $P < 0.01$). However, no such relationship occurred at open sites ($r_s = -0.41$, $N = 7$, $P > 0.1$). There was no significant difference in the rate of carcase depletion between forest and open habitats (Table 5.24), but this depended on group size and composition. However, sample sizes were very small and allow only tentative conclusions.

5.4 DISCUSSION

A number of avoidance mechanisms reduced competition when different vulture species fed at carcases. Most migrants foraged in open or semi-open savannas (Chapter 3, Sections 3.3.1, 3.3.5 and Chapter 4, Section 4.4.7) but a small number of birds foraged in the gallery forest. Thus, although residents avoided competition from migrants by selecting to forage in forest, there was potential for competition between the two races at feeding sites in forest areas and this chapter has concentrated on how such competition might be reduced.

In the dry season, residents fed at the same carcases as migrants in the forest and in the wet season they avoided large dead domestic livestock favoured by Black Vultures. During behavioural observations at carcases in gallery forest, residents were found to avoid interference competition by arriving first at baits and feeding at a high rate before migrant Turkey Vultures or King Vultures arrived.

5.4.1 Time taken to find carcases

Vultures took longer to locate carcases in gallery forest and this was undoubtedly related to the low density of birds in this habitat and/or fewer available carcases. Densities of vultures were much higher in semi-open and open savanna (Chapter 3), which increased their chances of locating food. In the latter habitats there was also less vegetative cover and a higher density of carrion (see Eisenberg *et al* 1979). Therefore, at open sites migrant Turkey Vultures needed to search more actively allowing them to arrive early at food sources to reduce intraspecific competition. That the time taken to locate food was related to density of vultures was shown by the significantly higher speed at which dry season carcases were located compared to wet season ones in similar habitats.

Houston (1986) found no difference in the time vultures took to find carcases in sites of varying vegetation cover and concluded that birds were equally efficient in all habitats. However, his study was carried out in the wet season when densities of vultures were much lower than in the dry season (Chapter 3, Sections 3.3.3, 3.3.7). In the present study, vultures of different species occurred at similar densities in all habitats in the wet season, but there was an increase in vegetative cover at this time of year, making it more difficult for vultures to locate carcases.

5.4.2 Arrival sequence

At gallery forest sites, resident Turkey Vultures were usually the first species to visit carcases. Subordinate species are more active searchers (see Stephens & Krebs 1987) and must arrive early at feeding sites. To meet energy requirements, they must avoid food patches with dominant competitors. Dominant species are able to arrive later in the sequence, because they can defend food against competitors or take over food sources already found by less dominant species. Some species, like King Vultures, arrive late in the sequence because they depend on *Cathartes* vultures to find food and probably do not use olfaction in foraging (Houston 1984), but they have the advantage of large body size and dominance status.

It is possible that very few migrants foraged over gallery forest because they were able to watch the activities of residents from outside the forest. Although searching *Cathartes* vultures were scattered over a wide area, birds soon were attracted to a site where other birds had begun to congregate. In more open savanna habitats in the dry season, this 'local enhancement' occurred much faster (at similar bait types to those placed in the forest) because of greater visibility. The number of birds visiting bait sites was determined by densities of vultures in the area, the group size and species component already feeding, and also the bait size. Against this a subordinate vulture, about to alight, must weigh its hunger state and chances of obtaining food. If food requirements exceed expected intake of food it would benefit individuals to forage elsewhere (see Pulliam & Caraco 1984). A search for alternative food sources by unsuccessful foragers, because of the presence of dominant competitors, may involve a decrease in fitness of individual birds, thus demonstrating competition (see Martin 1985).

5.4.3 Scavengers visiting carcases

In the dry season, the relative proportions of baits visited by resident Turkey and King Vultures reflected their habitat preferences (see Chapter 3, Section 3.3.5). The proportion of bait sites in different habitats visited by migrant and resident Turkey Vultures was significantly different and indicated that migrants visited carcases in all habitats equally. In the wet season, the large percentage of carcases visited by Lesser Yellow-headed Vultures strongly suggested that a migrant race moved into the study area in this season (see Chapter 3, Section 3.3.7).

Other scavenging species which visited carcases may have affected foraging behaviour of vultures although only small numbers of focal samples were obtained because, in forest areas, they rarely participated in interactions. In savanna vegetation types, Crested Caracaras *Polyborus plancus* were frequently present, often finding carcases before vultures. Individual Caracaras were often subordinate to migrant Turkey Vultures and usually only displaced migrants which had been partly satiated. However, many individual Caracaras were dominant to migrant Turkey Vultures so the two species probably have equal status (see Wallace & Temple 1986).

Great Black Hawks *Buteogallus urubitinga* were very aggressive and almost always caused all vultures to fly, but they were only recorded outside the gallery forest (see Thomas 1979). Occasionally Yellow-headed Caracaras *Milvago chimachima* visited bait sites and were sometimes first to locate the food. Although the larger Caracara species and the hawk were dominant to resident Turkey Vultures, both species were also present in the wet season, when vultures foraged outside the forest. Their presence therefore could not account for changes in foraging behaviour of residents described in Chapter 3 and 4.

5.4.4 Food types on which different vulture taxa were found

Both vulture group size (Table 5.22) and species composition varied greatly with carcase type. However, the relationship was not simply related to weight of carcases. Group size of Black Vultures was positively correlated with carcase weight (during focal observations), but numbers also depended on the ease with which carcases could be dismembered. For instance, during general observations, bait chickens attracted very large groups of Black Vultures because they had thin skins and were therefore quickly consumed.

A negative correlation was found between numbers of migrant Turkey Vultures and carcase weight, a finding which differed from that of Houston (1988). This could have been due to the large proportion of medium-sized carcases, the few very large carcases (horses and cows) and the absence of intermediate-sized carcases (ie 6-25 kg) used during focal animal samples. However, it is more likely due to differences in the numbers of different food types provided rather than their weight. For instance, in this study, migrant Turkey Vulture group size was significantly higher on carcases of medium-sized mammals (foxes and possums) than on carcases of domestic livestock. Further, group sizes of different vulture species were compared throughout observation periods and not maximum group size with carcase weight as in Houston's (1988) study. Elsewhere, (an unpublished study referred to in Stewart 1985) counts of vultures at carcases showed that group sizes of Turkey Vultures may be larger on large carcases and even outnumber Black Vultures. As Rabenold (1985) suggests, this may have been due to the numerical dominance of Turkey Vultures in the area used for the study.

Resource partitioning by feeding on carcases of different sizes is therefore not a mechanism separating the races of Turkey Vulture since both fed at similar carcases. It is important in reducing competition between Black Vultures and Turkey Vultures, since each species feeds selectively on different-sized carcases. Group sizes of migrant Turkey Vultures were significantly higher in savanna than in gallery forest on medium-sized small mammalian carcases. This indicated that, outside the forest in the dry season, there were more potential competitors for resident Turkey Vultures.

5.4.5 Interactions at food sites

There was a striking difference in the rates of encounter (attack rate and rate of being attacked combined) between the three taxa at gallery forest sites, although results varied somewhat in separate analyses for single carcase days. These differences could be explained by the small sample sizes obtained for single carcase days or because encounter rate increased when a single dominant feeding vulture attempted to defend several feeding sites. Migrants had higher rates of encounter than either resident Turkey or King Vultures (using the larger data set). No differences were found in rates of being attacked because this included both interspecific and intraspecific interactions. Although migrant Turkey Vultures did not have higher rates of agonistic encounters in open savanna compared to forest, the significantly higher encounter rate overall in this habitat was attributed almost entirely to migrants. In the forest, encounters involving migrants comprised 34% of the total, whereas in open savanna 80% of encounters involved migrants (Tables 5.14 and 5.15). Thus, higher encounter rates in the open savanna and larger group sizes of migrants probably make these habitats unprofitable for foraging residents.

A distinct interspecific vulture dominance hierarchy was found in all habitats. In the forest, the order of dominance was as follows;

King Vulture, migrant Turkey Vulture, resident Turkey Vulture, Black Vulture (rarely present). Generally, the incidence of agonistic interactions was highest intraspecifically. Migrants attacked resident Turkey Vultures significantly more than they attacked other migrants when the relative group sizes of each race present at carcases were taken into account. Migrants won all attacks (except one) which they initiated against residents. During continuous observations, 49 attacks were initiated by residents against migrants. These conflicts probably involved immature or otherwise low ranking migrants or possibly residents which were above average body weight, because most occurred on one observation day. Probably because migrants selectively attacked resident Turkey Vultures, the latter birds often stood away from feeding sites in a similar way to that observed in subdominant gulls at refuse tips (Greig *et al* 1984, 1986).

That aggression was usually highest between most similar forest vulture taxa was shown by the intensity of interactions. In most cases conflicts involving kicking and wing-flapping occurred intraspecifically. The relatively large number of high intensity (wing-flap and kick) conflicts between aggressor migrants and residents compared to migrants and other migrants showed that interference competition was strong between the races. The relatively large number of low intensity interactions among migrant Turkey Vultures or King Vultures compared to resident Turkey Vultures may have been because intention movements toward conspecifics were all that was necessary to establish dominance in larger vultures.

At bait sites outside the forest, dominance hierarchies differed according to carcase type and group size of vultures. The dominance of Turkey Vultures at medium-sized mammalian carcases over Black Vultures found appears to contradict published information elsewhere (Stewart

1978, Wallace & Temple 1986, Jackson 1988). Wallace & Temple (1986) accorded equal dominance status to Black and Turkey Vultures, but most observations were on large-sized carcases where Black Vultures congregate. In the present study, Black Vultures were found to exclude most Turkey Vultures from domestic livestock carcases by their ability to feed in a frenzy, in large numbers, when large amounts of soft, easily consumed food was available. However, during the present study in one-to-one conflicts Turkey Vultures almost invariably dominated Black Vultures.

The Black Vulture of lowland Central and South America, *Coragyps a. brasiliensis* is considerably smaller (see Chapter 6, Section 6.4.1) than *C.a. foetens* of the Andes (the race in Wallace & Temple 1986) or *C.a atratus* of North America. This probably accounts for differences in dominance status of Black and Turkey Vultures observed at the ranch. However, the subdominant status of Black Vultures in relation to Turkey Vultures is unusual because migrant Turkey Vultures were lighter than Black Vultures (Chapter 6).

General observations made in open savanna during the wet season (n=22 days), showed that resident Turkey Vultures were dominant to Lesser Yellow-headed Vultures (all 14 attacks by residents were won). Lesser Yellow-headed Vultures initiated attacks only against conspecifics. Resident Turkey Vultures rarely attacked Black Vultures (n=3) in the open, generally leaving carcases when Black Vultures arrived in large numbers.

5.4.6 Proportions of different activities in focal samples

When focal samples were split into different behaviour categories there were striking differences between taxa. Migrants spent least time feeding at carcases; as a proportion of total samples this was sigificantly different from residents or King Vultures. When they did feed, migrants were significantly more often involved in interactions than either of the other taxa.

The incidence of feeding without interacting with other individuals was higher in resident Turkey and King Vultures compared to migrants. These results indicated that at forest feeding sites migrants may have been at a disadvantage to resident Turkey and King Vultures (see Chapter 6, Section 6.4.2). Residents arrived before migrants and King Vultures dominated carcases later in the arrival sequence. However, there was no difference between the relative proportions of these activity classes in focal samples of migrant Turkey Vultures at open or forest sites, despite the absence of King Vultures at most savanna baits.

5.4.7 Feeding behaviour at carcases

Resident Turkey Vultures had a significantly higher peck rate than other forest scavengers, even when the effects of group size were taken into account. Compared to migrant Turkey and King Vultures the high feeding rate of residents was related to the fact that they arrived earlier than other vulture taxa and had to feed quickly before dominant competitors arrived. Although an individual feeding singly at a carcase had to spend more time looking up in order to detect arriving conspecifics, this was a lesser constraint than the presence of other vultures. Knight and Knight (1986) showed that in Bald Eagles *Haliaeetus leucocephalus* birds were more vigilant in larger groups to avoid piracy or injury by conspecifics rather than to detect predators. Vultures, like Bald Eagles, have no known predators (humans excepted), but other vultures frequently arrived suddenly at carcases and displaced unsuspecting birds which were feeding.

Although migrants had a lower peck rate (a correlate of larger group sizes and higher encounter rates) their dominant status over residents enabled them to feed for longer periods. This was also strikingly apparent in the King Vulture, which had very slow feeding rates over long periods. Peck rates were often recorded in individuals newly arrived at carcases so there were some biases towards resident Turkey Vultures. However, the multivariate analysis showed that peck rates were significantly different between taxa, despite variation in group size.

There was probably variation in the relative hunger-states of different individuals of the three vulture taxa. Low-ranking vultures, like resident Turkey Vultures had to search more actively for undiscovered carcases or those with smaller attendent groups and so may have been more hungry than dominants. Hunger-states of migrants also depended on their intraspecific dominance status and also how recently they had fed and therefore the general abundance of food in the area. The weekly variations in numbers of migrants in the study area (Chapter 3, Section 3.3.3) probably resulted in different levels of competition throughout the dry season.

The peck rates of different vulture species were related to their bill morphology, gape and preferences for different parts of carcases, in addition to metabolic needs. Houston (1988) measured the gape of small Cathartid vultures and found that increased gape size was not a correlate of larger body weight. King Vultures (the largest species) had the smallest gape size followed by Turkey Vultures, while Black Vultures had the largest. Gape was related to the parts of carcases consumed. Black Vultures are adapted to swallowing soft matter and have relatively fine bills. In contrast, the King Vulture uses its powerful bill to open the tough skin of larger mammals (such as Giant Anteaters *Myrmecophaga myrmecophaga*) and for feeding on cartilaginous and tendon tissue attached to bones (Houston 1988). Therefore a comparison of peck rates between different vulture species is only an estimate of the relative amounts swallowed. However, an accurate comparison may be made intraspecifically between migrant and resident Turkey Vultures which have similar bill morphology (Chapter 6, Table 6.3). The relative amounts of time spent feeding by different species is related to their metabolic requirements. Larger vultures would feed longer than smaller species, because of the relationship between body mass and metabolic rate (Kleiber 1970).

5.4.8 Effect of group composition on feeding behaviour

The results of the Stepwise Multiple Regression analysis showed that peck rate of resident Turkey Vultures was negatively correlated with two variables; numbers of migrants and King Vultures, but not with numbers of residents. The significant positive correlation between numbers of Black Vultures and peck rate in residents may be attributed to several factors; for example more Black Vultures may have visited forest carcases when only residents were present and the presence of a subordinate species may have induced residents to increase their feeding rate before the arrival of migrants. Migrants usually arrived after residents when group sizes were larger, and therefore had an overall lower peck rate.

Feeding rates were thus affected by the species composition of the group rather than overall group size. For instance, King Vultures were almost never pecked at by other species, fed during over 80% of observations, and participated in few high level interactions. King Vultures were not normally affected by arrivals of conspecifics because these were usually family groups comprising two adults and sometimes several generations of offspring (King Vultures can be aged up to six years by which time they have acquired adult head colouration and the body plumage becomes completely cream/white - see Wallace & Temple 1986).

The negative correlation between peck rate in migrants and King Vulture numbers may partly explain why few migrants foraged in the forest. In open habitats, group size of migrants had a significant negative effect on peck rate in other migrants. This indicated that in open habitats there was strong intraspecific competition between migrant Turkey Vultures on medium-sized carcases. No other species was found to have a significant effect on migrant peck rate in open savanna. Thus, in the gallery forest, King Vultures may have prevented migrants obtaining sufficient food to meet energetic requirements. Residents, on the other hand, mostly avoided King Vultures by arriving early at carcases.

For resident Turkey Vultures, the numbers of King Vultures and migrants present affected feeding rates considerably. Residents fed when there was more than one migrant present in a group on only 4% of observations, demonstrating the inhibitory affect of migrants on the feeding of residents. Increased encounter rates in residents due to migrant group size clearly prevented residents from feeding. Most residents left the ground and perched in trees above baits when several migrants arrived, and it is probable that they visited carcases the following day after roosting closeby, when baits had been depleted and migrants may have left.

In conclusion, this chapter demonstrates that there was less competition for resident Turkey Vultures from migrants in gallery forest compared to open savanna due to lower migrant group sizes at carcases and lower rates of agonistic encounter. Chapter 3 showed that densities of foraging *Cathartes* Vultures were significantly lower over the gallery forest than in the open. This enabled subordinate resident Turkey Vultures to locate food first and feed before other vultures arrived at carcases.

SUMMARY

1) Baits placed outside the forest were located by vultures significantly faster than those within the gallery forest. Furthermore, mean group sizes of vultures visiting medium-sized carcases in savanna habitats were significantly larger than in gallery forest. Migrant Turkey Vultures arrived signficantly faster at savanna sites than in the forest. These factors probably acted as a constraint on residents feeding outside the forest.

2) During the dry season, resident Turkey and King Vultures visited gallery forest carcases significantly more than carcases in open and semi-open habitats. However, there was no difference in the proportion of carcases visited by migrants in different habitats.

3) Group size of Black Vultures were significantly correlated with carcase weight in open savanna habitats. However, migrant Turkey Vulture numbers were negatively correlated with carcase weight. Thus migrant Turkey Vultures fed selectively at smaller carcases. During the dry season residents and migrants fed on similar carcases in the forest.

4) The rate of agonistic encounters between all vultures was higher on similar carcases at open savanna sites than in the gallery forest. During observations in dry season gallery forest, migrants attacked other individuals at a significantly higher rate than did resident Turkey or King Vultures (interspecific and intraspecific interactions combined), showing that they were more aggressive.

5) Usually the initiator of attacks won conflicts with recipient vultures. During encounters, migrants won all but 1 (N = 623) of the conflicts which they initiated with residents. On 48 (out of 49) occasions residents won attacks which they initiated with migrants. The majority of these occurred on one observation day when very low

numbers of migrants were present; this suggests that one resident of above average body size was responsible for these attacks and that low-ranking migrant Turkey Vultures were involved. Generally, residents were therefore subordinate to migrants. Migrants directed more attacks than expected against residents and less than expected against other migrant Turkey Vultures.

6) Feeding rates were strikingly different between taxa, being highest in subordinate and lowest in dominant taxa. Resident Turkey Vultures had the highest peck rates, followed by migrant Turkey Vultures. King Vultures had significantly lower peck rates than either of the other taxa. Most resident Turkey Vultures fed when group sizes were less than three birds. When group size was greater than three individuals there was no significant difference between peck rates of migrants and residents.

7) A multivariate analysis showed that the peck rate of residents was highly negatively correlated with numbers of both migrant Turkey and King Vultures, but there was no correlation with numbers of residents present at carcases. There was a significant decrease in the peck rate of migrants with group size of King Vultures in forest habitats, but in open savanna migrant peck rate was negatively correlated with numbers of migrants. This indicated that interference competition between migrants was higher in open savanna - see 2).

8) Resident Turkey Vultures arrived early in the sequence, fed faster and had a lower encounter rate than migrants. During focal samples King Vultures fed most often, followed by residents and migrants. Because they arrived later at gallery forest sites and had to compete with more individuals, migrants spent less time feeding and more time interacting and standing still. However, migrants compensated for this to some extent by being dominant to residents at food sites, enabling

them to feed for longer periods. They were subordinate to King Vultures though, which prevented them from feeding at gallery forest sites. Although King Vultures often foraged outside forest habitat, a very low proportion of open savanna baits were visited, and then usually only by single birds. In the forest, King Vulture family groups frequently visited carcases, and this may partly account for the low densities of migrants which foraged in this habitat.

CHAPTER 6 BODY SIZE AND CONDITION OF VULTURES

6.1 INTRODUCTION

Interspecific and intraspecific differences in biometric measurements may provide clues about the adaptive significance of particular traits and their role in ecological separation within or between avian species (see Wilson 1975). For species which have dietary overlap (eg. three *Buteo* species studied by Janes 1985), differences in wing-loading may allow exploitation of different habitats and be important in resource partitioning. Differences in wing-loading of Cathartid vultures may help explain habitat selection and foraging strategies (Chapter 3) as it does in raptors (Janes 1984). Although large body size is an advantage to vultures, because of their unpredictable food supply (Houston 1976 b), lower wing-loading enables birds to fly earlier in the day and avoid interference competition (Brown & Amadon 1968).

There are a number of different ways to measure body condition, and these usually involve an estimate of fat reserves, such as lipid indices of dead birds (Houston 1976 b, Evans & Smith 1975). To avoid unnecessary collecting of birds, other measures may be used such as abdominal profiles of birds in the field (eg. Barnacle Geese *Branta leucopsis* - Owen 1981), body weights corrected for size (Owen & Cook 1977, see Johnson *et al* 1985) and seasonal changes in body weight (Hanson 1962). Where there are appreciable differences in body size within species, body weight can be a misleading measure because of its variability due to other factors, such as how recently birds have fed (Owen & Cook 1977). In large birds like vultures, there are also considerable variations in skeletal size in birds of the same weight (see Houston 1976 b).

A measure of fat (or lipid index-see Johnson *et al* 1985) is useful to assess seasonal changes in body condition of birds or the physiological changes associated with migration (Odum *et al* 1964, Fry *et al* 1972, Diamond *et al* 1977, Blem 1980). Turkey Vultures do not feed on migration (Smith 1980, 1985 a, b) so it might be expected that birds which had recently arrived in South America would be in poorer condition than those trapped later in the dry season (ie. November/December caught birds compared to January.) Variation in body condition between migrant and resident vultures may indicate differences in the ability of these groups to exploit available food or cope with potential competition. The large increase in density of *Cathartes* vultures during the dry season due to the influx of migrant Turkey Vultures (Chapter 3) may affect food availability and body condition of resident Turkey Vultures by direct competition at feeding sites or indirectly by forcing them to forage in gallery forest.

Members of both the New and Old World vulture families show great size polymorphism (Kruuk 1967, Houston 1974, 1983, Wallace & Temple 1986) and interspecific dominance rank is a correlate of interspecific variation in body size when individuals scavenge in mixed-species flocks (Chapter 5, Section 5.4.4). In small Cathartid vultures there are also intraspecific differences in body size between different races and subpopulations (Wetmore 1964, Brown & Amadon 1968, Blake 1977). Differences in body sizes of migrant Turkey Vultures trapped in different months could provide evidence for the leap-frog migration believed to occurr in this species (Salmonsen 1955, Stewart 1977). Larger, northern avian races are often dominant to southern congeners where groups feed at clumped food sources (eg. Scandinavian over British Herring Gulls - Greig *et al* 1986) so a comparison of biometrics between migrant and resident Turkey Vultures may reveal considerable size differences. The aim of the present chapter was; i) To record biometrics for all vulture species and compare measurements of migrant and resident Turkey Vultures to see how they differed.

ii) To compare the body condition of resident Turkey and Black Vultures between months, and relate these to possible changes in food supply or level of competition.

iii) To compare body size of vultures caught at different times to see if different subpopulations foraged in the study area.

iv) To compare body size of migrants first caught in the autumn with later arrivals to see if early arriving birds differed in size from those which arrived later on.

6.2 METHODS

6.2.1 Procedure for measuring vultures

Trapped vultures were used to provide a range of biometric data (General Methods - Chapter 2, Sections 2.2.1-2.2.3). The following details decribe the methods used to measure different parameters.

1) Body weight; vultures were weighed in polypropelene sacks with a 5kg spring balance (precision 0.01 kg).

2) Wing span; vultures were placed ventral side uppermost, with both wings fully outstretched and measured between the tips of the longest primary in each wing.

3) Flattened and straightened wing; distance between carpal joint and tip of longest primary on closed wing.

4) Wing breadth measurements;

a) Leading edge to trailing edge at position of humerus with ulna/radius joint.

b) Leading edge to trailing edge at position of ulna/radius with carpus/metacarpals joint.

5) Head and bill - bill tip to posterior of skull.

6) Head width at widest point.

7) Bill depth - at widest point.

8) Bill length - two measurements were made a) tip of bill to proximal edge of nostril and b) from bill tip to top of nostril.

9) Tarsus - from the nucal notch on the intertarsal joint to joint with third toe.

10) Head and body - vultures were placed ventral side uppermost and measured from tip of tail to bill tip, with neck outstretched.

11) Tail length - from the base of the central pair of rectrices to the tip of the longest feather when the tail was closed.

12) Wing area was calculated for some individuals by extending the wings over paper and tracing the wing outlines. Wing area for all other individuals was estimated from measurements of wing span and width.

Measurements 2,3,4,9 and 10 were made with Vernier calipers. The remaining measurements were made with a flat rule or tape measure.

6.2.2 Analysis of results

The data were normally distributed enabling use of parametric statistics throughout. To obtain an index of body size a Principal Components Analysis was performed, firstly entering 11 body measurements in the analysis and then repeating this, with weight excluded. Body weight was not used in the measure of body size (Principal Component 1) for the condition indices. Body condition was estimated by regressing Principal Component 1 (a predictor of body size) against body weight for each vulture taxon; the residual values were used as a measure of the body (probably fat) condition of birds Thus, the index of body condition was the deviation about the regression line and was therefore a positive or negative value.

The body condition of resident Turkey Vultures was compared between months to see if there was any relationship with the presence or absence of migrants, or possible changes in food supply. For some taxa, data were pooled for the early dry season, mid-late dry season and late dry/early wet season because of small sample sizes for some months. Variation in body condition of Black Vultures and migrant Turkey Vultures was compared between different months to investigate any general pattern of response in relation to food supply. In addition, the body size of migrant Turkey Vultures was compared between dry season months to test the hypothesis that smaller individuals were first to arrive in South America.

Sample sizes were too small for birds with known wing area to compare wing-loading between different taxa. Therefore, an estimate of wing area was calculated in the following way: average wing width measurements (wing width measurements/4) x wing span. Wing loadings (in Newtons) were then calculated using the equation: weight (kg) x 9.81/ wing area (m^2) (Pennycuick 1972 a.). The former equation overestimated wing area and wing-loadings were therefore lower than those calculated for individual vultures by tracing wing outlines and weighing the tracings. Nevertheless, the measurements were comparable between different taxa.

6.3 RESULTS

Measurements were made on 128 Black Vultures, 153 migrant Turkey Vultures, 70 resident Turkey Vultures and 4 Lesser Yellow-headed Vultures. However, smaller sample sizes were available for the Principal Components Analysis because an incomplete set of measurements were taken from some individuals.

6.3.1 Differences between taxa

Of the four taxa, Black Vultures were the heaviest, followed by migrant Turkey Vultures, resident Turkey Vultures and Lesser Yellow-headed Vultures (Tables 6.1-6.3). Black Vultures had longer legs and shorter wings than the *Cathartes* species. Black Vultures had relatively short, broad wings, compared to *Cathartes* Vultures which had longer, narrower wings (Tables 6.1-6.3).

Migrants were significantly larger than residents in most body measurements (Table 6.3). However, there were no significant differences between the two races in head and bill, bill length measurement (1) and tail length. Differences between wing width measurements were not consistent and significance levels varied considerably between the two races (Table 6.3). This was due to the difficulty of standardising wing width measurements.

6.3.2 Differences in wing-loading between taxa

There was a striking difference in wing-loading between the taxa; Black Vultures had significantly higher wing-loading than any *Cathartes* taxa (Table 6.4). Among *Cathartes* vultures, migrant Turkey Vultures had a significantly higher wing-loading than residents, while Lesser Yellow-headed Vultures had a significantly lower wing-loading than resident Turkey Vultures (Table 6.4). The relationship between wing area and body weight varied considerably between taxa. In Black and migrant Turkey Vultures, there was a highly significant correlation between wing area and body weight (Table 6.4, Figure 6.1). The correlation was less significant for resident Turkey Vultures (Table 6.4, Figure 6.1). Thus, wing area was most highly correlated with body weight in species with highest wing-loading.

Table 6.1 Biometrics of Black Vultures *Coragyps atratus* (means ± SD, weight in kg, measurements in cm.).

Measurement	Mean	SD	N
Weight	1.63	0.16	144
Wing length	134.1	3.95	70
Flat wing cord	39.2	3.25	126
Wing width (LW)1.	26.8	0.87	84
2.	27.8	0.95	84
Wing width (RW)1.	26.7	0.91	83
2.	28.0	1.05	83
Head and Bill	10.66	0.34	83
Head width	4.00	0.20	83
Bill length 1.	2.54	0.27	42
2.	4.43	0.22	82
Bill depth	1.84	0.53	128
Tarsus	8.97	0.32	126
Head and body	58.2	1.85	71

Table 6.2 Biometrics of Lesser Yellow-headed Vulture *Cathartes burrovianus* (Mean ± SD, weight in kg, measurements in cm.)

Measurements	Mean	SD	N
Weight	0.95	0.09	4
Wing length	157.0	5.56	4
Flat wing cord	47.4	1.64	4
Wing width (LW)1.	26.9	1.73	4
2.	26.0	0.93	4
Wing width (RW)1.	27.1	1.42	4
2	26.3	0.61	4
Head and bill	9.00	0.24	4
Head width	3.47	0.04	4
Bill length 1	2.09	0.05	3
Bill depth	1.94	0.31	4
Tarsus	7.02	0.14	4
Head and body	56.3	1.47	4
Tail	21.5	0.92	3

Wing width 1 = Leading edge to trailing edge at position of humerus with ulna/radius joint.

2 = Leading edge to trailing edge at position of ulna/radius with carpus/metacarpals joint.

LW = left wing
RW = right wing

Table 6.3 Comparison of biometrics between migrant *Cathartes aura meridionalis* and resident Turkey Vultures *C. a. ruficollis* (Mean ± SD, weight in kg, measurements in cm, t = 'Student' t test).

	Migrant			Resident					
Measurements	Mean	SD	N	Mean	SD	N	t	df	P
Weight	1.42	0.17	150	1.22	0.10	64	8.91	212	***
Wing length	168.6	4.31	143	164.5	3.73	68	6.78	209	***
Flat wing cord	50.3	2.82	152	49.6	1.65	69	2.03	219	*
Wing width (LW) 1.	29.6	1.12	153	29.3	1.20	69	1.85	220	N.S
2.	28.9	1.27	153	28.3	1.19	69	3.24	218	**
Wing width (RW) 1.	29.6	1.02	150	29.1	1.54	70	2.69	218	**
2.	29.1	1.21	150	28.7	1.15	70	2.40	221	*
Head and bill	9.33	1.54	153	9.35	0.29	70	-0.01	220	N.S
Head width	3.83	0.16	152	3.64	0.13	70	8.51	220	***
Bill length 1.	2.30	0.14	67	2.26	0.17	44	1.43	109	N.S
Bill length 2.	3.66	0.16	75	3.47	0.18	18	4.70	91	***
Bill depth	1.60	0.11	151	1.50	0.08	70	7.02	219	***
Tarsus	7.38	0.30	151	7.22	0.27	70	3.88	219	***
Head and body	64.7	2.05	141	63.1	1.44	69	5.64	208	***
Tail	25.1	1.04	74	25.2	0.72	51	-0.74	123	N.S

LW = left wing
RW = right wing

Table 6.4 Relationship between weight and wing area in vultures.

Taxa	Body weight (kg.)		Wing length m^2		Wing area m^2		Wing loading N/m^2		
	m	SD	m	SD	m	SD	m	SD	N
Black	1.63	0.16	1.34	0.04	0.37	0.02	43.6	3.30	64
Migrant Turkey	1.42	0.17	1.69	0.04	0.49	0.03	28.2	3.14	140
Resident Turkey	1.22	0.10	1.65	0.04	0.47	0.02	25.1	2.00	60
Yellow-headed	0.95	0.09	1.57	0.06	0.42	0.02	22.3	1.12	4

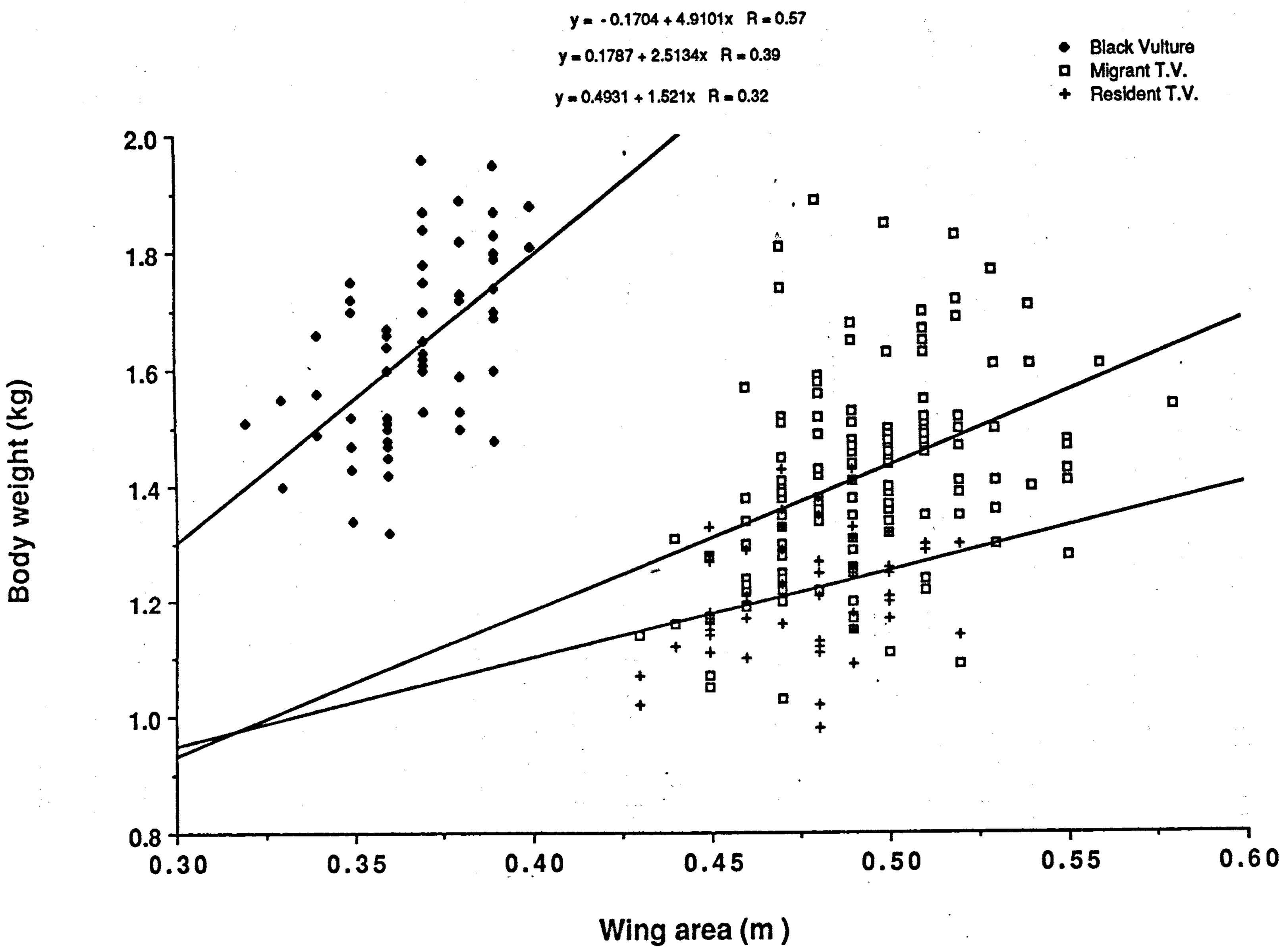
Correlation coefficients and regression equations for each taxa (wing area against body weight).

Black Vulture	$r = 0.60$, ***
Migrant Turkey Vulture	$r = 0.39$, ***
Resident Turkey Vulture	$r = 0.34$, **

Comparison of wing-loading between species ('Student' t tests)

BV vs MTV	$t = 32.0$, df 202, ***
MTV vs RTV	$t = 7.1$, df 198, ***
RTV vs LYH	$t = 2.7$, df 62, **

Figure 6.1 Relationship between weight and wing area in different vulture taxa



6.3.3 Body size differences

The Principal Components Analysis showed that of all the biometrics measured, wing span was the most consistent predictor of body size because it had the highest correlation with Principal Component 1 (PC1) for all taxa when body weight was excluded from the analysis (Table 6.5). Wing width measurements were also highly correlated with PC1 but the correlation varied between taxa and depended on whether weight was included in the analysis (Table 6.5). When weight was included, body length was also a good predictor of body size for Black and migrant Turkey Vultures (Table 6.5).

There was a significant correlation between weight and body size (PC1) for all taxa; Black Vultures ($r_{152} = 0.56$, $P < 0.0001$; $y = 1.64 + 0.04\ x$), migrant Turkey Vultures ($r_{136} = 0.48$, $P < 0.0001$; $y = 1.42 + 0.04\ x$) and resident Turkey Vultures ($r_{60} = 0.42$, $P < 0.0001$; $y = 1.21 + 0.02\ x$). In Black Vultures the variation in weight due to body size (r^2) was 29.8 %, in migrant Turkey Vultures it was 22.2%, but it was only 15.8% in resident Turkey Vultures. Thus, the variation in body size not explained by weight was larger in the smaller vultures.

6.4.4. Differences in body size and weights of vulture taxa between months

Body weights of trapped migrant Turkey Vultures were significantly different between months (Table 6.6, Figure 6.2). Table 6.6 shows that individuals caught in November and December were below average body weight and were significantly lighter than migrant Turkey Vultures caught in January. There was no significant difference in body size between migrant Turkey Vultures caught in different months (Table 6.7, Figure 6.3) but birds trapped in November were significantly larger than those caught in December ($t_{39} = -2.16$, $P < 0.05$ - Table 6.7). This indicated that larger Turkey Vultures arrived

Table 6.5 Loadings between Principal Component 1 and body measurements in three vulture taxa, including (1) and excluding (2) body weight (highest correlations only shown).

	Black Vulture		Resident Turkey Vulture		Migrant Turkey Vulture	
	PC1		PC1		PC1	
Parameter	1	2	1	2	1	2
Wing length	-0.36	-0.35	-0.40	-0.41		-0.34
Flat wing cord	-0.35					
Wing width LW1					-0.34	
LW2	-0.36	-0.41				
RW1					-0.34	
RW2					-0.33	-0.35
Body length			-0.40		-0.34	-0.34

Table 6.6 Variation in body weights of three vulture taxa trapped in different months.

	Black Vulture			Resident Turkey Vulture			Migrant Turkey Vulture		
Month	m	SD	n	m	SD	n	m	SD	n
October	-			1.26	0.10	7	1.51		1
November	1.44	0.03	2	1.21	0.10	5	1.36	0.12	21
December	1.53	0.18	13	1.19	0.07	10	1.37	0.14	28
January	1.58	0.16	26	1.18	0.11	2	1.41	0.18	43
February	1.62	0.17	4	1.24	0.09	4	1.52	0.15	19
March	1.66	0.14	92	1.17	0.10	20	1.42	0.20	35
April	-			1.25	0.12	10	1.61	0.12	3
May	1.72	0.12	6	1.32	0.08	2			
June	-			1.28	0.01	4			

Comparison of weights between months (one-way ANOVA).

Black Vulture $F_{2,140} = 7.89$, ***
Resident Turkey Vulture $F_{2,61} = 5.12$, **
Migrant Turkey Vulture $F_{4,145} = 2.87$, *

(Due to small sample sizes for Black Vultures and resident Turkey Vultures data were pooled for 1. early dry season-November, December, January; 2. mid/late dry season-February, March; 3. late/dry-wet season-April, May, June, October).

Table 6.7 Body size (Principal Component 1) of three vulture taxa trapped in different months.

	Black Vulture			Resident Turkey Vulture			Migrant Turkey Vulture		
Month	m	SD	n	m	SD	n	m	SD	n
October	-			-0.59	1.40	8	2.35		1
November	-			-0.38	1.37	4	0.89	2.46	21
December	-0.02	3.34	3	-1.79	2.10	10	-0.75	2.30	18
January	-0.27	1.71	21	-0.67	0.72	2	-0.03	2.56	42
February	-			0.25	1.05	7	0.02	2.31	19
March	0.14	2.07	42	0.66	2.15	19	-0.11	2.12	34
April	-			0.55	1.64	11	-1.08	0.63	3
May	-			1.06	0.18	2	-		
June	-			0.76	1.72	4	-		

Comparison between months in body size of different vulture taxa. ('Student' t test and one-way ANOVA).

Black Vulture t_{61} = 0.83, N.S.
Resident Turkey Vulture $F_{2,67}$ = 5.76, **
Migrant Turkey Vulture $F_{4,138}$ = 1.45, N.S.

(Due to small sample sizes for resident Turkey Vultures, data were pooled; 1. early dry season-November, December, January; 2. mid/late dry season-February, March; 3. late dry/ early wet season-April, May, June, October.)

Figure 6.2 Body wt. of migrant Turkey Vultures trapped in different months

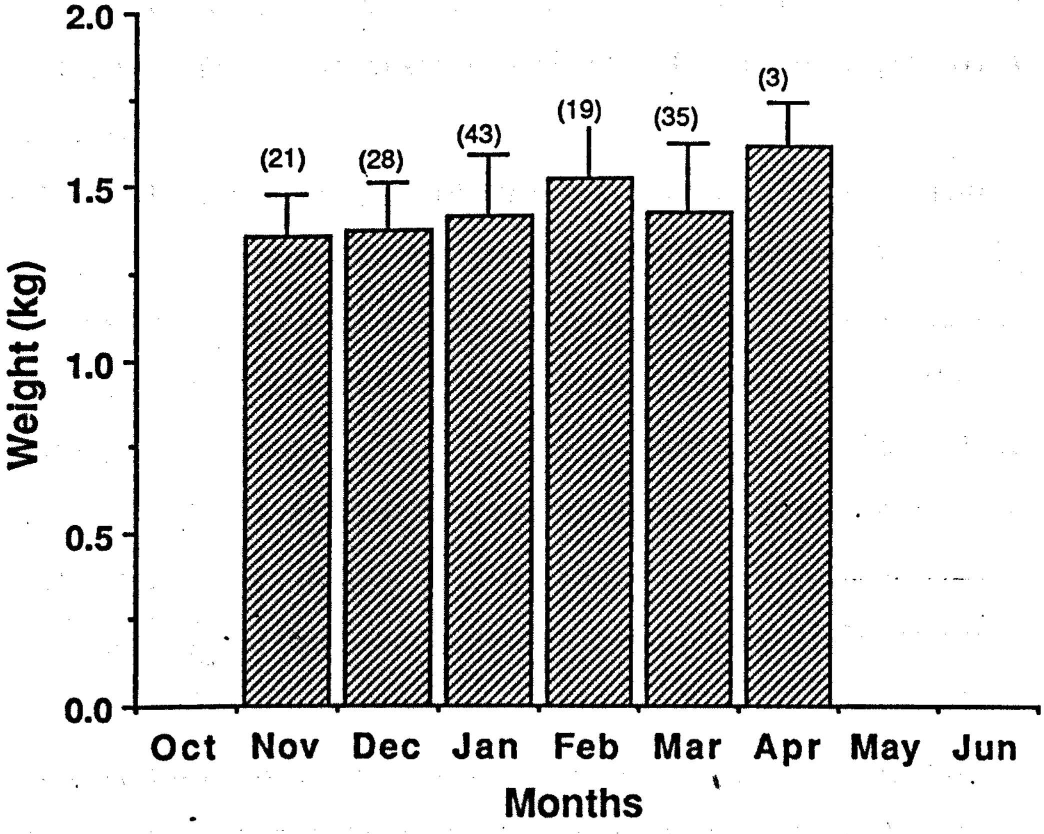
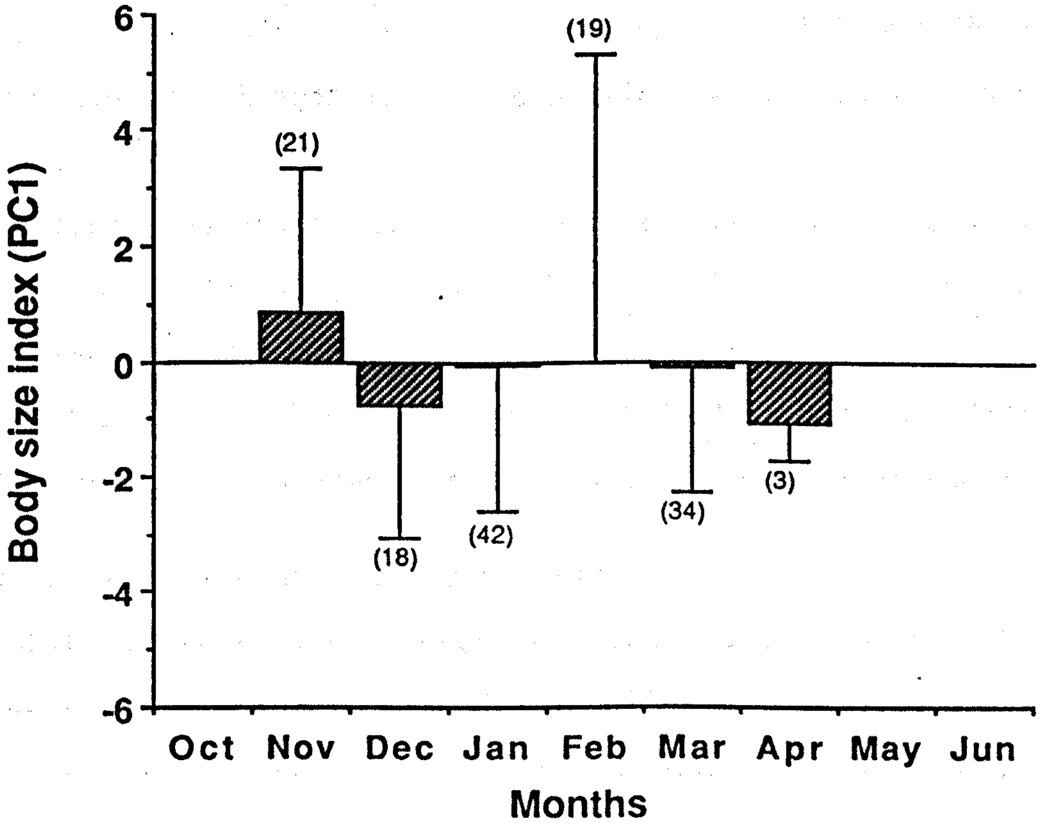


Figure 6.3 Body size indices (Principal Component 1) of migrant Turkey Vultures in different months



first at the ranch but did not remain in the area (Figure 6.3). The fact that trapped vultures in both months were of similar weights (Table 6.6) may reflect the greater distances flown by larger birds (see Section 6.3.5).

The body sizes and weights of trapped resident Turkey Vultures differed significantly between periods (data were combined for early dry season, mid/late dry season and early wet season - Tables 6.6 and 6.7). Resident Turkey Vultures of above average body size caught in March (Table 6.7, Figure 6.4), had low actual body weights (Table 6.5, Figure 6.5). All the birds from October to January, which were below average body size were trapped in the 1986/87 field season, while those from February to June were trapped in all three field seasons. When data were pooled to incorporate months with small sample sizes (see Table 6.7, 6.8), body weights of birds were significantly higher in the wet season than either early or late dry season months. However, vultures caught in the wet season were below average body size. Conversely, in the early dry season large resident Turkey Vultures had below average weights. These data suggested that there were considerable changes in body condition between months (see below).

The body weights of Black Vultures differed significantly between months (Table 6.6, Figure 6.6), being highest in the wet season (though sample sizes were small) and lowest in the early dry season. There was no significant difference in body size of birds trapped between the two months with adequate sample sizes (Table 6.7).

6.3.5 Variation in body condition between months

Despite small sample sizes, the trend was for substantial differences in average body condition in different months, in both resident and migrant Turkey Vultures (Table 6.8, Figure 6.7, 6.8).

Figure 6.4 Body wt of resident Turkev vultures trapped in different months

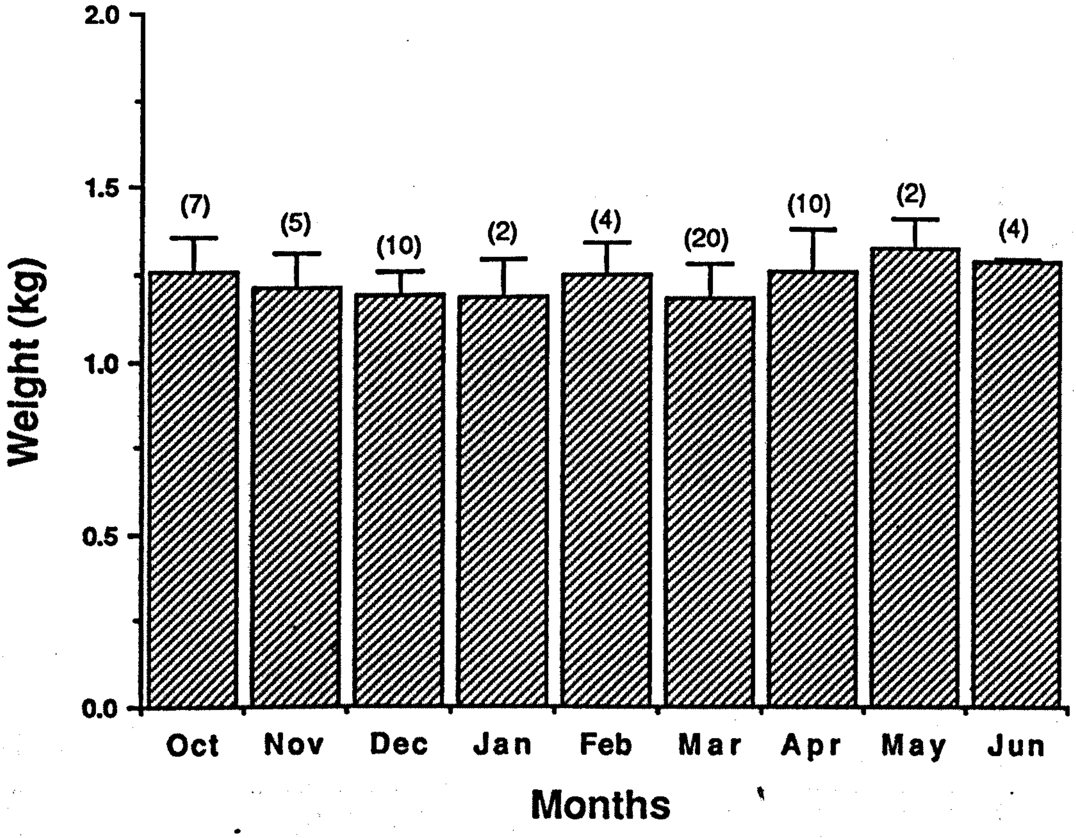


Figure 6.5 Body size indices (Principal Component 1) of resident Turkey Vultures in different months

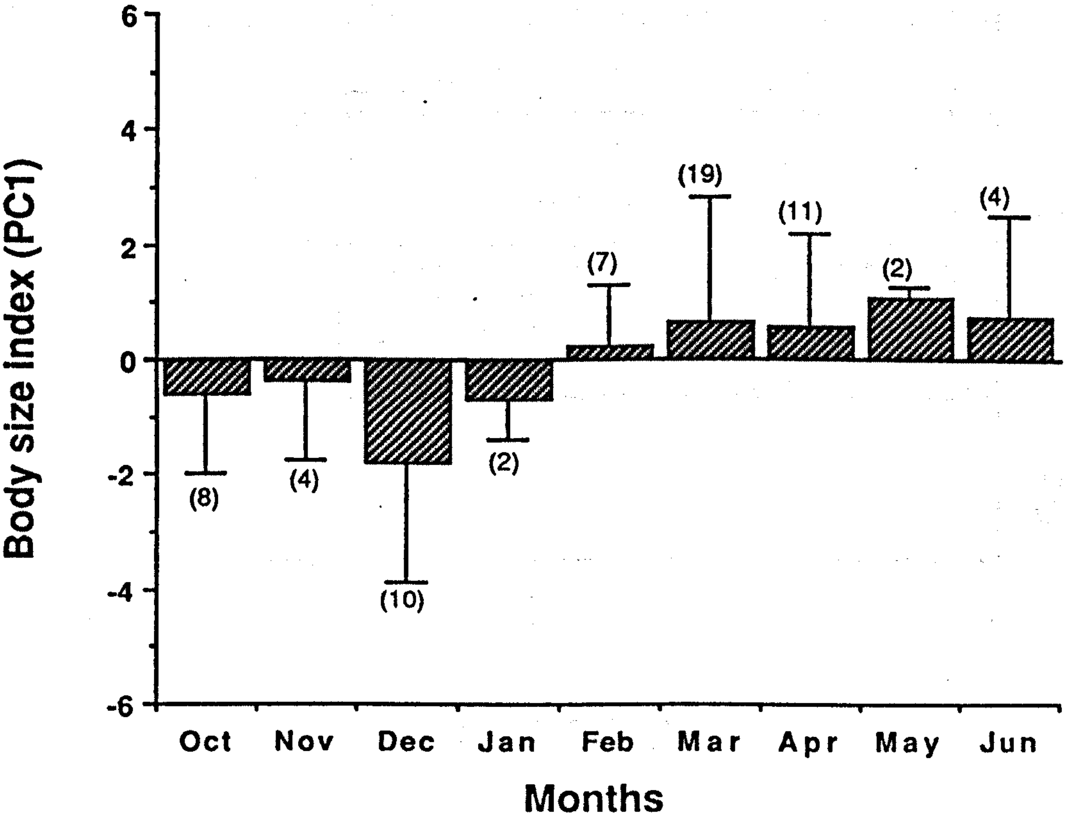
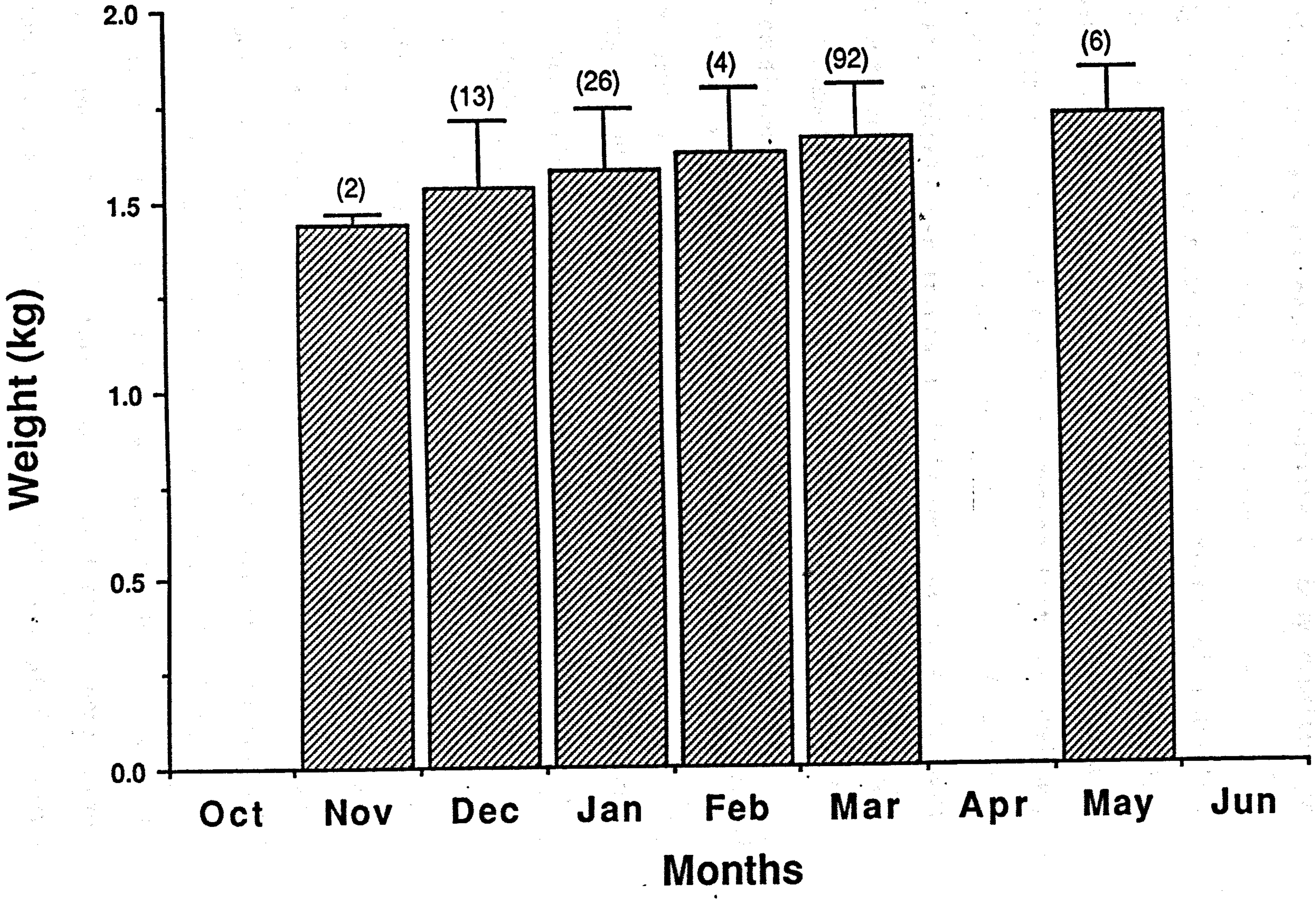


Figure 6.6 **Body wt of *Black Vultures trapped* in different months**



There were large differences between the body condition of migrants and residents trapped in the same month (Table 6.8, compare Figures 6.7 and 6.8). Sample sizes were too small to permit detailed comparisons between months for Black Vultures (Table 6.8). However, the general pattern was for great variability in body condition in each trap month when sufficient measurements were made. This variability was probably related to dominance status of individual Black Vultures; all birds were included in the analysis, including some juveniles and young adult birds. A comparison of body weights of Black Vultures in different months suggested that, on average, increasingly heavy birds were caught during the dry season (Table 6.6, Figure 6.6). Monthly variations in body weights of birds were comparable with condition indices (compare Figures 6.2 with 6.8; 6.4 with 6.7 for *Cathartes* Vultures), so this may indicate that birds were in better condition in the late dry season than early dry season.

Migrant Turkey Vultures had lowest body condition (probably least fat) in November after recently arriving in the Llanos from North America (Table 6.8). The average body condition of trapped migrants increased after arriving in South America and was highest in the late dry season (Table 6.8, Figure 6.8). Migrants trapped in March were in average body condition.

By contrast, resident Turkey Vultures were in best condition in the wet season months (October, May and June) when migrants were absent (Table 6.8, Figure 6.7). In the dry season, resident Turkey Vultures were in significantly poorer condition than in the wet season. Body condition was much lower in March than all other months, in contrast to migrant Turkey and Black Vultures (Table 6.8). A small number of resident Turkey Vultures caught in February were above average condition. Migrants trapped in this month were also in very good condition (Table 6.8).

Table 6.8 Body condition (residuals of body weight regressed against Principal Component 1) of three vulture taxa trapped in different months.

	Taxa								
	Black Vulture			Resident Turkey Vulture			Migrant Turkey Vulture		
Month	m	SD	n	m	SD	n	m	SD	n
October	-			0.34	1.24	10	0.05	-	1
November	-			-0.29	0.58	4	-0.57	0.57	21
December	0.45	1.38	2	-0.01	0.36	8	-0.22	0.82	17
January	-0.45	0.87	19	-0.25	0.98	2	-0.04	0.95	42
February	-			0.18	0.89	4	0.65	0.92	19
March	0.20	1.01	39	-0.57	1.08	19	0.01	1.14	33
April	-			0.34	1.24	10	1.52	0.87	3
May	-			0.92	0.88	2	-		
June	-			0.50	0.49	4	-		

Differences in body condition (comparison of regression lines of weight plotted against body size) between months (Covariance analysis, slopes significantly different).

Black Vulture $F_{1,56}$ = 0.72, N.S.
Resident Turkey Vulture $F_{2,57}$ = 4.44, *
Migrant Turkey Vulture $F_{4,131}$ = 2.95, *

(Due to small sample sizes, for resident Turkey Vultures data were pooled 1. early dry season-November, December, January; 2. mid/late dry season-February, March; 3. late dry/ early wet season-April, May, June, October.)

Figure 6.7 Body condition of resident Turkey Vultures trapped in different months

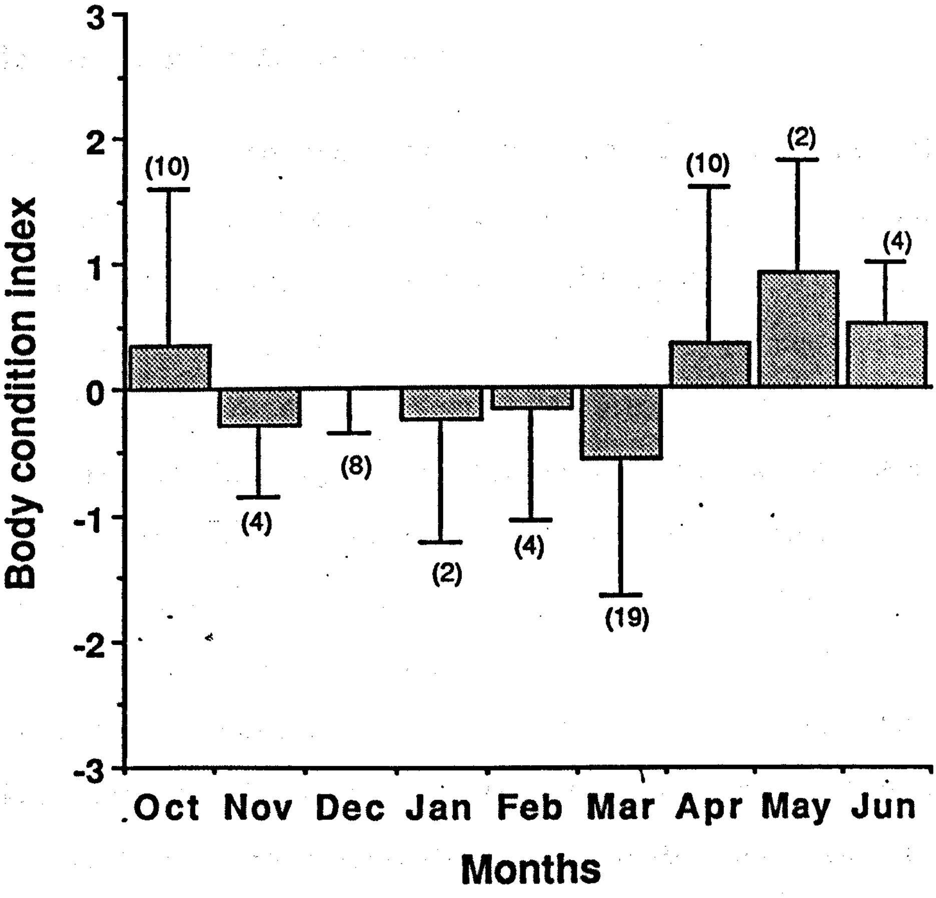
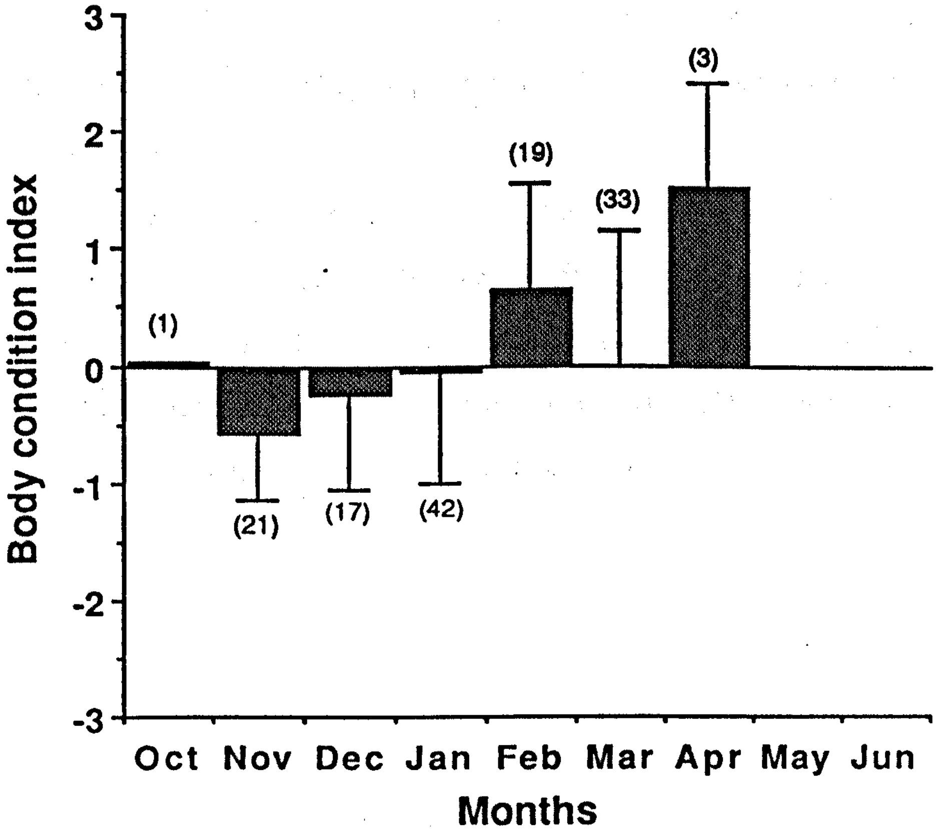


Figure 6.8 Body condition of migrant Turkey Vultures trapped in different months



6.4 DISCUSSION

6.4.1 Body size in relation to dominance

There were large differences in body size between different vulture taxa. Within taxa, no apparent sexual differences were found but identification of any bimodal trends in the data for different biometrics was complicated by the presence of subpopulations in the study area (particularly for migrant Turkey Vultures). However, there were large differences in body size between migrant and resident Turkey Vultures. Migrants were significantly larger in almost all measurements except bill length (one measurement), head and bill and tail length. This corresponded well with the fact (Chapter 5, Section 5.4.4) that migrants invariably won agonistic interactions with resident Turkey Vultures. Despite being heavier than migrant Turkey Vultures, Black Vultures were nevertheless subordinate during one-to-one agonistic encounters at carcases (Chapter 5, Section 5.4.4).

The nominate race of Black Vulture *C. a. atratus* weighs from 1.9-2.7 kg, or between 14-40% heavier than the South American *C. a. brasiliensis* (Jackson 1988). This may account for the dominance of Black Vultures over Turkey Vultures observed in North America (eg Stager 1964, Stewart 1978) but because the Turkey Vulture race in the north-eastern United States *C. a. septentrionalis* is also larger than *C. a. meridionalis* (one male 2.08, one female 1.99 kg-Hatch 1970) perhaps factors other than body size account for this difference. *C. a. atratus* may be more aggressive than *C. a. brasiliensis*.

6.4.2 Differences in wing-loading

The wing-loadings of the different vultures related well to their foraging strategies as found in raptors (Jaksic & Carothers 1974, Janes 1984). Most raptors show intersexual differences in wing-loading (Brown & Amadon 1968). For example, female Marsh Harriers *Circus aeriginosus* are less manoueverable than males and therefore probably need to forage over taller vegetation for concealment from agile prey (Schipper *et al* 1977). In Hirundines, wing-loading and shape is important in ecological segregation, since it determines flight speeds, agility and therefore foraging altitude and the types of insects taken in flight (Waugh 1978).

The low wing-loading of resident Turkey Vultures may enable them to utilise air movements over the canopy in the gallery forest. They may expend less energy than migrants, which have a significantly higher wing-loading. Residents also have relatively long tails compared to migrants, in relation to their body size, enabling greater manouverability. In terms of foraging energy expenditure, gallery forest may not provide optimal flying conditions for migrant Turkey Vultures and this may partly explain why higher densities of migrants foraged in more open savanna habitats (Chapter 3, Sections 3.3.5, 3.3.6). In open habitats, there may be greater wind velocity at low altitude because of fewer obstacles and they therefore may be more suitable to vultures with higher wing-loading, like migrant Turkey Vultures. Living for part of the year at high latitudes may place a constraint on body size and therefore wing-loading of migrants.

Lesser Yellow-headed Vultures have the lowest wing-loading of all Cathartid vultures and use low level air turbulence while searching for food. The low wing-loading of Lesser Yellow-headed Vultures enables them to exploit very weak air currents caused by small irregulaties in topography found in lowland areas (Pennycuick, in pers. comm. to Houston 1988). In the present study, Lesser Yellow-headed Vultures foraged mostly over open habitats (Chapter 3, Section 3.3.5, 3.3.6) and fed on very small food items such as small reptiles, amphibians, fish and possibly insects (this species has a similar diet in Belize; Clinton-Eitnaier pers. comm.). The foraging strategy of the Lesser Yellow-headed Vulture suggests that low level flight enables small items of carrion to be detected by olfaction or sight.

Black Vultures cannot maintain flapping flight because of their extremely high wing-loading (Mahoney 1983). These birds vigorously flap their wings and glide, alternately, to gain altitude (Fisher 1949) where they can forage by sight, using thermals. Houston (1985) found a significant difference in the height at which different vulture species foraged; the majority of *Cathartes* Vultures were seen below 150 m, compared to most Black Vultures which flew at significantly higher altitudes (greater than 300 m). Black Vultures probably have higher performance at cross country flight than *Cathartes* Vultures, because of their higher wing-loading, enabling them to arrive quickly at distant carcases. In the Serengeti, Hooded Vultures *Necrosyrtes monachus* cannot travel as fast as Griffon Vultures (eg. *Gyps africanus*) because of their low wing-loading (Pennycuick 1972 b).

Wing-loading also determines how early in the day vultures can begin to forage. In Chapter 3 (Section 3.3.1) it was shown that *Cathartes* Vultures fly much earlier in the day than species with higher wing-loading such as Black and King Vultures. However, although early foraging may be advantageous to subdominant *Cathartes* Vultures, it would not benefit other species (eg. Black and King Vultures) which depend on local enhancement to find food (unless a food source had depend on local enhancement to find food (unless a food source had been located the previous day - see Rabenold 1983 c).

6.4.3 Differences in body size between birds trapped in different months

There was no significant difference in body size of migrant Turkey Vultures when all months were compared because of high variability in each month. However, migrants trapped soon after arriving at the ranch (in November) were significantly larger in body size than birds caught in December. The former migrant Turkey Vultures were the largest trapped. This strongly suggested that these Turkey Vultures were from higher latitudes and perhaps migrated south earlier than southern populations because of deteriorating weather conditions. Furthermore, there were no differences in body weights of birds caught between November and December; thus after migration large Turkey vultures did not weigh more than smaller vultures, probably because they had utilised relatively more premigratory fat reserves after flying longer distances. The large vultures did not remain in the area but presumably flew further south.

There were significant differences in body weights and body sizes of resident Turkey Vultures caught in different months and this may have been partly related to variation between years. Small birds were caught between October-January in 1986/87, suggesting the possibility of some annual turnover in the population of residents. However, trapping biases toward small subdominant resident Turkey Vultures could also have accounted for this finding because, except during October, competition at feeding sites was likely to be highest during these months (see Chapter 3). This was due to the high densities of migrant Turkey Vultures present at the ranch in this period.

6.4.4 Body condition of vultures

Despite small sample sizes in some months for resident Turkey Vultures, some obvious trends in body condition were apparent. Generally, with the exception of four birds caught in February, body condition of residents was below average in the dry season months (when migrants were present). By contrast, in the wet season, trapped residents were in good condition. Birds of above average condition were caught in October at the end of the wet season. These differences could be partly explained by varying food abundance in different months. Some of the variation could be explained by breeding adults which may have been in poor condition when feeding dependent young. Resident Turkey Vultures probably begin breeding in February-April as noted by Smith (1980) in Panama (see Chapter 4, Section 4.5.7). Houston (1976 b) found that body condition of both Ruppell's Griffon *Gyps rueppellii* and White-backed Griffon *Gyps africanus* Vultures declined markedly in the breeding season.

The pattern of variation in body condition was not similar between different taxa examined in the same months. Resident Turkey Vultures foraged only in gallery forest during the dry season (Chapter 3, Section 3.3.5) and largely avoided migrant individuals at feeding sites (Chapter 5, Section 5.3.2), so it seems likely that their lower body condition in the dry season compared to wet season months was a genuine result which may be attributable to competition with migrants.

Although both migrant and resident Turkey Vultures were in below average condition in the early dry season, subsequent trends were distinctly different between the two races. Loss of condition after migration probably accounted for the low relative weights of migrant birds caught in November and December. In the following months the average condition of trapped birds was better, suggesting that they had obtained sufficient food to regain condition and restore fat levels prior to the return migration. An indication of increased food abundance later in the dry season was suggested by the significantly higher weights of Black Vultures in these months, but sample sizes were too small to calculate condition indices for this species over the period.

The body condition of migrant Turkey Vultures cannot be used to indicate the general level of food abundance in the study area because of their itineracy (shown by wing-tagged birds - Chapter 4, Section 4.3.1). Migrant Turkey Vultures probably foraged over an extensive area outside the ranch exploiting sporadic food sources. Furthermore, the carcase types exploited by Black Vultures in open savanna during the dry season were different to forest carcases eaten by resident Turkey Vultures (Chapter 5, Section 5.4.6) so that extrapolations between one species and another are not valid.

6.4.5 Biases of assessing body condition

There were some biases which might have affected the measurement of body condition. Firstly, vultures in poor condition might be more likely to enter traps. Thus, small capture samples were likely to be biased toward these unsuccessful foragers. This could account for the small body size of resident Turkey Vultures caught in the early dry season. In large captures, particularly in the case of Black Vultures, a wide range of individuals were caught and this accounts for the large variation in condition during each month. Secondly, the body condition of individual Black Vultures probably reflects their relative intraspecific social status as well as the abundance of food (see Chapter 1). By contrast, in *Cathartes* vultures dominance may be related to body size, but outcomes of intraspecific conflicts also depend on the relative hunger states of birds and no fixed hierarchies were observed (Chapter 5).

In Black Vultures, both adults and first year birds would likely be in relatively good condition, in contrast to wide-ranging subordinate young adults (see Rabenold 1983 b). In this analysis, young adult Black Vultures were not differentiated from older birds. Although juvenile Black Vultures were easily distinguished by the absence of deep rugosities on the bare skin covering their heads (see Rabenold 1983 a), they were probably in relatively good body condition because they were being fed by parent birds. Sample sizes were too small to compare body condition in different age-classes of Black Vultures. Turkey Vultures can be aged until they are 3 years old (Henckel 1981) but only juvenile migrants were identified in the present study (no juvenile residents were caught). The breeding state of resident Turkey Vultures may account for some differences in body condition.

Traps were baited with carrion in order to catch vultures, so most individuals had eaten before being handled. Normally, vultures vomited when caught and expelled their crop and stomach contents. Variability in the proportion of food vomited by different individuals could result in some biases in weight of trapped birds. Data were pooled for all years because of small sample sizes. This involves a number of assumptions. Food abundance and level of competition (eg. numbers of vultures present) may vary between months in different years and this might account for some of the variability within months.

In summary, while body condition of trapped migrants increased in months after birds had arrived in the Llanos, body condition of residents fluctuated considerably and was generally below average in the dry season. Furthermore, although the body size of resident Turkey

Vultures was significantly different between months, there was no corresponding significant difference in body weight. The results suggested the possibility that competition from migrants could affect body condition of residents by limiting their access to food.

SUMMARY

1) There were significant differences in body size dimensions between migrant and resident Turkey Vultures. Migrants were significantly heavier and longer-winged than residents. However, in some parameters there were no significant differences between migrants and residents. These included; head and bill length, culmen to bill tip and tail length.

2) A highly significant difference in wing-loading was found between the three taxa. Black Vultures had highest wing-loading, followed by migrant Turkey, resident Turkey and Lesser Yellow-headed Vultures. Wing area was most highly correlated with weight in the larger vultures (Black and migrant Turkey). The wing-loading of different taxa was related to their foraging strategies; the low wing-loading of resident Turkey Vultures compared to migrants may enable residents to exploit areas of weak air movements over gallery forest.

3) When body weight was regressed against body size, it was found that the variation in body size not explained by weight was largest in the smaller vultures. In migrant Turkey Vultures this was probably due to variation in condition of individuals from subpopulations temporarily foraging at the ranch. In resident Turkey Vultures, this indicated that large individuals were not heavier than birds of a smaller body size. There was therefore great variability in body fat reserves in resident Turkey Vultures.

4) Migrant Turkey Vultures caught after autumn migration (November) were significantly larger in body size than individuals which arrived

in December. The former individuals were the largest caught. This suggested that the larger birds caught during the autumn migration wintered further south, thus supporting a leap-frog migration hypothesis. However, large birds arrived first possibly because conditions in the autumn forced earlier migration than in more southerly populations. Small vultures (from the southern United States or Mexico) may have preceded large individuals but may have been in better condition and less likely to enter traps on arrival.

5) There were significant differences in body condition of vultures in different months. In autumn, trapped migrants were in relatively poor condition, but the condition of trapped birds increased with time spent in South America. A decline in condition of birds caught in March may be attributed to individuals which had wintered further south passing through on their return migration.

Body condition of resident Turkey Vultures was generally below average in the dry season, and was lowest in March. By contrast, condition of residents caught during the wet season months was above average, and was highest in October (at the end of the wet season) before the return of migrant Turkey Vultures. The fact that residents were in poor condition in March suggests that fat reserves were depleted after foraging in the gallery forest during the dry season. Larger captures of resident and migrant Turkey Vultures in consecutive months might indicate levels of food abundance and competition between the races and substantiate these tentative conclusions.

CHAPTER 7 MOULT

7.1 INTRODUCTION AND AIMS

The energetically demanding process of moult usually occurs at a time when there are low ecological constraints, mostly outside the breeding season or period of migration. Usually, birds moult at times of the year when food is most plentiful, so that in many larger, non-passerines which experience a long moult this means that moult may considerably overlap breeding (eg. Golden Eagles *Aquila chrysaetos*; Jollie 1947, Griffon Vultures *Gyps africanus*; Houston 1975 and Sparrowhawks *Accipiter nisus*; Newton 1986). Moult is also thought to be triggered by daylength (Stresemann & Stresemann 1966, Voitkevitch 1966). In the tropics, daylength is constant throughout the year, but other seasonal changes such as wet and dry seasons can alter the availability of food and hence the timing of breeding and moult. However, generally in the tropics there is greater overlap between these activities than in temperate regions (Foster 1975, Ginn & Melville 1983).

For temperate breeding species which winter in the tropics, a number of different strategies are employed to avoid moult on migration (Stresemann & Stresemann 1966). These include suspending moult (eg. Turtle dove *Streptopelia turtur* Swann & Baillie 1979), moulting before (eg. Redstart *Phoenicurus phoenicurus*) or after autumn migration (eg. Reed Warbler *Acrocephalus scirpaceus*). In North America, both Black and Turkey Vultures show regular descendent primary moult, all primaries are replaced on an annual basis and the process is thought to be relatively non-seasonal (Snyder *et al* 1986, Rea in prep). Davis (1974) found moult was continuous in Turkey Vultures in west Texas throughout spring and summer, but recorded comparatively more missing remiges from late-May to June. However, no detailed published account of moult in any small Cathartid vulture exists. No study has recorded moult in migrant Turkey Vultures overwintering in South America, or compared moult in resident vultures (which are unconstrained by a migratory period).

Moult spread over a long period probably does not exert a significant physiological stress on birds (Kendeigh *et al* 1977, King 1974, 1980). A long moult is the general rule in Cathartid vultures (Coles 1938, Davis 1974, Snyder *et al* 1986) but in comparison to residents, migrants would be likely to have fewer feathers in moult because of suspended moult before or during migration. Alternatively, to overcome the constraints of a migratory period they may undergo moult in a shorter time period (ie. before migration) than birds resident in South America.

In waders, Pienkowski *et al* (1976) found migrant populations had a more rapid moult than resident ones. Kozlova (1957) suggested that arrested moult during migration may provide greater flight efficiency than if some primary feathers were growing (when there would be gaps in the wing). Arrested moult occurs during other periods of ecological constraints; in Sparrowhawks *Accipiter nisus* this occurs when there is a peak demand for food from young (Newton & Marquiss 1982), and in the Californian Condor it may have reflected poor foraging in winter months (Snyder *et al* 1986).

The spread of dates over which moult occurred in three taxa and its duration in individual birds was investigated by examining the position of moulting feathers in captured birds. This chapter aims to investigate:

1) the relationship between moult schedules and other ecological events; for example, to relate moult in migratory vultures to migration periods.

2) Since bird populations from the same geographical area often show

similarities in the stage of moult (eg. Furness & Baillie 1981), a specific aim was to relate moult records in resident and migrant populations of Turkey Vultures to see how they differed.

3) Further, the chapter aims to establish a general account of moult patterns in Cathartid vultures in the absence of any published material and is a comparative study to the one carried out by Houston (1975) on White-backed *Gyps africanus* and Ruppell's Griffon Vultures *Gyps ruepellii*.

The pattern of moult can also be used for taxonomic studies between related genera; for instance in Cathartid vultures moult might be compared with moult in storks Ciconidae (see Rea 1983).

7.2 METHODS

7.2.1 Feather nomenclature

Small Cathartid vultures have 11 primary wing feathers (the 11th was small and difficult to find and has therefore been ignored here), 15 or 16 secondary feathers and 12 tail feathers.

Vultures were trapped in large funnel cage traps (Chapter 2, Section 2.2.1). Almost all the birds which were wing-tagged were also examined for moult in the remiges and rectrices. Body moult was difficult to score but a number on a scale of 1-3 was allocated to some individuals; 1) low; 2) medium; 3) heavy moult. The primaries, the first 15 secondaries and the tail feathers were examined and individual feather positions allocated a score from 0-5 as is the usual convention (Ginn & Melvile 1983) in the following way:

0) Old feather; It was not possible to accurately age feathers, although old feathers could be easily identified by their frayed and worn edges.

1) Old feather missing or new feather in pin stage;

2) New feather up to one third grown;

3) New feather between one and two thirds grown;

4) New feather more than two thirds grown, waxy sheath still remaining;

5) New feather fully developed, no waxy sheath (Ginn & Melvile 1983).

Primaries were numbered descendently (from the innermost outwards; 1-10) and secondaries ascendently (from the outermost inwards; 1-15) while the tail feathers were numbered from the central pair outwards (1-6 numbered inner-outer on each half of the tail). Positions of growing feathers were counted for both wings although moult usually occurs simultaneously in both primary tracts (eg. Coles 1938 for the Turkey Vulture, and generally in other avian genera - Ginn & Melvile 1983, Newton & Marquiss 1982).

7.2.2 Trapping schedule and feather growth in captive birds

An attempt was made to catch birds in each month, to obtain an even spread of samples for each month and to retrap birds to assess the rate of feather growth, but it was not always possible to achieve these objectives. Only a small number of resident Turkey Vultures were recaptured to enable the speed of feather growth to be recorded, so a number of individual birds were kept in captivity for two periods of three weeks to obtain more information on this aspect (3 migrant Turkey Vultures, 1 Black Vulture and 2 resident Turkey Vultures). Remiges and rectrices were measured from their base to the tip of the rachis; when growth increments were below 1 mm feathers were assumed to have reached full length (as in Lenton 1984).

Captive birds are subject to stress and this can adversely affect their feather growth (Newton 1966, 1967, 1968, Houston 1975, Ginn & Melville 1983), but an attempt was made to reduce this in the present investigation by minimising handling times. Resident Turkey Vultures did not respond well to captivity and few data were collected on this taxon. However, nine resident Turkey Vultures were recaptured (on 21 occasions) and as residents were not kept for more than a few days in captivity, analysis of recaptures provided most information about the speed and duration of moult in individual birds. Only two migrant Turkey Vultures (one immature) were caught on several occasions and moult was not recorded in the two recaptured Black Vultures because these were among a large number (c 50) of birds caught at the same time.

Analysis of moult data

7.2.3 Timing and speed of moult

The duration of moult in the three taxa was estimated by recaptures of marked individuals and linear regression analysis. Moult scores were calculated for each captured bird, the maximum primary score for each wing was 50 (recently completed moult with all new feathers) and minimum 0 (all old feathers). Moult scores were collected from both wings for each individual so the maximum score was 100. Moult score was plotted as the dependent variable against date (independent) although it was recognised that there are a number of pitfalls associated with this method (see Pimm 1976, Summers *et al* 1983; moult score does not necessarily increase linearly with time - see Underhill & Zucchini 1988).

The moult scores of migrant Turkey Vultures obtained from birds which were on passage to more southerly destinations in South America or on their return journey to North America, were compared with moult scores of birds caught in interim months (ie. December - February), to test if there were differences between these periods. The relationship between moult and date was assessed by combining data from three field seasons to estimate the duration of moult in the average individual from the population.

7.2.4 Sequence of moult

The order of shedding feathers was investigated by recording the feather position with the highest growing feather score (ie between 1-4), indicating that this was the first feather in the tract to be shed. Sometimes this was not possible because several feathers had been shed at the same time, grew at the same rate and were therefore assigned the same score. The order of shedding could not then be determined so wings in this condition were not included in the analysis. The stage of primary moult at which secondary moult began was investigated by recording the location of newly shed feathers or feathers in the pin stage in the secondary tract.

7.3 RESULTS

7.3.1 Sequence of moult and number of growing feathers

Moult was recorded for 120 Black Vultures, 132 migrant Turkey Vultures, 78 resident Turkey Vultures and 4 Lesser Yellow-headed Vultures (334 birds in total - the latter species will not be discussed here because of the small sample size).

The majority of birds were found to replace their primaries in order from the innermost outwards (ie. serially descendent moult). Most birds of all three taxa commonly had 1-3 primary feathers in growth (Median 1), Black Vultures had up to six feathers in growth, resident Turkey Vultures up to five and migrants up to four feathers in growth in each wing (Table 7.0). A number of birds showed 'stepwise moult' (when one wave of moult had not reached P10 before a new wave began at P1) and this occurred most often in Black Vultures (19% of birds examined), followed by resident Turkey Vultures (12%) and migrant Turkey Vultures (6%). A few birds showed irregular or

Table 7.0 The number of growing primaries at different moult stages.

Latest primary shed	Resident TV			Migrant TV			Black		
	M	Range	N	M	Range	N	M	Range	N
1	1.3	1-2	3	2.0	1-4	16	1.8	1-6	24
2	2.3	2-3	3	1.6	1-3	17	2.3	2-3	3
3	1.0	-	4	1.5	1-3	46	1.5	1-2	2
4	1.5	1-4	26	1.5	1-4	59	2.0	1-4	7
5	1.4	1-3	31	1.4	1-3	52	2.1	1-4	17
6	1.6	1-4	27	1.0	-	2	2.4	1-6	17
7	1.2	1-2	21	-	-	-	1.7	1-5	52
8	1.6	1-2	13	-	-	-	1.4	1-3	60
9	3.0	-	1	-	-	-	1.7	1-3	19
10	-	-	-	2.5	2-3	2	1.8	1-3	12

N = Number of wings examined M = mean number of growing feathers

Table 7.1 Numbers of growing feathers in primaries, secondaries and tail in vultures (M = mean, N = number of wings examined, H = Kruskal-Wallis ANOVA).

	Black			Migrant TV			Resident TV				
	M	Range	N	M	Range	N	M	Range	N	H	P
Primaries	1.7	0-6	240	1.2	0-5	264	1.5	0-4	156	31.9	***
Secondaries	2.3	0-7	240	0.8	0-7	264	1.6	0-6	156	144	***
Tail	2.5	0-6	117	0.8	0-6	132	1.0	0-8	76	81.3	***

Comparisons between vultures (Mann Whitney U test)

	Primaries	Secondaries	Tail
MTV vs RTV	U = 17200, ***	U = 12947, ***	N.S.
MTV vs BV	U = 23194, ***	U = 13195, ***	U = 3177, ***
RTV vs BV	U = 16580, *	U = 13616, ***	U = 2089, ***

'transilient' moult when feathers were missed in the descendent moult of the primaries (Stresemann & Stresemann 1966). Sometimes this could have been attributed to premature accidental loss of feathers.

Black Vultures had a significantly higher number of growing primary feathers than either resident or migrant Turkey Vultures (Table 7.1). Migrants had significantly lower numbers of primaries in growth than resident Turkey Vultures. The same trend between the three taxa was apparent for both the secondary and the tail feather tracts (Table 7.1). However, there was no significant difference between numbers of growing tail feathers in migrants and residents and both had significantly fewer growing tail feathers than Black Vultures (Table 7.1).

The start of secondary and tail moult occurred at some time after primary moult had begun but it was only possible to determine this for a small number of birds because individuals frequently had several feathers in growth in these tracts at the same time. If a single secondary or tail feather was in growth stages 2-4 there was no way of telling at what stage of primary moult growth began. The following are details from vultures which had only one secondary or tail feather in pin stage or missing (score 1) signifying the start of moult.

In 18 wings of Black Vultures, moult in the secondaries began after the fourth, fifth or sixth primary had been shed in 33% of cases, the seventh primary in 28% of cases, the eighth in 11%, and the tenth in 6%. It was only possible to determine the timing of secondary moult in 11 wings of resident Turkey Vultures, and for these, moult in the secondaries began after the sixth primary had been shed in 45% of cases, after the fifth in 36%, and the remainder after the fourth and tenth primary had been shed. In 15 wings of migrant Turkey Vultures moult began in the secondaries after the tenth primary had been

Table 7.2 Distance between foci in secondary tract of Black, migrant Turkey and resident Turkey Vultures. (M = mean number of feathers between foci, CL = 95% Confidence limits, N = number of distances between foci examined, G = mean number of growing feathers in wings with several foci, n = number of wings).

	Black	Migrant TV	Resident TV
M	3.24	3.12	3.81
CL	(3.00-3.50)	(2.71-3.60)	(3.35-4.34)
	N = 363	N = 90	N = 140
G	3.15	2.53	2.88
CL	(3.00-3.15)	(2.29-2.77)	(2.66-3.10)
	n = 166	n = 59	n = 74

Comparison of distances between foci between species (Student 't' test, data log-transformed)

MTV vs RTV $t_{228} = -2.01, P = 0.05$
MTV vs BV N.S.
RTV vs BV $t_{501} = -2.18, P < 0.05$

Table 7.3 Frequency with which moult began at different secondary feather locations in Black Vultures

	Feather number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
% wings starting with each feather	17	8	4	4	10	10	3	4	4	5	6	8	7	4	5
Number of of wings	21	10	5	5	12	12	4	5	5	6	7	10	9	5	6

reached in 40% of cases, after the fourth or fifth primary in 27% of cases each and after the sixth primary in 7%.

The general pattern in secondary moult was for vultures to have several moult centres or foci in each wing, although the number was very variable (up to seven in Black and resident Turkey Vultures or up to six in migrant Turkey Vultures - Table 7.1). In the majority of wings examined, each focus had only one growing feather (sometimes two but rarely more) and was usually separated by several feathers from the next focus. The precise number of feathers separating foci differed significantly between the three vulture taxa ($F_{2,595} = 3.55$, $P < 0.05$ - log-transformed data). Resident Turkey Vultures had significantly larger gaps between foci than migrants (Tukey test $P < 0.05$ - Table 7.2).

The location of active foci in the secondaries varied between species, but did not appear to occur at random. In Black Vultures, foci were commonest at feather S1, followed by feather S5 or S6 and then S12 (Table 7.3). In resident Turkey Vultures, the first secondary was also the commonest foci, followed by S3 or S5 and then S7 or S13 (Table 7.4). However, in migrant Turkey Vultures, S4 was the commonest feather in growth followed by S9 and S1 (Table 7.4). The probability of an active site having an adjacent feather in growth was calculated after Houston (1975). For wings with two growing feathers, Tables 7.5 and 7.6 show that the observed number of occasions when an active site had an adjacent feather in growth was significantly less than if there was an equal probability of feather growth at all sites (for details of how expected frequencies were calculated see Tables 7.5). This indicated that the location of foci in the secondary tract were not distributed at random.

The number of occasions on which it was possible to determine the precise order of shedding in the secondaries was limited by the large

Table 7.4 Frequency with which secondary moult began at different secondary feather locations in;

1. Resident Turkey Vultures

	Feather number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
% wings starting with each feather	28	4	11	5	11	3	8	3	4	5	1	3	8	4	4
Number of wings	21	3	8	4	8	2	6	2	3	4	1	2	6	3	3

2. Migrant Turkey Vultures

	Feather number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
% wings starting with each feather	13			18	1	2	9	8	14	8	9	8	2	6	1
Number of wings	11	-	-	16	1	2	8	7	12	7	8	7	2	5	1

Table 7.5 The relationship between numbers of actively growing feathers in the secondary tract and the distance apart of feathers in growth in Black Vultures

Number of feathers growing		Frequency of intervals separating active feathers														
	E	0	1	2	3	4	5	6	7	8	9	10	11	12	13	N
	6.4	4	3	7	4	6	2	0	3	4	2	0	4	3	3	45
3	39.7	16	21	22	16	9	10	5	15	8	7	3	-	2	-	134
4	51.5	23	28	16	11	12	9	7	4	-	1	-	-	-	-	111
5	39.4	15	16	12	7	3	4	4	-	-	-	-	-	-	-	61
6	4.2	-	3	2	-	-	-	-	-	-	-	-	-	-	-	5
7	6.4	3	2	-	-	1	-	-	-	-	-	-	-	-	-	6

E The expected frequency of feathers growing at adjacent sites was calculated after Houston (1975), and assumes that there are 14 available sites (disregarding the end sites of 15 examined feathers) in the wing for feathers to grow (each feather had two neighbours). Thus, if there was an equal probability of growth at each site and there were two feathers in growth in the wing, the probability of one feather having an adjacent feather in growth was 2 in 14; expected frequency was 45 x 2 / 14 = 6.4; for three feathers in growth (134 x 2/14) + (134 x 2/13) = 39.7.
For wings with two feathers in growth the observed number of occasions when the adjacent feather was in growth was significantly less than that expected; $X^2 = 51.9$, df 5, $P < 0.01$.

Table 7.6 The relationship between numbers of actively growing feathers in secondary tract and distance apart of feathers in growth in migrant 1) and resident 2) Turkey Vultures

Number of feathers growing

Frequency of intervals separating active feathers

Resident Turkey Vultures

	E	0	1	2	3	4	5	6	7	8	9	10	11	12	13	N
2	4.4	2	1	2	1	4	2	3	4	3	3	1	1	2	2	31
3	15.8	7	6	16	1	1	3	2	3	8	3	1	0	0	2	53
4	17.5	5	7	14	3	-	3	3	2	1	-	-	-	-	-	38
5	5.1	2	2	2	-	2	-	-	-	-	-	-	-	-	-	8
6	8.4	2	2	5	-	1	-	-	-	-	-	-	-	-	-	10

Significantly fewer occasions were recorded than expected of two feathers in wings growing adjacent to one another $X^2 = 21.9$, df 4, $P < 0.01$.

Migrant Turkey Vultures

	E	0	1	2	3	4	5	6	7	8	9	10	11	12	13	N
2	5.4	9	5	6	4	3	1	4	2	2	1			1		38
3	6.5	1	5	3	4	3	4	2	-	-	-			-		22
4	9.7	3	6	3	6	-	2	1	-	-	-			-		21
5	2.6	1	-	1	2	-	-	-	-	-	-			-		4
7	6.4	3	-	3	-	-	-	-	-	-	-			-		6

Significantly fewer occasions were recorded than expected of two feathers in wings growing adjacent to one another $X^2 = 14.5$, df 4, $P < 0.01$.

number of wings where growing feathers were at the same stage of growth (having been shed at about the same time and given the same feather score). However, in 39 Black Vulture wings, 24 resident Turkey Vulture wings and 22 migrant Turkey Vulture wings it was possible to determine the exact order of shedding, assuming that feathers which are shed first maintain their lead throughout the growth sequence.

There was a large amount of variation between individual birds in the location of growing feathers (Tables 7.3 and 7.4). When the first shed feather was partly grown, another feather was shed and this was usually at some distance from the first focus although occasionally it was the adjacent feather. Secondary 12 was usually the first (16% of wings) or second feather shed (24%) in Black Vultures, while the third was most commonly S1 or S8. Feather S1 or S5 was usually first to shed in resident Turkey Vultures (21% of wings respectively), second was feather S5 (21%) and third, feather S11. Finally, migrant Turkey Vultures usually shed feather S4 or S11 first (23% each respectively) and feather S10 second (23%). (Few migrant Turkey Vulture wings contained more than two growing feathers.)

Tail moult was sometimes apparently irregular, but this could have been due to birds losing feathers prematurely through fighting at carcases. The sequence of tail moult varied between species (Tables 7.7 - 7.9). In resident Turkey Vultures the central tail feathers were most often the first to moult (Table 7.7), while in migrant Turkey Vultures (Table 7.8), No 3 was most often shed first (both halves of tail combined). Both resident and migrant Turkey Vultures had few tail feathers in moult (Table 7.1) so it was not possible to determine the remainder of the sequence in the two races. The tail feather most often shed first in Black Vultures was No 2 while the second commonest to be shed was the outermost feather (No 6) (Table 7.9).

Table 7.7 The sequence of moult in two halves of the tail in resident Turkey Vultures (Numbers = birds in each category).

Order of shedding	Innermost		Feather number		Outermost	
	1	2	3	4	5	6
Right side						
First	9	5	5	2	3	3
Second	1		1		1	
Left side						
First	8	2	1	3	4	-
Second	1	1			2	

Table 7.8 The sequence of moult in two halves of the tail in migrant Turkey Vultures

Order of shedding	Innermost		Feather number		Outermost	
	1	2	3	4	5	6
Right side						
First	1	5	9	4	9	3
Second	3			1	1	1
Left side						
First	2	3	6	6	4	1
Second		2	2		1	

Table 7.9 The sequence of moult in two halves of the tail in Black Vultures

Order of shedding	Innermost		Feather number		Outermost	
	1	2	3	4	5	6
Right side						
First	11	14	7	6	10	15
Second	7	4	5	1	2	9
Third	1				1	
Left side						
First	16	17	9	3	9	9
Second	2	2	5	4	4	3
Third			1			

7.3.2 Symmetry of moult

The correspondence of growing feathers between the two wings and each half of the tail was investigated by assigning each bird a category as in Newton & Marquiss (1982). Tables 7.10-7.12 show the proportion of individuals in each category:

1) Birds with corresponding feathers in each wing or half of tail with the same score;

2) Birds with corresponding feathers at different stages of growth;

3) Birds with one or more non-equivalent feathers of the same or different moult scores.

The general pattern for all species was for primaries to have greatest symmetry, the tail was intermediate and the secondaries had least symmetry (Tables 7.10-7.12) with the exception of migrant Turkey Vultures. The latter species showed the same degree of symmetry in the tail as the secondary tract (Table 7.10). The level of symmetry in the primary feathers of vultures was high when equivalent feathers of different scores were considered (60% for migrants, 59% for residents and 53% for Black Vultures) but lower in the case of equivalent feathers of the same scores (Tables 7.10-7.12). However, most of the discrepancies were due to birds having one wing slightly out of phase with the other wing (eg. a primary in one wing dropped slightly out of phase with the other wing). A number of birds also showed stepwise moult (see earlier, Section 7.3.2) and often in these cases one wing would begin the second wave of moult before this started in the other wing.

In the case of primary feathers, there was no significant difference in the proportion of birds in each category between different taxa. Migrant Turkey Vultures had the highest percentage of equivalent primary feathers at the same growth stage, followed by

Table 7.10 Symmetry of moult in two wings and two halves of tail in migrant Turkey Vultures

	Primaries	Secondaries	Tail
Number of birds examined (with growing feathers in 3 tracts)	108	75	46
% with equivalent feathers of same score	43.5	5.3	4.3
% with equivalent feathers of different scores	16.7	1.3	2.2
% with non-equivalent growing feathers	39.8	93.4	93.5
Correlation coefficient	0.84 *** (n = 107)	0.58 *** (n = 74)	0.55 ** (n = 47)

Correlation coefficients based on birds which had growing feathers in one wing and either half of tail (data log-transformed).

Table 7.11 Symmetry of moult in two wings and two halves of tail in resident Turkey Vultures

	Primaries	Secondaries	Tail
Number of birds examined (with growing feathers in 3 tracts)	71	63	37
% with equivalent feathers of same score	39.4	9.5	18.9
% with equivalent feathers of different scores	19.7	7.9	5.4
% with non-equivalent growing feathers	40.8	82.6	75.7
Correlation coefficient	0.98 *** (n = 71)	0.27 * (n = 63)	0.35 * (n = 38)

Table 7.12 Symmetry of moult in two wings and two halves of tail in Black Vultures

	Primaries	Secondaries	Tail
Number of birds examined (with growing feathers in 3 tracts)	117	106	98
% with equivalent feathers of same score	33.3	2.8	6.1
% with equivalent feathers of different score	19.7	1.9	4.1
% with non-equivalent growing feathers wings	47.0	95.3	89.8
Correlation coefficient	0.98 *** (n = 116)	0.44 *** (n = 105)	0.27 ** (n = 98)

N.B. Correlation for secondaries r = 0.84 with n = 106 points (one extreme point was removed).

Table 7.13 Proportion of wings in which feathers were growing and those in which no feathers were growing in the primary tract (%).

	Migrant TV	Resident TV	Black
% Wings examined with no moult	12 (32)	3 (4)	2 (4)
% Wings in moult with no growing feathers	10 (27)	7 (8)	4 (9)
% Wings with growing feathers	78 (205)	90 (124)	94 (211)

Comparison between wings with growing feathers, wings with none and those with suspended moult

MTV vs RTV $X^2 = 6.80$, df 2, $P < 0.001$
MTV vs BV $X^2 = 11.20$, df 2, $P < 0.0001$
RTV vs BV $X^2 = 1.11$, df 1, N.S.

resident Turkey Vultures and finally Black Vultures, but the differences were not significantly different.

However, a significantly higher proportion of resident Turkey Vultures (N = 63) had equivalent secondary feathers growing in either wing (compared to non-equivalent feathers) than either migrant Turkey (N=75) or Black Vultures (N=106). ($X^2 = 3.89$, df 1,$P < 0.05$ with Yate's correction, and $X^2 = 7.49$, df 1, $P < 0.01$ respectively). More resident Turkey Vultures showed symmetry in either half of the tail than either of the other vulture taxa ($X^2 = 5.25$, df 1, $P < 0.05$ when compared with migrant Turkey Vultures and $X^2 = 4.43$, df 1, $P < 0.05$ when compared with Black Vultures). Tables 7.10 -7.12 show data from all birds combined and therefore do not take into account their different states of moult. With an increased number of feathers growing in the wing the chances of feathers growing at non-equivalent positions in either wing or each half of the tail is clearly much greater.

Symmetry was also measured by comparing moult scores between each wing or either half of the tail using linear regression. There was a high correlation between primary scores for each wing and a lower correlation for secondary scores in all taxa. However, there was no correlation between scores for either half of the tail for Black Vultures (Table 7.12), resident or migrant Turkey Vultures (Tables 7.10 and 7.11 respectively).

7.3.3 Frequency of suspended moult

Completely suspended moult (when there were only fully grown feathers present, some old and the remainder new) occurred rarely in any vulture taxa, but absence of growing feathers in the primaries was common, especially in migrant Turkey Vultures (Table 7.13). Usually vultures had at least one growing feather in the secondaries or tail

Table 7.14 Proportion of wings in which feathers were growing and in which growing feathers were absent in secondary tract in vultures (N).

	Migrant TV	Resident TV	Black
% Wings examined with no moult	39 (102)	27 (34)	7 (15)
% Wings in moult but no growing feathers	16 (44)	2 (2)	7 (15)
% Wings with growing feathers	45 (118)	71 (88)	87 (194)

Comparisons between wings with growing feathers and wings with none

MTV vs RTV $X^2 = 30.1$, df 2, $P < 0.0001$
MTV vs BV $X^2 = 94.8$, df 2, $P < 0.0001$
RTV vs BV $X^2 = 31.0$, df 2, $P < 0.0001$

Table 7.15 Proportion of birds in which feathers were growing and those in which no feathers were growing in the tail

	Migrant TV	Resident TV	Black
% Birds examined with no moult	36 (47)	56 (33)	12 (13)
% Birds in moult with no growing feathers	29 (38)	3 (2)	3 (3)
% Birds with growing feathers	35 (45)	41 (24)	85 (94)

Comparison between birds with growing tail feathers, those with none and those with suspended moult

MTV vs RTV $X^2 = 17.0$, df 2, $P < 0.001$
RTV vs BV $X^2 = 38.5$, df 2, $P < 0.0001$
MTV vs BV $X^2 = 65.2$, df 2, $P < 0.0001$

Comparisons between proportion of birds with growing tail feathers and those with none

MTV vs RTV $X^2 = 0.64$, df 1, N.S.

feathers. The proportion of birds with growing wing or tail feathers, those with completed moult (all new feathers) and those with suspended moult in particular tracts was very different between taxa (Tables 7.13-7.15). A significantly higher proportion of migrant Turkey Vultures had suspended primary moult, had completed primary moult or were not moulting when examined than either resident Turkey or Black Vultures (Table 7.13). However, there was no significant difference between resident Turkey and Black Vultures. Findings were similar for the secondary feathers except that there was a significant difference between proportions of resident Turkey and Black Vultures in the three categories (Table 7.14). A higher proportion of resident Turkey Vultures showed suspended or no secondary moult than Black Vultures (Table 7.14).

There was no difference in the proportion of birds with tails in moult and those not in moult between migrant and resident Turkey Vultures (Table 7.15). When the three categories (moulting, suspended moult, completed moult) were compared however, significantly more migrant Turkey Vultures had tails in suspended moult. In both residents and migrants a significantly higher proportion of tails examined showed suspended or no moult than was the case for Black Vultures (Table 7.15). In summary, migrants had suspended moult in the primary or secondary tract more often than either resident Turkey or Black Vultures. Although sample sizes were small there was a highly significant difference between the proportions of migrants examined with suspended primary moult in months when birds were arriving from North America or on return migration (ie. October/November and March/April repectively) than in interim months (Table 7.16). Thus, some migrants do appear to delay moult while on migration. Table 7.17 shows that resident Turkey Vultures were on average half way through moult in the early dry season, while migrants were in an early stage

Table 7.16 Proportions of migrant Turkey Vultures with primary moult started, moult completed and suspended moult in different periods (%).

	- Migration -		Overwintering period						- Migration -		
	1-15 Oct	15-30 Nov	1-15 Dec	16-31 Dec	1-15 Jan	16-31 Jan	1-15 Feb	16-28 Feb	1-15 Mar	16-31 Mar	1-15 Apr
Birds in which moult started	1 (50)	10 (72)	2 (100)	21 (95)	5 (62)	28 (87)	16 (100)	1 (100)	19 (79)	4 (49)	1 (50)
Birds with arrested moult	0	2 (14)	0	0	1 (13)	4 (13)	0	0	3 (13)	1 (13)	
Birds with new feathers	1 (50)	2 (14)	0	2 (5)	2 (25)	0	0	0	2 (8)	3 (38)	1 (50)

Comparison between the proportion of vultures in suspended moult examined on migration (moving north or south) and those examined during overwintering period revealed that significantly more vultures had no growing wing feathers in the former than the latter period ($X^2 = 14.2$, df 1, $P < 0.001$).

Table 7.17 Monthly moult scores (maximum 50, including only wings with growing primaries) for migrant and resident Turkey Vultures in the dry season (Mean + 95% Confidence limits).

	Month				
	Nov	Dec	Jan	Feb	Mar
Migrant TV	13.4 (12.2-14.8) N = 9	13.1 (9.7-17.5) N = 21	15.7 (13.6-18.3) N = 30	13.5 (10.1-18.0) N = 18	21.4 (19.8-23.2) N = 21
Resident TV	28.8 (18.8-44.2) N = 5	17.7 (10.4-30.4) N = 10	19.0 N = 1	23.8 (17.9-31.6) N = 6	26.7 (24.8-28.7) N = 23

of moult.

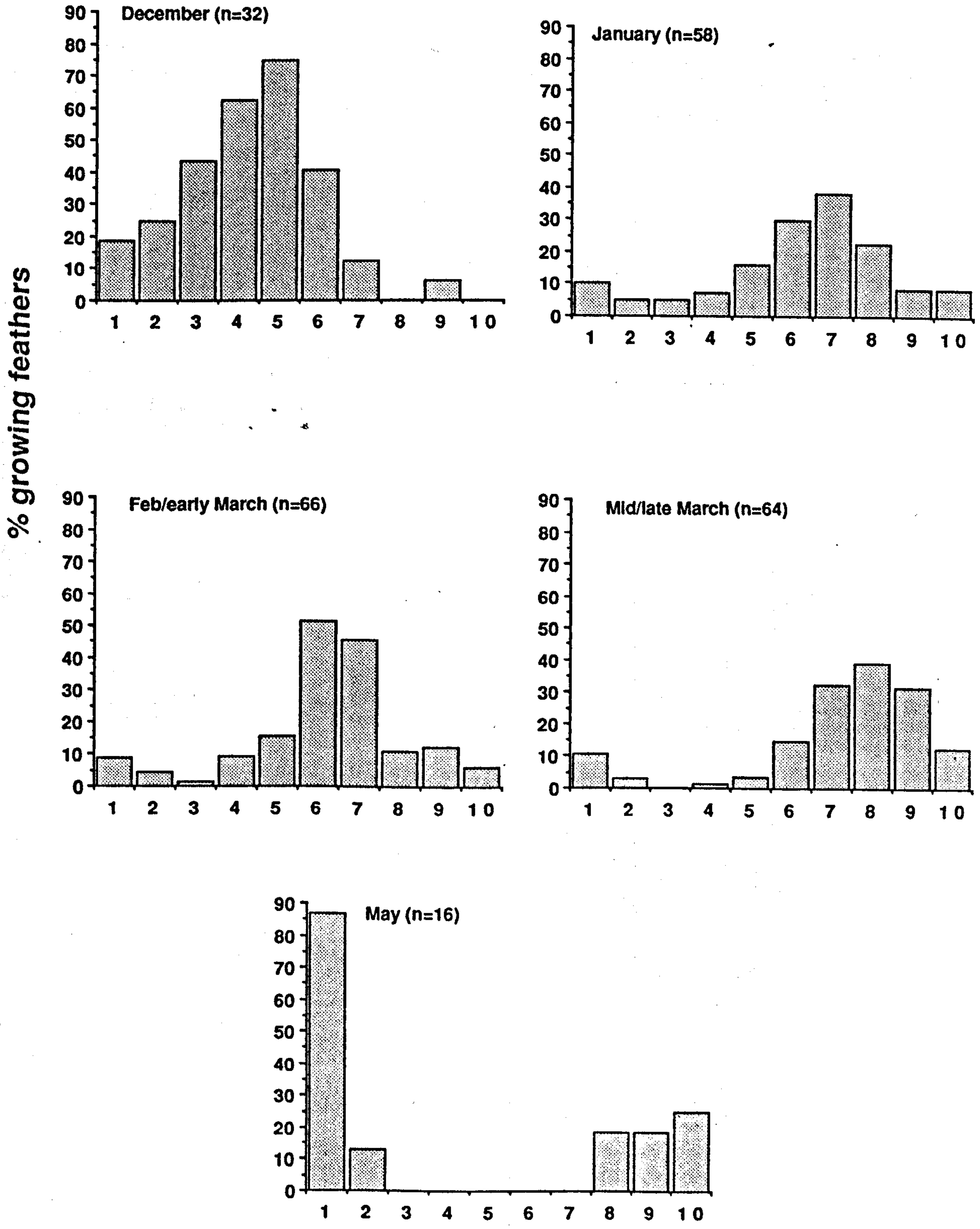
7.3.4 The duration and timing of moult from recaptures of marked individuals

Figures 7.1 to 7.3 show the percentage of growing primary feathers at each location during months when moult was recorded in Black, resident Turkey and migrant Turkey Vultures. Although sample sizes for some months were too small to make meaningful comparisons, there appeared to be great variability in the stage of moult in birds caught in different months and this was confirmed by the linear regression analysis of moult scores against date. A few individuals were captured when they were starting moult (the inner primary not fully grown and all other feathers old); two migrants had started moult in December/early January and one in February and one resident in mid-December, but these birds were atypical and appeared not to follow the general trend of moult in other vultures caught at the same time.

Changes in the moult scores of six recaptured resident Turkey Vultures are shown in Figure 7.4. There was high variability in the rate of increase in moult score partly because birds were at different stages of moult when captured. A direct comparison between individuals was also not possible for a number of other reasons (see Discussion). There was a significant correlation between the number of days between recaptures and increase in moult score units ($R_s = 0.90$, $N = 8$, $P = 0.01$) and a significant positive correlation between numbers of new primaries in growth and number of days between recaptures ($R_s = 0.87$, $N = 7$, $P < 0.05$) as would be expected.

Results from recaptures show that two birds (individual 23 and individual 127) had undergone a complete moult between trappings; individual 23 between 3 March 1986 and 10 December 1986; individual

Figure 7.1 Percentage of growing feathers in primary tract at each feather location in Black Vultures (by month)
n= no. of wings examined



December (n=32)

January (n=58)

Feb/early March (n=66)

Mid/late March (n=64)

May (n=16)

Figure 7.2 Percentage of growing feathers in primary tract at each feather location in resident Turkey Vultures (by month)
n=no. of wings examined

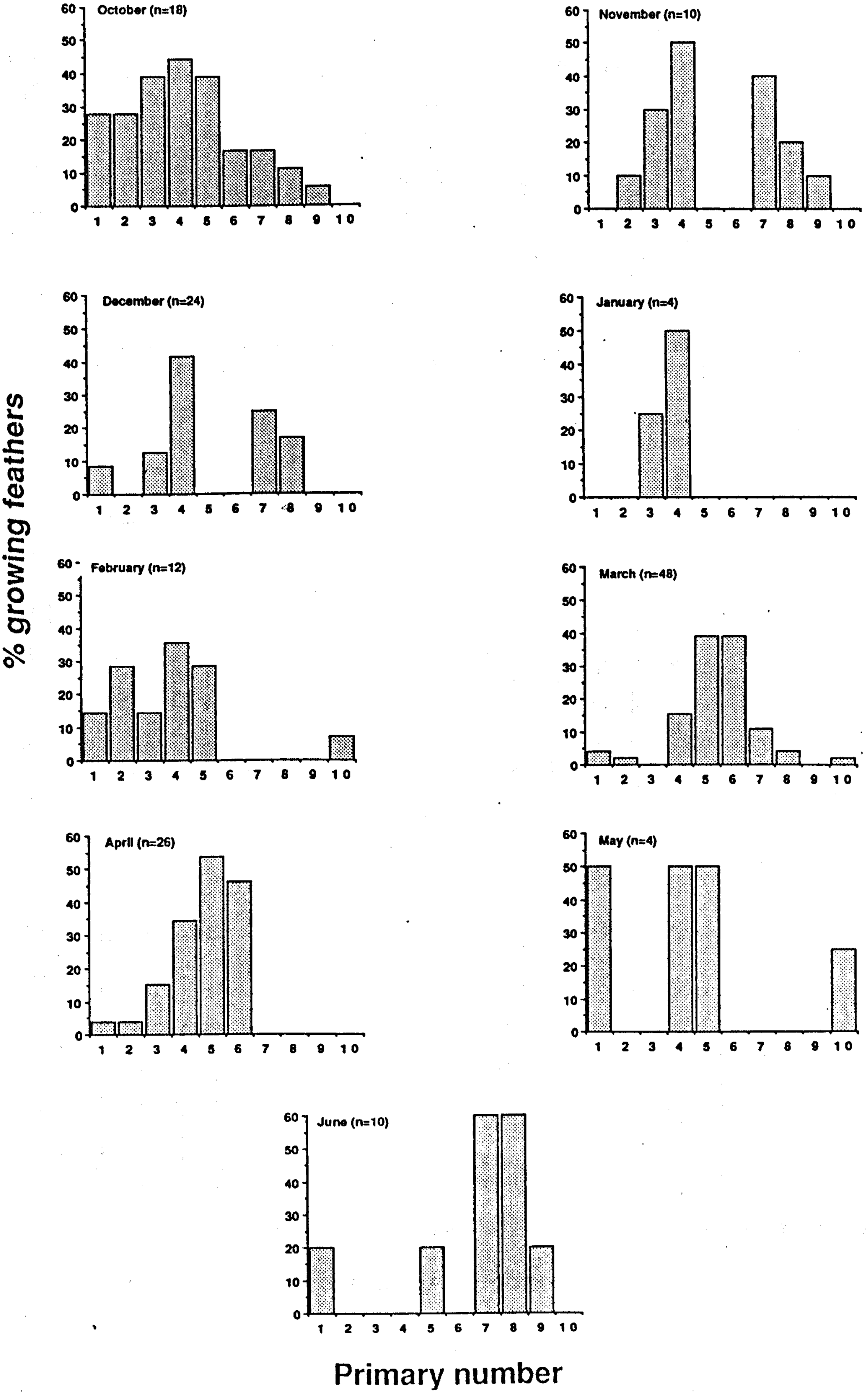


Figure 7.3 Percentage of growing feathers in primary tract at each feather location in migrant Turkey Vultures (by month)
n= no. of wings examined

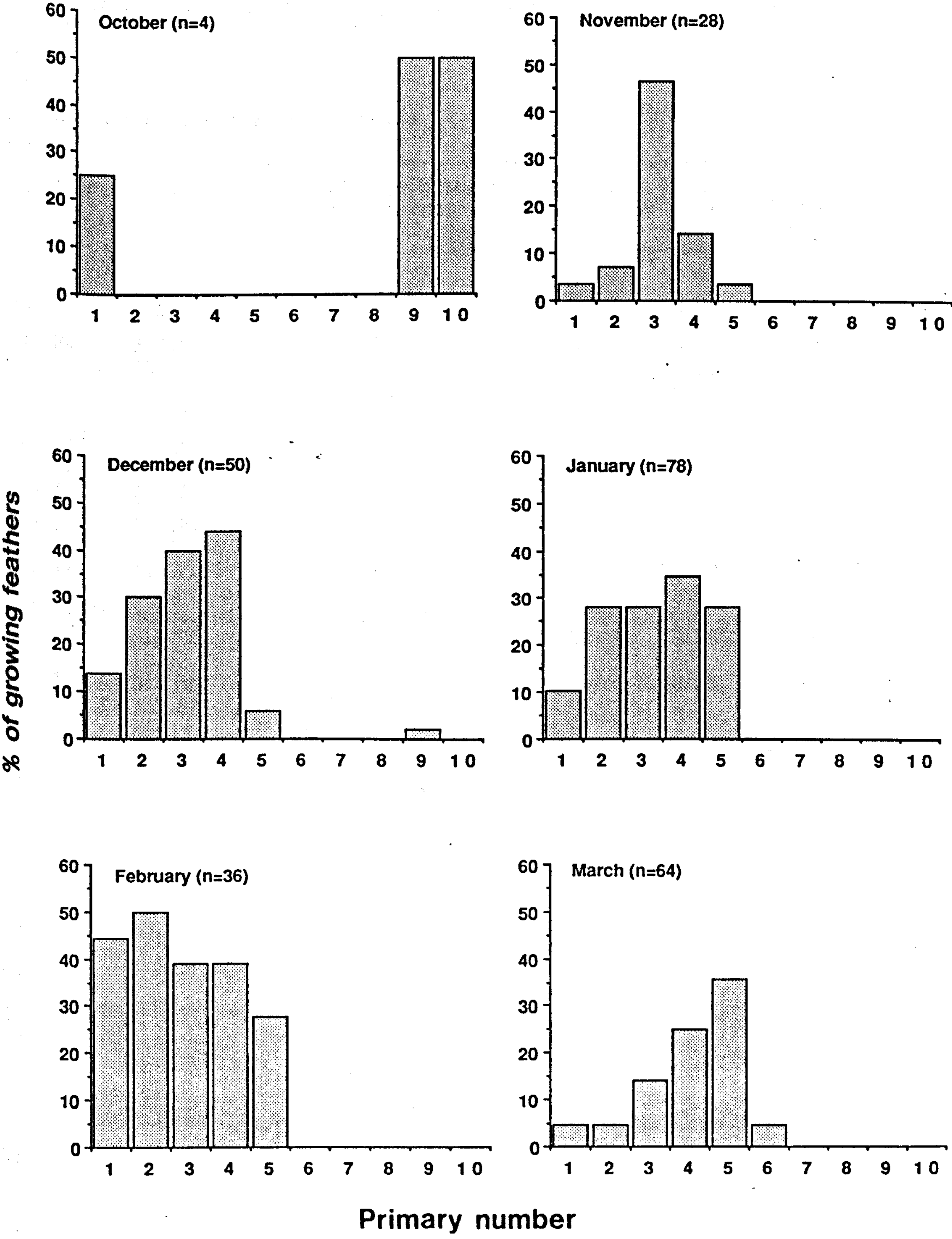
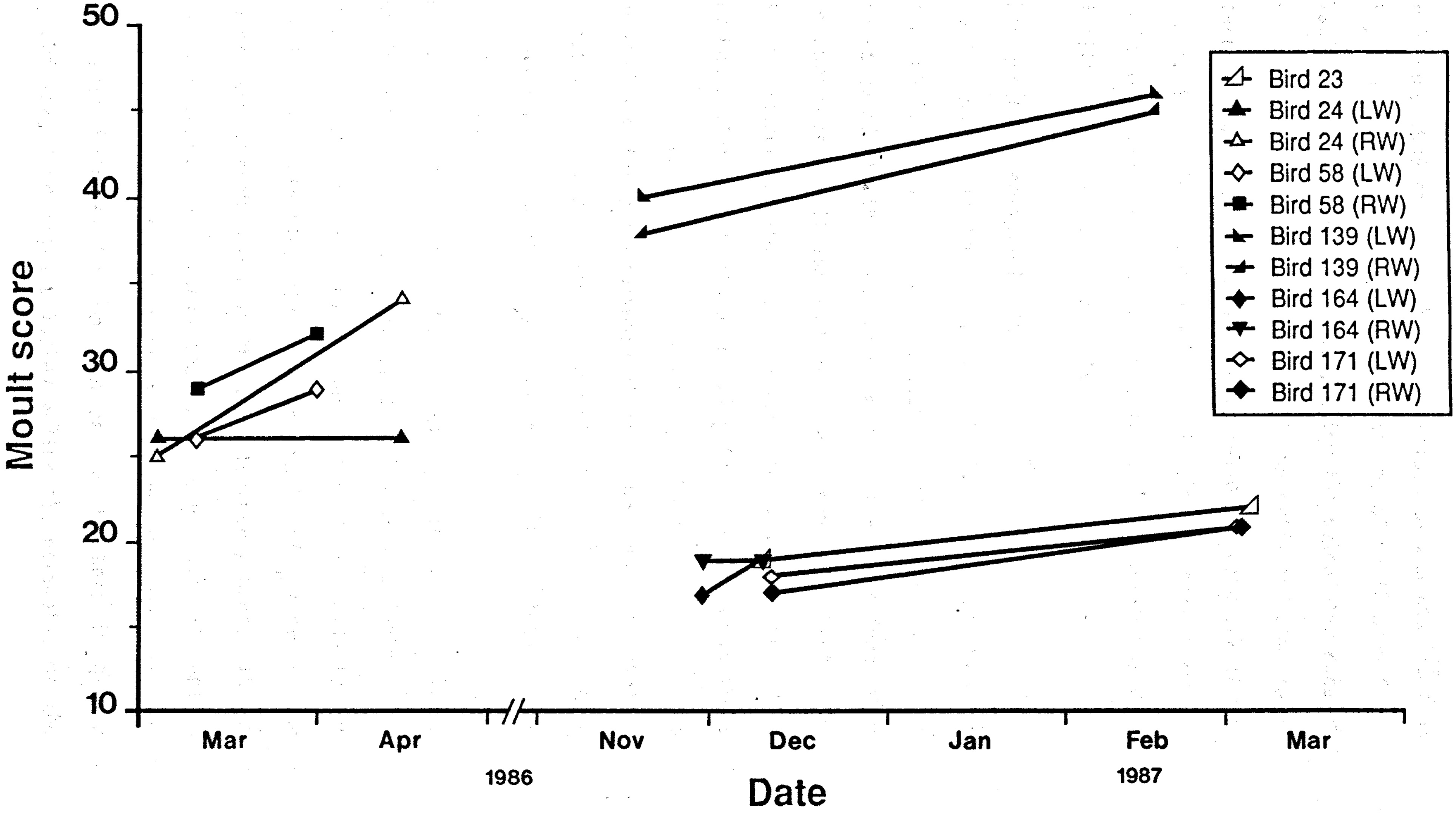


Table 7.18 Change in primary moult scores of recaptured resident Turkey Vultures.

Birds recaptured within 3 months

Iden	Dates caught	No. of days between recaptures	Increase in moult score units	Rate of increase/ day	No new remiges
23	10.12.86 5.3.87	85	6	0.07	2
24	3.3.86 15.4.86	32	9	0.28	3
58	10.3.86 1.4.86	25	9	0.36	1
139	18.11.86 16.2.87	90	13	0.14	4
164	29.11.86 10.12.86	13	2	0.15	0
168	16.12.86 21.12.86	6	0	-	0
171	11.12.86 3.3.87	82	7	0.09	2
Birds recaptured after > 3 months					
23	3.3.86 10.12.86	223	130	0.58	18
127	8.6.86 3.3.87	268	74	0.28	14

Figure 7.4 ***Changes in the moult scores of* recaptured resident Turkey Vultures**



127 between 8 June 1986 and 3 March 1987 (periods of 223 and 268 days respectively). Both birds were at different stages of moult when first captured (Tables 7.18: Figure 7.4). Thus, using the calculated rate of increase in moult units per day, for bird 23 the estimated time taken from the start to end of moult was 172 days, while for bird 127 it was 357 days. Thus, there is probably much variabilty in time taken to complete moult in different individuals (Figure 7.4). There may also be seasonal differences in speed of moult.

7.3.5 Feather growth in captive birds

Table 7.19 shows that there was remarkably little variation in the rate at which feathers grew (Figures 7.5 - 7.8). In migrant Turkey Vultures the range of growth rates for primary feathers was from 32-45 mm, for secondaries 35-51 mm and for tail feathers 21-45 mm. Differences in feather growth rates between individuals was partly because they had different numbers of growing feathers. A few feathers were measured towards the end of their growth period so it was possible to estimate (very approximately) the time taken to complete growth. For actively growing feathers for which the fully grown length was not recorded, an estimate was made of final length from neighbouring feathers.

The estimates of time taken to complete growth shown in Table 7.19 do not include the period between dropping an old feather and visible start of feather growth. (Birds were not held in captivity for sufficiently long to determine the precise length of growth of one primary feather and the shedding of the next feather.) Hence, it was not possible to calculate accurately the duration of moult in captive birds from the time taken for individual feathers to grow. However, assuming that most vultures had on average two feathers in growth (Table 7.1) and that (for migrant Turkey Vultures), estimates of the

Table 7.19 Mean growth rate / day of feathers in captive Black and migrant Turkey Vultures with calculated growth period (see text). N = number of times feather measured (at 3 day intervals).

Bird	Date	Species	Feather No.	Growth rate /day	N	Estimated time to complete growth
A	31/12/ - 21/1	Migrant	P4 (LW)	0.43	6	62.3
			P4 (RW)	0.45	6	59.6
			TF 3	0.45	6	51.1
B	31/12/ - 21/1	Migrant	P5	0.41	5	82.6
			S14	0.35	5	62.0
C	12/2 - 2/3	Migrant	P5	0.32	6	35.3
			S9	0.51	6	44.1
			S13	0.46	6	47.4
			TF5	0.21	6	114.8
D	22/2 - 24/2	Resident	P5 (LW)	0.40	2	-
			P5 (RW)	0.35	2	-
			P1	0.30	2	-
E	12/2 - 2/3	Black	P9	0.35	6	-
			S4	0.37	6	55.1
			S10	0.37	6	55.1
			S14	0.32	6	63.8
			TF2	0.21	6	81.0

Figure 7.5 Feather growth in captive Migrant Turkey Vulture

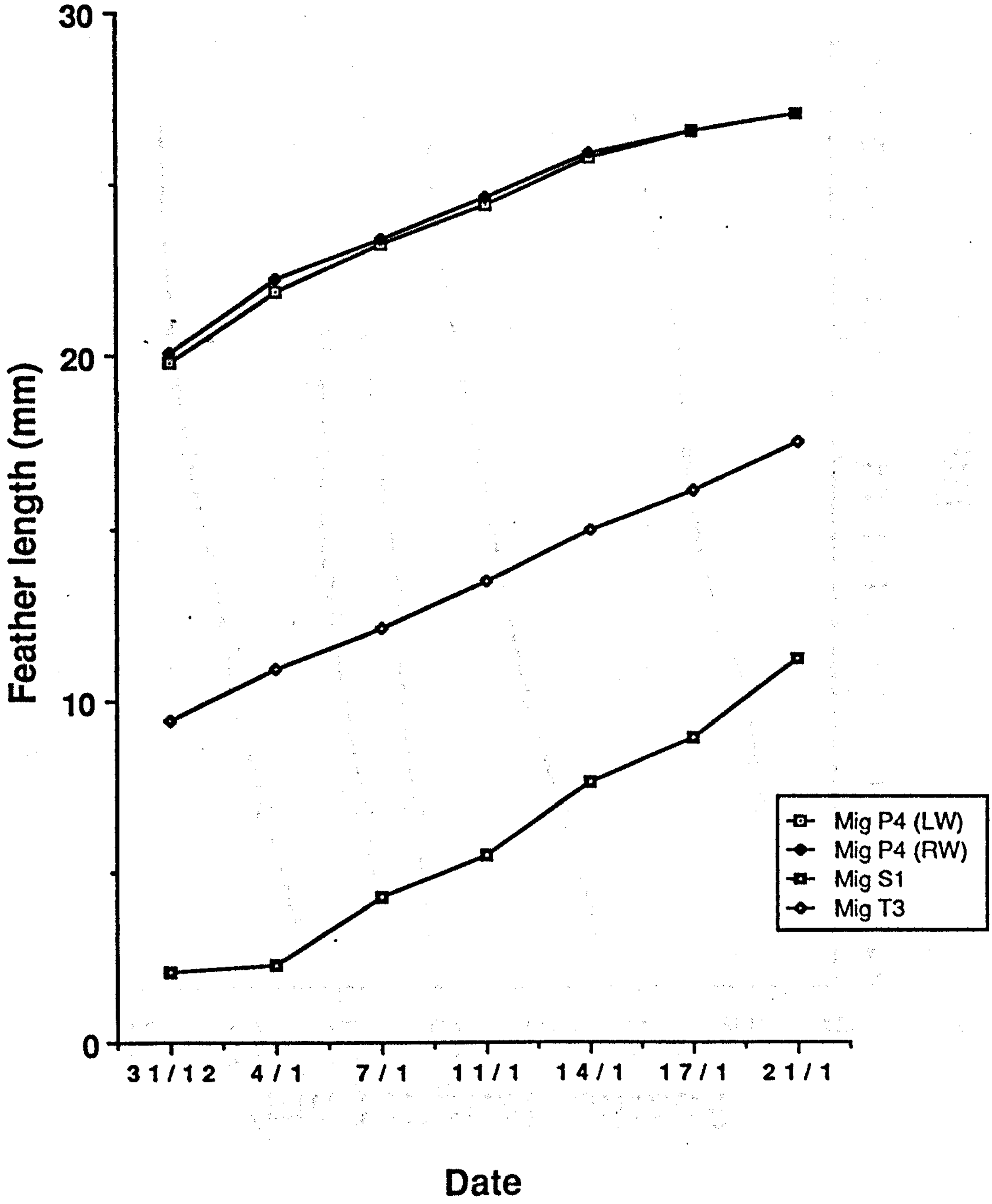


Figure 7.6 Feather growth in captive migrant Turkey Vulture

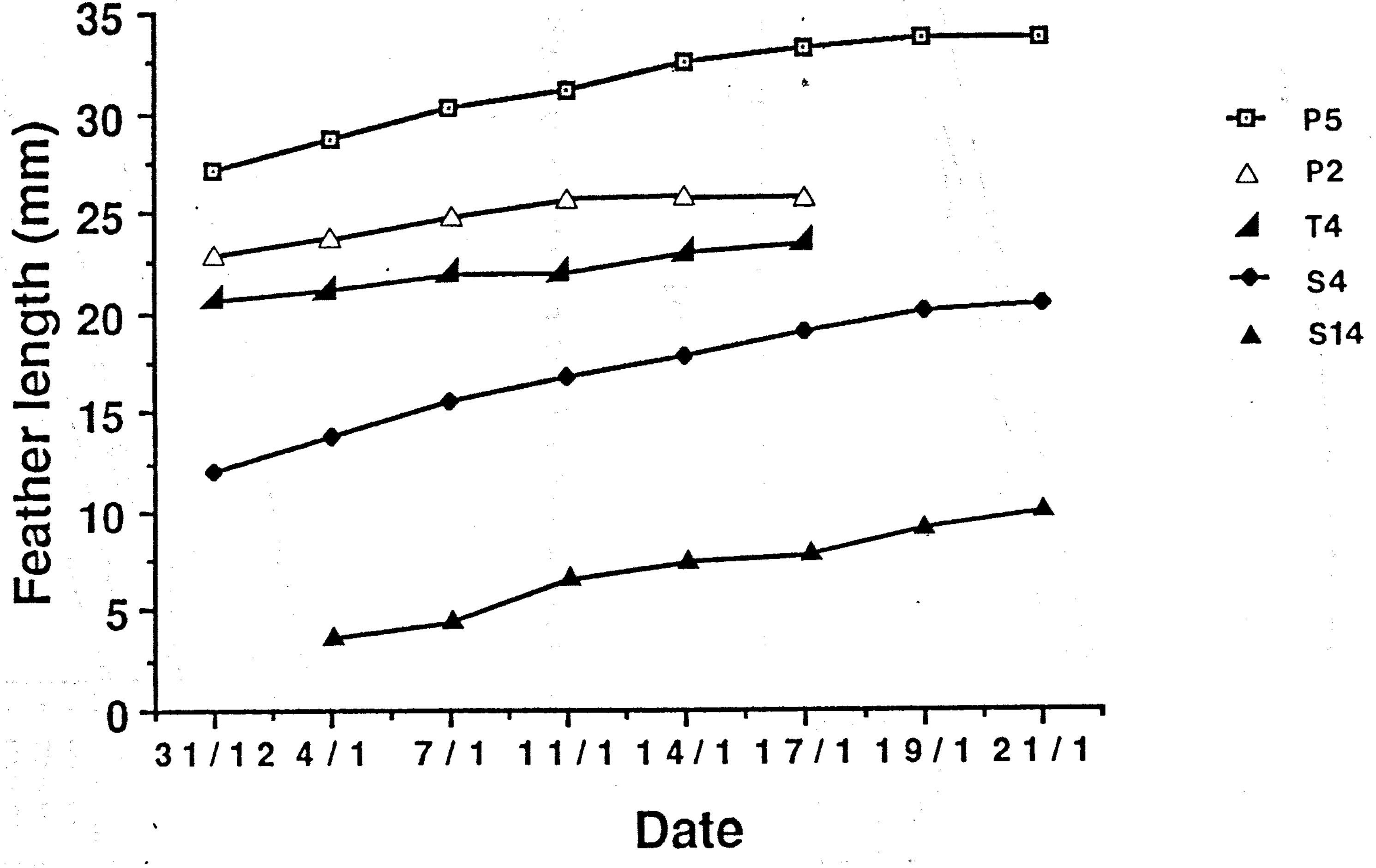


Figure 7.7 Feather growth in captive migrant Turkey Vulture

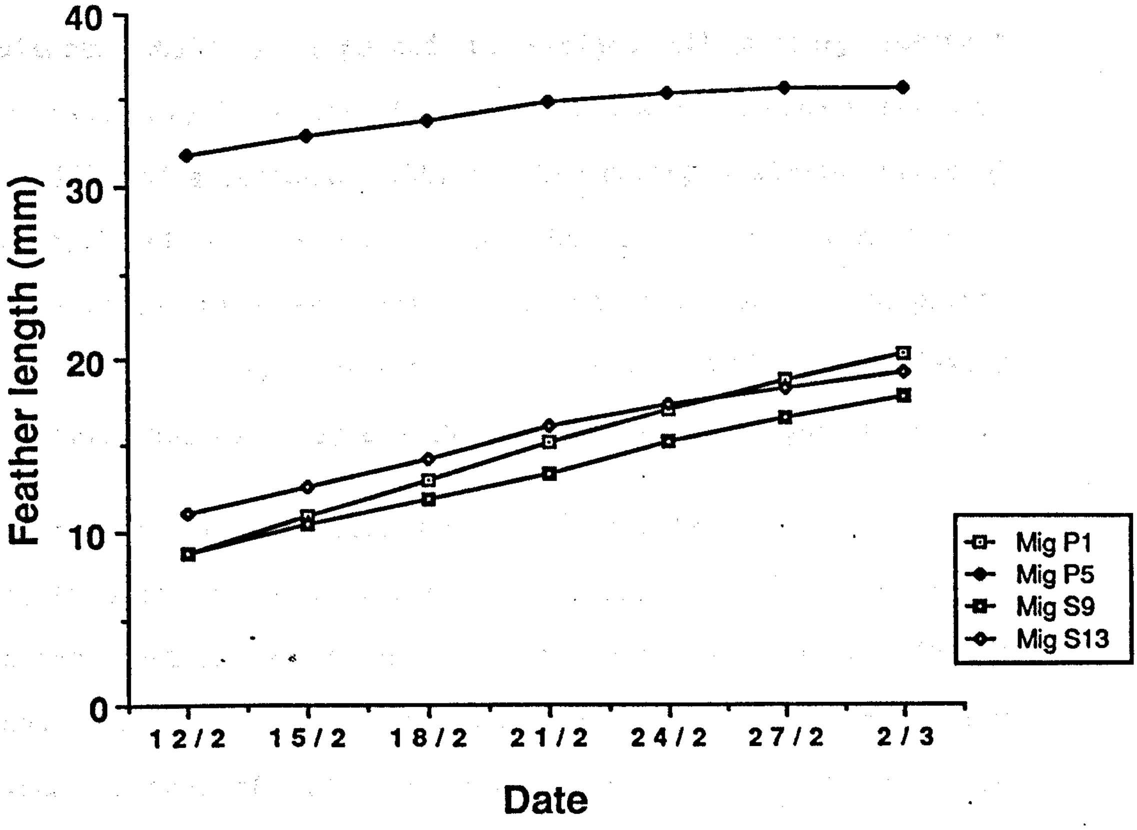
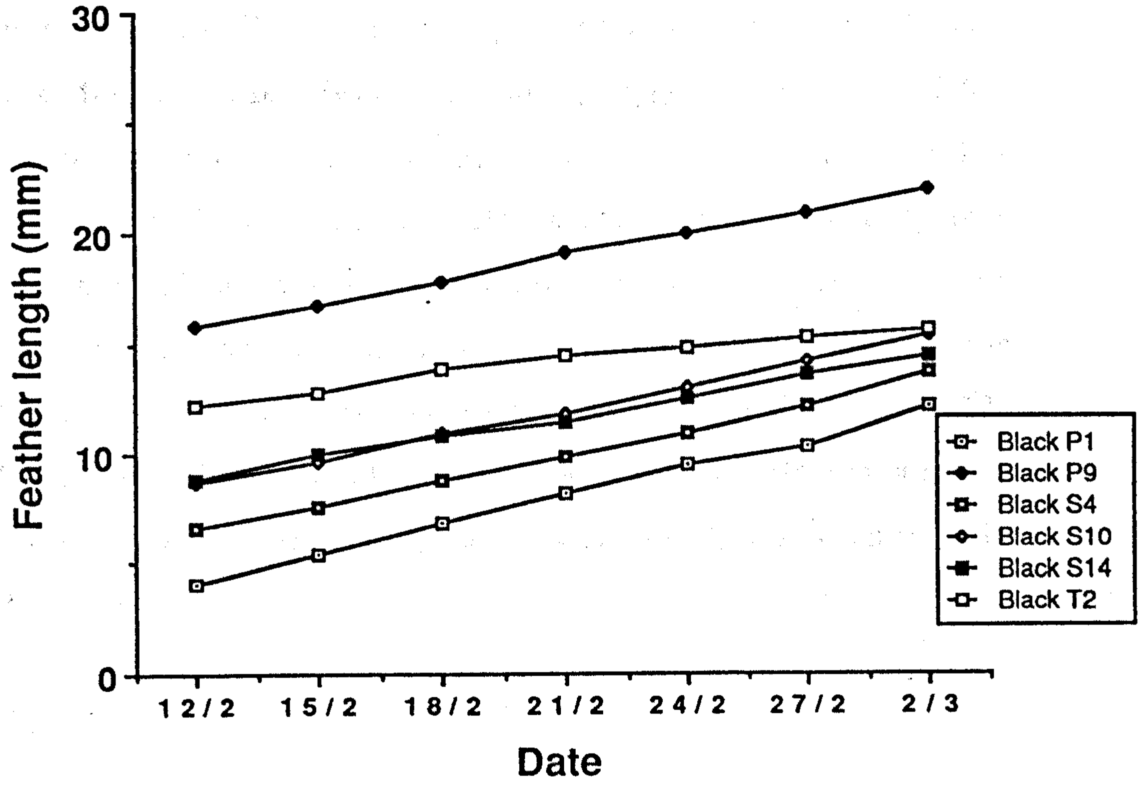


Figure 7.8 Feather growth in captive Black Vulture



length of time required by feathers to grow to full length average 60 days, vultures would be expected to replace all primary feathers within approximately 11 months. Comparison between the growth rates of a primary (P1) and a secondary (S9) feather during a similar stage of growth (individual 221, Figure 7.10) showed that the former grew signficantly faster than the latter (Wilcoxons test for matched pairs, $T = 0$, $N = 6$, $P < 0.01$). Primaries would be expected to grow faster than secondaries because they are the most important flight feathers.

7.3.6 Linear regression of moult score against date

Vultures were not examined over a sufficiently long period to determine the start and end of moult for the average individual in the population. Considering data recorded from both wings together (ie maximum moult scores of 100), regressions were significant for both Black and resident Turkey Vultures but there was no significant relationship between moult score and date for migrant Turkey Vultures (Figures 7.9-7.11). However, when wings in which growing feathers were absent were excluded (ie. suspended primary moult) regressions were significant for all taxa (Black Vultures, $r_{114} = 0.22$, $P < 0.02$; migrant Turkey Vultures, $r_{101} = 0.17$, $P < 0.05$; resident Turkey Vultures, $r_{71} = 0.27$, $P < 0.05$). Scatterplots of moult score against date showed that although there was variation in the moult scores of individuals examined on particular dates, the general pattern was for moult scores to be positively correlated with date (Figures 7.12-7.14). Thus, even though Black and resident Turkey Vultures moulted continuously throughout the year, there was remarkable synchrony in the moulting process.

Figure 7.9 ***Plot of moult score against date***
for Black Vultures (using all wings)

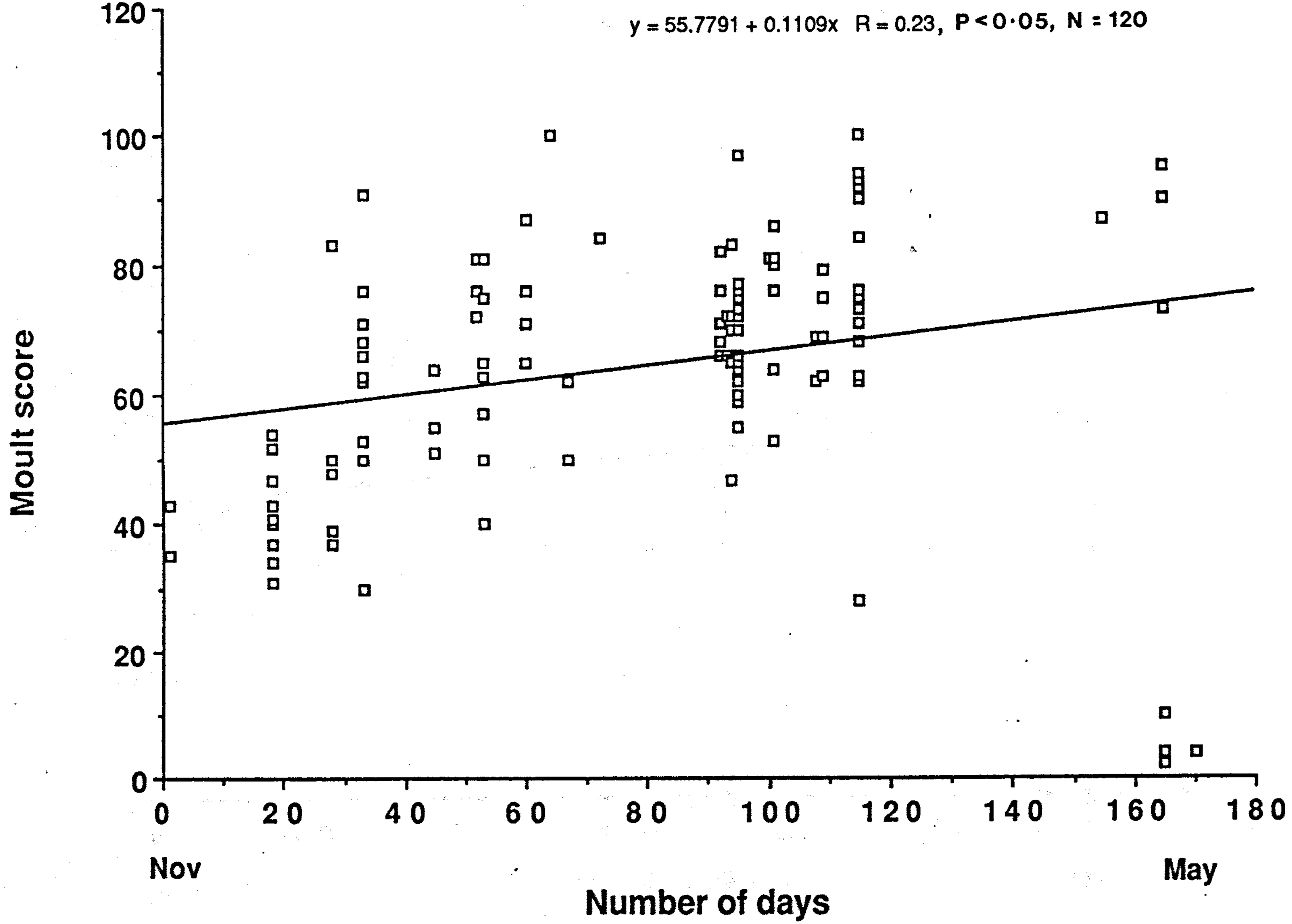
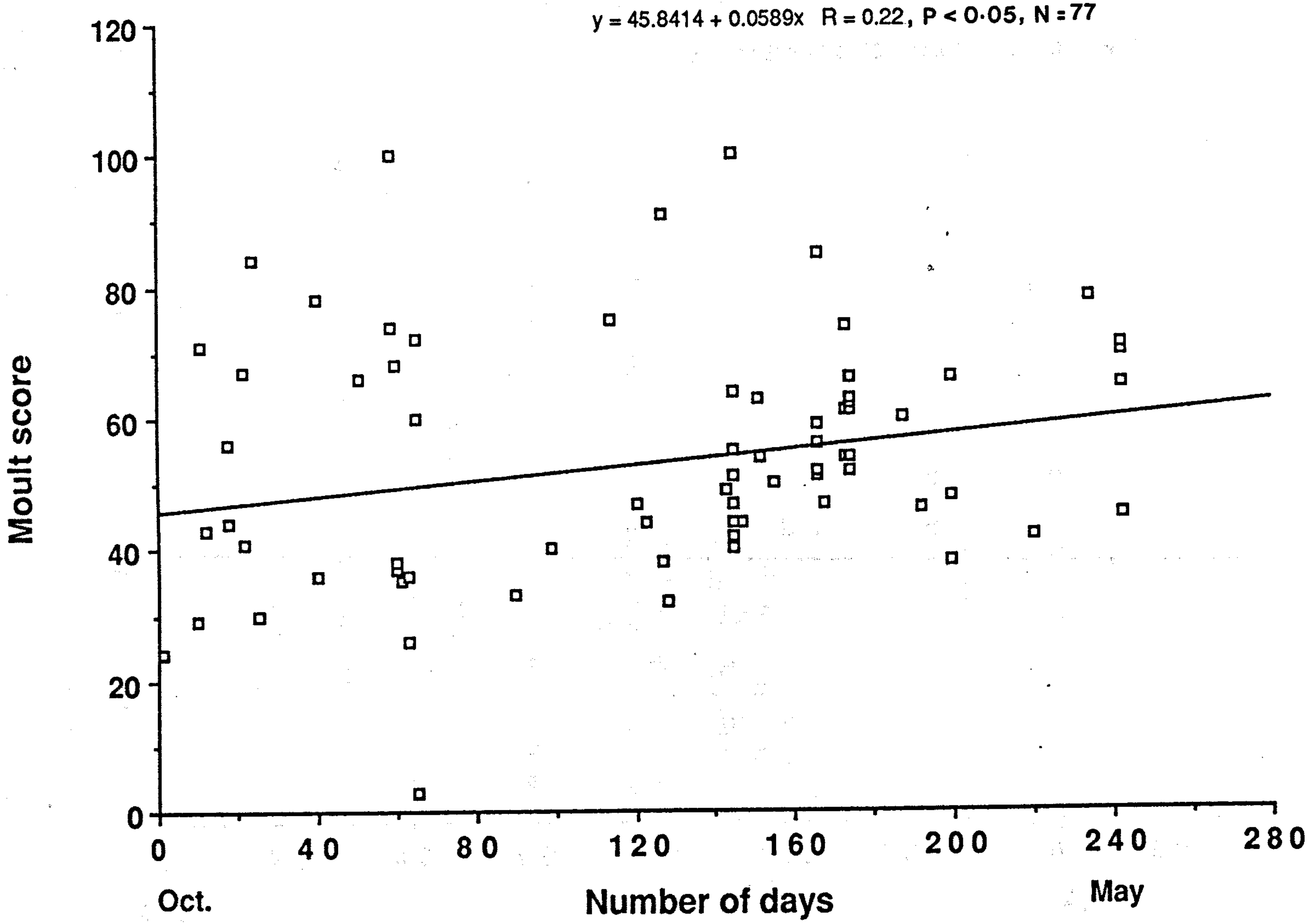


Figure 7.10 *Plot of moult score against date for resident Turkey Vultures (using all wings)*



$y = 45.8414 + 0.0589x$ $R = 0.22$, $P < 0{\cdot}05$, $N = 77$

Fig. 7.11 ***Plot of moult score against date for migrant Turkey Vultures (using all wings)***

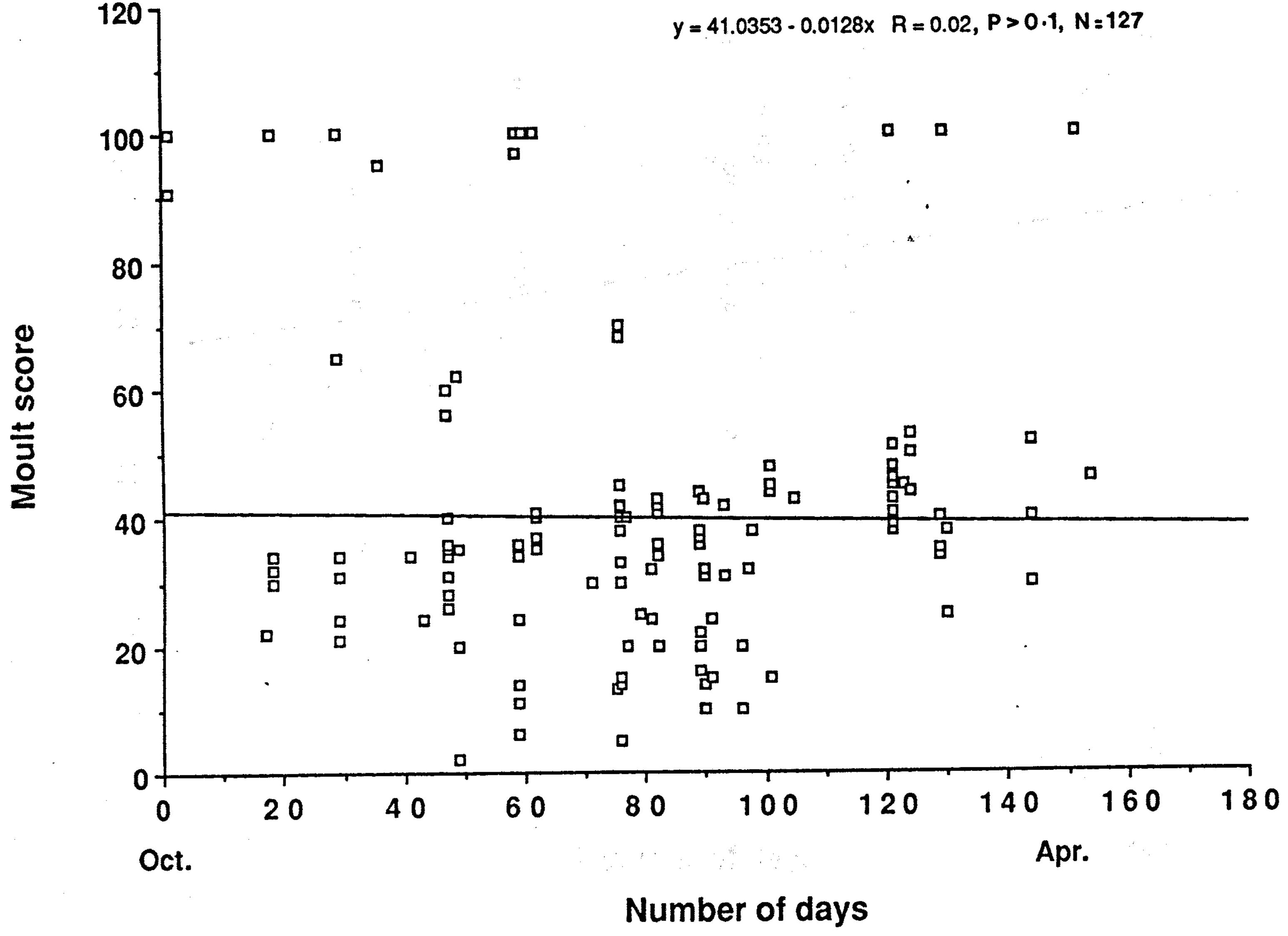


Figure 7.12 Plot of moult score against date for Black Vultures (using only wings with growing feathers)

$y = 27.9219 + 0.052x$. $R = 0.22$, $P < 0{\cdot}05$, $N = 116$

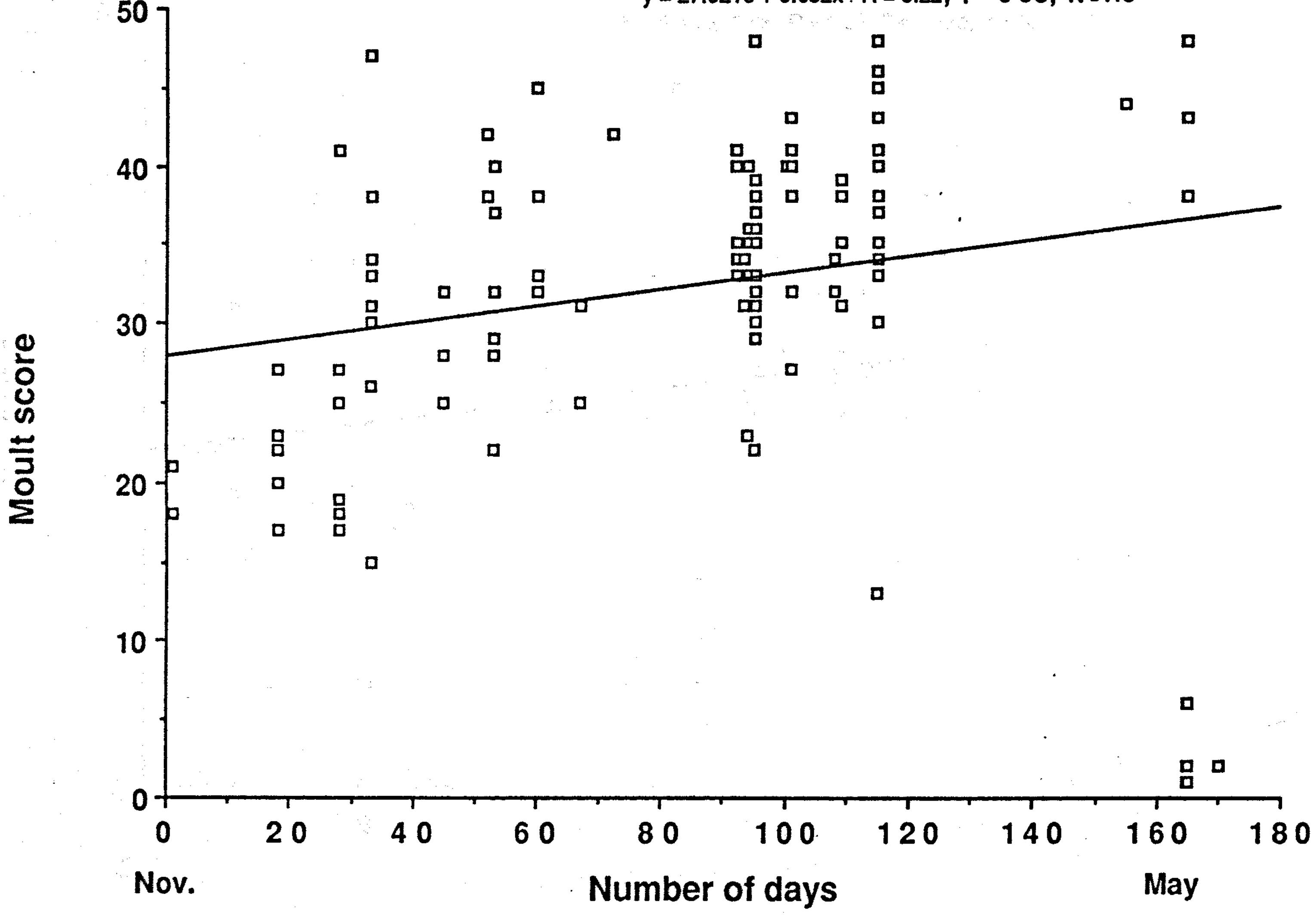


Figure 7.13 *Plot of moult score against date for* resident Turkey Vultures (using only wings with growing feathers)

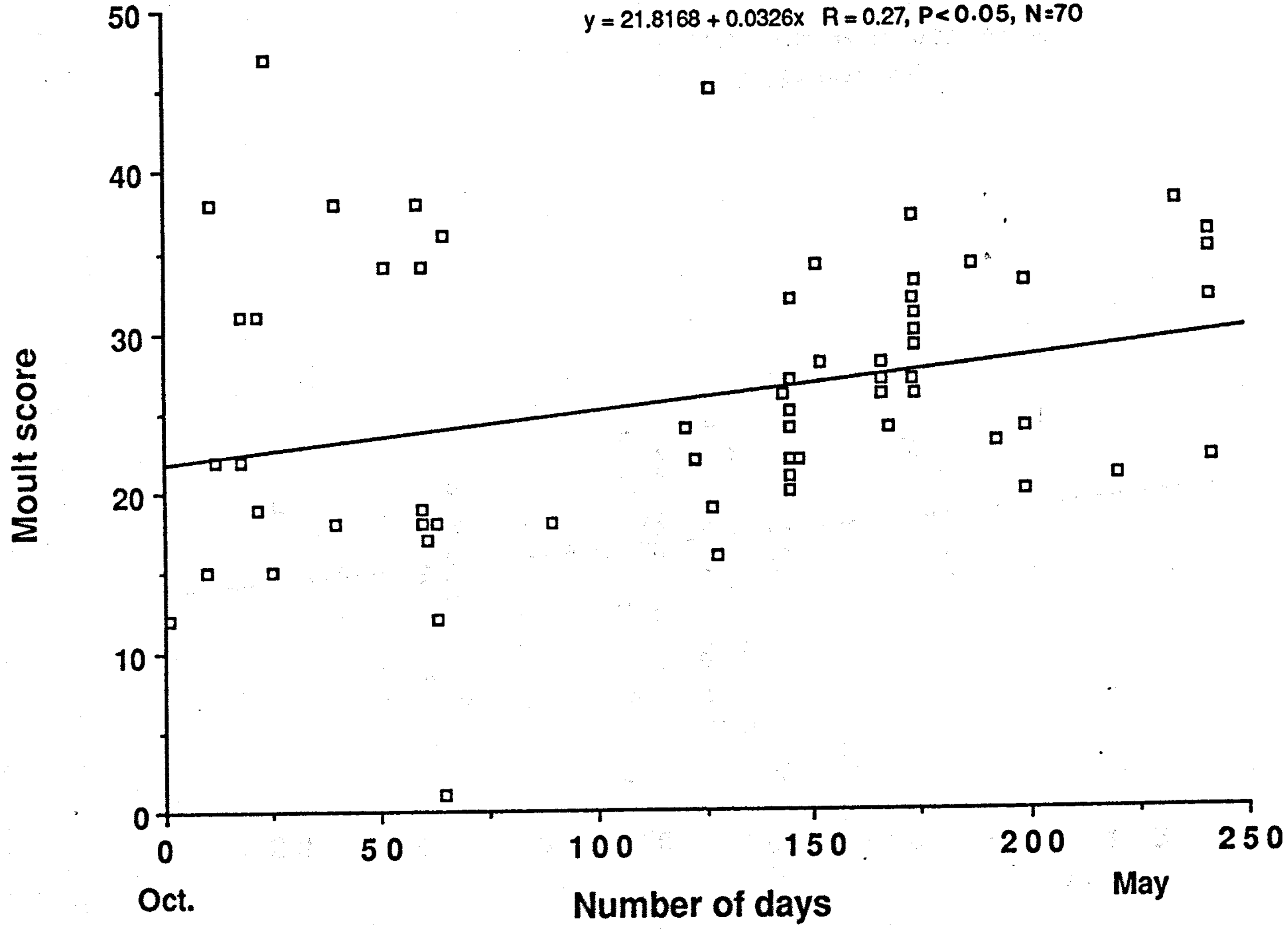
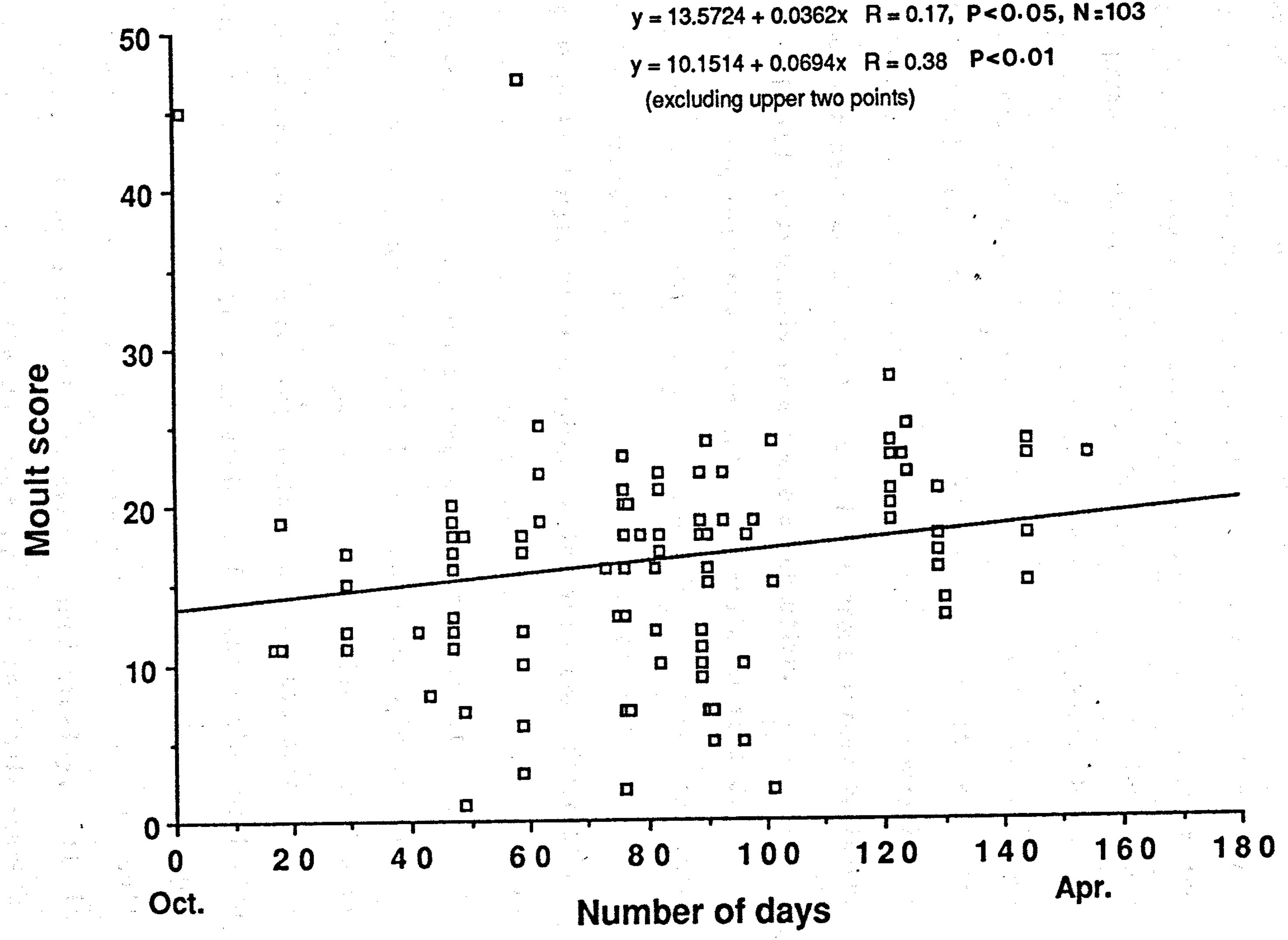


Figure 7.14 Plot of moult score against date for migrant **Turkey Vultures (using only wings with growing feathers)**



7.4 DISCUSSION

Moult in small New World vultures appears to be a continuous process (except in migrant Turkey Vultures), in which birds replace all their primary feathers on an annual basis. The general pattern of primary moult was serially descendent, although some birds showed stepwise moult. Secondaries were not moulted in the 'basic sequence' (ie. from the outermost, S1 progressing inwards towards the body - S15) but independently and secondary moult began sometime after the onset of primary moult, often continuing until after the latter had been completed. Chandler (in Rea 1983) found that in captive Black and Turkey Vultures, secondary foci were commonest at S1 and S5, followed by S11 (S9 and S10 were moulted independently). Moult progressed ascendantly. In the present study, in Black Vultures, secondary foci were also commonest at S1 and S5, but for migrant Turkey Vultures, findings differed considerably from those of Chandler.

By comparison with New World vultures, moult in some Old World vultures takes considerably longer as would be expected from their larger size (generally larger birds take longer to complete moult - Ginn & Melvile 1983): Houston (1975) calculated that White-backed Griffon Vultures took three years to renew completely all primary feathers and up to seven years to complete secondary moult).

There were a number of difficulties associated with calculating the duration of moult in the present study. Usually the period of moult is determined by regressing moult score against date (Ginn & Melville 1983) but this gives an estimate for the whole population rather than an individual bird. Where the regression line intercepts moult scores of 0 and 50, the start and completion of moult respectively can be recorded. However, paradoxically, it is preferable to use date as the dependent variable and moult score as the independent variable and vice versa to give a better estimate of moult duration for individuals (Pimm 1976). Moult was recorded for resident Turkey Vultures over nine months, for migrants over six months and for Black Vultures over four months but none of these periods were sufficiently long to measure accurately the duration of the process. When moult score was regressed on date there were several differences between taxa, but the general pattern was a large degree of variability in the spread of moult scores from birds examined on the same date.

Despite the variability in moult scores the significant positive correlation (combining data from three field seasons) between moult score and date for Black and resident Turkey Vultures demonstrates the similarity between the speed and synchrony of moult in vulture populations from the same geographical area. In contrast, the correlation between moult score and date was not significant for migrant Turkey Vultures, which may indicate that these birds came from different areas of the United states. However, when birds with primary tracts containing full grown feathers (old or new) were excluded linear regression lines were significant for all taxa.

When data were log-transformed (to fit moult scores to a normal distribution) there was no significant correlation between moult score and date for Black Vultures. This was because the distribution of dates when Black Vultures were caught were not normally distributed since birds tended to be caught in large numbers on a few days, rather than a more even spread of catch dates as for resident and migrant Turkey Vultures. Additionally, moult was recorded for Black Vultures during a period of only three months. The slow moult of vultures and variability in starting dates between individuals explains why log-transformed moult score regressions with date were not significantly correlated for this species.

The estimation of moult duration using changes in moult score from recaptured individuals suffers from a number of shortcomings and involves some invalid assumptions (moult score does not increase linearly with date - see Underhill & Zucchini 1988). Assigning growing feathers to score categories does not take into account the different lengths and masses of feathers and the time they take to grow. Furthermore, estimating moult duration from recaptures of the same individual could lead to wide differences in estimates between birds because of the nature of feather growth. This is because feathers grow slowly at the end of growth (Heinroth 1906) and they are therefore allocated scores of 4 for longer periods than scores of 2 or 3. There was also a possibility that moult in vultures is affected by season, particularly as there are changes in the food supply in the wet season in the study area, but only two recaptured birds had moulted during a wet season so this could not account for differing rates of increase in moult score units.

The numbers of growing feathers at any one time in individuals of different species could be related to wing-loading and flight strategy (Chapter 6, Section 6.4.2). For instance, Black Vultures, which have a high wing-loading and forage by soaring at high altitude (see Houston 1988), cannot exploit areas of weak lift close to the ground or vegetation in the manner adopted by *Cathartes* Vultures. It is therefore possible that a complete wing is not as important to predominantly soaring vultures as it is in the *Cathartes* taxa and this may explain why Black Vultures have significantly more rectrices and remiges in growth. By contrast, the flight strategy of Turkey Vultures, which have a significantly lower wing-loading than Black Vultures (see Chapter 6, Section 6.3.2) may be a constraint on the number of feathers in growth at any one time.

During three field seasons most (70%) Turkey Vultures which were on migration (captured after recently arriving from North America or on their way north in the spring) had at least one actively growing primary feather while the remainder were in a state of suspended moult or had all new feathers. However, the proportion of birds with all new feathers was much higher than birds examined in the overwintering period (when they had been present in South America for some time). In newly arrived Turkey vultures, a new moult was just beginning and wings were comprised mostly of old feathers. Although migrants did not completely arrest moult as Newton & Marquiss (1982) observed in Sparrowhawks, a large number of birds had no growing feathers in the primary tract. This suggests that migrant Turkey Vultures could suspend moult in the primary tract so that their wing feathers provide a uniform surface necessary for efficient flight when gliding (see Houston 1975). In other migrants, like Sparrowhawks from Northern Europe, moult precedes the spring migration so that birds do not have to undergo a long journey with partially moulted wings (Newton 1986).

A larger proportion of migrant Turkey Vultures had primary tracts in which growing feathers were absent (part old and part new feathers, or all new feathers) than was the case for resident Turkey or Black Vultures. This may indicate that even though moult appears to be continuous in the former vultures, the migratory habit may have imposed some constraints on moult. The presence of one or two actively growing feathers in the secondary tract is probably not important since these gaps are covered by other feathers in flight. Migrants were also found to have on average fewer feathers in growth during the dry season than either residents or Black Vultures. This supports other findings which suggest that migrants have fewer feathers in growth, allowing efficient flight over large distances. Presumably, because of their long wings and the fact that few feathers are in growth at any one time, some Turkey Vultures are able to undertake a substantial migration while moulting.

SUMMARY

1) All vultures replaced primary feathers on an annual basis, and this was demonstrated by recording moult throughout the dry season, from recaptures of marked individuals and measurements of growing feathers in captive birds. Examination of recaptured resident Turkey Vultures showed that there was individual variation in the time taken to complete moult. It was not possible to investigate the duration of moult using the usual method of a linear regression of moult score against date because birds were not examined over a sufficiently long period. Data were not collected on moult in breeding vultures, but Black Vultures caught in February (when other breeding adults were known to be feeding young) showed no sign of suspended moult.

2) Compared to resident Turkey and Black Vultures, migrant Turkey Vultures had significantly fewer growing feathers. During the dry season, more migrants had wings with no growing feathers than either of the other taxa. Proportionately more migrants which had recently arrived in, or about to depart from South America, showed suspended primary moult than birds which had been overwintering in the general area for a longer period. This suggests that migrants could suspend moult at least during migration periods so that they could fly as efficiently as possible. Most migrants had some feathers in growth, usually secondary or tail feathers, indicating that a small number of growing feathers in these tracts may not affect flight efficiency on migration.

3) For all taxa, when equivalent growing feathers were compared, generally the primaries showed greatest symmetry followed by the tail and then the secondaries. Results differed somewhat when moult scores were correlated between each wing and each half of the tail. There was

a lower correlation between the secondary tract in each wing than for the primaries but no correlation was found between each half of the tail. This agrees well with what is probably the relative importance of each feather tract in flight. For instance, it is most important that primary feathers should be moulted symmetrically in terms of flight aerodynamics.

4. Black Vultures had highest numbers of growing feathers followed by resident Turkey Vultures and lastly migrant Turkey Vultures. Black Vultures also showed the greatest degree of irregular or stepwise moult.

CHAPTER 8 GENERAL DISCUSSION

Ecological Separation in small Cathartid vultures

Overlaps in resource utilisation between different vulture taxa were reduced by a number of avoidance mechanisms, which included habitat selection, feeding on different carcase types and differential feeding times. At mixed-species feeding flocks, dominance hierarchies mediated competition. There was much variation in the relative importance of these different mechanisms among different taxa.

During the dry season, there were striking differences in the density of vultures in different habitat types (Chapter 3, Sections 3.3.1, 3.3.5). The general pattern was for foraging *Cathartes* Vultures (mostly migrant Turkey Vultures) and Black Vultures to occur at high densities in savanna habitats, in contrast to low densities over the gallery forest area. There were significant differences in density of *Cathartes* Vultures, but not Black Vultures between habitats (Chapter 3, Section 3.3.5). This was attributed to the more even dispersion of *Cathartes* compared to Black Vulture flocks which were highly clumped. Migrant Turkey Vultures foraged over savanna habitats more than expected from its availability, if their dispersion had been random. By contrast, resident Turkey Vultures foraged almost entirely over gallery forest. Lesser Yellow-headed Vultures showed no significant habitat selection, but were seen most often in open marsh and sandhill areas.

During the wet season there was a striking difference in densities of *Cathartes* Vultures (Chapter 3, Section 3.3.6) and differences between habitats were less marked. The emigration of migrants resulted in a six-fold decrease in the density of *Cathartes* Vultures. Resident Turkey Vultures showed a foraging shift from forest habitats to open savanna. This may have been a release effect in the absence of migrants. In both dry and wet seasons King Vultures were only seen over gallery forest.

Migrant Turkey Vultures moved through the ranch in large numbers during the autumn and spring migration (Chapters 3 and 4). However, even in the period when migrants were assumed to be relatively sedentary in the study area (ie the 'wintering' population), the very low proportion (16% - Chapter 4, Section 4.3.1) of resightings of marked individuals strongly suggested that these vultures ranged over very large areas, or were nomadic within South America. The proportion of migrants resighted was significantly less than the proportion of resident Turkey Vultures which were resighted.

Individual marked migrants which did stay at the ranch moved over significantly smaller distances than either Black or resident Turkey Vultures (Chapter 4, Section 4.3.2). A few migrants therefore showed high site fidelity (even between years) and exploited locally abundant food in open savanna, often close to ranch houses. Black Vultures may be more likely to cover larger distances because of their high altitude foraging. The majority of sightings of marked resident Turkey Vultures were made in gallery forest where there was lower food availability; intersite distances were therefore higher than for migrants seen in the open.

During the wet season, Black Vultures moved significantly greater distances than in the dry season (Chapter 4, Section 4.3.5) suggesting a decline in the availability of food and increased intraspecific competition. Food supplies were probably lower in the Llanos during the wet season. Additionally, the dramatic decrease in density of *Cathartes* Vultures meant that there were fewer birds searching by olfaction for carcases. This reduced the chances of Black Vultures being led to hidden food.

Marked Black Vultures were seen more often than expected in open and semi-open habitats (Chapter 4, Section 4.3.7 - based on the null hypothesis that the distribution of sightings was proportional to habitat area). By contrast, wing-tagged resident Turkey Vultures showed less habitat selection in the wet season, whereas in the dry season they were seen significantly more than expected in gallery forest. The behaviour of radio-tagged resident Turkey Vultures supported the hypothesis of a niche shift; they occupied ranges within the gallery forest during the dry season but after migrants departed, before any seasonal changes were detected, birds foraged in open savanna (Chapter 4).

In Chapter 5 the behaviour of vultures feeding at carcases was discussed. A comparison between forest and savanna sites during the dry season showed that carcases were discovered more quickly in the open (Chapter 5, Section 5.3.1). More than 80% of forest carcases were discovered first by resident Turkey Vultures even though counts indicated similar densities of migrants and residents in the forest (Chapter 3, Table 3.6). Thus, residents seemed to search more actively than migrants, probably because of their subdominant status. In the dry season, most carcases in open savanna were visited by Black and migrant Turkey Vultures (Chapter 5, Section 5.3.3). On the other hand, resident Turkey Vultures visited most gallery forest baits but few open ones. Again in the wet season differences were striking; residents visited open savanna carcases frequently (Chapter 5, Table 5.4).

Taxa were ecologically separated by carcase type. During the dry season, group sizes of Black Vultures (in the open) and King Vultures (in the forest) were positively correlated with carcase weight (Chapter 5, Section 5.4.6). However, group sizes of migrant Turkey Vultures (in the open) were negatively correlated with carcase weight, and there was no correlation between carcase weight and group size of resident Turkey Vultures.

Group sizes of *Cathartes* Vultures and the rate of agonisitc encounters between all vulture taxa was higher outside the forest suggesting that competition from migrant Turkey Vultures in the savanna was a constraint on residents feeding in these habitats (Chapter 5, Section 5.4.2). This was also suggested by detailed behavioural observations at forest carcases. Resident Turkey Vultures had high feeding rates when alone or in small groups before any migrants arrived (Chapter 5, Section 5.3.8). Migrant Turkey Vultures generally arrived later, spent more time engaged in aggressive interactions than residents and as a consequence had lower feeding rates. By contrast, King Vultures had extremely low feeding rates but because of their social dominance could feed uninterrupted by energetically costly disputes. The feeding rate of residents was significantly and negatively affected by increased numbers of migrants and King Vultures, but not by other residents (Chapter 5, Section 5.3.9). Most agonistic interactions were intraspecific. Migrants attacked residents significantly more than they attacked other migrants, indicating strong competition between the races.

Chapter 6 showed that there were large differences in morphology between different Cathartid vultures (Section 6.3.1). Migrant Turkey Vultures were significantly larger than residents in most body dimensions, which accounted for their social dominance (Table 6.3). Differences in wing-loading between taxa were striking and reflect foraging strategies (Chapter 6, Section 6.3.2). Lesser Yellow-headed Vultures had lowest wing loading, followed by resident Turkey Vultures, migrant Turkey Vultures and finally Black Vultures. The low wing-loading of the *Cathartes* Vultures enables them to fly at low altitude searching for carrion using olfaction, whereas Black Vultures depend almost entirely on thermals to forage. The body condition of resident Turkey Vultures was generally below average in dry season months, but birds caught in months when migrants were absent had above average condition (Chapter 6, Section 6.3.5). Migrant Turkey Vultures trapped after autumn migration were in comparatively poor condition whereas later in the dry season average condition of marked birds improved.

To summarise, despite the occurrence of intraspecific and interspecific aggression in Cathartid vultures at feeding sites, evidence for competition affecting the overall fitness of individuals was circumstantial, since little was known about survivorship or reproduction of marked birds in relation to their intraspecific or interspecific ranking. However, some evidence for competition was the following;

1) Despite a probable abundance of available food in the dry season, most migrant Turkey Vultures had large home ranges. By inference, the nomadic movements of subpopulations of migratory Turkey Vultures, and leap-frog migration in particular, suggest the importance of intraspecific competition (see Greenberg 1986). This is because birds from more northerly populations have to overfly the winter ranges of southerly ones, and this constitutes an energetic cost. Most wing-tagged migrant Turkey Vultures were not resighted indicating that they were heading further south or at least were itinerant within South America. The first individuals trapped at the ranch after returning from breeding grounds were significantly larger than later arriving birds (Chapter 6, Section 6.4.4) and these birds did not remain in the study area.

2) During the dry season, residents were forced to seek food in a forest habitat which held fewer migrants. Increased competition when migrants are present may therefore affect body condition of residents;

future comparisons between body condition of vultures in dry and wet seasons might show this, but ultimate factors such as food supply would also need to be measured. The body condition of resident Turkey Vultures was generally below average in the presence of migrants, but was above average in the wet season when migrants had departed. Food supply is probably most abundant in the dry season due to increased animal mortality.

3) The concept of niche breadth broadening (ie. competitive release) when competition is decreased was supported by the observation of a niche shift in resident Turkey Vultures during the wet season (see later-migrant and resident interactions).

4) Interspecific dominance hierarchies in vulture guilds also indicated the importance of competition. For instance, because dominant individuals have greater resource holding potential (see Fretwell 1972), subdominants may incur costs to overall fitness. Subdominant individuals (eg. resident Turkey Vultures) are forced to leave feeding sites and search elsewhere for food.

Food supplies for vultures are unpredictable so it is clearly difficult for them to specialise. Vultures are generally considered to be opportunisitic. However, the present study showed that at least some taxa specialised by foraging in particular habitats (resident Turkey Vultures), or feeding on particular carcase types (eg. Lesser Yellow-headed Vulture). This reduction in overlap probably reduced competition between different taxa.

Differential migration in the Turkey Vulture

The study of variation in intraspecific migration, where some individuals are long distance migrants while others are more or less sedentary has been reviewed recently by a number of authors (Morton 1980, Ketterson & Nolan 1983, Myers *et al* 1985). Although the factors determining partial migration (selective pressures operating differently on part of a population) may be quite different across bird genera there have been several attempts to define a general evolutionary model; some workers have favoured a single factor approach (eg. Gauthreaux 1978, 1982) while others have proposed a more plausible combined-factor approach (Baker 1978). Ketterson & Nolan's data on Dark-eyed Juncos *Junco h. hyemalis* were best explained by Baker's model (1978), in which males, which were larger and dominant to females, wintered at higher latitudes.

The body-size hypothesis, which proposes that because males are larger and have greater fasting ability (Calder 1974), they do not migrate as far as females, has mixed support. Theoretically, in species with the highest sexual dimorphism males should migrate least (Dolbeer 1982) and have higher fasting ability but this is not always true; in Juncos, Stuebe & Ketterson (1982) found no intersexual difference in fasting ability. However, there is support for this hypothesis among raptors which have reversed sexual dimorphism; females winter closer to breeding grounds (Newton 1979, Piccozi 1984). The second single-factor hypothesis favoured by Gauthreaux (1978, 1982), proposes that social dominance is the most important factor behind differential migration. Thus, during the winter, subdominants have to leave breeding areas when conditions deteriorate and competition for food increases. Thirdly, there is the arrival time hypothesis, in which strong intrasexual competition sets a premium on males (or females in polyandrous species) arriving early at breeding grounds on their return migration (Myers 1981). Selection pressures are therefore for males to migrate shorter distances so that they will not be disadvantaged when returning to breed.

From this preamble it appears that none of these hypotheses alone explain the complex differential migration of Turkey Vultures.

Although the species is not markedly sexually dimorphic, there are six races which differ considerably in body size. Individuals in some races also vary in size latitudinally (see later). Among these races there are partially migratory subpopulations, some individuals remaining in North America throughout the winter (in the southern and middle United States), while others are completely migratory (eg. retreating from the far north) and some tropical subpopulations which are year-round residents.

The mechanisms underlying differential migration of Turkey Vultures at higher latitudes may well be different from those at lower ones; proximate factors in the north force all vultures to emigrate irrespective of body size or condition. Evidence from the northern United States suggests that they migrate in response to decreased temperatures and reduction in daylength (Jackson 1988). In the more equable climate of their southern range, other factors may be important in determining which subset of birds migrate. In some partially migratory populations, social dominance may be important. The vultures which migrate may be subdominant birds as proposed by Gauthreaux (1982). However, intermediate-ranking birds may suffer most competition and be the class most likely to migrate rather than subdominant birds (Ketterson & Nolan 1982).

Baker's (1978) model defines an equation in which the overall fitness of a bird is enhanced if it migrates to a better quality habitat rather than staying in the currently occupied habitat. Thus, there is a migration threshold at which benefits accrueing to individuals which migrate are greater than costs. To test the validity of a migration threshold for Turkey Vultures, survivorship of different subpopulations must be determined and comparisons made between individuals which migrate and those which are sedentary.

Generally, though there are few available data (eg. Stewart 1977) Turkey Vultures show a form of leap-frog migration in which it is the larger individuals which migrate furthest south (Salmonsen 1955). This occurs commonly among raptors; for example in Europaean Kestrels *Falco tinnunculus*, larger northern individuals overwinter in southern France, while smaller birds fly only as far as northern France (Mead 1973). Following Bergmann's rule, body-size of Turkey Vultures shows a distinct clinal trend in size; in northern latitudes Turkey Vultures are larger and there is a progressive decrease in body-size southward. Thus, at wintering sites such as the Llanos in Venezuela, the vultures which remain in the area would be expected to be smaller than birds which have to fly further south to find food. Chapter 6 suggested that it was indeed the smaller individuals which stayed in the study area.

To my knowledge, nothing is known about the body sizes of vultures which overwinter in the United States, relative to the individuals which migrate. That it is adults which remain and only prebreeders that migrate can only be speculative (Jackson 1988), since a large number of marked individuals would be needed to confirm this. Whether particular subpopulations of Turkey Vulture migrate or remain in their breeding areas is probably a function of an optimal balance of several selective pressures (costs of migration, survival on the wintering grounds and the effect of the return time to breeding areas on reproductive fitness) which vary between individuals according to their age and intraspecific status (see Ketterson & Nolan 1983).

General factors inducing Turkey Vulture migration

Cox (1985) discusses five separate theories relating to the evolution of migration; increased seasonality, optimal energy budget, intraspecific and interspecific competition, predation and food supply and finally the time - allocation model. Of these, he favours a combination of competition theory and the time-allocation model (migrants wintering in the tropics have increased survivorship relative to temperate residents - Greenberg 1980). Exploratory migration (see Baker 1978) in the Turkey Vulture may have been triggered by increased seasonality and intraspecific competition. In addition, changes in vegetation and climate associated with the Pleistocence glaciation may have led to isolation of subpopulations and subspecific differentiation in Turkey Vultures, thus isolating tropical residents from other subpopulations (see Mengel 1964).

The current range expansion of Turkey Vultures in the northern United States and Canada (Wilbur 1983) demonstrates their opportunism and ecological plasticity in adapting to different climates (see Hatch 1970), though the reasons for this are equivocal (Bagg & Parker 1951). Historically, Turkey Vulture populations have responded to fluctuations in ungulate herds (eg. Bison *Bison bison*) in North America and recent trends in animal husbandary; in some areas there has been a decline in numbers of vultures due to improved animal hygiene (Wilbur *et al* 1983).

In the wintering area of central Venezuela, the constraints of nest site availability and food supply have probably resulted in high selective pressures for vultures to migrate. Many raptor populations are limited by lack of breeding sites (Newton 1979). Turkey Vultures nest at low density (Coles 1938, Davis 1983 a) and in North America use remote caves, cliffs and hollow trees as nest sites, although they also nest on the ground (Jackson 1983, 1988). In the tropics, ground-nesting birds have high nest mortality and this may also apply to vultures; thus birds which migrated north would enhance their reproductive fitness.

Although there are selective pressures for birds to show high site fidelity (Alerstam & Enckell 1979), the advantages to overall fitness in such individuals are reduced if this behaviour occurs in seasonally fluctuating climates. Nevertheless, birds which show high fidelity to particular areas have better knowledge of food sources, shelter and predator avoidance. So that they are not disadvantaged to residents, migrants must have higher reproductive rates and be able to overcompensate for the losses suffered during migration (Alerstam & Enckell 1979).

In both the New and Old World, individuals of species which migrate to the tropics have higher survivorship than resident individuals of the same species from the same latitude (Greenberg 1980). Compared to temperate migrant subpopulations, resident Turkey Vultures in the tropics probably have increased survivorship but lower reproductive rates. This may explain the large difference in population sizes of resident and migrant Turkey Vultures (Chapter 3). The ultimate factors determining population sizes in each race are very different; residents have low reproductive outputs and are less opportunistic than migrants. By contrast, migrants have increased their reproductive output by flying north to breed and thereby reducing intraspecific competition (see Lack 1968). For differential migration to have evolved, the migration threshold must vary between individual Turkey Vultures. Selection pressures must therefore fluctuate to maintain both a migratory and a resident strategy.

Migrant-Resident Interactions

Some of the assumptions and preconceptions about the Nearctic-Neotropical migration system stemmed from the simultaneous development of theoretical ecology and migration studies during the 1950s and 1960s (Greenberg 1986). Recently, however, migrants have been viewed as species with established niches in tropical communities which take advantage of northern seasonal productivity to breed (Keast & Morton

1980, Rappole *et al* 1983, Greenberg 1986). Thus, migrants do not necessarily have ecological counterparts in the tropics and the niche space occupied by them is not filled by residents on their departure north in the spring (Rappole *et al* 1983). Many recent studies have shown that neotropical migrants and residents reduce potential competition by habitat segregation or foraging behaviour (eg. Barlow 1980, Stiles 1980, Tramer & Kemp 1980) and territoriality has been demonstrated in a number of migrant species (eg. Rappole & Warner 1980).

Turkey Vultures are among several polytypic migrant bird species with temperate migratory subpopulations which are sympatric with tropical resident congeners. There are numerous examples of northern temperate or sub-arctic bird taxa wintering further south where they are sympatric with their southern counterparts (eg. Sylven 1978, Monaghan *et al* 1983). These northern races are invariably larger than the more southern ones and therefore dominate them in direct interactions at clumped food sources or by territoriality. An example is that of the Scandinavian race of Herring Gull *Larus argentatus argentatus*, which dominates British Herring Gulls *Larus a. argenteus* feeding at refuse tips (Greig *et al* 1986).

A striking difference between the present study and other studies of migrant-resident interactions is that in the same species migrants were larger and therefore possible competitors of residents. In Africa, there are several examples of larger migrant species overwintering sympatrically with smaller resident congeners (eg. Beeaters Meropidae and Orioles Oriolidae - see Moreau 1972). Generally, in passerines from the Old World, potentially competing migrants and residents which occur sympatrically in winter will often be members of the same family but rarely of the same species (except Laniidae - Moreau 1972).

There is no quantititave evidence that competition occurs between these species and Moreau (1972) suggests several mechanisms for ecological separation. However, in some cases migrants may considerably outnumber residents (eg. *Hirundo rustica*) and this may lead to competition for food resources (see Curry-Lindahl 1981). In Penninsular Malaysia, migrant Barn Swallows *Hirundo rustica* and Pacific Swiftlets *Apus pacificus* fed at the same altitude as resident species but there was no evidence of any temporary resource abundance (Waugh & Hails 1983). The timing of the peak occurrence of young in both resident swallows and swiftlets does coincide with the absence of migrants (Hails 1983) and this may not be coincidental (Waugh 1983). Three species of Palearctic hirundine spend the temperate winter in southern Africa at a time when native hirundines are breeding and this presumably increases the demand for aerial insect food (Waugh 1978). Most hirundines resident in southern Africa are separated altitudinally. Where air space overlap occurs between migrants and residents the latter do not breed during the period of sympatry suggesting that food may be limiting (Waugh 1978).

In raptors, there are several examples of Palearctic migrants overlapping with their tropical congeners (eg. Marsh Harriers *Circus aeriginosus* and Black Kite *Milvus migrans* - see Moreau 1972), but there are no quantititave studies of the interactions between them. In the case of Marsh Harriers, migrants considerably outnumber residents, a similar situation to that occurring in Turkey Vultures. Resident Black Kites may be more closely associated with humans than migrants and this may reduce competition. Among ecologically similar migrant and resident raptors, overlap is reduced by geographical separation (see Newton 1979), such as in Ospreys *Pandion haliaetus* which forage on the coast and thus avoid competition with Fish Eagles (Thiollay 1978). Both immigrant Pallid *Circus macrourus* and Montagu's Harriers

C. Pygargus forage in dry grasslands and overlap little with resident harriers (Brown 1970). Where overlap occurs between migrant harriers of different species, presumably food is abundant (Newton 1979).

Most migrants and resident bird species reduce competition by ecological separation; for instance Tramer & Kemp (1980) showed that in the Red-eyed Vireo *Vireo olivaceous* complex (which has North American migratory and South American resident subspecies), taxa used different feeding methods to avoid competition. However, there has been little experimental work to demonstrate competition in migrants and resident bird species in the tropics so that many such conclusions are conjectural (Greenberg 1986). Not surprisingly, few Neotropical passerine studies have recorded many agonistic encounters between migrants and residents (Rappole, Warner & Morton 1983) apart from those at resource concentrations such as fruiting trees or army ant swarms (eg. Willis 1966, Morse 1971, Leck 1973).

Some examples of niche shift in resident passerines attributed to migrants can be explained by alternative hypotheses (see Gochfield, 1985), such as changes in food abundance or the ecological requirements of birds. For example, Lack & Lack (1972) implied that Yellow Warblers *Dendroica petechia* were restricted to mangroves by the large numbers of migrants on Jamaica. However, on islands where there are fewer migrants (eg. the Lesser Antilles) Yellow Warblers also occupy mangroves (see Gochfield 1985) and the habitat shift observed by Lack & Lack (1972) might have been due to breeding requirements. Other examples of habitat shift by residents are more convincing (eg. Terbor gh & Faaborg 1980, Rabol 1987). While there was a possibility of seasonal changes in ecological requirements playing a role in foraging shifts in resident Turkey Vultures, these cannot explain the almost exclusive use of gallery forest during the dry season when the subspecies were sympatric.

That carrion was less abundant in the forest was suggested by the fact that few migrant Turkey (or Black) Vultures foraged there. It is therefore possible that migrant Turkey Vultures which foraged in the forest were subdominant birds which were unable to compete with dominant migrants in open savanna (too few resightings were made to substantiate this). In the forest, the high probability of King Vultures visiting carcases may also have acted as a constraint on migrants foraging in this habitat. What seemed to be a wet season invasion of vacated niche space by resident Turkey Vultures, previously occupied by migrant Turkey Vultures in the dry season, was a phenomenon sometimes recorded among other migrant-resident systems. However, no quantitative studies have been undertaken on seasonality or annual changes in the relative abundance of carrion and this is crucial to an full understanding of the vulture guild. The only way in which seasonal changes in mammalian mortality can be assessed is through variation in density (Eisenberg pers. comm.). Although the dry season is a period of food shortage for herbivores and therefore highest mortality, wet season flooding restricts movements of mammals and may increase mortality (eg. White-tailed Deer - Eisenberg pers. comm.). The effects of season vary in different mammal groups so it may be difficult to isolate the effects on food availability for vultures. For example, on Barro Colorado island rain during the dry season can result in fruiting failure and mass mortality of animals (Foster 1980).

Increasing the number of marked resident and migrant Turkey Vultures would enable a measure of correlation between social dominance and individual fitness (body condition) to investigate further competition between the races.

In conclusion, during the dry season, large influxes of migrant Turkey Vultures in the Llanos of Venezuela apparently had a significant effect on a resident subspecies, which depended on gallery forest as a foraging area. Thus, other migrant bird species may compete strongly with resident birds particularly where both groups are congeners and where migrants greatly outnumber residents. Although both migrant Turkey and Black Vultures are preadapted to coexist with humans, the specialised habitat requirements and low densities of King Vultures indicated that these birds are vulnerable to forest clearance and susceptible to local extinctions as elsewhere (see Marmol 1974, Wilbur *et al* 1983). Considering the widespread destruction of Llanos (Redford 1985) and other ecosystems in the neotropics, this study emphasizes the importance of assessing the ecological requirements of tropical resident and migrant birds so that future conservation planning can ensure their survival.

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APPENDIX TABLES

(CHAPTER 3)

Table 1.1 Densities of Black Vultures (birds/km^2) by month in three habitat types in large (up to 1 km) arcs (mean densities with 95% Confidence limits, n = total number of arc counts in each habitat).

	Vegetation types					
Month	Forest	n	Open	n	Semi-open	n
October	0.07 (0.02-0.14)	72	0.10 (0.04-0.18)	99	0.29 (0.13-0.55)	69
November	0.15 (0.08-0.26)	104	0.33 (0.19-0.54)	821	0.36 (0.18-0.65)	89
December	0.09 (0.04-0.16)	120	0.17 (0.10-0.27)	165	0.27 (0.14-0.46)	115
January	0.11 (0.06-0.20)	128	0.09 (0.05-0.15)	155	0.12 (0.05-0.22)	101
February	0.14 (0.08-0.22)	168	0.22 (0.13-0.33)	199	0.16 (0.09-0.27)	129
March	0.08 (0.03-0.15)	96	0.12 (0.05-0.21)	100	0.10 (0.03-0.20)	60
April	0.05 (0.01-0.10)	72	0.10 (0.03-0.21)	75	0.17 (0.06-0.36)	45
May	0.13 (0.06-0.24)	96	0.06 (0.01-0.13)	92	0.03 (0.00-0.08)	52
June	0.13 (0.03-0.30)	48	0.16 (0.09-0.24)	66	0.20 (0.07-0.43)	46

(data log-transformed)

Comparison between Black Vulture densities in different habitat types in each season (two-way ANOVA).

Dry season (November-April);	Habitat effect	$F_{2,2030} = 4.99$, **
	Month effect	$F_5 = 4.97$, ***
	Habitat x Month	$F_{10} = 0.89$, N.S.
Wet season (October, May, June);	Habitat effect	$F_{2,631} = 1.26$, N.S.
	Month effect	$F_2 = 0.31$, N.S.
	Habitat x Month	$F_4 = 3.41$, **

Table 1.2 Densities of Black Vultures by month in three habitat types in 1 km arc (mean densities with 95% Confidence limits, n = number of positve vulture counts excluding zero values) during wet and dry season.

			Vegetation types			
Month	Forest	n	Open	n	Semi-open	n
October	7.5	9	9.0	20	10.3	20
	(4.0-13.8)		(6.4-12.6)		(7.1-15.0)	
November	7.7	22	11.6	39	12.5	28
	(5.9-10.1)		(8.7-15.4)		(8.3-18.8)	
December	8.0	18	14.6	33	12.6	31
	(5.5-11.8)		(10.9-19.7)		(9.2-17.3)	
January	11.0	21	12.2	21	11.6	17
	(7.4-16.4)		(7.6-19.7)		(6.7-20.3)	
February	9.5	32	14.3	46	12.2	26
	(7.5-12.0)		(10.6-19.3)		(8.4-17.6)	
March	7.9	13	9.9	17	6.0	10
	(5.3-11.7)		(7.2-13.5)		(4.2-8.6)	
April	9.8	6	18.3	10	5.7	11
	(6.0-15.9)		(9.6-35.0)		(3.7-8.9)	
May	9.4	18	15.3	7	11.3	3
	(6.4-13.6)		(9.9-23.8)		(2.8-45.6)	
June	15.0	8	9.5	7	9.2	11
	(10.7-21.0)		(6.3-14.3)		(6.5-13.1)	

(Data log-transformed)

Table 1.3 Proportion of zero counts by month in three habitats (1km arc) for Black Vultures.

Month	Forest	n	Open	n	Semi-open	n
October	87.5	72	84.8	99	71.0	69
November	78.8	104	69.3	127	68.5	89
December	85.0	120	80.0	165	73.0	115
January	83.6	128	86.5	155	83.2	101
February	81.0	168	76.9	199	79.8	129
March	86.5	96	83.0	100	83.3	60
April	91.7	72	86.7	75	75.6	45
May	81.3	96	84.8	92	94.2	52
June	83.3	48	89.4	66	76.1	46

Table 1.4 Densities of *Cathartes* Vultures (birds/km^2) by month in three habitat types in large (up to 1km) arcs (mean densities with 95% Confidence limits, N = total number of arc counts in each habitat)

			Vegetation types			
Month	Forest	N	Open	N	Semi-open	N
October	0.02 (0.01-0.03)	216	0.04 (0.02-0.07)	297	0.06 (0.03-0.09)	207
November	0.09 (0.06-0.13)	312	0.21 (0.15-0.29)	381	0.20 (0.13-0.28)	367
December	0.08 (0.06-0.12)	360	0.24 (0.18-0.31)	495	0.24 (0.17-0.34)	465
January	0.11 (0.07-0.14)	384	0.21 (0.15-0.28)	465	0.19 (0.13-0.26)	303
February	0.06 (0.04-0.08)	504	0.17 (0.13-0.21)	597	0.18 (0.13-0.24)	387
March	0.05 (0.03-0.07)	288	0.06 (0.04-0.09)	300	0.05 (0.02-0.07)	180
April	0.03 (0.01-0.05)	216	0.01 (0.004-0.03)	225	0.01 (0.0001-0.03)	135
May	0.02 (0.01-0.03)	216	0.04 (0.02-0.07)	297	0.06 (0.03-0.09)	207
June	0.01 (0.002-0.03)	144	0.03 (0.01-0.05)	198	0.03 (0.01-0.05)	138

(data log-transformed)

Comparison between densities in different habitat types for each season (two-way ANOVA).

Dry season (November to April;

Habitat effect $F_{2,6126}$ = 29.60, **
Month effect F_5 = 26.65, ***
Habitat x Month F_{10} = 2.49, **

Wet season (October, May, June);

Habitat effect $F_{2,1911}$ = 5.95, **
Month effect F_2 = 5.83, **
Habitat x Month F_4 = 0.64, N.S.

Table 1.5 Densities of *Cathartes* vultures by month in three habitat types in 1 km arcs (mean densities with 95% Confidence limits, n = number of positive counts excluding zero values) during wet and dry season.

			Vegetation types			
Month	Forest	n	Open	n	Semi-open	n
October	6.0 (4.4-8.2)	9	7.3 (5.7-9.3)	25	5.5 (4.6-6.6)	23
November	9.0 (7.5-10.8)	46	15.7 (13.3-18.5)	85	14.9 (12.0-18.5)	58
December	8.9 (7.5-10.8)	49	16.6 (14.4-19.1)	118	14.9 (13.2-16.6)	85
January	9.2 (7.7-10.9)	61	15.7 (13.6-18.3)	104	12.3 (10.2-14.7)	66
February	7.7 (6.6-9.1)	56	11.7 (10.3-13.3)	123	9.7 (8.3-11.4)	86
March	6.3 (4.9-8.0)	27	8.1 (6.5-10.1)	34	6.5 (4.9-8.7)	16
April	5.7 (4.2-7.7)	15	8.5 (5.7-12.8)	7	5.5 (4.4-6.9)	4
May	8.8 (5.2-14.9)	5	17.1 (9.7-30.2)	7	4.7 (3.9-5.8)	11
June	5.4 (4.2-7.0)	5	12.1 (7.7-18.8)	10	5.8 (3.7-9.1)	8

Table 1.6 Proportion of zero counts by month in three habitats (1 km arc) for *Cathartes* vultures.

Month	Forest	n	Open	n	Semi-open	n
October	95.8	216	91.6	297	88.9	207
November	85.3	312	77.7	381	78.3	267
December	86.4	360	76.2	495	75.4	345
January	84.1	384	77.6	465	78.2	303
February	88.9	504	79.4	597	77.8	387
March	90.6	288	88.7	300	91.1	180
April	93.1	216	96.9	225	97.0	135
May	98.3	288	97.5	276	92.9	156
June	96.5	144	94.9	198	94.2	138

Table 1.7 Densities of vultures in different habitat types (1 km arc) in the dry season (Mean density/km^2 in each habitat with 95% Confidence limits, n = number of positive vulture counts excluding zero values).

			Vegetation type			
Species	Forest	n	Open	n	Semi-open	n
Black Vulture	8.9 (7.8-10.3)	112	13.1 (11.3-15.1)	166	10.8 (9.1-12.9)	123
Cathartes vultures	8.2 (7.5-8.8)	254	13.9 (13.0-14.9)	471	12.0 (11.0-13.2)	315
King Vulture	8.4 (6.5-10.8)	28	-		-	

Table 1.8 Proportion of zero counts in different habitat types (1km arc) in the dry season (n = total number of arc counts).

Species	Forest	n	Open	n	Semi-open	n
Black Vulture	83.7	688	79.8	821	77.2	53
Cathartes vultures	87.7	2064	80.9	2463	80.5	1617
King Vulture	96.0	688	-		-	

Table 1.9 Densities of vultures in different habitat types (1 km arc) in the wet season (Mean densities of vultures/km^2 in each habitat with 95% Confidence limits, n = number of positive vulture counts excluding zero values).

			Vegetation type			
Species	Forest	n	Open	n	Semi-open	n
Black Vulture	9.8 (7.5-12.9)	35	11.2 (8.7-14.3)	36	10.0 (7.7-13.1)	34
Cathartes Vultures	6.4 (5.2-8.0)	19	9.4 (7.6-11.8)	42	5.3 (4.6-6.2)	42
King Vulture	5.7	6	-		-	

Table 1.10 Proportion of zero counts in different habitats for three vulture species during the wet season (N = total number of arc counts).

			Vegetation type			
Species	Forest	n	Open	n	Semi-open	n
Black Vulture	83.8	216	86.0	257	79.6	167
Cathartes vultures	97.1	648	94.6	771	91.6	501
King Vulture	97.2	216	-		-	

Table 1.11 Densities of vultures in different habitat types (200m arc) in the dry season (Mean densities of vultures/km^2 in each habitat with 95% Confidence limits (n = number of positive vulture counts excluding zero values).

Taxa	Vegetation type Forest	n	Open	n	Semi-open	n
Black	51.5 (39.7-66.8)	18	64.4 (51.7-80.3)	64	50.3 (17.6-69.8)	14
Migrant Turkey	33.9 (31.1-41.6)	22	54.6 (47.4-62.8)	94	55.1 (29.5-78.9)	12
Resident Turkey	35.3 (30.3-41.1)	20	31.8	1	31.8	3
Yellow-headed	31.8	3	34.4 (29.5-40.1)	9	31.8	1
King	39.9 (31.3-50.8)	11	-		-	

Table 1.12 Percentage of zero counts in each habitat type (200m arcs) for each vulture taxa

Taxa	Vegetation type Forest N = 200	Open N = 301	Semi-open N = 55
Black	91.0	78.7	74.5
Migrant Turkey	89.0	68.8	78.2
Resident Turkey	90.0	99.7	94.5
Yellow-headed	98.5	97.0	98.2
King	94.5	-	-

Appendix Figure 1.1

Road casualties on Calabozo-San Fernando highway

Counts of road casualties on a 41 km stretch of highway revealed distinct seasonal differences in mortality in different months (Appendix Figure 1.1). Two of the most important species (Spectacled Caiman and Possum) were most frequently killed in June, indicating increased movement of these species in the early wet season. The highest number of Crab-eating foxes found on the highway was in April at the end of the dry season. These findings indicated that there were seasonal changes in the movements of animals at different times of year. Caiman are known to be relatively mobile in the dry season (Thorbjarnsson pers. comm.). Flooding may force animals such as possums to vacate their dry season ranges (see Eisenberg *et al* 1979). Foxes may alter their ranges seasonally in response to changes in the movements of their prey. These factors may make the former species more vulnerable to road accidents.

KEY TO FIGURE 1.1 (APPENDICES)

ROAD CASUALTY ANIMAL SPECIES

1) COW *Bos indicus*
2) DOG *Canis domesticus*
3) CAT *Felis domesticus*
4) CRAB-EATING FOX *Cerdocyon thous*
5) RACOON *Procyon cancrivorus*
6) PREHENSILE-TAILED PORCUPINE *Coendou prehensilis*
7) GRISON *Grison vittatus*
8) POSSUM *Didelphus marsupialis*
9) GIANT ANTEATER *Myrmecophaga tridactyla*
10) LESSER ANTEATER *Tamandua tetradactyla*
11) ARMADILLO *Dasypus novemcinctus*
12) BLACK VULTURE *Coragyps atratus*
13) TURKEY VULTURE *Cathartes aura meridionalis*
14) BIRD SPECIES (SMALL PASSERINES)
15) BIRD SPECIES (LARGE NON-PASSERINES)
16) SPECTACLED CAIMAN *Caiman crocodilus*
17) TEGU LIZARD *Tupinambis teguixin*
18) SNAKE SPECIES
19) IGUANA *Iguana iguana*
20) LIZARD SPECIES

Figure 1.1 Number of road casualties/10 km on Calabozo-San Fernando highway in different months