

**ECOLOGICAL FACTORS INFLUENCING
THE REPRODUCTIVE ECOLOGY, TERRITORIALITY
AND FORAGING BEHAVIOUR OF FISCAL SHRIKES.**

BY

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PREFACE

The experimental work described in this thesis was carried out in the Department of Biology, University of Natal, Durban, during October and November 1995, and from August 1996 to December 1997. The work was supervised by Dr. Rob H. Slotow (Department of Biology, University of Natal, Durban) and Professor Mike R. Perrin (Department of Zoology and Entomology, University of Natal, Pietermaritzburg).

These studies represent original work by the author, and have not been otherwise submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

Devenens 9th April 1999.

ABSTRACT

This thesis describes the behavioural ecology of South African fiscal shrikes through detailed field observations and experimental manipulations, and discusses these in the context of reproductive ecology, life history strategies, territoriality, and foraging theory. A population of fiscal shrikes was observed during the period October 1995-October 1997 in a 336 Ha area of grazed bushveld near Pietermaritzburg, South Africa. Fiscal shrike reproduction coincided with the onset of the rainy season. Nests were placed in the centre or north-west regions of tree canopies and contained three or four eggs. Incubation and brooding were performed by females, and shading behaviour was observed in hot weather. Hatching and fledging success averaged 48%. High, exposed nests were less successful than other nests as they were prone to damage during inclement weather. There was a trend in life history strategies between equatorial and South African fiscal shrikes (an increase in clutch size, incubation and brooding durations, and territory size and a decrease in breeding season length), and between northern hemisphere Laniinae (increased intensity in the northern hemisphere), that could be explained by variability in precipitation and temperature, and clutch survival.

Fiscal shrikes maintained individual or pair-held territories throughout the year using visual and vocal signalling. Territories averaged 2.2 Ha in area and almost all contained man-made structures. Territory size was inversely proportional to tall tree density, as trees were used for foraging. Fiscal shrikes resided in areas with few natural perch sites by utilising fence lines and overhead cables. When perch density was manipulated fiscal shrikes decreased and increased territory size accordingly. Fiscal shrikes were sit-and-wait foragers and primarily used perch-to-ground forays. The diet of breeding birds consisted of large invertebrates. Small items were consumed and larger items were cached or fed to offspring or females. Fiscal shrikes were central place foragers. Prey size increased in patches over 35 m from the nest. Perch height affected search area, which in turn affected foraging methods, search duration and subsequent movements. Perches may be the limiting resource for other sit-and-wait foragers and the manipulation of perch density could act as a conservation strategy for declining populations.

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I am grateful to the management and staff of Ukulinga Research Farm for allowing me free access to their farm at all times, which proved to be a superb field site, and for helping with materials for my perches. The Department of Zoology and Entomology at Pietermaritzburg gave me a base from which to study, and the technical staff provided me with unhesitating assistance, especially Billy, whenever I could find him! Thanks to Natal Parks Board, especially to Chris Pullen of Weenen Game Reserve and Dave Balfour of Hluhluwe-Umfolozi Game Reserve, for logistical support and allowing me to record and run experiments on fiscal shrike song in their reserves.

Numerous people helped with fieldwork for short periods during the course of this study. Stephanie Johnson and Lynn Broomhall ran a pilot study during the summer of 1994 to determine the feasibility of working with fiscal shrikes. David Mahlanza and Gift Dandala helped me map territories and erect perches during winter 1997, and educated me in the Zulu and Xhosa folklore of many birds. Lawrence Wahlberg, Iain Stephens and Sally Davis helped with fieldwork on a few occasions.

Douglas Chapmann of the Cedara Agricultural Research Farm very kindly updated my weather records for Ukulinga from the Institute of Soils, Climate, and Water (Pretoria) on numerous occasions during the course of this study. Terry Oatley of the Avian Demographic Unit at the University of Cape Town offered me the chance to rummage through 1500 nest record cards for the fiscal shrike. John Clugg of the Department of Agricultural Economics, University of Natal, taught me how to digitise maps and use GIS. Colleen Downs and Craig Symmes allowed me access to their ringing records for measurements of fiscal shrikes culmens'. The Durban Museum kindly loaned me their microphone and tape recorder for song playback experiments. Thanks.

Financial assistance was obtained in part from the University of Natal, who awarded me a graduate assistantship towards payment of tuition fees. Dr Rob Slotow and Mike Perrin donated funds from their F.R.D. research grants to cover the running costs of the project. The KwaZulu-Natal Ornithological Trust was kind enough to award me a small grant for a field trip to Weenen Game Reserve, and I received funds for writing this thesis from the Gay Langmuir Bursary Fund.

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CHAPTER 1: INTRODUCTION.

This thesis describes the behavioural ecology of southern African populations of the fiscal shrike *Lanius collaris* through detailed field observations and experimental manipulations, and discusses these in the context of life history strategy studies, territoriality, and foraging theory. The fiscal shrike was an ideal subject for study. Very little is known about its behaviour and ecology (but see Marshall & Cooper 1969; Cooper 1971). Only two detailed investigations have been performed (MacDonald 1980; Zack 1986) and these were of equatorial populations that are different subspecies and, possibly, a separate species to southern African fiscal shrikes (Harris & Arnott 1988; Harris 1995). However, the fiscal shrike is a common, prominent species of gardens, grassland, woodland and bushveld and occurs over 64% of the land mass of southern Africa (Parker 1997) and 99% of KwaZulu-Natal (Cyrus & Robson 1980). Its habit of perching conspicuously together with its abundance allowed a large sample of detailed observations to be collected. In addition, the nest record card (NERC) collection of Birdlife South Africa (formerly the South African Ornithological Society) contained a database of over 1500 breeding records of the fiscal shrike, which allowed comparisons of breeding biology amongst regions of southern Africa.

The initial objective of this study was to describe aspects of the behavioural ecology of fiscal shrikes. Although meaningful in its own right, a study on the behavioural ecology of South African fiscal shrikes allows specific theories of ecology and evolutionary biology to be tested. I was able to determine the reproductive ecology of fiscal shrikes by observing breeding behaviour and recording nest construction and egg, chick and fledgling development. The incidents of nest failure were recorded and factors causing failure were discovered. Life history strategies in birds are known to vary with latitude, and two studies (Yom-Tov 1987; Yom-Tov et al. 1994) have suggested that there are differences in the pattern of life history strategies between the northern and southern hemispheres. I was able to detect a pattern of life history strategies with latitude by contrasting equatorial fiscal shrike studies with this study of fiscal shrikes in KwaZulu-Natal. By comparing literature accounts of northern hemisphere Laniinae with the results of this study I quantified a difference between life history strategies in the two hemispheres and determined possible causal factors.

Fiscal shrikes are predatory and raptorial passerines that hunt from exposed perch sites to attack ground-dwelling prey. By studying factors influencing fiscal shrike foraging, for example perch height, we may gain a greater understanding of factors influencing the sit-and-wait foraging mode. This in turn could be applied to other sit-and-wait foragers for which study is either impractical, such as species inhabiting remote forests (e.g. laughing falcon *Herpetotheres chachinnaus* of the Neotropics), or uncommon species (e.g. cuckoo hawk *Aviceda cuculoides*, dark chanting goshawk *Melierax metabates*, and many of the Laniinae).

Fiscal shrikes hold small territories by raptorial standards, which facilitates the collection of a large sample of foraging behaviour. I was able to study the foraging methods of fiscal shrikes by direct observation and determine factors which favoured their employment. I erected artificial perch sites in territories in order to determine (1) how perch structures influenced foraging behaviour, and (2) whether fiscal shrikes behaved as Central Place Foragers (CPF) according to various theories (Orians & Pearson 1979; Lessells & Stephens 1983). Finally, by a combination of direct observation and video-recording, I described the hunting success rate and diet of breeding fiscal shrikes.

Many of the Laniidae are suffering from a global decline in numbers (Yosef 1994). In central Europe many breeding populations have decreased by approximately 50% in the past 15 years (Yosef 1994; Carlson 1995; Rothhaupt 1995), and in the past century some species have become locally extinct through their former range (e.g. red backed shrikes in the British Isles (Peakall 1995)). The two North America species of shrike, the loggerhead shrike *L. ludovicianus* and great grey (northern) shrike *L. excubitor*, are declining at a rate of up to 5% per year (Peterjohn & Sauer 1995; Temple 1995). The main factors hypothesised to contribute to the decline are habitat change, overuse of pesticides and climate change/global warming (Yosef 1994). The latter carries conflicting reports of the decline in shrike species, as both declines (Peakall 1995; Peterjohn & Sauer 1995) and increases (Lorek 1995) in population numbers have been attributed to climate change. Pesticides are known to have detrimental effects on reproduction in birds (Malik 1995), for example, DDT reduces calcium deposition in eggshell causing egg failure. In addition pesticides reduce the abundance of invertebrates. Shrikes, like other raptors, are especially susceptible to pesticide abuse because their diet consists primarily of invertebrate prey, and as such pesticides could be affecting population declines.

Habitat loss at either breeding or wintering grounds in migratory populations, or residential grounds in non-migratory populations, is thought to be the major factor leading to the decline in shrike populations (Yosef 1994; Carlson 1995; Haas & Ogawa 1995; Laporte & Robert 1995). Human induced land changes include the loss of hedgerows and scattered bushes to commercial farming practices, the loss of natural pastures, and indigenous deforestation and commercial afforestation. Most of the Laniinae require fairly open ground with scattered trees or bushes, which are used as vantage points. The loss of such perch sites has been responsible for some population declines, by limiting shrike densities when there is a negative relationship between territory size and perch density (Yosef 1993; Yosef & Grubb 1994; Bechet 1995; Rothhaupt 1995; Schon 1995). To assess the importance of perch density in determining fiscal shrike territory size I performed a manipulation by erecting and removing bamboo perches at Ukulinga Research Farm. By observing territories I was also able to describe the territorial strategies used by fiscal shrikes throughout the year, and the behaviour employed to maintain territories.

THE FISCAL SHRIKE.

The fiscal shrike is a member of the genus *Lanius* (family Laniidae) (Table 1.1), which is composed of 26 species of typical shrikes and is one of the three genera of the subfamily Laniinae (Harris & Arnott 1988; Cramp & Perrins 1993; Yosef & Lohrer 1995). DNA-DNA hybridisation studies suggest that the Laniidae belong to the superfamily Corvoidea and are most closely related to the Vireonidae and Corvidae (Sibley et al. 1991). *Lanius* shrikes are widely distributed in Eurasia and Africa and extend into North America and New Guinea (Cramp & Perrins 1993). They are small to medium sized passerines whose masses vary only by a factor of four, from 20-25 g to 90-100 g (Cade 1995). They are predatory in nature; commonly called butcher-birds, their generic name is derived from the Latin '*lanius*' meaning butcher. The fiscal shrike is divided into eight subspecies (Table 1.1) (McLachlan & Liversidge 1958; Mackworth-Praed & Grant 1960, 1973) and is distributed throughout southern and eastern Africa, extending westwards into Sierra Leone and northwards into Ethiopia, but does not inhabit north-western Africa (Heim de Balsac & Mayaud 1962). Five subspecies occur in southern Africa, and four in South Africa (McLachlan & Liversidge 1958), with the nominate of the species *L. c. collaris* occurring in the Eastern and Western Cape. The fiscal shrike is medium sized and has a black head, back and tail, grey rump, white underparts and a white 'V' on the back, from which it takes its Latin name *collaris*, meaning collared

Table 1.1. Classification of the fiscal shrike *Lanius collaris* Linnaeus 1766 (after Sibley et al. 1988).

Kingdom	Animalia
Phylum	Chordata
Subphylum	Vertebrata
Class	Aves
Subclass	Neornithes
Infraclass	Neoaves
Parvclass	Passerae
Superorder	Passerimorphae
Order	Passeriformes
Suborder	Passeri (Oscines)
Parvorder	Corvida
Superfamily	Corvoidea
Family	Laniidae
Subfamily	Laniinae
Genus	<i>Lanius</i>
Species	<i>Lanius collaris</i>
Subspecies ^a	<i>L. c. collaris</i> , <i>L. c. vigilans</i> , <i>L. c. predator</i> , <i>L. c. subcoronatus</i> , <i>L. c. aridicolus</i> , <i>L. c. smithii</i> ^b , <i>L. c. capelli</i> ^b <i>L. c. humeralis</i> ^b

^a According to McLachlan & Liversidge (1958), Mackworth-Praed & Grant (1960, 1973).

Clancey (1980) recognises four subspecies in the southern African region, with *L. c. vigilans* classified as *L. c. predator*.

^b Subspecies falling wholly outside the southern African region and the Sudan.

(Harris & Arnott 1988; Ginn et al. 1989; Maclean 1993). The tail is long and narrow and is swung when the bird is excited (Harris & Arnott 1988). The bill is black and is strong, laterally compressed and hooked, with a tomial tooth and notch, similar to a raptor (Cramp & Perrins 1993; Cade 1995). Females have slightly duller plumage than males and have chestnut-coloured flanks (Harris & Arnott 1988), except for *L. c. smithii*, which is not sexually dimorphic (MacDonald 1980). Immature birds are brown and barred although the adult pattern is discernible (McLachlan & Liversidge 1958; Harris & Arnott 1988; Ginn et al. 1989; Maclean 1993).

The fiscal shrike is very abundant throughout much of the southern African region (Cyrus & Robson 1980; Parker 1997), although it is rare in the Kruger National Park (Kemp 1974), much of Botswana (Penry 1994), northern Namibia, south eastern Zimbabwe and the Zambezi valley (Parker 1997). It favours grassland and moist woodlands (Parker 1997), and uses elevated structures such as trees, fence lines, and overhead cables as observation posts from which to hunt (Harris & Arnott 1988). It is a sit-and-wait predator and its diet consists primarily of large insects, although it will also capture other invertebrates, amphibians, reptiles, birds, and mammals (Harris & Arnott 1988; Ginn et al. 1989). Like most of its congeners, the fiscal shrike impales prey in caches which may be consumed at a later date or left uneaten. Caches could function as larders (Bevan & England 1969; Applegate 1977), could aid prey manipulation (Bevan & England 1969), may be a sexual signal (Yosef & Pinshow 1989), or could facilitate the destruction of toxins in noxious prey (Yosef & Whitman 1992). Individuals and pairs of fiscal shrikes hold territories of between less than 1 Ha and 13 Ha depending on the habitat (Harris & Arnott 1988). Fiscal shrikes are resident and non-migratory in South Africa (Harris & Arnott 1988), although small scale movements occur in Botswana (Parker 1997). Breeding can occur during all months throughout southern Africa, although it usually takes place between August and December (Harris & Arnott 1988; Maclean 1993; Parker 1997). The normal clutch consists of 3-4 eggs, which are coloured pale cream to green with darker speckles (Winterbottom 1988).

STUDY PERIOD.

1) Ukulinga.

Data collection began in December 1994 when Miss Stephanie Johnson and Miss Lynne Broomhall performed a pilot study by observing breeding fiscal shrikes at Ukulinga for six weeks to determine the feasibility of studying the species. The data collected during the pilot study included the location and occupation of fiscal shrike territories in the south-west of Ukulinga, which is included in this thesis, plus incidental observations of the behaviour of adult birds that are not reported here.

My observations began in October 1995 and lasted for nine weeks, encompassing the height of the breeding season. I resumed at the beginning of the following breeding season (August 1996) and continued until it finished (mid-January 1997). Mr Laurence Wahlberg assisted with field observations during December 1996. Perches were erected in five territories during this time to assess their effects on foraging. Between mid-January 1997 and June 1997 fiscal shrikes were observed on an casual basis to record any incidences of breeding activity, and the occupancy and location of territories. Song playback experiments occurred at Ukulinga during this period. During June and early July 1997 experimental manipulations on territory size were performed on ten territories by the addition and removal of artificial perches. On completion these perches remained erected to assess their importance for foraging during the breeding season. From mid-July onwards fiscal shrike territories were observed systematically for signs of the onset of breeding and observations on breeding behaviour occurred until mid-October 1997.

2) Other study sites.

Weenen, Itala and Hluhluwe-Umfolozi Game Reserves were used as locations for playback experiments in this study. Playback experiments occurred at Weenen and Hluhluwe-Umfolozi Game Reserves during December 1996, again at Weenen Game Reserve during March 1997, and at Itala Game Reserve in April 1997. Playback experiments were used as a teaching exercise at Weenen Game Reserve for University of Natal Biology B.Sc. Honours students, who participated with the collection of such data.

STUDY SITES.

1) Ukulinga Research Farm.

Almost all of the fieldwork for this project was performed at Ukulinga Research Farm (30°24'E 29°40'S), situated 5 km south-east of Pietermaritzburg in the province of KwaZulu-Natal, South Africa. Ukulinga covers 336.2 Ha and varies in altitude from 710-850 m (Fig. 1.1), covering the eastern slopes and plateau of the hill that forms the basis of Bisley Nature Reserve. The hill is composed of Mispah shale with doleritic intrusions through the lower slopes. The predominant soil forms are Glenrosa and Mispah. One perennial stream, the Mkondeni spruit, fed by two seasonal spurs formed the south-eastern boundary of Ukulinga; the seasonal Blackburrow stream arose in the north-east, and another seasonal stream began in the south-western corner of the farm. A natural perennial spring leading to a small area of wetland was located on top of the plateau, which although dammed gave rise to another watercourse that joined the Blackburrow stream outside Ukulinga.

The natural vegetation of Ukulinga is classified as Dohne sourveld (Acocks type 44b) (Acocks 1988), and consists of *Acacia sieberiana*, *A. nilotica*, and *A. karoo* dominated bushveld with pockets of denser woodland containing *Calodendrum capense*, *Canthium mundianum*, *Cussonia spicata*, and *Kiggelaria africana* among others. Many species of tree and shrub that were not indigenous to the region occurred at Ukulinga, including large numbers of black wattle *A. mearansii*, gum *Eucalyptus spp.*, syringa *Melia azedarach*, bugweed *Solanum mauritianum*, and lantana *Lantana camara*. The plateau and steeper hillsides of Ukulinga were occupied by open grassland with scattered trees, and thicker areas of riverine thornveld occurred in valleys and towards the boundary with Bisley Nature reserve. The sourveld grasses were dominated by *Themida triandra*, *Heteropogon contortis*, *Tristachia leucothrix*, and *Eragrostis spp.*, and aloes including the rare *Aloe pruinosa* were found in this habitat.

At least 180 species of birds occurred at or over Ukulinga, including three species of *Lanius* shrikes (*L. collaris*, *L. collurio*, *L. minor*) and a further nine members of the family Laniidae (*Lanarius ferrugineus*, *Dryoscopus cubla*, *Nilaus afer*, *Tchagra tchagra*, *T. senegala*, *Telophorus zeylonus*, *T. sulfureopectus*, *T. olivaceus*, *Malaconotus blanchoti*). Larger mammalian inhabitants included bushbuck *Tragelaphus scriptus*, common reedbuck *Redunca arundinum*, common duiker

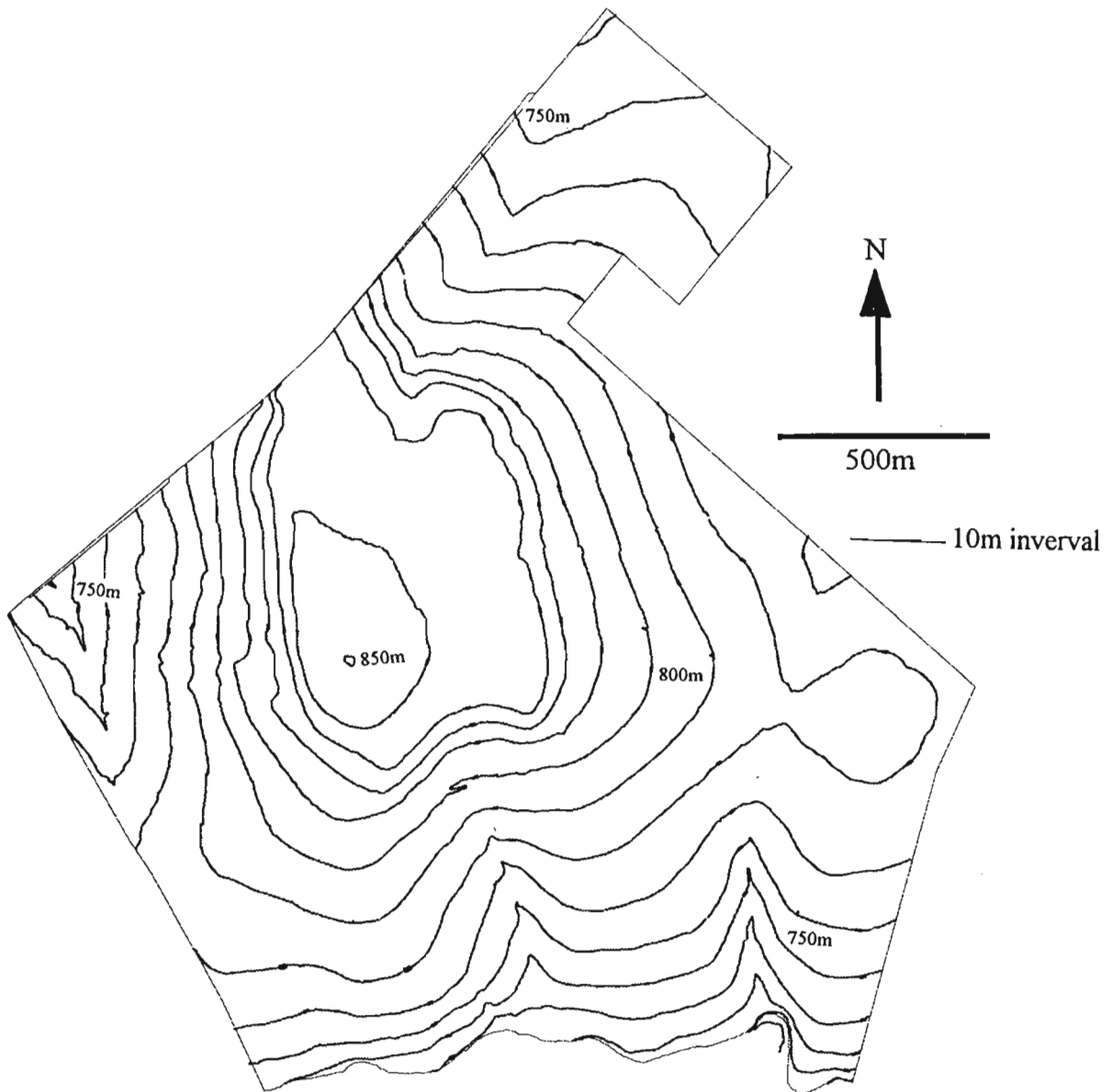


Figure 1.1. Contour map in 10 m increments of Ukulinga Research Farm. The mapping and digitising of these features were performed by the Department of Agricultural Economics, University of Natal, Pietermaritzburg, South Africa.

Sylvicapra grimmia, oribi *Ourebia ourebia*, porcupine *Hysrix africae australis*, vervet monkey *Cercopithecus aethiops* and possibly black-backed jackal *Canis mesomelas*. Many smaller mammals inhabited the area including the rock dassie *Procavia capensis*, scrub hare *Lepus saxatilis*, mongooses *Gallerella sanguinea*, *Herpestes ichneumon*, and numerous rodents of which *Mastomys spp.* and *Otomys spp.* were the most abundant.

Ukulinga was the University of Natal, Faculty of Agriculture's research and teaching farm. Most of the farm was used for cattle, sheep, and goat grazing by the departments of Animal Science and Range and Forage Resources at the University of Natal, and remained as relatively undisturbed bushveld. This was subject to controlled and accidental burning during the winter periods, for which the farm did not possess long term records. The remainder of the farm was divided between horticultural science, poultry and pig farming, crop production and abandoned low-density plantations, plus private residences and farm buildings.

Climate.

Ukulinga receives between approximately 10 h of daylight in the winter and 14 h of daylight in the summer. Ukulinga's climate is transitional between the temperate inland areas of South Africa and the tropical coastal regions. KwaZulu-Natal lies within the summer rainfall region of South Africa (over 85% of precipitation falling between October and March), although rain occurred in most months during the study (Fig. 1.2). The hill on which Ukulinga is situated lies within a narrow mist-belt and receives on average 700-750 mm of rain per year (Fig. 1.2). Precipitation does not fall as snow and frosts are uncommon and did not occur during this study. The Pietermaritzburg area receives a large number of thunderstorms during the spring and summer months arising from the Drakensburg Mountains, 50 km to the north west. During such storms it was not uncommon for over 15 mm of rain to fall, and over 80 mm of rain was recorded during one 24 h period in December 1995 (Fig. 1.3). This is still less than the maximum previously recorded during a 24 h period in December at Ukulinga (Fig. 1.3). Ukulinga receives hot, humid summers and warm winters (Fig. 1.4). During the study the average diurnal range was 9.7°C in the summer and 11.3°C in the winter (Fig. 1.4). The maximum temperature recorded during the study was 40°C, although the average maximum daily summer (October-March) temperature was 25.1°C. Winter (April- September) daily maximum temperatures averaged 22.4°C, and the minimum temperature recorded during the study period was 2.4°C (note that data were not available for the winter months of July and August 1996, and May 1997).

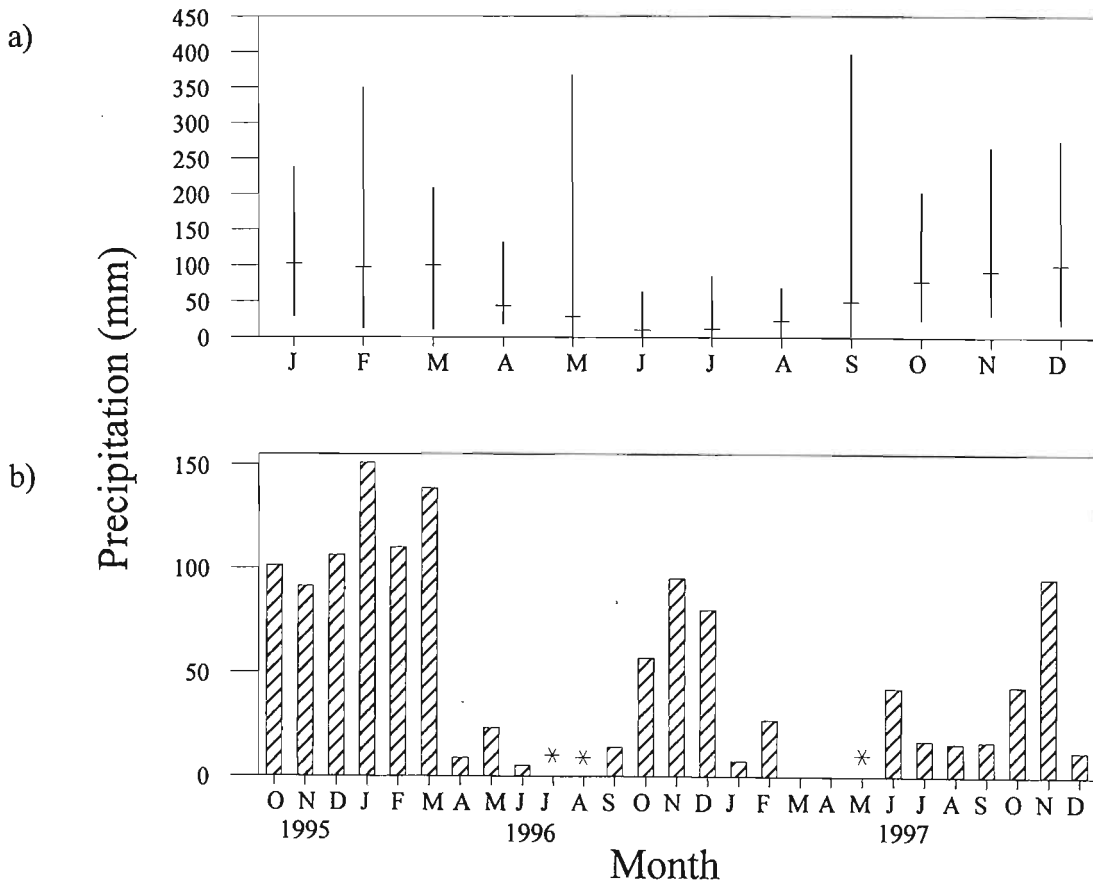


Figure 1.2. Monthly precipitation at Ukulinga Research Farm during (a) the period January 1959-December 1995 (horizontal lines indicate average monthly precipitation and vertical lines connect the highest and lowest recorded monthly precipitation), and (b) the study period (October 1995-December 1997). * indicates missing data.

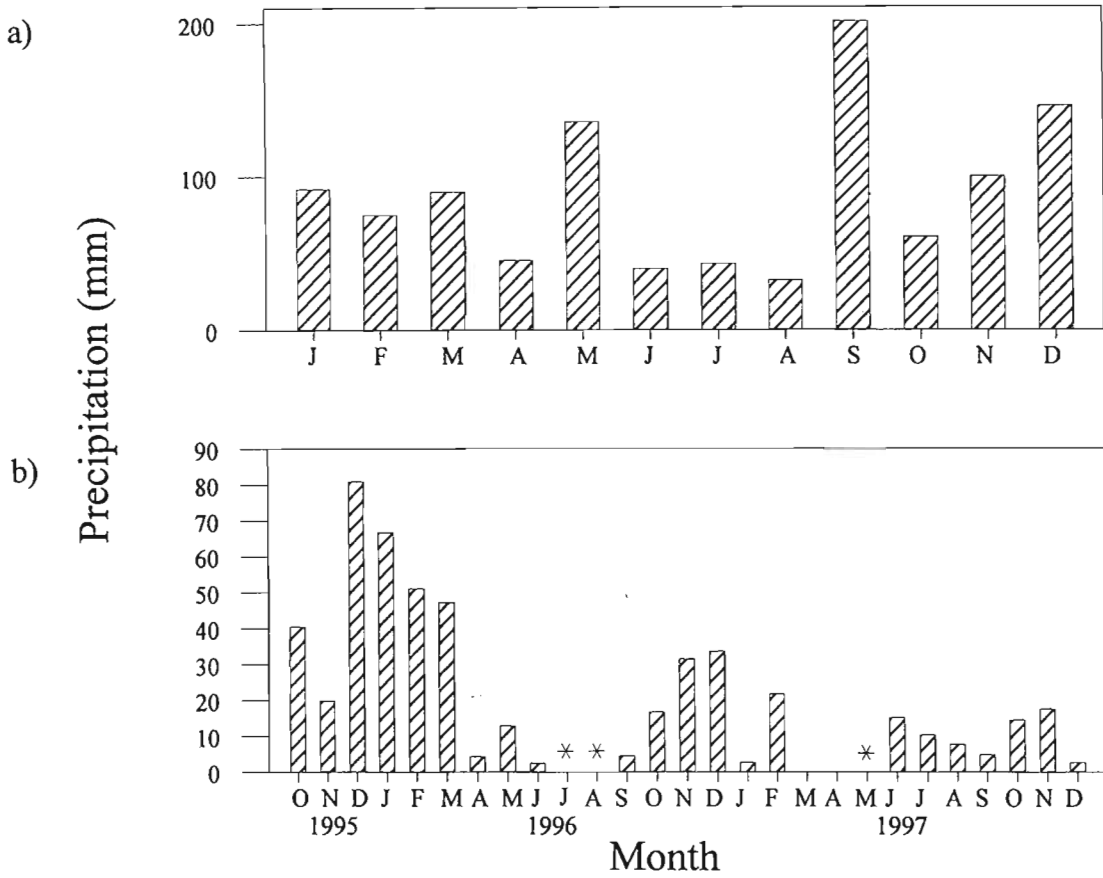


Figure 1.3. Maximum precipitation on any one day (0-24 h) at Ukulinga Research Farm during (a) the period January 1959-December 1995 and (b) each month of the study (October 1995-December 1997).

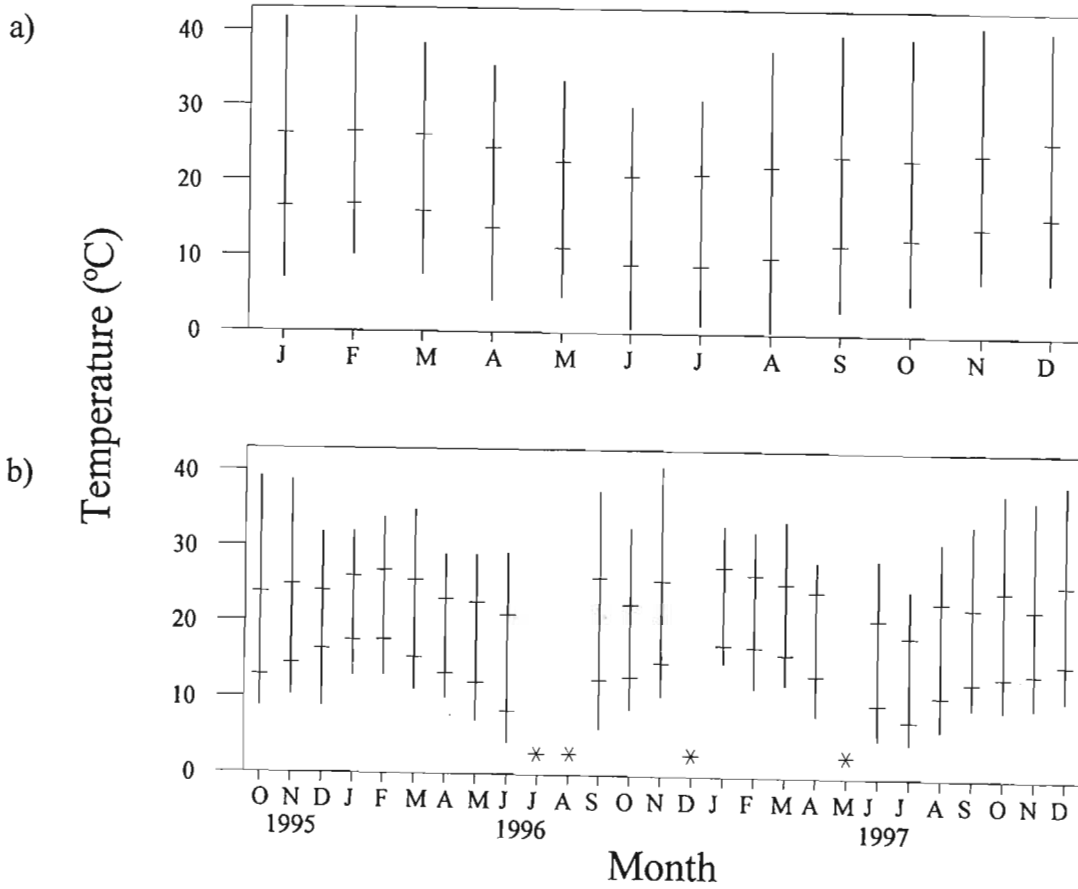


Figure 1.4. Average daily maxima, minima and monthly temperature extremes at Ukulinga Research Farm during (a) the period January 1959-December 1995 and (b) the study period (October 1995-December 1997). Horizontal lines indicate average daily maximum and minimum temperatures and vertical lines connect highest and lowest recorded temperatures in each month. * indicates missing data.

2) Hluhluwe-Umfolozi Game Reserve.

Hluhluwe-Umfolozi Game Reserve (28°22'S, 32°25'E) is situated in northern Zululand, 280 km north of Durban. Hluhluwe and Umfolozi were established as protected areas in 1895, making them the oldest game reserves in Africa. Hluhluwe-Umfolozi Game Reserve covers 96453 Ha and varies in altitude from 60-650 m above sea level. The Hluhluwe section is hilly and receives on average 950 mm of rain annually, whilst the Umfolozi section is flatter and more open and receives on average 650 mm of rain per year. Three perennial rivers, the Hluhluwe, the Black Umfolozi and the White Umfolozi, fed by numerous seasonal streams are situated the reserve. Many of the streams have been dammed, and other natural and maintained seasonal pans occur in the reserve. Hluhluwe-Umfolozi is situated on the coastal scarp interface and as such incorporates a large diversity of flora and fauna. Over 1250 species of plants have been documented in the reserve which incorporates indigenous mist belt and coastal scarp forests, *Acacia* bushveld, riverine forest and open grasslands. The predominant tree species occurring in habitats suitable for fiscal shrikes are *Acacia karoo* and *A. nilotica*, and the predominant grass is *Themida triandra*. Over 25000 Ha of Umfolozi is classified as a wilderness zone and contains pristine *Acacia* bushveld and grasslands, with no permanent roads or habitations.

Hluhluwe-Umfolozi is the only reserve in KwaZulu-Natal to contain the Big Five - black rhino *Diceros bicornis* and white rhino *Ceratotherium simum*, elephant *Loxodonta africana*, Cape buffalo *Syncerux caffer*, lion *Panthera leo* and leopard *P. pardus*. Other large predators include spotted hyaena *Crocuta crocuta*, black-backed jackal, cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus* and Nile crocodile *Crocodylus niloticus*. Primates are represented by the chacma baboon *Papio cynocephalus* and vervet monkey *Cercocebus aethiops*. Large herbivores include hippopotamus *Hippopotamus amphibius*, giraffe *Giraffa camelopardalis*, Burchell's zebra *Equus burchelli* and 11 species of antelope (Family Bovidae), and other large mammals are represented by aardvark *Orycteropus afer*, civet *Civettictis civetta*, genet *Genetta spp.*, several species of mongoose (Family Viverridae), porcupine *Hystrix africaeaustralis* and warthog *Phacochoerus africanus*. More than 300 species of birds occur in the reserve, including fiscal shrikes, lesser grey shrikes and red backed shrikes from the genus *Lanius*, and eleven other members of the Laniidae.

3) Itala Game Reserve.

Itala Game Reserve (27°35'S, 31°07'E) measures 29653 Ha in area and is situated in on the banks of the Pongola river in northern Zululand, just south of Swaziland. Itala has been inhabited since the stone age, and most recently until 1973 by farming and gold mining communities. In 1973 Natal Parks Board took control of Itala and began reclaiming eroded land, removing signs of habitation and reintroducing wildlife that had been eradicated. Today the reserve is primarily a conservation area, with secondary objectives of education, research and recreation.

Itala varies in altitude from 400 m to 1400 m and contains a wide variety of soils arising from a diverse geology. Dolerite cliffs dominate the Ngotshe escarpment which forms the reserve's southern boundary. The Karroo sequence sandstones stretch from the lower reaches of the escarpment to the Pongola river which forms the reserve's northern border. A further five river tributaries and numerous seasonal streams run through the reserve to join the Pongola. Itala represents three distinct vegetation types and numerous sub-types, including open *Protea caffra* grasslands, acacia bushveld (*A. nilotica* and *A. karoo* dominated), wetlands and riverine forest. Approximately 320 species of tree are found in Itala, making it the most tree species diverse reserve in KwaZulu-Natal.

Itala is home to 80 species of mammal, 20 of which have been re-introduced since the reserve was established. Large carnivores are represented by leopard, cheetah, caracal *Caracal caracal*, black-backed jackal, brown hyaena *Hyaena brunnea* and spotted hyaena, and Nile crocodile. Large herbivores include white and black rhino, elephant, giraffe, Burchell's zebra and 16 species of antelope. Itala is home to two primates, the vervet monkey and chacma baboon. Three hundred and fifteen species of birds have been recorded in Itala, including 29 species of raptor. Of the genus *Lanius*, fiscal shrikes are resident and red-backed shrikes are summer migrants. Ten other members of the Laniidae are present in Itala throughout the year.

4) Weenen Game Reserve.

Weenen Game Reserve (28°48'S, 30°07'E) covers 4906 Ha of the KwaZulu-Natal Midlands/Highveld and is situated 30 km north-east of Escourt. Weenen has been occupied by Man since Stone Age times. Since 1850 it was farmed intensely and by 1948 erosion was such a problem that the Department of Agriculture took over the land to research and demonstrate soil reclamation methods. Soil erosion was stabilised and gradually the natural veld began to

recover. In 1975 Natal Parks Board took control of the land and Weenen Game Reserve was proclaimed. Today the reserve is primarily managed as a conservation area with the secondary aim of eco-tourism, although soil erosion damage limitation continues and influences the diversity of species being re-introduced.

Weenen varies in altitude from 1000-1240 m. In the south and south east dolerite hills are transected by the Bushman's river, whilst the northern and western regions are flatter and underlain by shale. Three major streams run through the reserve and merge to form the Amanzanyama River in the north east and water is also available from numerous dams and waterholes. Rainfall in the region is erratic, varying between 429 mm and 1129 mm a year. Temperatures fall to 1°C in winter and rise to 37°C in summer.

Weenen contains a particularly fine example of Valley Bushveld vegetation, and also *Acacia* bushveld characterised by *A. karoo*, *A. nilotica* and *A. tortilis* woodland and thickets, grassland dominated by *Hyparrhenia hirta* in the thickets and *T. triandra* on dolerite derived soils, and large stands of paperbark *A. sieberiana* woodland. Weenen has a total of 35 species of mammal, including the following herbivores: black and white rhino, buffalo, giraffe, Burchell's zebra and 11 species of antelope, including the rare roan antelope *Hippotragus equinus*. Carnivores include spotted hyaena, black backed jackal, serval *Leptailurus serval*, genet, yellow mongoose *Cynictus penicillata*, slender mongoose *Galerella sanguinea* and cape clawless otter *Aonyx capensis*, and insectivores are represented by aardvark, porcupine and aardwolf *Proteles cristatus*. Currently 267 species of birds reside in the reserve, and the avifauna is unique in KwaZulu-Natal in that species ranges' from the interior (e.g. titbabbler *Parisoma subcaeruleum*, blackthroated canary *Serinus atrogularis*) overlap with those from the subtropical coastal regions. Fiscal shrikes are the only member of the genus *Lanius* to reside in the reserve, although red-backed shrike and lesser grey shrike are summer migrants. Ten other members of the family Laniidae have been observed in Weenen Game reserve.

OTHER SOURCES OF DATA: NEST RECORD CARDS (NERC).

Fiscal shrike reproductive data were extracted from the nest record card collection of Birdlife South Africa, formerly the South African Ornithologists Society (SAOS). NERC provide an extensive database of breeding information from a large geographical area, which would otherwise be impossible to collect. One study has previously analysed fiscal shrike breeding information from NERC (Cooper 1971), but the analysis was restricted to cards submitted before 1969. Furthermore, a large proportion of NERC analysed were from Zimbabwe (belonging to the Rhodesian Ornithologists Society). I am interested in geographical variation in life history traits between the equatorial regions of Africa, previously studied in Kenya (Zack 1986) and Ghana (MacDonald 1980), and South Africa which lies in the sub-tropics/temperate zone. Zimbabwe lies in wholly within the tropics and so the contrast with equatorial studies would be less profound, which is why NERC from Zimbabwe were omitted from this study.

NERC are housed at the Avian Demography Unit (ADU) at the University of Cape Town. NERC are primarily used by amateur ornithologists to record observations of nesting birds, although a small percentage of the cards contain data extracted from scientific investigations and museum collections. The NERC collection spans 117 years, from its origin in 1881 to the present day. However, the bulk of records were collected between 1951 and 1979 (Dr. T. Oatley, ADU, pers. comm.). A nest record card is a pre-printed postcard containing a table to record the date and observations of the breeding stage, breeding behaviour (e.g. nest building, incubating) and nest contents (e.g. eggs, chicks). Although NERC design has been modified over time all cards asked for the geographical location of the nest and most asked for the height of the nest above ground level and the nest structure. Many contributors also recorded further details, such as the species of tree or shrub in which the nest was placed. The majority of completed NERC contained one or two observations of one nest, but a small number were detailed and contained daily observations of a nest that had been revisited throughout the breeding season.

There were over 1500 NERC for the fiscal shrike, from South Africa, Namibia and Zimbabwe (Rhodesian Ornithologists Society). The following information was extracted from South African and Namibian cards in the collection: duration of nest building, incubation and

brooding phases; laying and hatching order; nest tree species and height of nest above ground level; clutch size, number of eggs to hatch and chicks to fledge; egg dimensions; and accounts of parasitism. For some analyses only part of the collection was examined due to time constraints. In such cases cards were searched systematically by SAOS region and records were omitted randomly from regions with a disproportionate representation (e.g. Western Cape), thereby ensuring a large sample of cards were selected from each region.

This thesis is divided into three main chapters (Chapters 2, 3 & 4) that cover three broad subject areas. Chapter 2 describes the reproductive ecology of the fiscal shrike in southern Africa from field observations and an analysis of nest record cards (NERC). Life history data (e.g. clutch size, breeding season length) are then compared with information about equatorial populations of fiscal shrikes and literature accounts of northern hemisphere Laniinae, and the results are discussed with reference to hypotheses concerning life history patterns and latitude. In Chapter 3 I describe the territorial strategies of fiscal shrikes and report the results of an experimental manipulation performed to assess the importance of perch sites in controlling territory size. Chapter 4 describes the foraging behaviour of fiscal shrikes. Different hunting strategies are reported and, by erecting artificial perches in territories, factors which select for their employment are determined. Finally, fiscal shrike foraging behaviour is discussed in the light of past and present opinion on optimal foraging theory. Chapter 5 is a conclusion that integrates the results of the whole study and discusses its relevance to the global decline in the true shrikes.

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CHAPTER 2: FACTORS INFLUENCING THE REPRODUCTIVE ECOLOGY OF FISCAL SHRIKES IN SOUTHERN AFRICA: A CONTRAST WITH EQUATORIAL AND NORTHERN TEMPERATE PASSERINES.

ABSTRACT.

The reproductive ecology of the fiscal shrike *Lanius collaris* was described from a field study at Ukulinga Research Farm, KwaZulu-Natal, South Africa, and also using nest record cards (NERC) from South Africa and Namibia. Fifty-four per cent of fiscal shrike territories were held by pairs throughout the year at Ukulinga, which increased to 95% during the breeding season. Nests were built on average 1.65 m above ground level at Ukulinga, which was significantly lower than for the rest of KwaZulu-Natal, an effect of a greater abundance of lower nest sites. Nests were placed in the centre of a tree significantly more often than in the periphery, and within the periphery nests were placed significantly more often in north and west quadrants than east and south quadrants. Throughout South Africa the breeding season of the fiscal shrike lasted five months, although clutches were initiated one month earlier in winter rainfall regions than in summer rainfall regions. Females shaded and incubated clutches, which averaged 3.4 eggs, and shading was negatively related to ambient temperature. Eggs hatched asynchronously and chicks fledged 17.7 days after hatching. Males fed their partners and both parents fed offspring. Sixty-five per cent of nests were unsuccessful in fledging any offspring, and successful nests fledged on average 2.2 chicks. Highly exposed nests in elevated positions were less successful than other nests, due to damage during heavy rain and strong winds.

Changes in life history strategies of birds with latitude are a consequence of environmental variables occurring at the latitude, rather than latitude per se. Compared to the equator high latitudes have greater fluctuations in day length and lower annual rainfall. Furthermore, lower latitudes receive a large number of high intensity rain or thunderstorms. The southern hemisphere, because of the absence of land masses at high latitudes and the triangular form of continents, does not deviate from climatic predictions based on latitude. As such it receives a less variable climate than the northern hemisphere, and lacks the continental temperate zones of

the northern hemisphere characterised by harsh, cold, winters. Life history strategies of fiscal shrikes differed between equatorial and southern African populations. In southern Africa fiscal shrikes laid larger clutches and had shorter breeding seasons than in equatorial Africa, and this was evaluated with respect to different hypotheses that account for the variation in life history strategies with latitude. For fiscal shrikes and other passerines these trends could be explained by the variability of the environment, and the probability of nest survival could account for clutch size variation.

INTRODUCTION.

Life history strategies differ between and within species occurring at different latitudes. In the northern hemisphere clutch size tends to increase with latitude (Lack 1948; Ricklefs 1980; Kulesza 1990), and breeding season length decreases with latitude (Ricklefs 1980). The few studies that have been carried out on southern hemisphere species have also documented trends in life history strategies with latitude, such as increasing clutch size (Moreau 1944; Yom-Tov 1987; Yom-Tov et al. 1994).

Traditionally, life history strategies have been correlated with latitude rather than with actual selective processes, such as the photoperiod, temperature and rainfall that vary with latitude. The photoperiod is the period of daily illumination that an organism receives and is extremely predictable, varying only by minutes depending on cloud cover. At the equator the photoperiod lasts 12 h 07 min and is constant throughout the year. With increasing latitude it shows a seasonal change, with longer day lengths in summer than in winter. This occurs because the earth is tilted at a constant angle of 23.5° on its axis as it revolves around the sun. Summer day length increases with increasing latitude to 24 h above 70°N or 70°S , whereas winter day length shows the reverse trend (Pearce & Smith 1990).

The main climatic factors influencing life history strategies are temperature and rainfall. Temperature and rainfall patterns correlate approximately with latitude giving rise to different climatic regions, although many other factors (e.g. ocean currents, altitude) influence local weather patterns (Miller & Parry 1975; Burroughs 1991). Equatorial regions between approximately 5°S and 10°N are straddled by a permanent low pressure belt and experience consistently hot and moist weather. Equatorial temperatures average 27°C , vary by only a few degrees throughout the year, and have a diurnal range of 8° to 10°C (Miller & Parry 1975). There is no winter and no defined dry season. Although temperatures remain stable, rainfall is variable and extreme, averaging over 1500 mm a year, and can be prodigious. Typically, equatorial regions receive daily afternoon storms, and thundery outbreaks are common. Most of the region has 80 or more electric storms a year, ten times the number in the British Isles (Miller & Parry 1975).

Between the equatorial band and about 30°N and 30°S , under the influence of trade-winds and semi-tropical high pressure systems, lie the tropics (Miller & Parry 1975). The tropics are

characterised by a seasonal climate with warm, dry winters and equatorial-type summers. Annual and diurnal temperature ranges are greater than in equatorial regions, and summer diurnal temperature ranges can be 25°C with daytime temperatures in excess of 40°C. Between 1000 mm and 1500 mm of rain falls on the tropics each year, mostly during the summer months and in a manner similar to the heavy storms of the equatorial region (Miller & Parry 1975). However, rainfall in the tropics can be unreliable and, combined with high evaporation levels, the tropics are prone to drought. Summer rain in the form of monsoons affect some tropical regions especially south-east Asia, which are typified by having extremely heavy and prolonged rains that may arise suddenly.

Between latitudes of 30° and 40° climates are characterised by hot, dry summers and mild, wet winters, and are called Mediterranean (Miller & Parry 1975). These have greater annual variation in temperature than tropical regions, but lower rainfall (400-800 mm per year). Precipitation falls as showers or for prolonged periods, and the thunder and heavy rainstorms of lower latitudes are less common.

The temperate zone encompasses latitudes between 40° and 60°, and these climates can be divided into maritime temperate climates, characterised by mild wet winters and warm summers, and the continental temperate, which display cold winters and hot summers (Miller & Parry 1975). In the southern hemisphere the absence of continents at high latitudes and the circumpolar form of Antarctica reduce the variation in annual temperature ranges (Burroughs 1991). In addition, land masses in the southern hemisphere are typically triangular whose tips point south, and this enforces the modulating effect of the sea in stabilising land temperatures. The continental temperate regimes that are common in the northern hemisphere are absent, and mid-latitude southern hemisphere climates tend to be more equable than in the northern hemisphere (Miller & Parry 1975). Annual variation in temperature is greatest in continental regions, whereas maritime regions are characterised by their changeable, unreliable weather that lacks extremes. Rainfall varies throughout the temperate region, from 400 mm in some continental regions to 2500 mm in maritime regions, but lacks exceptionally heavy downpours, instead having more consistent rain throughout the year.

Polar and sub-polar regions above 60°N or 60°S have the greatest annual variation in temperature in the world, with Verkhoyansk, Siberia (68°N) boasting an absolute range of 106°C (Miller & Parry 1975). Summer temperatures are often above 20°C in the sub-polar

region and between 0° and 10°C nearer the poles, but winters are harsh, with permafrosts, snow-covered ground, and temperatures falling to -40° to -50°C. Precipitation varies from 50-300 mm, and falls largely as snow (Miller & Parry 1975).

In summary, annual global temperature patterns are stable at the equator and increase in variability and extremes with increasing latitude, although more slowly in the southern hemisphere than in the northern hemisphere. Precipitation is greatest at the equator and decreases moving towards the poles, although the tropics are prone to drought because of high evaporation and unreliable annual rainfall. Violent storms and thunderstorms are common at the equator and decrease in occurrence and severity with increasing latitude, becoming uncommon in most temperate zones.

Clutch size is the most intensively studied life history trait in birds, and a trend between increasing clutch size and increasing latitude has been demonstrated (Moreau 1944; Lack 1948; Klomp 1970; Ricklefs 1980; Kulesza 1990). Lack hypothesised that clutch size in birds allows the maximum number of young to survive, where the limiting factor is the parents ability to feed their offspring. Because the photoperiod increases with latitude during the summer breeding months, higher latitudes have longer days than lower latitudes; parent birds can forage for longer periods and, hence, raise larger clutches. The duration of time available for foraging could also be restricted by long periods of heavy rain, as this may reduce the time a parent bird can devote to foraging, and so the number of young that can be provisioned (Foster 1974). As precipitation and heavy periods of rain decrease with increasing latitude, birds living at high latitudes would have longer periods available for foraging and so should raise larger clutches. Photoperiod, temperature and rainfall combine to determine the productivity of an environment, and this concept has been used by Ricklefs (1980) to predict clutch size variation in birds. In most species populations are regulated by resources at the most limiting time of the year. In areas of high annual productivity (low latitudes) mortality is low and individuals encounter high levels of competition for resources. At higher latitudes, population densities are lower from increased winter mortality, and competition is less. The optimal clutch size is therefore greater at higher latitudes where competition is reduced by resource limitation during long, unproductive winters (Ricklefs 1980).

If day length, the usual proxy for latitude, is driving patterns of life history strategies there should be no difference between clutch size at similar latitudes in the northern and southern

hemisphere. However, if rainfall or temperature are responsible there could be a contrast, with northern hemisphere patterns increasing at a faster rate with latitude than southern hemisphere patterns. There is some evidence that life history strategies differ between the northern and southern hemisphere. Although there is a trend of increasing clutch size with increasing latitude in both hemispheres, the magnitude of this trend is greater in the north than in the south (Yom-Tov et al. 1994). Clutch size increased by three eggs for every 18-30° increase in latitude in the northern hemisphere (Klomp 1970), whereas clutch size in Australian birds increased by 0.8 eggs per 30° latitude (Yom-Tov 1987).

The fiscal shrike *Lanius collaris* is a common and widely distributed medium-sized passerine, found throughout much of sub-Saharan Africa (Harris & Arnott 1988; Maclean 1993; Penry 1994; Parker 1997). The fiscal shrike provides the ideal subject for the study of life history strategies. Pairs hold small territories at high densities throughout the year in much of South Africa, and populations are non-migratory (Parker 1997). In addition, fiscal shrikes are easy to locate through their habit of perching on the top of trees and overhead cables, and they tolerate a high level of human interference.

Compared to most northern hemisphere passerines the fiscal shrike has been poorly studied. The breeding biology of equatorial populations of the fiscal shrike is known from two investigations. The ecology of *L. c. smithii* (MacDonald 1980) was studied in Ghana, and the breeding biology of *L. c. humeralis* (Zack 1986) is known from field studies in Kenya. Therefore a database exists for the comparison of life history traits in South African populations with populations from equatorial latitudes. The breeding biology of fiscal shrikes in southern African is less well known. Breeding information from nest record cards (NERC) in southern Africa was described three decades ago (Cooper 1971), post-fledgling development in captive *L. c. predator* has been described (Cooper 1971), and brief accounts exist of breeding in *L. c. predator* (Marshall & Cooper 1969; Hargrove et al. 1972). However, many life history parameters such as incubation and brooding durations have not been recorded in Mediterranean/temperate populations of the fiscal shrike. By comparing the life history strategies of South African populations of the fiscal shrike to those of equatorial populations this study will determine whether latitude is the factor responsible for trends in life history strategies, or whether other influences are the cause.

There are 26 species of *Lanius* shrikes, distributed throughout Eurasia, Africa, and North

America (Cramp & Perrins 1993). An abundance of information exists about palaeartic and neoartic species, which has been encouraged by the recent global decline in shrike populations (Cramp & Perrins 1993; Bassin 1995; Busse 1995; Carlson 1995; Haas & Ogawa 1995; Laporte & Robert 1995; Lefranc 1995; Peakall 1995; Peterjohn & Sauer 1995; Yosef 1994). This extensive database on shrike biology will allow a comparison of the reproductive ecology of fiscal shrikes with that of their congeners, and a comparison between northern and southern hemisphere trends in life history strategies. In addition, extrapolation of the results of this study could be used to help conserve remaining populations of declining shrike species.

Effects of selective processes on the life history strategies of fiscal shrikes:

1) Latitude/photoperiod.

The trend of increasing clutch size with latitude (photoperiod) in the northern hemisphere predicts that clutch size should increase by three eggs for every 18°-30° increase in latitude from the equator (Klomp 1970). If this applies to fiscal shrikes in the southern hemisphere, clutch size in South Africa should be larger than in equatorial Africa. Maximum clutch size in eastern and western subspecies of equatorial populations of the fiscal shrike was three ($\bar{X} \pm SE = 2.58 \pm 0.19$ eggs, $N=12$; 2.67 ± 0.16 eggs, $N=9$ - eastern and western races respectively) (MacDonald 1980; Zack 1986). Therefore, fiscal shrikes in KwaZulu-Natal, South Africa (30°S), should lay clutches of at least six eggs, three more than those in Ghana (05°N) and Kenya (00°S). In addition, as South Africa traverses over 11° latitude, within South Africa clutch size should vary by at least one egg, from at least five in the north to six or seven in the south.

2) Environmental variability (temperature and precipitation).

Variability in annual temperature and precipitation increases from the equator to the poles, and from the southern hemisphere to the northern hemisphere. Therefore the proportion of the year that is available for breeding should decrease with increasing latitude, and breeding season length should increase with decreasing latitude. The length of the breeding season (>95% of all clutches) of fiscal shrikes in Ghana was eight months (MacDonald 1980); southern African populations of fiscal shrikes should therefore have a breeding season of less than eight months. Furthermore, the breeding season length of northern hemisphere Laniidae should be less than southern hemisphere populations.

If birds respond to increased environmental variability by increasing clutch size (e.g. because of a shorter breeding season or longer days in which to forage), clutch sizes near the equator will be smaller than towards the poles, and also smaller in the southern than the northern hemisphere. Clutch size increased by 0.8 eggs per 30° increase in latitude in Australia and South America (Yom-Tov 1987, Yom-Tov et al. 1994). Following this trend fiscal shrikes in South Africa should lay clutches of three or four eggs, and no variation in clutch size should occur from northern to southern latitudes within South Africa. Breeding season length should decrease with increasing latitude

Environmental variability may also affect the territorial strategy of birds. Fiscal shrikes defend exclusive territories throughout the year and all activities, including reproduction and feeding, occur within these territories. If resources are highly variable within or between years (e.g. because of extreme or unpredictable variation in rainfall), fiscal shrikes should maintain a territory that encompasses the minimum area required for the acquisition of resources during the most limited period, i.e., a “worst case” scenario. As fluctuations in the environment are smaller at the equator than at higher latitudes, and as southern Africa is subject to the El Niño Southern Oscillation (ENSO) which brings drought periodically to the region, fiscal shrikes should hold larger territories in South Africa than in the tropics. In Ghana, *L. c. smithii* held territories of 0.6 Ha ($\bar{X} \pm SE = 0.59 \pm 0.04$ Ha, $N=9$) (MacDonald 1980), therefore the mean size of fiscal shrike territories in South Africa should exceed 0.6 Ha. In the continental temperate zone territories might never be able to reach the dimensions required to encompass resources during the harsh winters associated with such zones, and these populations should migrate to avoid such extremes in temperature.

3) Predation risk.

An alternative explanation for the trend of increasing clutch size with latitude is the predation-risk hypothesis (Skutch 1949; Ricklefs 1970; Martin 1983; Lima 1987). If nest predation is high, selection could act on the production smaller clutch sizes, so that energy reserves are maintained for future nesting attempts (Skutch 1949). Nest predation might be higher at lower latitudes because of a larger guild of predators arising from a more productive environment (Skutch 1949). Theoretically, nest predation alone has been shown to account for all variation in clutch size (Lima 1987). Fifty-eight per cent of an equatorial population of fiscal shrike's nests were predated (MacDonald 1980). If predation risk is driving clutch size in fiscal shrikes, South African populations should have larger clutch sizes only if predation levels are lower.

4) *Clutch survival.*

Although predation is a major cause of nest loss in altricial birds, I believe that the predation-risk hypothesis could be improved by considering all nest losses, and not only those caused by predation. In regions where nest losses are common, individuals should lay small clutches and retain reserves for future nesting attempts in case a clutch is lost. Nest loss may be more frequent in equatorial and tropical regions than at higher latitudes because many nests are lost or damaged in heavy rain storms, in addition to any increased predation risk. Therefore if the total risk of nest loss is influencing clutch size I would expect to find an inverse correlation between clutch size and nesting success, and find clutch size increasing (1) with latitude and (2) from the southern to northern hemisphere. Nest loss could also influence the pattern of incubation and brooding in birds. If the mortality of eggs or chicks is higher than of fledged young, selection may favour a reduction in the duration of either stage. Therefore if nest loss is influencing the pattern of incubation and brooding in fiscal shrikes, I would expect to see a positive correlation between nest success and incubation or brooding duration.

This study is important in two respects. (1) It will describe the reproductive ecology of southern African populations of the fiscal shrike. (2) It will determine whether the behaviour of southern African races of the fiscal shrike differs to the behaviour of equatorial ones, and will evaluate the possible causes of the trends in life history strategies of birds with latitude. A summary of the predictions of the above hypotheses on life history strategies is shown in Table 2.1.

Table 2.1. Predictions of the effects of hypotheses on life history strategies.

Region	Life history strategy	Latitude/ Photoperiod	Environmental variability	Predation	Clutch survival
	Clutch size	Increase	Increase	Proportional to predation	Proportional to clutch survival
South Africa compared to equatorial Africa	Breeding season length	Decrease	Decrease	-	-
	Incubation/ brooding duration	Increase ^a	Increase ^a	Inversely proportional to predation	Inversely proportional to clutch survival
	Territorial strategy	Increase size	Increase size	-	-
	Clutch size	No difference	Increase	Proportional to predation	Proportional to clutch survival
Southern hemisphere compared to northern hemisphere	Breeding season length	No difference	Decrease	-	-
	Incubation/brooding duration	No difference	Increase ^a	Inversely proportional to predation	Inversely proportional to clutch survival
	Territorial strategy	No difference	Increase size and migratory	-	-

^a increased duration due to increased clutch size.

METHODS.

Study area.

This study was performed at Ukulinga Research Farm, 5 km south-east of Pietermaritzburg, South Africa (30°24'E, 29°40'S, elevation 775 m). Ukulinga consisted of Dohne sourveld, characterised by *Acacia karoo*, *A. nilotica*, and *A. sieberiana* bushveld with *Themida triandra* dominated sour grasslands (Acocks type 44b) (Acocks 1988), and was used for animal science and range and forage resources research. The remainder of the farm was partitioned between horticulture, poultry and pig science, plant breeding, crop production, agricultural engineering, and private residences.

Ukulinga field data.

Observations occurred between October and November 1995, and between August 1996 and October 1997. Fiscal shrike territories were located throughout the year and were classified according to their occupation as follows: belonging to a single bird, belonging to a pair, or belonging to a small family group comprising of offspring and one or both parents. Territories were assigned a number for identification purposes. Boundaries were determined by observing territory holders for at least three hours, and recording the outermost perches defended or hunted from. If a fiscal was inactive or did not use part of its suspected territory during this period the bird was displaced by walking towards it repeatedly, until it turned back on itself at a boundary or was chased from an adjacent territory. Territory maps were drawn by connecting the outermost perches defended or hunted from and mapped onto a 1:2500 map of Ukulinga using landmarks and actual measurements. These were digitised using Bentley Workstation and territory areas were calculated.

Territory holders were observed to determine the following chronological breeding information: onset of pairing and courtship (pair formation, and nuptial feeding to egg laying respectively), onset and duration of nest building (transportation of nest material and incorporation into a nest), egg laying, incubation, (from first day of incubation to first egg hatched), brooding (date of first egg hatched to first chick fledged), date when chicks fledged (first chick to leave the nest), and dates of subsequent nesting attempts. The following physical characteristics of the nest were recorded: tree species, tree height, nest height above ground, nest orientation in tree (bearing from trunk), exposure (% visible from a lateral view). Note that

all bearings are given relative to magnetic north. The success or failure of each part of the breeding cycle was noted and possible causes of failure (e.g. predation or weather) were determined. Nests that were waterlogged or damaged after inclement weather were assumed to have been lost due to inclement weather, whereas eggs or chicks lost from undamaged nests, or nests showing damage inflicted by a terrestrial predator (e.g. broken nest walls) were assumed to have been lost to predation. Nests found with unincubated eggs or dead chicks were assumed to have been abandoned.

The behaviour of breeding fiscal shrikes (see Table 2.2 for definitions) was recorded from courtship to post-fledging care of offspring. Observations were carried out between 0700 h and 1700 h (at least one hour after sunrise and before sunset), although usually between 0800 h and 1200 h, during October and November 1995 (16 territories, 17 breeding attempts), August to December 1996 (four territories, eight breeding attempts), and August to October 1997 (five territories, five breeding attempts). Male and female *L. c. vigilans* were dimorphic and easily discernible in the field, as only the female had chestnut coloured flanks and her plumage was duller than the male's. The plumage of adult fiscal shrikes is pied, black above and white below, whereas juveniles have cryptic brown plumage (Maclean 1993).

Females and nests or fledglings were observed from a distance of 20 m to 50 m for 2 h periods using 10x25 binoculars. No hide was necessary because fiscal shrikes were tolerant of human intruders and quickly habituated to my presence by foraging within 15 m of where I sat. All activities and time of occurrence were recorded onto tape. Male behaviour was recorded using focal sampling with activity recorded every minute for 15 consecutive minutes (Altmann 1974). If more than 3 min elapsed when the bird was not visible sampling was restarted for an additional 15 min, whereas if less than three missing data points occurred, that focal session was extended so that 15 samples were obtained. In addition seven nests in seven territories were each videoed on two to four occasions using a Sony 8 mm camera to observe behaviours not visible with binoculars. During such periods the behaviour of the territory holders was observed simultaneously with binoculars, in order to relate nest activity to other behaviours, e.g. foraging (see Chapter 4). Temperature was recorded on an hourly basis by the Institute of Soils, Climate, and Water (Pretoria), from the weather station at Ukulinga.

Hatching success was calculated as the percentage of all eggs laid that hatched. Fledging success was calculated as the percentage of all chicks that hatched and survived to leave the

Table 2.2. Definition of terms describing fiscal shrike behaviour.

Behaviour type	Behaviours	Classification
Vigilance	Lookout	Perched, searching for prey in air, on foliage, or on ground.
Sexual	Incubation & brooding	Sat/stood in nest containing eggs or chicks
	Copulation	Male mounting female
	Courtship	Nuptial feeding, allogrooming, nest displays, pair-bonding, and advertisement calls (see Harris 1995 for definitions)
	Nest building	Incorporation of nesting materials into nest
Foraging	Forage	Duration of forage sortie (including feeding if occurred whilst on ground)
	Feeding	Self, nuptial, or offspring feeding
	Caching	Impaling prey on spike
Flight	Flying	Non-foraging flight
Territorial	Interaction	Interspecific or intraspecific interactions
	Advertisement	Territorial song (Harris 1995), often accompanied by static ^a marking
Maintenance	Preening	Self-preening.

^a Static marking was when a bird perched prominently on a tall object displaying exposed scapular feathers.

nest. The number of fledglings per successful nest was calculated as the mean number of fledglings to arise from successful nests only (i.e. nests which were successful in fledging at least one chick).

The population of fiscal shrikes at Ukulinga was not colour-banded so individual recognition was not possible. This study does not focus on long term territory dynamics, associations, dispersal, or inter-territory movements. It was therefore decided unnecessary to stress individuals by capture and ringing. Once incubation began it is unlikely that a pair bond was broken, and pairs are assumed to have remained together for the duration of a nesting attempt. Therefore, as almost all pairs were observed during the same time periods it is unlikely that any one individual was sampled excessively, reducing the occurrence of pseudoreplication (Hurlbert 1984). The same individual may have been re-sampled in different years. However, fiscal shrikes appear to have a large population turnover, in that following fledging some territories at Ukulinga contained just one parent tending offspring. In Kenya fiscal shrikes are known to divorce following unsuccessful nesting attempts, and 26% of a population of 19 fiscal shrikes changed territory at least once during a two and a half year study (Zack 1986). Furthermore, fiscal shrikes residing in the same territory for more than one year were subject to different climatic and land use conditions between years (Fig. 1.2, 1.3 & 1.4, Chapter 1).

NERC data.

Data were extracted from the Nest Record Card (NERC) collection of Birdlife South Africa, formerly the Southern African Ornithological Society (SAOS), which is housed at the Avian Demography Unit (ADU) at the University of Cape Town. NERC are used primarily by amateur ornithologists to record observations of nesting birds, although a very small percentage contain data extracted from scientific literature or museum records. Most records were collected between 1951 and 1979, although NERC collection began in 1881 and still continues (Dr. T. Oatley, ADU, pers. comm.). NERC design has been modified over time, but all cards contained a table to record observations of nest-building, incubation and brooding, and most asked for nest height and details of the nest structure. All asked for the geographical location of the nest.

There were over 1500 NERC for the fiscal shrike. Most cards contained one or a few observations on one nest, although a few contained detailed accounts of nests that had been revisited on a daily basis throughout the breeding season. Many contained information that was

not requested, such as the species of tree where the nest was placed, or measurements of egg dimensions. The following information was extracted from fiscal shrike NERC, from South Africa and Namibia: duration of nest-building, incubation, and brooding phases; laying and hatching order; nest tree species and height of nest above ground; number of eggs laid, number of chicks hatched, and number of chicks fledged; egg dimensions; and accounts of brood parasitism.

For some analyses only part of the fiscal shrike NERC collection was examined. This was solely due to time constraints, and in these cases cards were searched systematically and records which were omitted were from regions with a disproportionate representation (for example, the Western Cape), and within a region records were chosen randomly. However, all regions were represented. Rhodesian (Zimbabwean) Ornithological Society records, also housed at the ADU, were omitted for all analyses as they had been previously been subject to analysis (Cooper 1971). They also represented an area wholly within the sub-tropics, and inclusion of this data would reduce the effectiveness of a contrast to equatorial species.

Data analysis.

Unless otherwise stated, all statistical analysis were two-tailed with $\alpha=0.05$. Raw data were subjected to Kolmogorov-Smirnov one-sample test for normality prior to further analysis (Steele & Torie 1980). When analyses of variance were performed, residuals were subjected to Kolmogorov-Smirnov tests for residual normality, and Barlett's test for homogeneity of variance (Sokal & Rohlf 1995). In order to run parametric analyses, data which were not normally distributed were subjected to transformation. Proportional data were arc-sine square root transformed, and data with a large range were logarithmically transformed (e.g. territory area, which showed a 30-fold increase in size at Ukulinga). All transformations which were applied to data are stated. Data which were not normally distributed or could not be transformed to achieve normality were subject to non-parametric analysis, and medians and interquartile ranges (median, Q1-Q3) are quoted when describing such data. Data which were normally distributed and which agreed with all other assumptions for the appropriate statistical tests, were analysed with parametric analyses, and means and standard errors are quoted when describing such data.

Methods used for choosing an appropriate statistical test followed Sokal & Rohlf (1995) and Siegal & Castellan (1988). Associations were tested using the G-test. Comparisons of

distributions were tested with the Kolmogorov-Smirnov test, differences between categories were tested with analyses of variances (ANOVA (parametric), and Wilcoxon-Mann-Whitney and Kruskal-Wallis tests (non-parametric)). Functional relationships between continuously distributed variables were tested using linear regression.

Log-linear modelling was employed to test for associations between three or more categories of data. Log-linear modelling, which requires categorical data only, is a powerful non-parametric analysis, similar to a multiple analysis of variance (MANOVA) or multiple regression (Knocke & Burke 1980, Bakeman et al. 1992). Log-linear modelling computes the probability of all interactions occurring between x variables at y levels (expected frequencies), and compares these to observed frequencies, thereby being similar to a G-test except using more than two classes or levels of variables. A model is specified between the variables, and terms outside the model are introduced sequentially, with single effects followed by interactions in a hierarchical manner (Knocke & Burke 1980). The probability of the specified model occurring is computed every time a variable is factored in. The model is said to describe the data when the fitted model is not significantly different to the specified model, i.e. $P > 0.05$ (Knocke & Burke 1980). The effect of each alternative model is deduced by comparing the change in the test statistic L^2 , (i.e. $\Delta L^2 = L^2$ of the baseline model - L^2 of the interaction) under DF (DF of the baseline model - DF of the alternative model) using the χ^2 distribution table. This calculates the probability of the effect of the interaction being due to chance. If $P > \alpha$ there is no significant effect of the interaction, however, if $P < \alpha$ the interaction has a significant effect on the baseline model.

An example of the application of log-linear models.

A data set contains categorical information on nest success (variable A), nest height (variable B), and nest exposure (variable C) in fiscal shrikes. It is of interest to determine whether nest height, nest exposure, or a combination of these factors, had a significant effect on nest success. This could be analysed using log-linear modelling to see the effects of the interactions on breeding success. The model [A][BC] would be specified as the baseline model. Alternative models (e.g. the interactions [AB][BC] (nest height on nest success) and [AC][BC] (exposure on nest success)) would be compared to the baseline model. The resulting test statistic L^2 is compared to L^2 of the baseline model after the addition of each variable, and the probability of ΔL^2 (the change in L^2) occurring by chance is found in a χ^2 distribution table under DF (DF for baseline model - DF for alternative model). If ΔL^2 at DF is less than α , the effect of the interaction is not due to chance alone, and therefore the interaction has a significant effect.

RESULTS AND DISCUSSION.

Pairing status and territoriality.

The decision of whether to remain on a territory or migrate during a period of limited resources or severe climatic conditions may be considered as an economic decision. Both options carry costs and benefits; remaining on a territory might reduce the condition of the owner, but benefits include retention of the territory for the future. Migration is an energetically costly strategy which increases the risk of mortality, although resources may be more plentiful or conditions more favourable at the migration destination. The decision to remain at or leave an area is a trade-off between the associated costs and benefits of each option. In regions subject to severe climatic conditions or resource shortages populations of a species may migrate, whereas in other areas the same species may be resident. Variation in the photoperiod increases with increasing latitude, leading to resources being limited for a greater proportion of the year at high latitudes than at the equator (Ricklefs 1980). Therefore populations of birds at the equator should be sedentary, whereas populations at high latitudes should migrate.

The size of territory occupied by an individual is a reflection of available resources. When resources are plentiful territories are usually small, either because of increased intruder pressure or because resource requirements can be met in a smaller area. Where the environment is variable resources can be limited for part of the year. Territory size should therefore increase with increasing environmental variability to allow sufficient resources for a "worst case" scenario. Territories held near the equator should be smaller than those held at more northern or southern latitudes.

Fiscal shrike territories were held by individuals or pairs throughout the year at Ukulinga Research Farm. Boundaries fluctuated slightly amongst years, but locations remained similar throughout the study. Nests or other signs of breeding were not discovered in eleven of the 63 territories at Ukulinga during the period 1994-1997, and therefore these were termed non-breeding territories. Nests were not discovered in a further 16 fiscal shrike territories, but due to insufficient observation effort it is possible that in one or more years reproduction occurred in those territories. Therefore the breeding status of these was termed unknown. Territories that contained a nest in one or more years of the study were termed breeding territories. Figure 2.1 shows the location of fiscal shrike territories in 1997, and whether the territory was ever

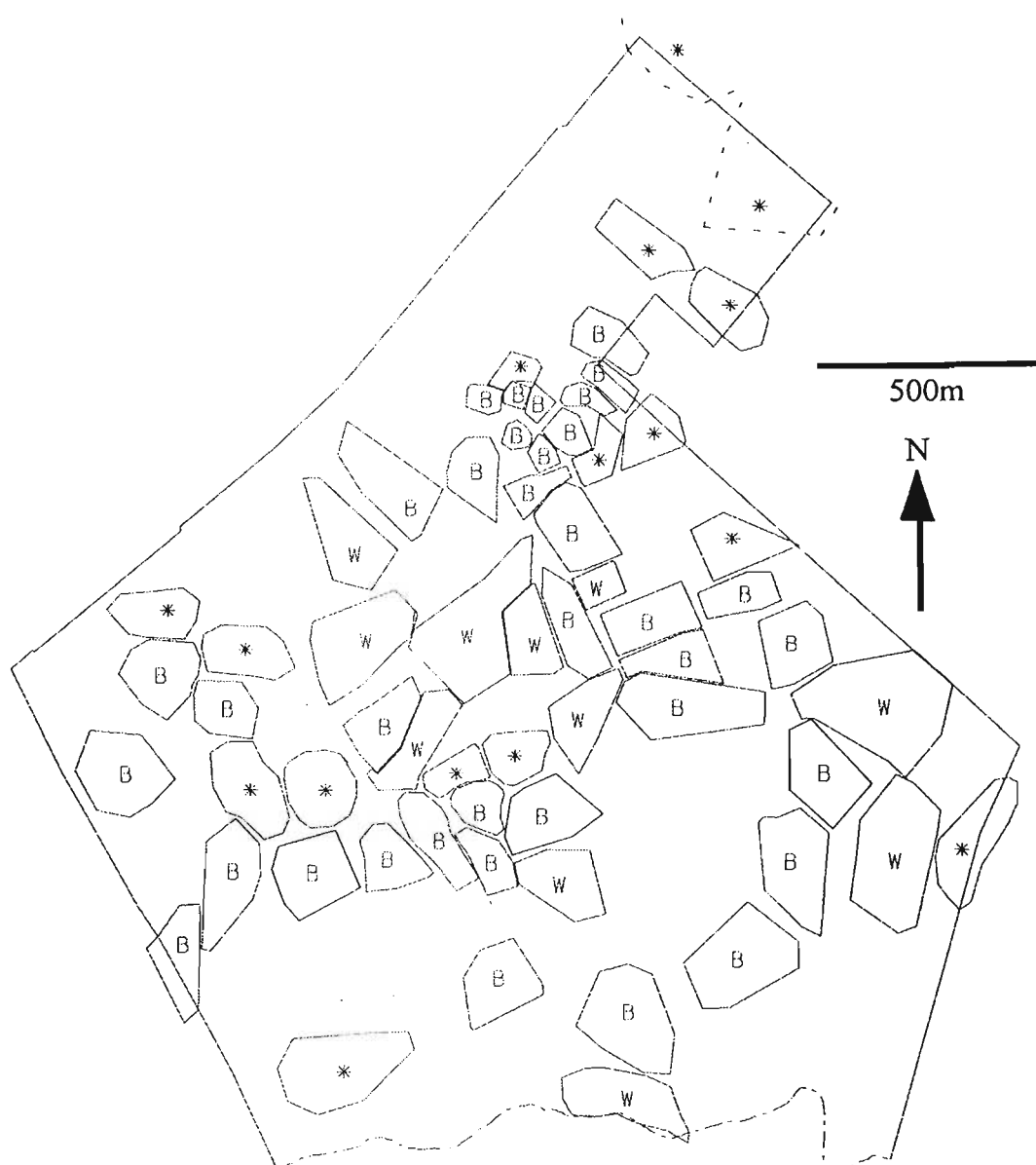


Figure 2.1. Organisation of breeding and non-breeding fiscal shrike territories at Ukulinga Research Farm. Breeding territories (B) contained at least one nest during the breeding seasons of 1994-1997, whereas non-breeding (W) territories did not. Territories for which there is inadequate information concerning nest occurrence are indicated by an asterisk (*). Boundaries shifted slightly during the study period but core areas remained the same. This map shows the boundaries of territories during July 1997. Dashed lines indicate estimated boundaries.

occupied by breeding birds during the period 1994-1997. Breeding territories were occupied throughout the year in all 36 cases, whereas six non-breeding territories were only occupied during winter periods, four were occupied throughout the year, and the occupancy period of one territory was not known.

Fiscal shrikes are resident in southern Africa and are monogamous and territorial (Harris & Arnott 1988). Fifty four per cent of all territories at Ukulinga were occupied by pairs of fiscal shrikes outside the breeding season (January-July) (Fig. 2.2). Additional pairing occurred during spring and early summer, and by November-December there was a significant increase in the proportion of territories held by pairs or families to 95% of all territories (G-test: $G_1=23.2$, $P<0.001$). Resources for fiscal shrikes in South Africa must be reasonable to allow residency and the maintenance of pair-held territories throughout the year. The maintenance of pair-held territories outside the breeding season by fiscal shrikes is in contrast to many other species of Laniinae. The migratory red-backed shrike *L. collurio*, lesser grey shrike *L. minor*, great grey shrike *L. excubitor*, and woodchat shrike *L. senator*, usually hold individual territories on their wintering grounds (Harris & Arnott 1988; Atkinson 1993; Cramp & Perrins 1993; Schon 1995). Resident great grey shrikes in Germany remain on breeding grounds throughout the year, but pair bonds dissolve and males and females hold separate territories outside the breeding season (Ullrich 1971). Loggerhead shrikes *L. ludovicianus* held in captivity in San Diego were sexually incompatible when not breeding and males and females were housed in separate cages, whereas fiscal shrikes were fully compatible and were housed together at all times (Azua & Lieberman 1995).

The majority of studies of the Laniinae have occurred in the palaeartic and neoartic regions that have continental climates with severe winters. Most of these populations are migratory (Cramp & Perrins 1993), and differential migration of the sexes leading to solitary winter territories are common in migratory birds (Gauthaux 1982; Ketterson & Nolan 1983). Pairs of fiscal shrikes may maintain territories and inter-sexual compatibility outside the breeding season to increase their chances of opportunistic breeding if favourable conditions prevail. Note that fiscal shrikes have bred from June to April in South Africa (NERC analysis) and in every month of the year in Zimbabwe (Cooper 1971). In Kenya *L. c. humeralis* was able to breed throughout the year except during periods of moult, and breeding was opportunistic, occurring with the onset of the rains (Dittami & Knauer 1986).

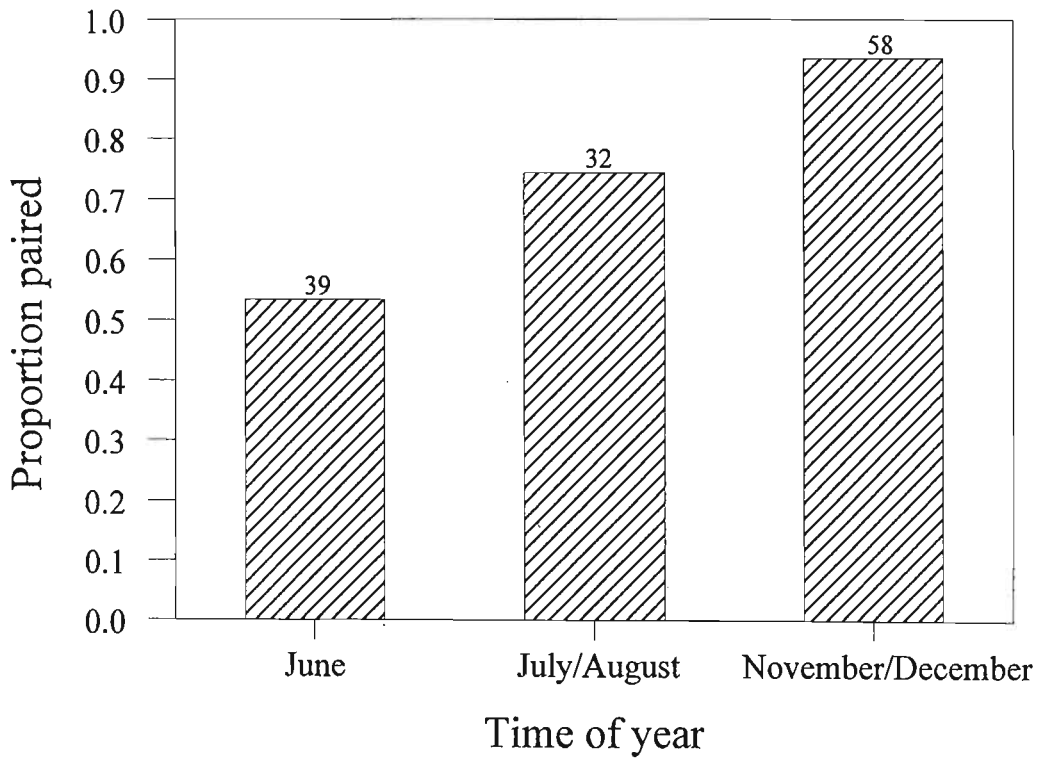


Figure 2.2. Proportion of fiscal shrike territories held by pairs throughout the year (1995-1997). Numbers above bars indicate sample sizes. There were significantly more pair-held territories in November-December than in June (G-test: $G_1=23.2$, $P<0.001$).

Fiscal shrikes held territories between 0.3 Ha and 6.3 Ha at Ukulinga ($\bar{X} \pm \text{SE} = 2.2 \pm 0.2$ Ha, $N=61$), larger than those of equatorial populations in Ghana ($\bar{X} \pm \text{SE} = 0.59 \pm 0.04$ Ha) (MacDonald 1980). This agrees with the prediction that territory size increases with latitude and environmental variability, and this and other aspects of territoriality are discussed further in Chapter 3.

Courtship and copulation.

Initiation of courtship was apparent when food sharing began. Females uttered a begging call "naaa" (call 7, Harris 1995), like that of juvenile passerines, whilst rapidly quivering their wings and crouching in a low position with head raised. Females followed their partner around the territory, begging, until food was offered. During the period of courtship feeding, females would also forage for themselves. Courtship feeding is common in the Laniinae of the palaeartic (Harris & Arnott 1988; Schon 1995; Cramp & Perrins 1993), although there is no information regarding courtship feeding in equatorial populations of the fiscal shrike. The male great grey shrike also calls and wing-quivers during courtship feeding (Cade 1962).

Courtship feeding has been implicated as an important factor in reproductive success for many species of birds. Courtship feeding in Ospreys *Pandion hiliaetus* functions primarily to ensure mate fidelity (Poole 1985). In some species such as hole-nesting hornbills (family Bucerotidae (Maclean 1993)), the female is sealed in the nest and is entirely dependent on male provisioning, whereas in most others the female also forages for herself. Courtship feeding functions in pair bond reinforcement (Lack 1940), to channel excess resources into reproductive output (Thornhill 1976; Gwynne 1986), or to allow a female to assess the quality of her partner or territory before commencing reproduction (Wiggins & Morris 1986). The intensity of courtship feeding in blue tits *Parus caeruleus*, great tits *P. major*, and marsh tits *P. palustris* was greater during egg laying than pair formation and courtship, which does not support the pair bonding hypothesis as courtship feeding should be greater during early periods (Krebs 1980; Nilsson & Smith 1988). However, great tits and blue tits require the extra energy from courtship feeding to produce eggs, as females are unable to meet the energetic costs of both daily maintenance and egg production, thereby supporting the second hypothesis (Krebs 1980). Nisbet (1973) discovered that courtship feeding in common terns (*Sterna hirundo*) correlates with clutch size, clutch mass, and the survivorship of the last chick. Male courtship feeding was manipulated in the red-backed shrike by food supplementation (Carlson 1989). Clutch size was significantly greater (average of 0.9 egg larger) in experimental groups than in

controls, who received no extra food. This implies that the increase in resources received by females during courtship feeding is channelled directly into reproduction (*sensu* Thornhill 1976; Gwynne 1986).

Copulations were recorded only four times during 59 h of observing of fiscal shrikes at Ukulinga. The female had begun egg laying by the time three of the copulations occurred (one unknown), and copulations followed courtship feeding in all instances. After food was exchanged the male uttered soft calls and his partner responded by crouching, after which copulation occurred, lasting for 3-8 s. Copulations in *L. c. humeralis* last 3-7 s (Zack 1986). Schon (1995) recorded 57 copulations in a ten year study on the great grey shrike, 84% of which followed courtship feeding. Bull-headed shrikes *L. bucephalus* copulate approximately 20 times per breeding cycle (Yamagishi et al. 1992). A pair of great grey shrikes that were observed during all daylight hours over an entire season had a copulation rate of 0.05/h to 0.2/h, which peaked in the morning and fell during the day, then rose again in the late afternoon (Lorek 1995). Overall, 32 copulations were recorded during the entire season and copulations always occurred after courtship feeding (Lorek 1995).

The Laniinae therefore appear to have a low copulation rate. Frequent copulation is a paternity guarding strategy seen mostly in species that are spatially clumped with asynchronous breeding cycles, and which are prevented from mate guarding by ecological constraints (e.g. colonial species, Miller 1985). The intense territorial strategy of the shrikes probably reduces the occurrence of extra-pair copulations (EPCs), although EPCs have been observed in great grey shrikes (Lorek 1995) and documented in the bull-headed shrike (Yamagishi et al. 1992). Male great grey shrikes guarded their partners during the fertile period by maintaining close proximity (Lorek 1995), which is an alternative strategy used to guard against cuckoldry. The fiscal shrike did not appear to use either the frequent copulation strategy or the proximity marking strategy to ensure paternity, but its intensive territoriality may have prevented most intrusions.

Nesting.

Three male fiscal shrikes were observed displaying at potential nest sites before nest construction commenced. A nest-display began when a male collected nesting material and entered a bush or tree from low in the canopy. Males moved slowly through the bush until arriving at a place suitable to build a nest, where material was deposited and crouched on by the

male. A wing-quivering display followed, accompanied by soft calling and tail fanning, after which the male moved slowly to the top of the bush or tree and perched prominently for a few minutes. Nine such displays were observed by one of the males during a 1 h period in the early afternoon, although displays were also observed in the morning in another individual. Male red-backed shrikes built platforms similar to those of the fiscal shrike, and male red-backed shrikes, lesser grey shrikes, and great grey shrikes performed nest-place displays (Cramp & Perrins 1993; Schon 1995). Nest displays may function to entice the female into initiating nest-building and breeding.

Fiscal shrikes constructed open cup-shaped nests of grass and small twigs, roughly lined with light coloured material, often feathers, string, and soft plant parts (e.g. dandelion seeds). Nest construction occurred at the same place as observed nest displays in two territories, but not in a third, so not all trees where nest displays were performed became nest trees. Both males and females constructed nests, sometimes re-using material from old nests as well as gathering fresh material. Analysis of NERC showed that nest construction in the fiscal shrike lasted 3-21 days ($\bar{X} \pm SE = 8.45 \pm 1.06$, $N=22$). Protracted egg-laying, where a period of over three months passed between nest completion and clutch initiation, has been observed in Zimbabwe (Steyn 1976). However, egg-laying at Ukulinga usually began within two weeks of nest completion. Zack (1986) reported that fiscal shrike nests were completed sometimes in as little as two days. Migratory woodchat shrikes, lesser grey shrikes, and red-backed shrikes complete their nests within three to seven days. This lower variability in nest construction duration may be due to time constraints resulting from a shorter breeding season in the short summers of high latitudes, and migration pressures. Most migrant palaeartic shrikes only spend 25% of the year on breeding grounds, and so must complete reproduction quickly (Harris & Arnott 1988), especially as breeding grounds are also used to improve the condition of individuals before migration. The speed with which fiscal shrikes can complete a nest in Kenya may be an adaptation for opportunistic breeding, so that reproduction can occur quickly in response to improved climatic conditions.

Nests at Ukulinga were placed 0.75 m to 5 m above ground level (median, $Q1-Q3 = 1.65$ m, 1.25-2.5 m, $N=32$) (Fig. 2.3). There was a significant difference in nest height amongst regions of southern Africa (Kruskal-Wallis test: $H_5=55.16$, $P<0.001$) with birds nesting higher in KwaZulu-Natal and the Transvaal than in the Western Cape (Fig. 2.4). Nest height at Ukulinga was significantly lower than in other parts of KwaZulu-Natal (Wilcoxon-Mann-Whitney test:

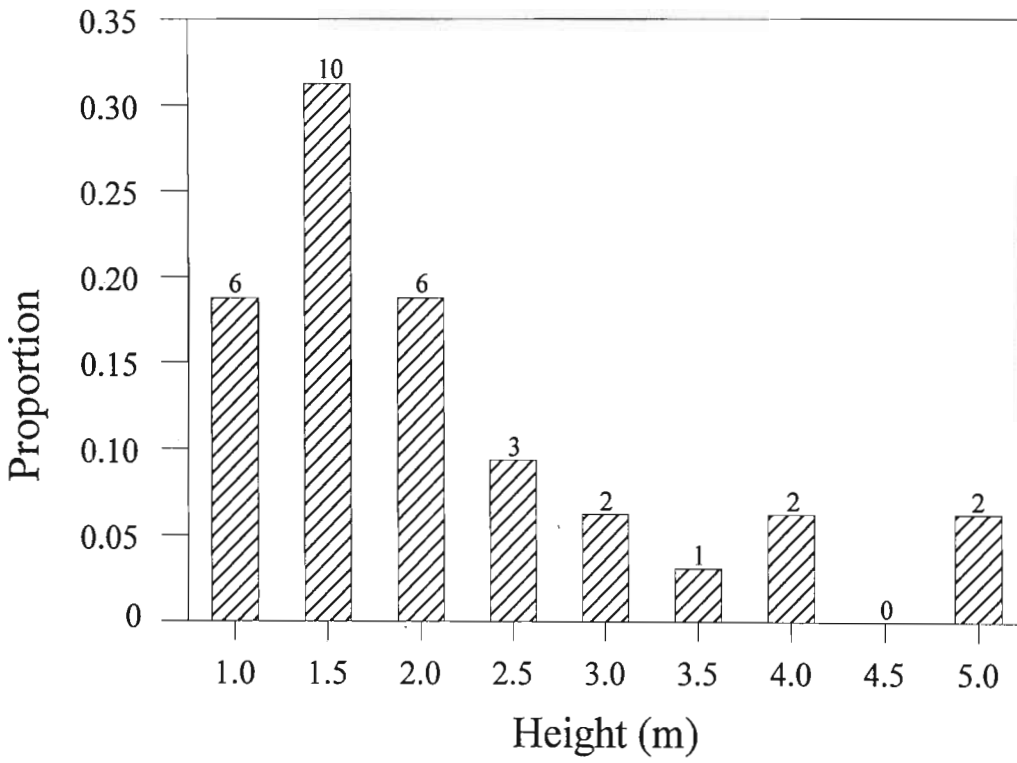


Figure 2.3. Height of 32 fiscal shrike nests above ground level at Ukulinga Research Farm.

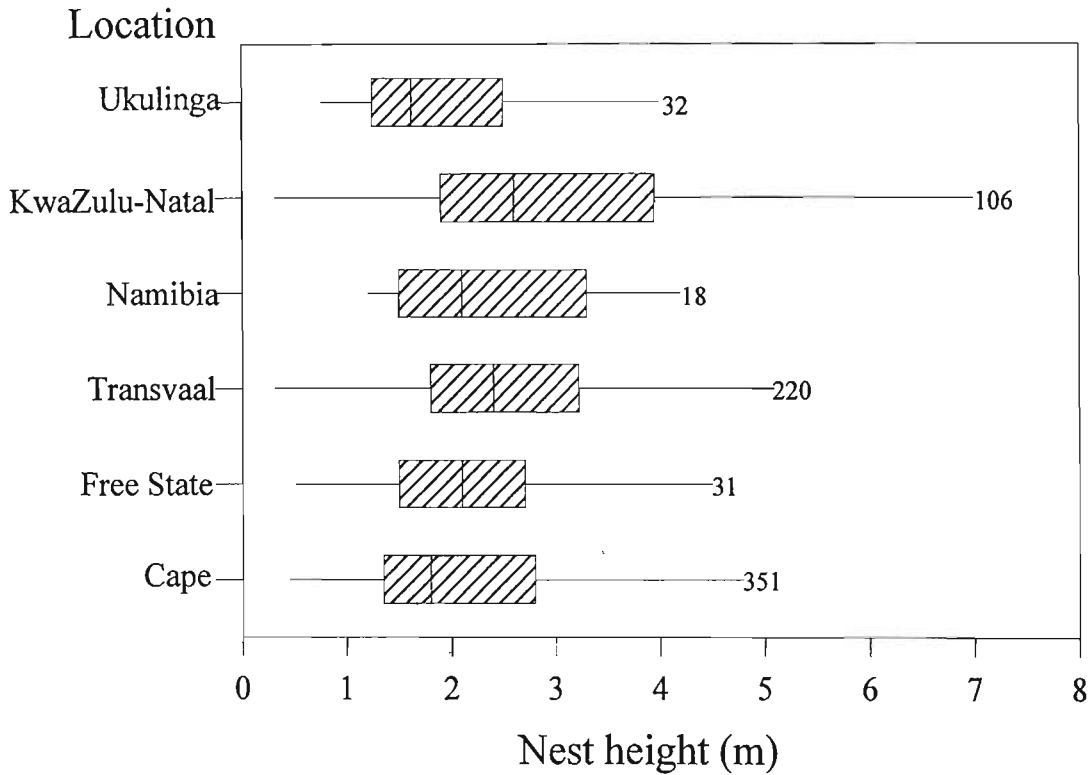


Figure 2.4. Height above ground level at which fiscal shrikes nested in different regions of southern Africa. Data were extracted from Nest Record Cards (KwaZulu-Natal, Namibia, Transvaal, Free State, Cape) and collected at Ukulinga Research Farm, Pietermaritzburg (Ukulinga). Numbers indicate sample sizes. Box-and-whisker plot vertical line represents median, box encloses 1st to 3rd quartiles, and horizontal line connects the lowest and highest observations defined by the lower limit $Q1 - 1.5(Q3 - Q1)$ and the upper limit $Q1 + 1.5(Q3 - Q1)$ (Minitab Inc.).

$W=1502.0$, $P<0.001$). Nest height was probably a consequence of the availability of suitable nesting places. Ukulinga had a large proportion of short trees due to recent bush encroachment.

The height of shrubs and trees used for nesting at Ukulinga varied from 0.5-20 m (Fig. 2.5) (median, Q1-Q3=3 m, 2-5.3 m, $N=33$). Fifty species of trees and shrubs were recorded in fiscal shrike territories at Ukulinga, and eleven of these were used in 31 nesting attempts. Nest placement in a species was not predicted by species abundance ($G_{11}=56.34$, $P<0.001$) (Fig. 2.6). Fewer nests were placed in *Acacia sieberiana* and *Eucalyptus spp.* than expected, whilst more *A. nilotica* were chosen as nest trees. *A. sieberiana* & *Eucalyptus spp.* had less dense canopies than *A. nilotica* at Ukulinga, and *A. nilotica* may provide increased protection or support for the nest. Eight nests were placed in flora not indigenous to the region, which was not significantly different to the number expected based on the proportion of non-indigenous species (G-test: $G_1=0.923$, NS).

Six hundred and fifty-four NERC out of a sample of 847 indicated the species or type of tree in which fiscal shrikes had nested. Twenty-nine trees were identified to the species level (scientific name), another 22 to the genus, 19 species were identified by their common name, and a further eight by category, such as thorn tree or epiphyte. As there was no information concerning the abundance of these species in the habitats where fiscal shrikes nested, it is impossible to determine whether placement was determined by species abundance. Thirty-three of the 77 species, genera, or categories (42.9%) were flora not indigenous to the region, and one category (three records, 0.4%) was artificial man-made structures (e.g. wooden beam in shed). All others were flora indigenous to South Africa and Namibia (56.7%). Fiscal shrikes were adaptable in their nesting requirements with 832 nests located in trees and shrubs, four in creepers, four in epiphytes, three in man-made structures, two on tree stumps, one in bamboo, and one in reeds (total nests=847).

Since colonial times the fiscal shrike has expanded into suburban habitats (Harris & Arnott 1988), and is frequently seen in plantation clearings. In the Eastern Cape and Lesotho where deforestation has occurred the fiscal shrike is less abundant, thereby indicating some sensitivity to land use changes (Parker 1997). In Mediterranean Europe the lesser grey shrike is less tolerant of urbanisation than either the woodchat shrike or the red-backed shrike, but unlike the fiscal shrike none of these three species occupy areas of high urbanisation (Guerrieri et al. 1995). Land-use changes have affected the abundance of many raptorial birds in South Africa

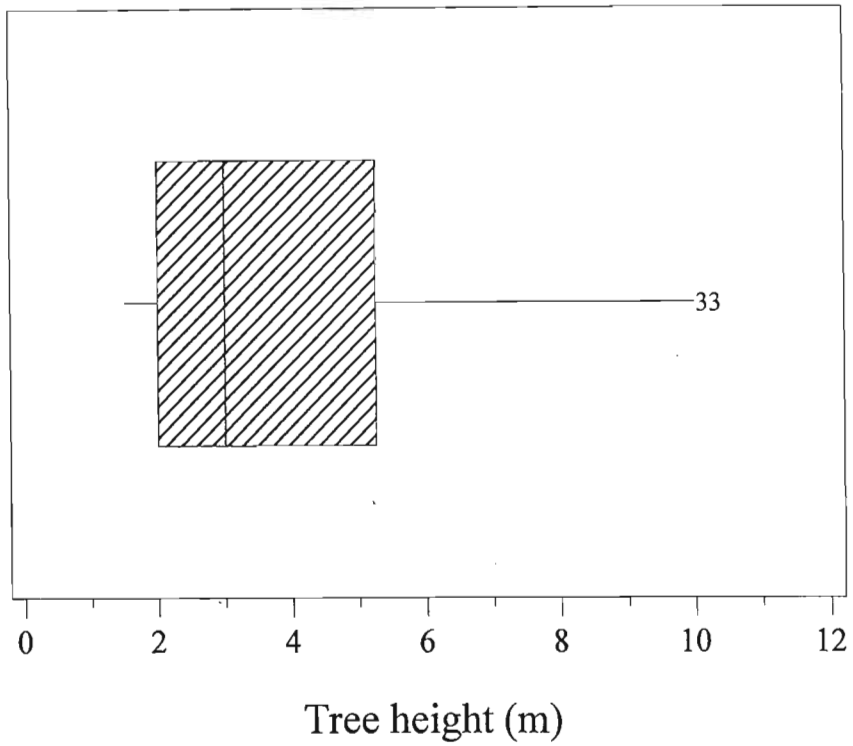


Figure 2.5. Height of trees and shrubs where fiscal shrikes placed their nests at Ukulinga Research Farm. Numbers indicate sample size. For a description of box-and-whisker plots see Fig. 2.4.

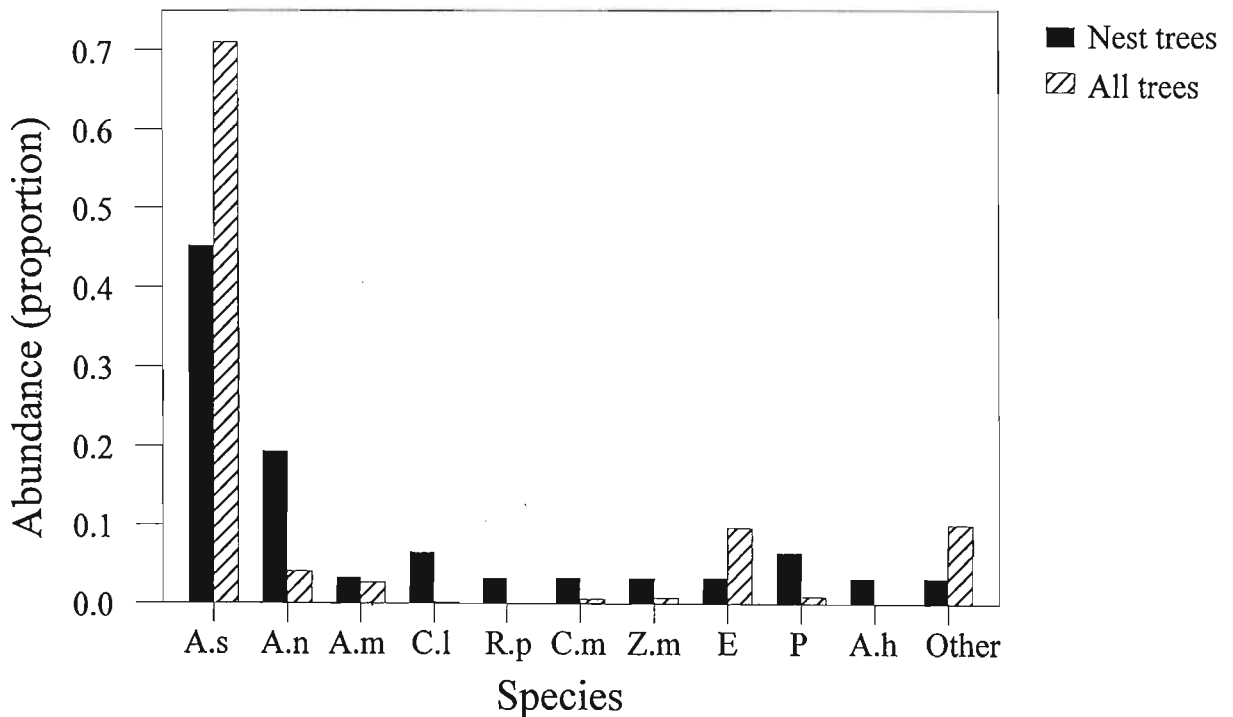


Figure 2.6. Proportion of 31 fiscal shrikes nests found in ten species of tree at Ukulinga research Farm, compared to each species abundance (2226 trees sampled). Nest placement was not predicted by species abundance (G-test: $G_1=54.24$, $P<0.001$). A.s=*Acacia sieberiana*, A.n=*A. nilotica*, A.m=*A. mearansii*, C.l=*Citrus limon*, R.p=*Rhus pentherai*, C.m=*Canthium mundiamun*, Z.m=*Ziziphus mucronata*, E=*Eucalyptus spp.*, P=*Pinus spp.*, A.h=*Araucaria heterophylla*, Other includes 40 species of tree.

(Brandl et al. 1985a). The tolerance of fiscal shrikes to urbanisation and land-use changes might have enhanced its apparent success (Brandl et al. 1985b), whereas species of the Laniinae which are less tolerant are in decline (Yosef 1994).

The fiscal shrike often does not conceal its nest very well. At Ukulinga nests were often visible ($\bar{X} \pm \text{SE} = 42.8 \pm 5.2\%$ exposed, $N=29$). The breeding season began prior to leaf growth in deciduous trees, and this increased the exposure of nests built early in the season. Nests were not evenly distributed within the canopies of nest trees (Fig. 2.7). Significantly more nests were placed in the centre of the canopy, than any of the four quadrants (G-test: $G_4=28.87$, $P<0.001$). Many species of birds orientate their nests in relation to environmental variables, placing their nests to either absorb or avoid solar radiation (Maclean 1974; Inouye 1976; Yanes et al. 1996). Other species situate their nests away from prevailing winds (Ricklefs & Hainsworth 1969; Conner 1975). Female white crowned sparrows preferred nest sites on the north-eastern side of trees, which firstly protected nests from the prevailing wind, and secondly exposed nests to the morning sun but shaded them from the midday heat (note that this study was in the northern hemisphere, with the sun to the south) (Zerba & Morton 1983). Nests at Ukulinga were placed significantly more often in north and west regions than in south and east regions of trees ($G_1=9.01$, $P<0.01$). The prevailing wind at Ukulinga originated from the south-east, and placement in north and west regions could have been an adaptation to avoiding this and the rains associated with it. Hummingbirds (family Trochilidae) in the Rocky mountains, USA., utilised nest locations that minimised heat loss by conduction, convection, and radiation in the pre-dawn environment (e.g. beneath overhanging vegetation) (Calder 1973).

Laying.

The ground colour of a fiscal shrike's egg is cream to beige, and eggs are marked with varying degrees of olive to brown speckles that often concentrate around the widest circumference of the egg to form a ring. Eggs were oval in shape ($\bar{X} \pm \text{SE} = 23.6 \pm 0.07$ mm length, $\bar{X} \pm \text{SE} = 17.8 \pm 0.04$ mm breadth, $N=263$). Egg-laying at Ukulinga began in August, and continued though to December (Fig. 2.7). There was a significant difference between the breeding season of fiscal shrikes in winter and summer rainfall regions of South Africa (Kolmogorov-Smirnov two-sample test: $D=0.254$, $P<0.001$) (Fig. 2.8). The breeding season (>95% of all records) lasted five months in both winter and summer rainfall regions. However, in winter rainfall regions egg-laying was initiated in July during the rainy season, whereas in

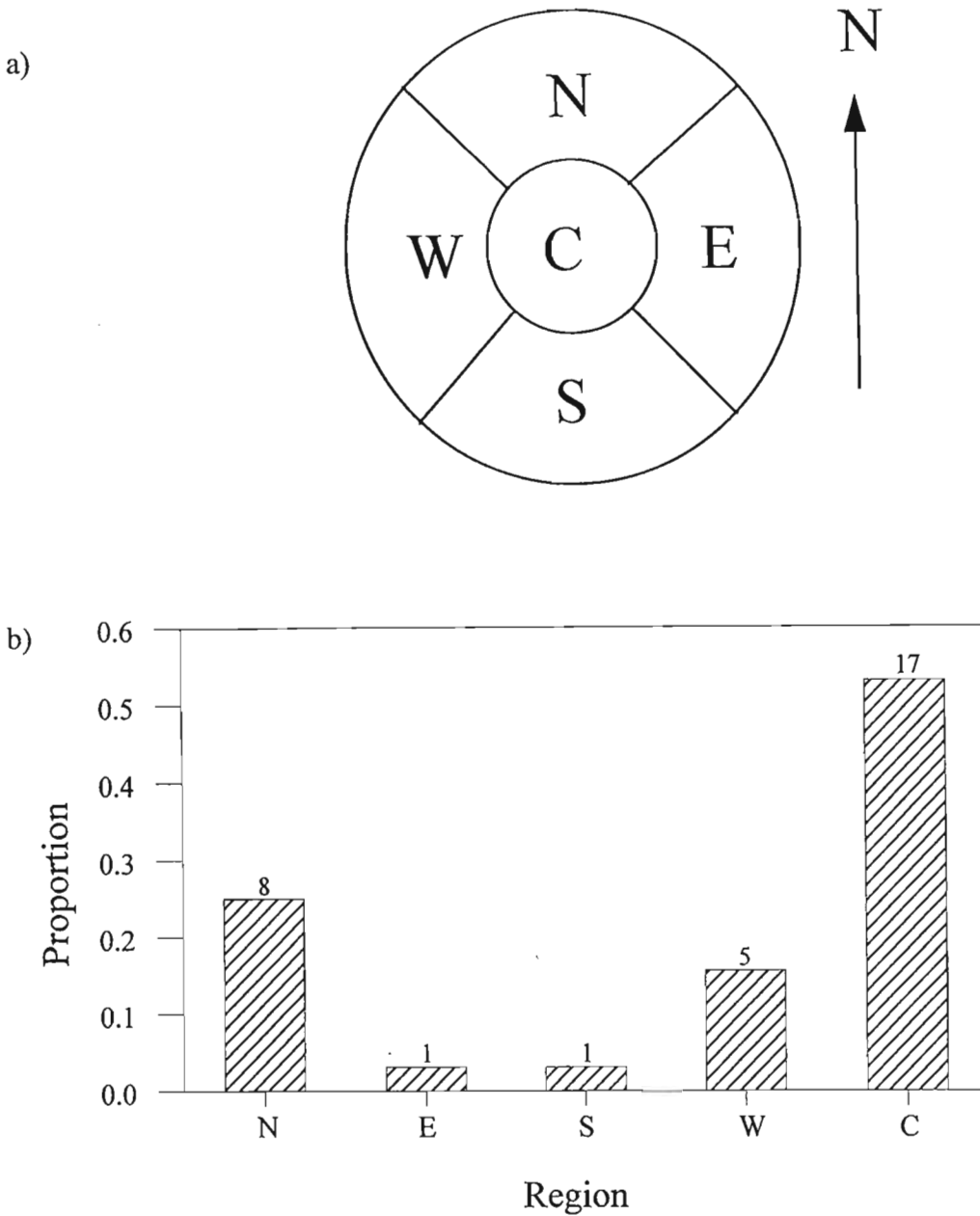


Figure 2.7. Nest placement. (a) Division of tree canopy into centre region, and north, east, south and west quadrants (each equal in area). (b) Nest placement in area of tree canopy (as defined above) of 32 fiscal shrike nests at Ukulinga Research Farm. Fiscal shrikes placed their nests in the centre of a tree significantly more often than expected if placement was random (G-test: $G_4=28.87$, $P<0.001$), and in the north and west quadrants significantly more than the south and east quadrants (G-test: $G_1=9.01$, $P<0.01$).

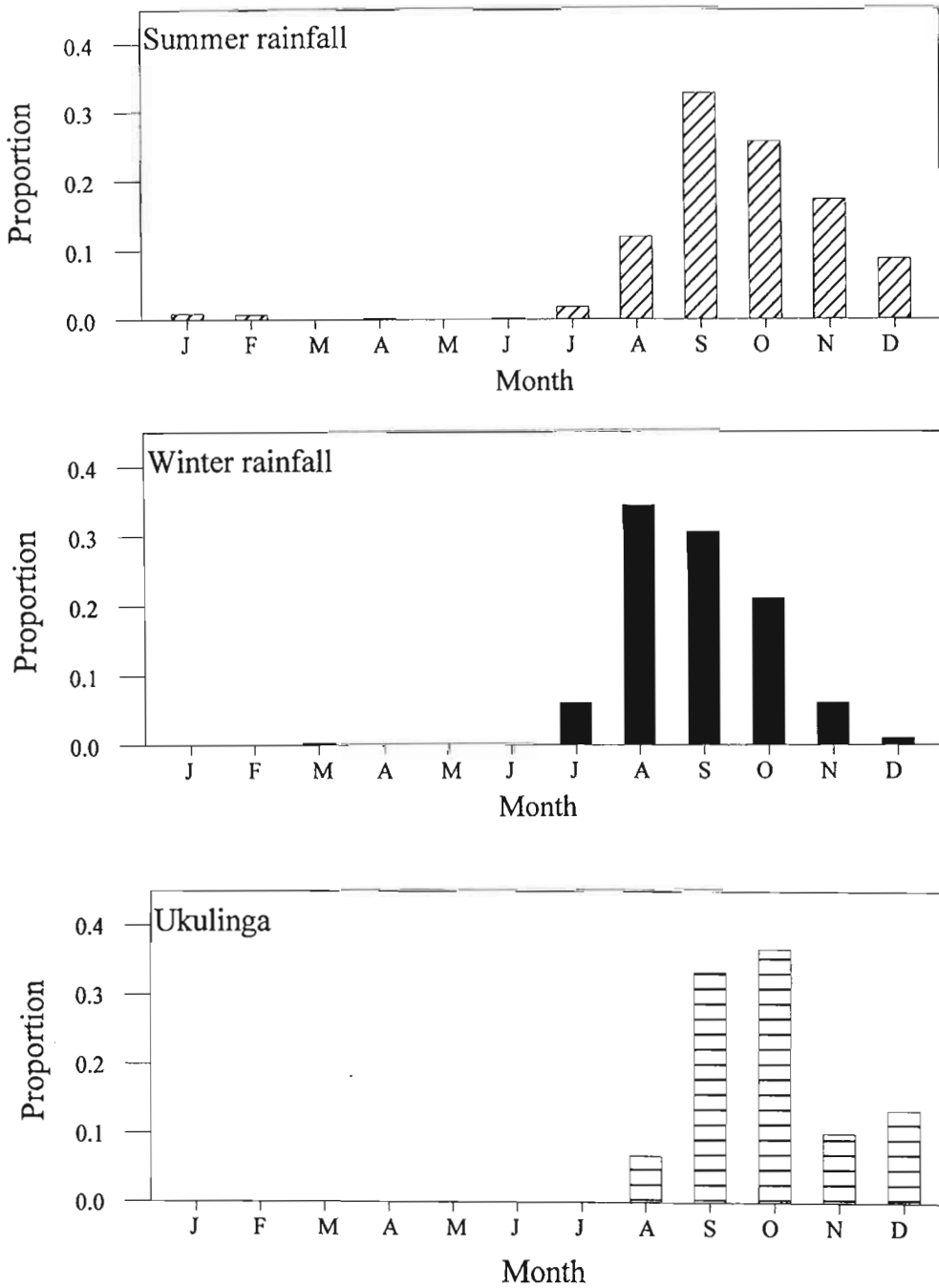


Figure 2.8. Proportion of all nesting attempts (first egg laid) by month for fiscal shrikes in summer rainfall regions (736 records), winter rainfall regions (571 records), and at Ukulinga Research Farm (24 observations). Summer and winter rainfall regions data were collated from Nest Record Cards (NERC).

summer rainfall regions egg-laying began in August prior to the onset of the rains. Parker (1997) also documented geographical variation in the breeding season of the fiscal shrike. There was a trend of increasing breeding season length (months where over 10% of records collected were from breeding birds) from four to five months, moving from the south-west to the north-east of the southern African region (when central and northern Namibia were omitted). Central Namibia had a bimodal distribution of breeding records, with peaks in December-January, and in mid-June. In northern Namibia the breeding season was very short, and breeding was only recorded in two months, October and April. Onset of breeding in Namibia may be in response to rainfall, as Namibia has an arid climate with much of the country receiving less than 250 mm of rain per year, and insects, which are the primary prey of fiscal shrikes, increase in abundance with increasing precipitation (Samways 1994).

Fiscal shrikes that initiate nesting during the rainy season (e.g. winter rainfall regions) endure different climatic and nutritious conditions than to those that breed with the onset of rain (e.g. summer rainfall regions), because of the association between insect abundance and precipitation (Samways 1994). Highest prey levels for fiscals breeding in winter rainfall regions fall during the early stages of reproduction, whereas those nesting in summer rainfall regions time chick hatching and fledging, the periods when resource requirements are greatest, to coincide with the peak in prey abundance. In Kenya initiation of fiscal shrike breeding coincided with the onset of heavy rains (Zack 1986; Dittami & Knauer 1986), although fiscal shrikes in Ghana bred during the driest and wettest months of the year (MacDonald 1980). Fiscal shrike breeding is therefore not necessarily confined to periods of rainfall. Their ability to exploit seasonably abundant food sources outside the normal breeding season demonstrates their opportunistic nature, which could be an important factor leading to their success whilst many of the Laniinae are in decline (Yosef 1994).

Thirty one NERC contained detailed information on egg-laying patterns of fiscal shrikes. Eggs were normally laid on consecutive days (74% of records), although a gap of one day was reported between laying the first and second eggs (16% of records) and between the penultimate and final eggs (10% of records). There was no significant difference between completed clutch sizes at Ukulinga ($\bar{X} \pm SE = 3.41 \pm 0.16$, $N=24$) and South Africa (NERC) ($\bar{X} \pm SE = 3.70 \pm 0.04$, $N=374$) (Kolmogorov-Smirnov two-sample test: $D=0.056$, NS) (Fig. 2.9), or amongst regions of South Africa (Kruskal-Wallis test: $H_4=6.13$, NS).

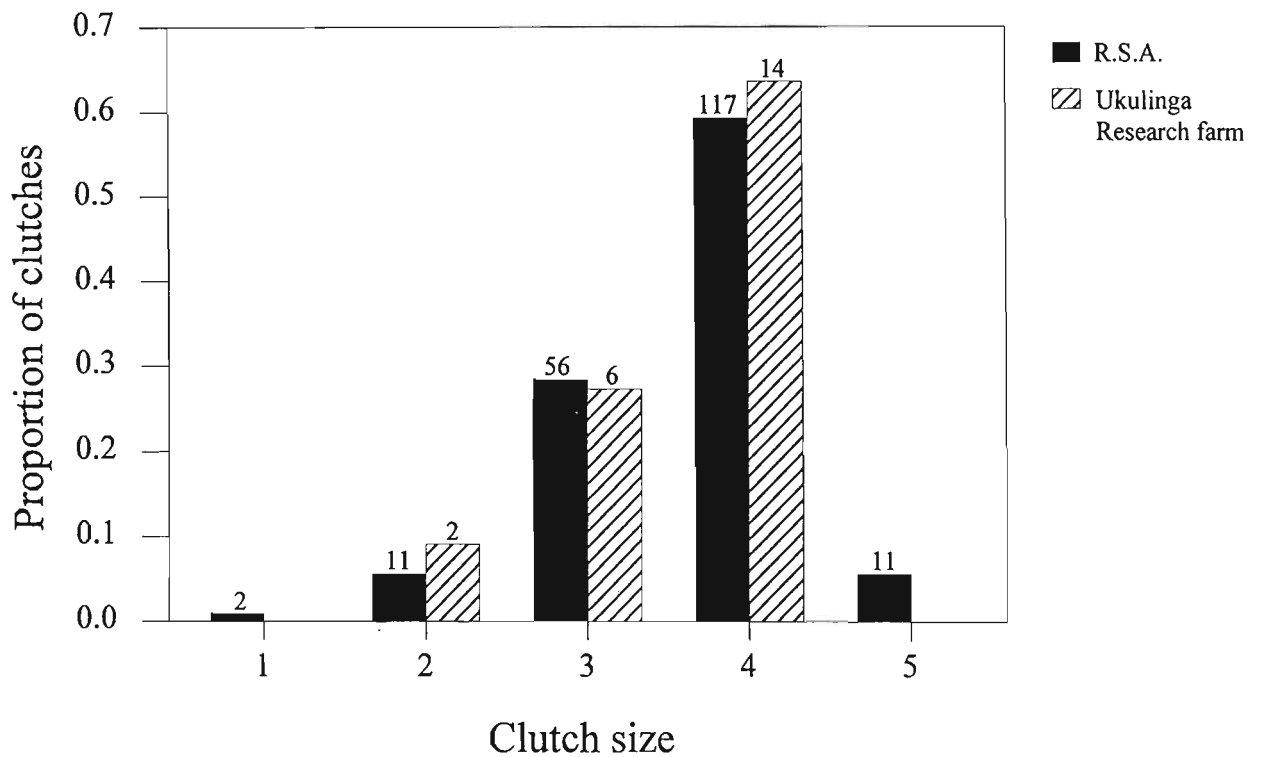


Figure 2.9. Completed clutch sizes of fiscal shrikes in South Africa (ZA) (197 records), and a population at Ukulinga Research Farm (22 records). Data for South Africa were extracted from Nest record Cards (NERC). There was no significant difference in the distribution of clutch sizes between South Africa and Ukulinga (Kolmogorov-Smirnov two-sample test: $D=0.056$, *NS*).

Clutch size in the Laniinae is variable and ranges from three (MacDonald 1980; Zack 1986) to seven or more eggs per clutch (Cade & Swem 1995). Most of this variation appears to be a function of latitude (Fig. 2.10). Northern hemisphere species show an increase of one egg for every 16° increase in latitude (Cramp & Perrins 1993). With only two data points for southern hemisphere populations of the Laniidae it is impossible to calculate the difference between clutch size trends in the northern and southern hemispheres. However, the two data points for fiscal shrikes in South Africa lie below the 95% confidence limits for trends in the northern hemisphere, although eight data points from the northern hemisphere also do, but this may suggest that the relationship of clutch size and latitude differs between the northern and southern hemispheres.

The fiscal shrike is host to one brood parasite, the jacobin cuckoo *Clamator jacobinus*. No nests at Ukulinga were parasitized by this or any other species of brood parasite occurring at Ukulinga (e.g. redchested cuckoo *Cuculus solitarius*, diderik cuckoo *Chrysococcyx caprius*, klaas's cuckoo *C. klaas*, greater honeyguide *Indicator indicator*, lesser honeyguide *I. minor*). Brood parasitism was not observed in Ghanaian or Kenyan populations of the fiscal shrike (MacDonald 1980; Zack 1986). Seven out of 902 NERC from South Africa showed that a fiscal shrike nest had been parasitized by the jacobin cuckoo. No other brood parasites were detected. In each case a fiscal nest contained one cuckoo egg, larger and rounder than a fiscal's egg (27.4 mm x 21.6 mm), and non-mimetic (glossy white in colour). Many species of brood parasites (e.g. European cuckoo *Cuculus canorus* (Davies & Brooke 1988)) evict one of their hosts eggs when parasitizing a nest, presumably to reduce the chance of detection by the host. If jacobin cuckoos were not evicting eggs I expected a significant difference between the distribution of parasitized clutch sizes and unparasitized clutch sizes, as parasitized clutches should be on average one egg larger than non parasitized clutches. There was no difference between the distribution of parasitized and unparasitized clutch sizes in the South Africa (Kolmogorov-Smirnov two-sample test: $D=0.322$, *NS*), which would suggest that the jacobin cuckoo is an egg evictor, as stated by Jensen and Jensen (1969). The jacobin cuckoo is not reported to evict it's hosts eggs elsewhere, however, as this and Jensen & Jensen's (1969) analyses are based on NERC, and as jacobin cuckoos lay before host clutch completion (Jensen & Jensen 1969), analyses undoubtedly include incomplete host clutches. This would mask the effects of egg eviction by lowering mean clutch size in parasitized nests. It is also possible that hosts adjust the size of their clutch in response to parasitism or the perceived threat of parasitism (Power et al. 1989).

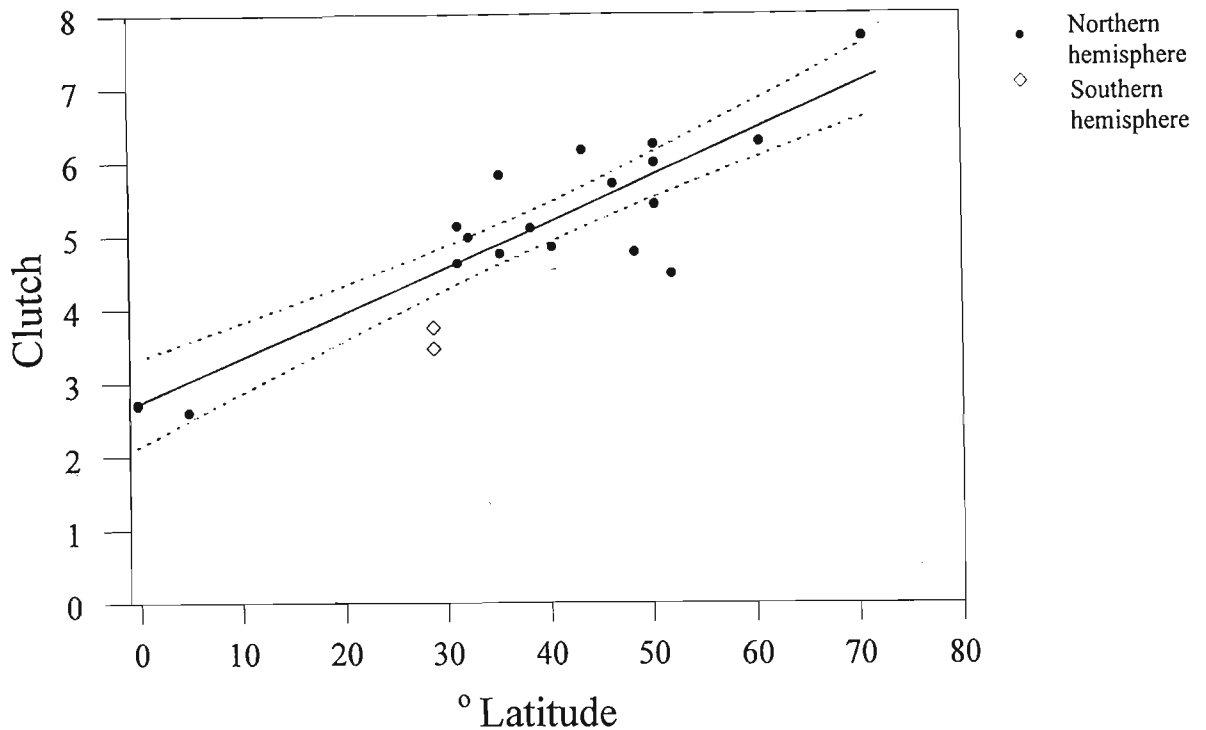


Figure 2.10. Trend in clutch size and latitude for seven members of the Laniinae (21 studies), with regression line (solid) and 95% confidence intervals (dashed) of clutch size for northern hemisphere species overlaid. Clutch size in northern hemisphere Laniinae significantly increased with latitude (Regression: $F_{1,16}=52.8$, $R^2=0.767$, $P<0.001$). Clutch sizes for southern hemisphere studies lay outside the confidence intervals for the northern hemisphere pattern. This suggests that a separate relationship may exist between the two hemispheres, although many of the northern hemisphere studies also lay outside the 95% confidence intervals.

Incubation.

Incubation was performed entirely by female fiscal shrikes at Ukulinga, and females spent a large proportion of their day on the nest ($\bar{X} \pm \text{SE} = 0.802 \pm 0.046$, $N=14$) (Fig. 2.11). Male fiscal shrikes fed incubating females on average 2.5 times per hour ($\bar{X} \pm \text{SE} = 2.45 \pm 0.534$, $N=14$), although females also hunted for themselves. Females solicited feeds with a begging call “naaa” (call 7, Harris 1995) and responded to food by frantically calling and quivering their wings. There was no significant relationship between male feeding rate and the proportion of time a female spent on the nest (Regression: $F_{1,20} = 0.62$, $R^2 = 0.03$, NS), although a positive correlation between incubation rate and male feeding was discovered in Kenyan fiscal shrikes (Zack 1986). Females left their nest for a variety of reasons at Ukulinga, frequently to forage or preen (Fig. 2.12).

The pattern of incubation in passerines may be constrained by the following factors: energetic factors, e.g. male assistance (Moreno 1989; Lyon & Montgomerie 1985; Lozano & Lemon 1995), ambient temperature (Morton & Pereyra 1985), and predation (Weathers & Sullivan 1989). In red-backed shrikes, lesser grey shrikes, great grey shrikes, and woodchat shrikes in the northern hemisphere incubation was performed predominantly by the female, but males have been recorded incubating for short periods (Cramp & Perrins 1993). The higher ambient temperature for fiscal shrikes breeding in South Africa, compared to other Laniinae in the northern hemisphere, might allow females more time off the nest for the same amount of embryonic growth. This allows the female to forage for herself whilst still performing all of the incubation duties so male incubation is unnecessary. Wheatear *Oenanthe oenanthe* incubation periods were constrained by foraging, and could have been shortened if males had fed their incubating partner (Moreno 1989). Various studies have shown a correlation between incubation feeding and the female's incubation behaviour (e.g. Lyon & Montgomerie 1985; Nilsson & Smith 1988). There was a positive correlation between male feeding rate and female attentiveness in pied flycatchers *Ficedula hypoleuca* (Lifjeld & Slagsvold 1986). Marsh tits reduced their incubation period duration when the frequency of incubation feeding was high (Nilsson & Smith 1988). Female snow buntings *Plectrophenax nivalis* that had been widowed at the end of egg laying (i.e. had not received incubation feeding from the male) spent significantly more time off eggs than females that had been widowed when chicks hatched (Lyon & Montgomerie 1985). As a consequence the incubation period was significantly longer in females that had been widowed at the end of egg laying. Furthermore, significantly more females who lacked male incubation feeding lost an egg during incubation which resulted in a

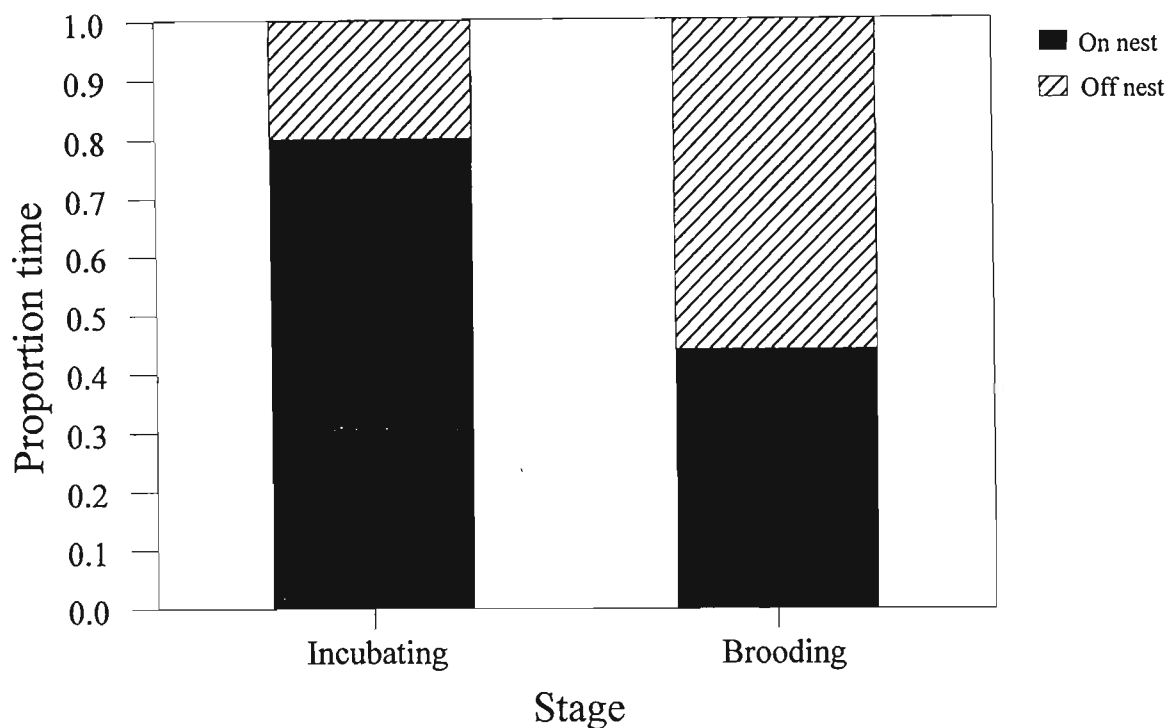


Figure 2.11. Activity budget of incubating and brooding (1-8 day old chicks) female fiscal shrikes at Ukulinga Research Farm. Females spent a significantly larger proportion of their time incubating compared to brooding (ANOVA: $F_{1,20}=18.55$, $P<0.001$). Proportional data were arcsine square-root transformed to normalise.

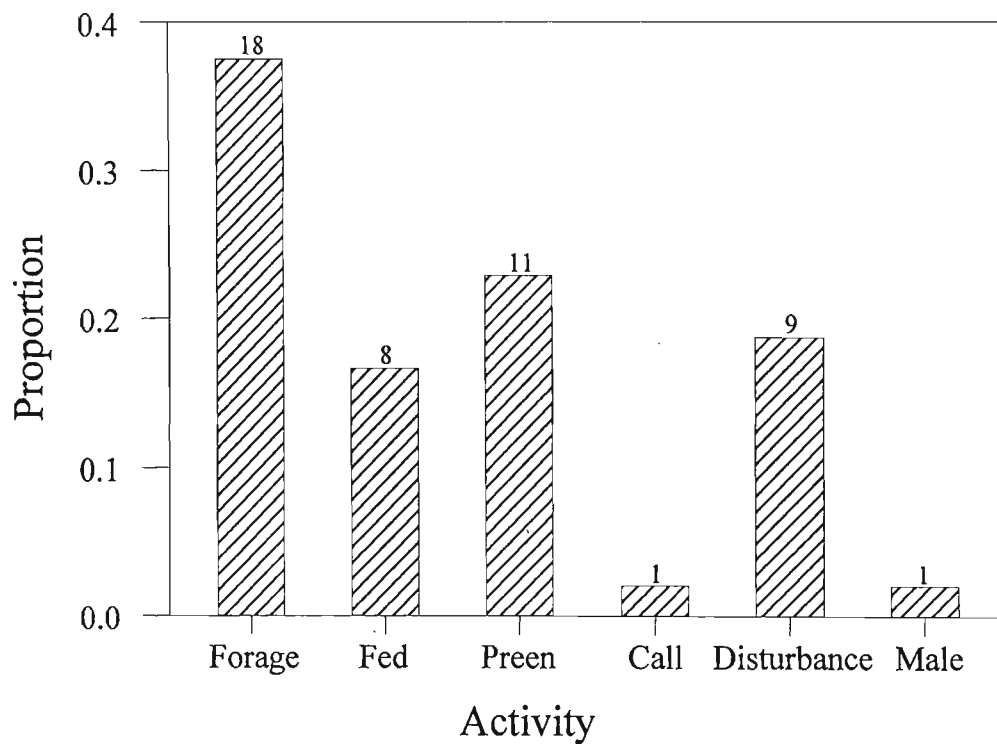


Figure 2.12. Activities for which fiscal shrikes left the nest during incubation and the first eight days of brooding at Ukulinga Research Farm (sample sizes above bars). ‘Forage’ was to hunt for herself or offspring, ‘fed’ was to be fed by her partner, ‘preen’ was to preen and stretch, ‘call’ was to solicit feeds by calling, ‘disturbance’ was in response to human or traffic disturbance, ‘male’ was to allow the male to feed offspring.

lower hatching success.

Female fiscal shrikes spent on average 80% of their time on the nest, but not all of this time was spent incubating eggs. Females shaded eggs and chicks, and this behaviour was significantly related to ambient temperature (ANOVA: $F_{1,20}=20.39$, $P<0.001$) (Fig. 2.13). In hot weather females spent a larger proportion of their time shading eggs and chicks than in cool weather. There was no difference between the proportion of time females shaded when incubating eggs or brooding chicks (ANOVA: $F_{1,10}=0.18$, *NS*). A nest attentiveness of 80% is high for any species of bird, especially for a species where only one sex incubates eggs (Slotow et al. 1995). However, fiscal shrikes construct open cup-shaped nests and place these in exposed positions in trees, often prior to leaf growth, therefore subjecting eggs to high levels of solar radiation. Females could be constrained to spending such large proportions of their time on the nest to prevent eggs from overheating. Shading has been well documented in a variety of species, especially those inhabiting open habitats in arid regions (e.g. crowned plover *Vanellus coronatus*, blackwinged plover *V. melanopterus*, lesser blackwinged plover *V. lugubris* (Ward 1990) and in habitats exposed to intense solar radiation (e.g. high altitude, white-crowned sparrows *Zonotrichia leucophrys oriantha* (Zerba & Morton 1983)). However, I have been unable to find any accounts of shading in the Laniinae. Incubation and shading are important behaviours, in that they prevent eggs from being exposed to lethal extremes of temperature and solar radiation. Egg development is severely restricted below 25°-27°C (White & Kinney 1974) whilst temperatures above 45°C are lethal (Zerba & Morton 1983). Shading by white-crowned sparrows reduced egg temperature to below the lethal level of 45°C, whereas the temperature of eggs exposed to solar radiation exceeded this.

It is possible that female fiscal shrikes stood raised over eggs and chicks in order to regulate their own body temperature (see Downs & Ward 1997). Periods of shading were often accompanied by panting by female fiscal shrikes, presumably to help regulate their own body temperature. White-crowned sparrows also panted when shading eggs (Zerba & Morton 1983). Zebra finches *Poephila guttata* panted and erected their head feathers when incubating at ambient temperatures greater than 40°C, and turned eggs at cooler temperatures (Vleck 1981). Vleck (1981) proposed that Zebra finches adjusted the position of eggs to facilitate the transfer of heat to cold eggs and excess heat away from hot eggs. Female fiscal shrikes turned their eggs on 50% of occasions before incubation resumed after a period of shading in hot weather (12/24 times, $N=3$ females, observed for 192 min).

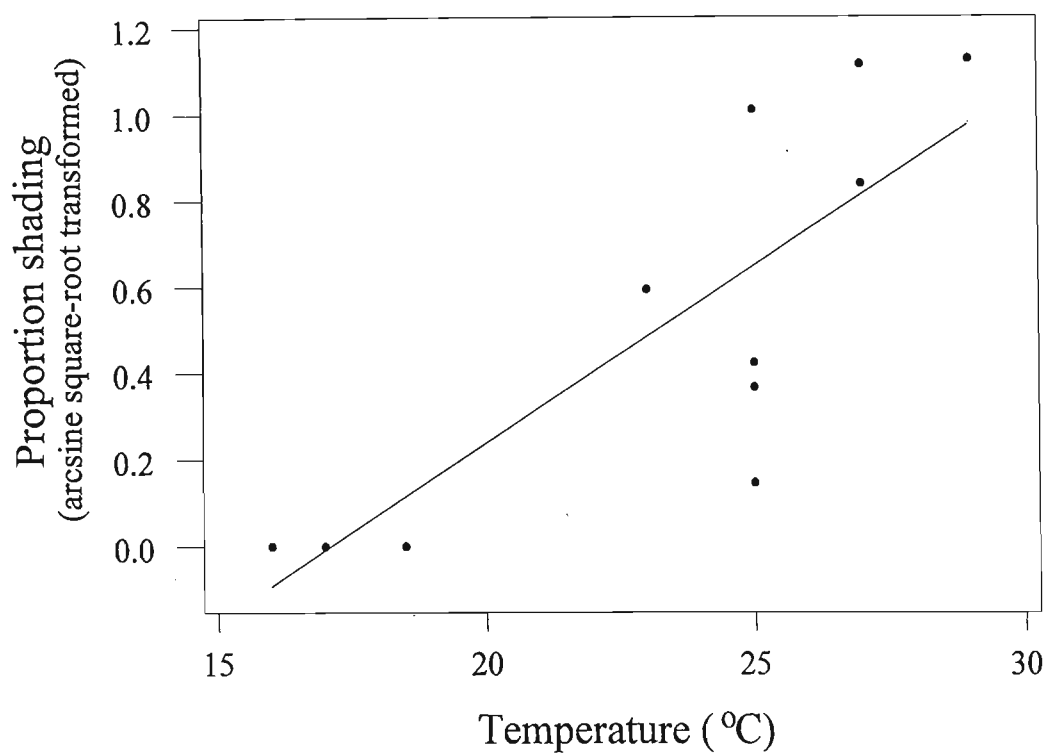


Figure 2.13. Proportion of time female fiscal shrikes shaded eggs and 1-8 day old chicks, out of total time spent on the nest (N=6 females). Proportional data were arcsine square root transformed to normalise. As temperature increased, females spent significantly more time shading (Regression: $F_{1,10}=24.17$, $R^2=0.71$, $P<0.001$).

Hatching.

Fiscal shrike eggs hatched 16 to 19 days after being laid (NERC: $\bar{X} \pm SE = 17.3 \pm 0.198$ days, $N=16$). In most cases eggs hatched over two days (66%), or together (29%), although three records (5%) recorded eggs hatching on consecutive days (NERC, 62 records). Hatching asynchrony is a widespread phenomenon among altricial birds (e.g. Slagsvold 1986). There have been many hypotheses for its evolution, of which three have received much attention and testing. (1) Hatching asynchrony could facilitate brood reduction, thus reducing the chance of total nest failure (Howe 1976). If offspring survivorship declines with offspring age, chicks die off one by one when food is scarce. However, hatching asynchrony was not necessary for brood reduction in the pied flycatcher although it increased parental efficiency (Amundsen & Slagsvold 1991), and was only necessary during periods of food shortage in the American kestrel *Falco sparverius* (Wiebe & Bortolotti 1995). (2) Hatching asynchrony could be an adaptation for nest failure. Species that are subject to high levels of nestling predation should hatch eggs asynchronously and incubation should begin early to reduce the time that some nestlings are in the nest (Slagsvold 1986). (3) It could be a consequence of incubation constraints. Incubation may begin before clutch completion to minimise the mortality of embryos (Arnold et al. 1987), and consequently hatching would occur asynchronously. This egg viability hypothesis (Veiga 1992) has received support from studies on the House sparrow *Passer domesticus* (Veiga & Viñuela 1993). All of the species of shrike for which there is information hatch their eggs asynchronously (Table 2.3).

Fiscal shrikes are altricial and chicks hatched naked and blind, with pink skin and no feathers. Eggs that did not hatch were removed, and egg shell was removed or eaten within a few days of other eggs hatching. One egg shell was found 20m from a nest at Ukulinga, within 24 hours of the egg hatching. Forty eight per cent of eggs laid at Ukulinga hatched ($\bar{X} \pm SE = 1.64 \pm 0.257$ hatched/nest, $N=25$), whereas the hatching success for South Africa (from NERC) was 82% ($\bar{X} \pm SE = 3.04 \pm 0.041$ hatched/nest, $N=490$). However detailed NERC containing data from revisited nests were scarce, which would underestimate the proportion of nests where all eggs failed to hatch. This would result in a bias towards a higher hatching success rate in NERC. Because of this it is preferential to compare NERC results with hatching success of successful nests at Ukulinga (i.e. nests that were successful in hatching at least one chick). Hatching success for successful nests at Ukulinga was closer to hatching success for NERC ($\bar{X} \pm SE = 2.41 \pm 0.173$ hatched/nest, $N=17$).

Table 2.3. Incubation and brooding parameters for some of the Laniinae.

Species	Region	Initiation ^a	Incubation length	Hatching Synchrony	Sex of incubator/ brooder	Brooding length
<i>Lanius collurio</i> ^b	Western palaeartic	before	14 days	asynchronous	female	14-15 days
<i>Lanius minor</i> ^b	Western palaeartic	before	15-16 days	asynchronous	female	16-18 days
<i>Lanius excubitor</i> ^b	Western palaeartic	before	15-17 days	asynchronous	female	15-18 days
<i>Lanius senator</i> ^b	Western palaeartic	before	14-15 days	no information	female	15-20 days
<i>Lanius nubicus</i> ^b	Western palaeartic	after	14-15 days	no information	no information	18-20 days
<i>Lanius collaris</i> ^c	Equatorial Africa	no information	13-14 days	no information	one sex only ^d	16-17 days
<i>Lanius collaris</i> ^e	South Africa	before	16-19 days	asynchronous	female	15-20 days

^a incubation initiation relative to clutch completion.

^b information collated from Cramp & Perrins (1993).

^c Zack (1986).

^d sexes indistinguishable but only one parent ever incubated.

^e this study.

At Ukulinga fiscal shrikes laid on average 3.4 eggs but only hatched 1.6 eggs, and in South Africa (NERC) laid 3.7 eggs but only hatched 3.0 eggs. Therefore fiscal shrikes laid one or two eggs more than they hatched. This may be an insurance policy against egg infertility. Three eggs out of 15 laid by a captive pair of *L. c. humeralis* were infertile (Azua & Lieberman 1995). Several species of eagles laid clutches of two eggs but very rarely reared both young (Meyburg 1974; Gargett 1978). If both eggs hatch the larger chick may kill its sibling, although egg infertility in eagles can be high and as many as 10% of eggs fail to hatch (Godfrey et al. 1991). It is unlikely that partial clutches of fiscal shrike eggs were lost to predation as MacDonald (1980) and Zack (1986) found nest failure was always complete.

Incubation length and initiation relative to egg-laying can be inferred from hatching data. Eggs hatched over two days in two thirds of nests (NERC) inferring that incubation began before clutch completion. This was observed at Ukulinga, where incubation often began when the penultimate egg was laid. Eggs hatched on average 17.3 days after being laid, which would imply that in most cases incubation lasted (date began to date first egg hatched) 15.3 days. This agrees with Winterbottom (1988) and Skead (1943), but is significantly lower than reported by Brooke's (1958) analysis of Rhodesian (Zimbabwean) NERC. The incubation period of *L. c. humeralis* in the tropics (13-14 days) was shorter than *L. c. vigilans* in KwaZulu-Natal (Zack 1986), which was predicted by the environmental variability and predictability hypotheses. Incubation parameters of some Laniinae are shown in Table 2.3. Four of the five species initiated incubation before clutch completion, and the hatching pattern of all species for which there were data was asynchronous. Incubation in European-breeding *Lanius* lasted 14-17 days, longer than for equatorial congeners.

Brooding.

As with incubation, the task of brooding chicks was only performed by female fiscal shrikes. The proportion of time a female spent on the nest when brooding chicks was significantly less than when incubating eggs (ANOVA: $F_{1,20}=20.39$, $P<0.001$) (Fig. 2.11). This might have been a consequence of either increased foraging demands or reduced thermoregulatory requirements of chicks as opposed to eggs. Females shaded their chicks, and the proportion of time they shaded chicks was no different to the proportion of time they shaded eggs (ANOVA: $F_{1,20}=0.18$, *NS*) (Fig. 2.13).

Brooding females were fed by their partner and foraged for themselves. Both males and females fed their offspring, although during the first few days after hatching males usually fed via their partner rather than directly. There was no difference between allofeeding rates during incubation and the first week of brooding (ANOVA: $F_{1,20}=0.04$, *NS*). Young fiscal shrikes responded to the presence of a parent (either visual or tactile) by begging frantically. One week after hatching young uttered a “naaa” begging call (call 7, Harris 1995), like that described above for the female. Both parents removed faecal sacs from their brood after feeding, which were usually eaten although sometimes discarded.

By 15 days of age young fiscal shrikes were fully feathered. Their plumage was brown and barred, although signs of the adult pattern were present. Fifteen to 20 days after hatching they left the nest (NERC: $\bar{X} \pm SE = 17.7 \pm 0.263$, $N=20$), although they usually remained within the nest tree for a few days. During this period they responded to perceived danger by becoming motionless. The length of the brooding period of fiscal shrikes in South Africa agrees with Skead (1943) and Marshall and Cooper (1969). As predicted by latitude/photoperiod and by environmental variability hypotheses the brooding duration in Kenya was shorter than in South Africa and lasted 16-17 days (Zack 1986). In European-breeding shrikes brooding was always performed by the female, and like the fiscal shrike lasted 15-20 days (Table 2.3).

Forty per cent of chicks at Ukulinga survived to fledge ($\bar{X} \pm SE = 0.684 \pm 0.214$ fledglings per nest, $N=25$), compared to 63% of chicks in South Africa ($\bar{X} \pm SE = 1.94 \pm 0.075$ fledglings per nest, $N=156$). Again, statistics derived from NERC data must be viewed with caution as a bias for smaller numbers of fledgling might have occurred because of the difficulty in locating fledglings once they had left the nest, and cases where no chicks fledged would be under-represented. Successful nests at Ukulinga (those that fledged at least on chick) fledged up to three chicks ($\bar{X} \pm SE = 2.13 \pm 0.227$ chicks).

For the first month after fledging young fiscals followed their parents from tree to tree begging incessantly. Within a month of fledging they attempted to forage, although they were still fed by their parents albeit at a reduced rate. Juvenile fiscal shrikes remained on their KwaZulu-Natal territory for three or more months after fledging, even when parents attempted to double brood, but were driven off before moulting into adult plumage.

Male activity.

Male fiscal shrikes had an active role in breeding. They contributed from building nests, though nuptial feeding, to post-fledgling care, and the importance of male courtship and incubation feeding has already been discussed. The proportion of a male's time spent performing sexual activities significantly reduced from courtship to post-courtship (ANOVA: $F_{1,34}=10.96$, $P<0.01$ (Bonferoni adjusted due to unplanned post hoc analysis)) (Fig. 2.14). There were no other significant changes in the proportion of time spent on any other activity. Territorial behaviour was exhibited throughout the breeding season, and continued throughout the year (Chapter 3).

Breeding success.

Sixty five per cent (17 out of 26 nests) of nests at Ukulinga were unsuccessful at fledging any offspring, and sixteen fledglings were produced in the seven successful nests. The causes of failure in fifteen nests were adverse weather (40%), predation (53%), and parents abandoning a second clutch whilst still raising their first fledged clutch (7%). Hatching and fledging success of fiscal shrikes in Zimbabwe and South Africa were similar. The clutch survival hypothesis predicts that nest losses are higher in unpredictable environments, and that predictability increases from the equator to the poles. There was a large degree of variation in parameters of success in the Laniinae (Table 2.4), both within a species and between species. Hatching success varied from 27% (*L. collaris*, Kenya) (Zack 1986) to 95% (*L. collurio*, U.K.) (Cramp & Perrins 1993), fledging success varied from 10% (*L. collaris*, Kenya) (*L. collaris*, Kenya) to 88% (*L. ludovicianus*, USA) (Gawlick & Bildestein 1991; Azua & Lieberman 1995), and the number of chicks fledged per successful nest varied from one (*L. collaris*, Kenya) (Zack 1986) to 4.7 (*L. ludovicianus*, S. Carolina) (Gawlick & Bildestein 1991). Therefore, nest success increases with increasing latitude.

Predation by crows (Corvidae), rodents, and snakes, was the main factor in 65 nesting failures of the red-backed shrike in England (38%), followed by egg collection (20%), and infertility, adverse weather and disturbance (11%) (Cramp & Perrins 1993). The cause of failure in 28% of nests was unknown. In another study, 72% per cent of red-backed shrike nest failures were due to predation, eight per cent to human disturbance, and 20% to climatic factors (Cramp & Perrins 1993). The lesser grey shrike had poor breeding success in Europe and nests were lost to predation, disturbance, and adverse weather, the same factors implicated in nest failure in the woodchat shrike (Cramp & Perrins 1993).

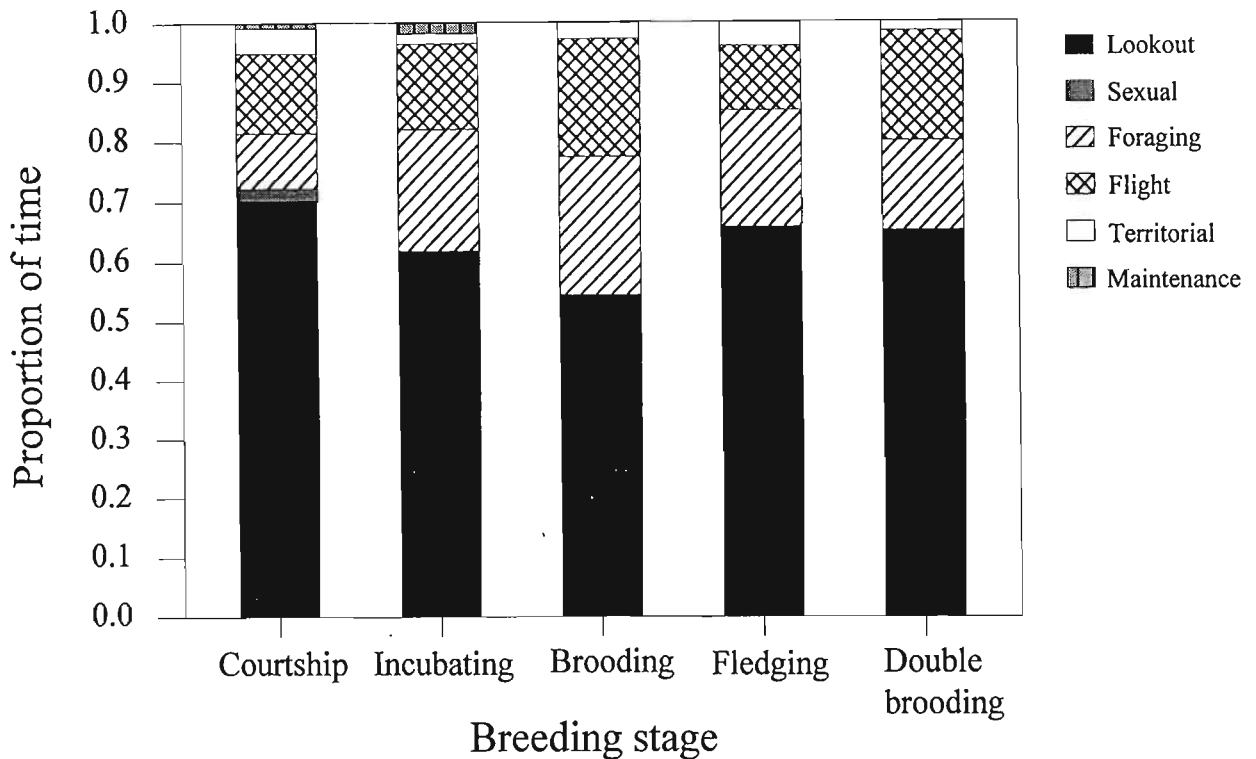


Figure 2.14. Activity budget of breeding male fiscal shrikes at Ukulinga Research Farm. The proportion of time spent performing sexual activities significantly declined from courtship to post courtship (ANOVA: $F_{1,34}=10.96$, $P<0.001$ (Bonferroni adjusted due to unplanned post-hoc comparison)). Activity was described as 'Lookout' when a male scanned for prey, 'Sexual' when copulating, courtship feeding and nest-building, 'Foraging' when hunting, feeding and caching, 'Flight' when flying, 'Territorial' when pursuing intruders or advertising by singing, and 'Maintenance' when preening or stretching.

Table 2.4. Breeding success rates of the Laniinae.

Species	Country	Hatching success	Fledging success	Breeding success	# fledged/ successful nest
<i>Lanius collaris</i>	South Africa ^a	48%	48%	23%	2.13
	Zimbabwe ^b	42%	56%	24%	1.75
	Kenya ^c	83%	10%	8%	1
	Ghana ^d	27%	60%	16%	*
<i>Lanius</i>	S. Carolina ^e	95%	88%	84%	4.7
<i>ludovicianus</i>	San Diego ^{f,g}	25%	88%	22%	1.75
<i>Lanius collurio</i>	U.K. ^h	95%	87%	83%	4.1
	France ^{h,i}	62% ^e	54%	35%	4.2
<i>Lanius excubitor</i>	Spain ^h	67%	49%	33%	*
<i>Lanius senator</i>	Germany ^j	69%	42%	29%	3.4
	Czecho- slovakia ^h	58%	50%	29%	2.4

^a this study

^b Marshall & Cooper (1969)

^c Zack (1986)

^d MacDonald (1980)

^e Gawlick & Bildstein (1990)

^f Azua & Lieberman (1995)

^g captive reared

^h Cramp & Perrins (1993)

ⁱ percentage of eggs which hatched and survived to 6-9 days of age.

^j Ullrich (1971)

* data missing or in a form unable to be presented.

The effects of physical characteristics of the territory and nest placement on breeding success were investigated using log-linear analysis. Variables were categorised as nest success (A), nest height (B), nest exposure (C), nest placement (D), and territory size (E) (Table 2.5). There was no significant effect of territory size on success, either as a first order effect, or as a first or second order interaction, so territory size was dropped from the analysis.

Factors were introduced into the baseline model [A][BCD] in a hierarchical manner. Factors that had a significant effect have a ΔL^2 probability of less than 0.05. Full results are summarised in Table 2.6. There was no significant effect of nest height on nest success [AB], of nest exposure on nest success [AC], or of nest placement on nest success. The only significant interaction of factors affecting nest success in the fiscal shrike at Ukulinga was the interaction of nest height and nest exposure [ABC] on nest success. Exposed, high nests, and concealed, low nests were less successful than other nests (Fig. 2.15). During the night of 18th October 1995 10.2 mm of rain fell at Ukulinga, and the following night a further 40.6 mm of rain was recorded. A systematic search for nests on the morning of 20th October revealed that two nests (one with eggs, one with chicks) had been washed out of trees, and two nests (one with chicks, one with eggs) were undamaged. The nests that had been lost were situated at branch ends in tall trees and were exposed (mean exposure=50%). These nests had become waterlogged, and the small twigs and branches on which they were placed had been unable to support them in the tree. The two surviving nests were placed in small bushes in a fork of the trunk and were less exposed (mean exposure=25%). High, exposed nests were less successful, possibly because they were more prone to adverse climatic conditions. In total, five tall exposed nests were lost to adverse weather, one to predation, and the cause of the failure of the seventh was not known. Two nests were built low to the ground in short trees and were concealed. Both of these failed to hatch any chicks. One nest was lost to predation whilst the other was lost to adverse weather.

Table 2.5. Criteria used for categorisation of breeding data for log-linear modelling. Cut-off points for continuously distributed data were chosen based on means (normally distributed data) or medians (not normally distributed data), plus behavioural observations.

Variable	Category 1	Category 2
Breeding success	unsuccessful	successful
Nest height	low (≤ 1.8 m above ground)	high (> 1.8 m above ground)
Nest exposure	concealed ($\leq 40\%$ visible)	exposed ($> 40\%$ visible)
Nest placement	centre (centre $\frac{1}{5}$ of canopy)	periphery (outer $\frac{4}{5}$ of canopy)
Territory size	small (≤ 2 Ha)	large (> 2 Ha)

Table 2.6. Log linear analysis of the effects of nest height (B), nest exposure (C), and nest placement (D) on nest success in fiscal shrikes (success at raising offspring) (A). These factors form the baseline model [A][BCD]. Alternative models were contrasted with the baseline model by subtracting L^2 for the alternative model from L^2 of the baseline model (ΔL^2).

Baseline model = [A][BCD]: $L^2=11.686$, $DF=7$, $P=0.1114$					
Alternative model	Effect	ΔL^2	DF^a	P^b	R^2^c
[AB][BCD]	Nest height on nest success	0.872	1	NS	0.075
[AC][BCD]	Nest exposure on nest success	0.000	1	NS	0.000
[AD][BCD]	Nest placement on nest success	2.440	1	NS	0.209
[ABC][BCD]	Interaction of nest height and exposure on nest success	6.554	1	$P<0.05$	0.972
[ACD][BCD]	Interaction of nest exposure and nest placement on nest success	1.016	1	NS	0.498
[ABD][BCD]	Interaction of nest height and nest placement on nest success	0.795	1	NS	0.480

^a $DF=DF$ baseline model - DF alternative model.

^b P is calculated by ΔL^2 at DF under χ^2 distribution.

^c R^2 , which gives a comparison between alternative models, was calculated from the following equation (Knocke & Burke 1980):

$$R^2 = \frac{L^2 \text{ baseline model} - L^2 \text{ alternative model}}{L^2 \text{ baseline model}}$$

Note that R^2 values do not sum to 1.

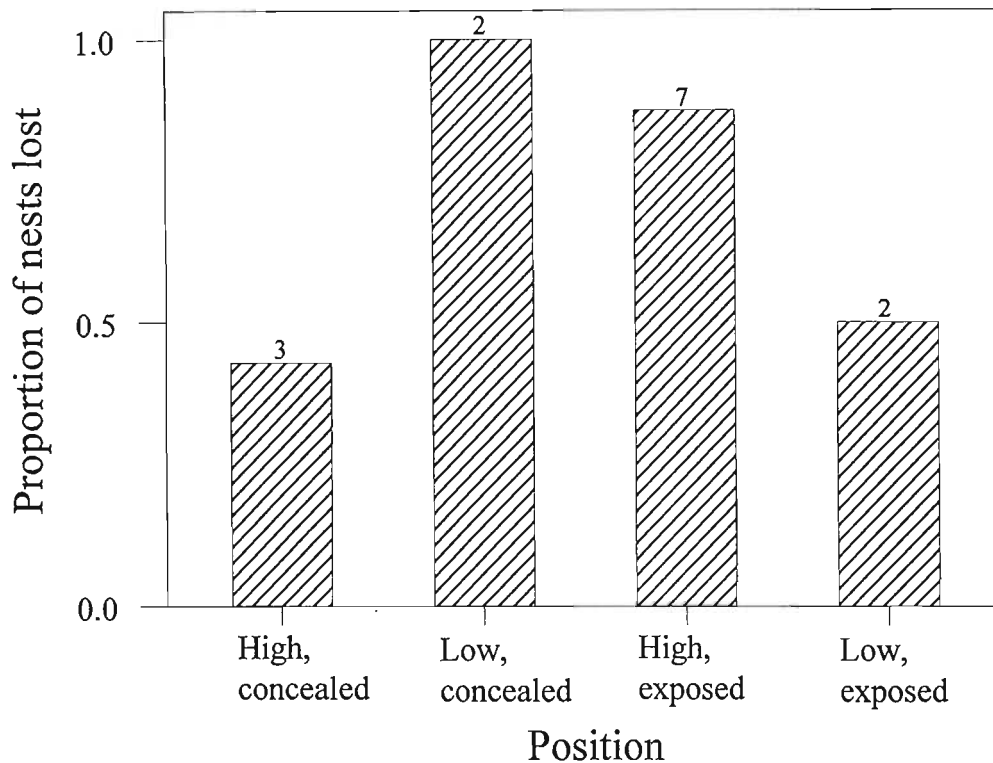


Figure 2.15. The effect of nest height and exposure on nest loss for fiscal shrikes at Ukulinga Research Farm. Numbers above bars indicate sample sizes. Significantly more high, exposed nests and low, concealed nests were lost compared to other nests (Log-Linear analysis: $\Delta L^2=6.55$, $DF=1$, $P<0.05$). High, exposed nests were prone to high winds and rain (5/7 losses). High nests were those greater than 1.8 m above ground level and low nests were classified as equal to or below 1.8 m above ground level. Nests were classified as exposed if they were more than 40% visible laterally, and concealed if they were equal to or less than 40% visible laterally.

Factors affecting life history traits.

General discussion.

Patterns of life history strategies in birds differ with latitude. Clutch size tends to be smaller at the equator than at higher latitudes (Moreau 1944; Lack 1948; Klomp 1970; Ricklefs 1980; Kulesza 1990) and the length of the breeding season decreases with increasing latitude (Ricklefs 1980). The trends in clutch size have been well documented in the northern hemisphere, where an increase of three eggs per clutch has been documented for every 18°-30° increase from the equator where birds lay two or three eggs per clutch (Klomp 1970). However, in the southern hemisphere in Australia clutch size increased by 0.8 eggs every 30° increase in latitude (Yom-Tov 1987). Clutch size in Laniinae of the northern hemisphere increased by one egg for every 16° increase in latitude (1.9 eggs per 30° increase in latitude) (This study). Fiscal shrikes laid clutches of on average four eggs in South Africa, one egg larger than populations 30° north at the equator (MacDonald 1980; Zack 1986). There was no difference in clutch size between northern and southern regions of South Africa, as predicted by trends observed in the northern hemisphere. This demonstrates that latitude alone does not determine the pattern of clutch sizes in the Laniinae. The length of the breeding season of fiscal shrikes decreased from the equator to South Africa. The possible factors driving life history strategies can be applied to the trends in life history strategies and latitude, and evidence for each will be evaluated with reference to the fiscal shrike.

The photoperiod.

The availability of food for parent birds to feed their offspring is a direct consequence of the productivity of the environment, which in turn is proportional to the photoperiod and latitude. Lack (1947, 1948) hypothesised that clutch size in birds allows the maximum number of young to survive, and in altricial species the limiting factor in clutch size is the parent's ability to feed offspring. In productive environments with a long photoperiod parents are able to forage for longer periods and thereby obtain food for a larger clutch than birds foraging in an environment where the photoperiod is short. Manipulative experiments have shown that many species produce smaller clutches than they are able to raise (Finke et al. 1987; Briskie & Sealy 1989; Ydenberg & Bertram 1989; Godfray et al. 1991). In addition, future reproductive success (Røskaft 1985; Hegner & Wingfield 1987; Sanz & Moreno 1995), survival of the parents (Nur 1988) or offspring (Cronmiller & Thompson 1980) can be affected if birds produce the maximum number of young per clutch. Therefore Lack's original hypothesis might be

applicable for species producing one clutch in a lifetime, but must be modified to include future reproductive success and survival for those that produce more than one clutch. Manipulations on clutch size in fiscal shrikes have not been performed in either the tropics or South Africa, so it is impossible to evaluate Lack's (1947, 1948) clutch size hypothesis in this manner.

However, as the ability of parent birds to feed their offspring can be limited by the photoperiod which is equal in the northern and southern hemispheres there should be no difference in clutch size trends of the Laniinae in either hemisphere. This study has shown that clutch size differs between northern and southern hemisphere species of birds, and therefore contradicts Lack's hypothesis.

Temperature and precipitation variability.

Clutch size may vary in relation to the abundance of resources at the most limiting time of the year (Ashmole 1963). In most species populations are regulated during the winter months when resources are low, and clutch sizes are determined by resources available during the breeding season relative to population density (Ricklefs 1980). Ricklefs (1980) tested this hypothesis by comparing geographical variation in clutch size with seasonal variation in the environment. Clutch size was inversely related to winter conditions, but independent of conditions in the summer, and clutch size was a direct consequence of population density during the breeding season. Ashmole's (1963) hypothesis as formulated by Ricklefs (1980) relies on environmental variability as the key to understanding clutch size variation in birds. Non-migratory populations, or those that do not suffer severe winters, should have a greater survivorship than those that do. As a consequence there should be stronger competition from conspecifics for resources during the breeding season due to greater numbers (Ricklefs 1980). Hence, non-migratory populations or those in favourable climates would be capable of feeding fewer young and compensate by laying smaller clutches.

Another theory concerning nest success and clutch size variation is the "bad year effect", which attributes reduced clutch size to year-to-year variability in conditions for chick survival (Boyce & Perrins 1987). The geometric mean of fitness is often more appropriate than the arithmetic mean of fitness amongst years when fitness varies through time (Gillespie 1977). When there is a large variation in reproductive success individuals laying large clutches may have a lower geometric mean fitness, as the geometric mean decreases as the variance increases. Great tits that laid large clutches were affected by poor survival years far more than those which laid smaller clutches (Boyce & Perrins 1987), and in a variable environment this could have

selected for smaller clutches than the most productive clutch size.

Annual temperature and photoperiod patterns in equatorial climates are less variable than in southern Africa, so adult survivorship should be greater nearer the equator and clutch sizes smaller. Although clutch sizes should be smaller in equatorial populations overall productivity need not be less than temperate populations as breeding seasons should be longer (Ricklefs 1980). Clutch size of fiscal shrikes increased from the equator to South Africa, and with latitude in northern hemisphere Laniidae. Furthermore, it would appear that clutch size increased more rapidly in the northern hemisphere than the southern hemisphere, which is an indication that shrike clutch sizes are adapting to annual variation in temperature and precipitation patterns. The breeding season of fiscal shrike populations in South Africa was five months, and in Kenya and Ghana was eight months (Macdonald 1980; Zack 1986). Breeding season length declines with increasing latitude in northern hemisphere *Lanius*, such that populations of the great grey shrike breeding in Alaska had only six weeks in which to reproduce each year (Cade & Swem 1995).

The permanent territories held by pairs of fiscal shrikes in South Africa were larger than those held in equatorial Africa. This could be a response to increased variability in resource levels due to the more variable temperature and rainfall patterns of South Africa. In the northern hemisphere where temperature and precipitation fluctuations are greater, most populations migrated to lower latitudes to escape the harsh winters. Those that remained held much larger territories than did fiscal shrikes in South Africa.

In conclusion, variability in temperature and rainfall patterns can successfully predict the relationship between clutch size, territory strategy, and breeding season length in the Laniidae, and can account for differences in these between the northern and southern hemispheres.

Predation.

Predation was first proposed as a factor controlling clutch size by Skutch (1949) and has since gained much support (Ricklefs 1970; Martin 1993; Lima 1987). Increased nest predation may select for reduced clutch size so that energy reserves could be maintained for future nesting attempts (Skutch 1949). Slagsvold (1982) evaluated the advantages of producing smaller clutches in regions where predation levels were high, and produced the following results: smaller clutches needed smaller nests, which needed less energy to complete, attracted fewer

predators, had shorter egg-laying and nestling periods, and better fed offspring that called less and required fewer forays, and therefore attracted fewer predators. The reserves that had been saved by producing a smaller clutch, added to the faster production rate, would leave more time and energy for future reproductive efforts. Predation is known to have different effects on different stages of the life cycle (Law 1979; Reznick et al. 1990). If predation acted on adults causing low adult survival, natural selection should favour early maturation and high reproductive effort, whereas if predation acted primarily on juvenile survival, selection should favour late maturation and a low reproductive effort. Guppies that had been exposed to high adult predation levels were moved to an area where predation acted on juvenile survival (Reznick et al. 1990). Eleven years later the life history strategy of the population had changed to delayed adult maturation and the production of smaller brood sizes with larger offspring. When clutch size in nidicolous birds was modelled, increased predation and increased adult survivorship were found to reduce optimal clutch size, whereas increased food supplies increased optimal clutch size (Lima 1987). Furthermore, predation as the sole cost of reproduction was adequate for the existence of an optimal clutch size.

Nest success of fiscal shrikes in Ghana varied between 10-17% and 58% of losses were due to predation (MacDonald 1980). In Kenya nest success was 15% and although no data were given most losses were attributed to predation. At Ukulinga, South Africa, 35% of nests were successful, and predation accounted for 53% of losses. Nest loss is therefore greater in South Africa than near the equator, but predation levels appear to be similar. The predation hypothesis states that clutch size should be greater where predation levels are lower, and so does not adequately describe the patterns of clutch size in southern hemisphere fiscal shrikes.

Clutch survival hypothesis.

Although predation levels were similar in populations near the equator and in South Africa, overall clutch losses were greater near the equator. According to the clutch survival hypothesis that I outlined in the introduction, clutch survival could drive a reduction in clutch size. Incorporation of northern temperate species of the Laniinae into these analyses strengthens the relationship between clutch size and the incidence of clutch survival.

The clutch survival hypotheses predicts that incubation and brooding durations should decrease when nest loss is high. Brooding and incubation durations increased with increasing latitude in the fiscal shrike. As predation levels were similar between the tropics and southern temperate

zones, the predation hypothesis again fails to adequately describe the pattern of decreased incubation and brooding durations with decreased latitude. However, extension of the hypothesis to include all forms of nest loss predicts the observed trend in the southern hemisphere.

In summary, a trend exists between life history traits and latitude, but as the extent of these patterns differs between the northern and southern hemisphere, latitude cannot be the sole driving force behind the relationship and instead is a consequence of actual selective processes such as the photoperiod. As shrikes are able to raise more than one brood in their lifetime, Lack's original hypothesis on clutch size may not apply, although this was not tested by experimental manipulations on clutch size in the fiscal shrike. However, the disparity between life history strategies in the two hemispheres provides evidence that Lack's hypothesis does not apply to the Laniidae or to other species, as the photoperiod (productivity), which limits parental foraging and hence clutch size, does not differ between the northern and southern hemispheres. The variability in annual patterns of temperature and rainfall adequately described the trends observed in clutch size, territorial strategy, and breeding season duration. Predation alone could not account for the variation in clutch size or incubation and brooding durations in populations of fiscal shrikes occupying different latitudes. However, when all nest losses were considered (i.e. the clutch survival hypothesis), the increase in clutch size and incubation and brooding durations were explained. In reality the determination of patterns of life history traits is complex, and undoubtedly relies on more than one consideration. Environmental variability and the occurrence of severe climatic events probably combine in their influence on the pattern of life history strategies with latitude in birds .

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CHAPTER 3: TERRITORIALITY IN THE FISCAL SHRIKE: PERCHES ARE THE LIMITING RESOURCE.

ABSTRACT.

Fiscal shrikes *Lanius collaris* held territories as pairs and individuals throughout the year in grassland and bushveld habitats at Ukulinga Research Farm, South Africa. They used visual and vocal territorial signals to maintain boundaries, counter-singing to the playback of local song, and actively chased conspecific intruders. Interspecific aggression was displayed towards similar sized and smaller birds approximately once every 2 h, and was more frequent than intraspecific aggression. Fiscal shrikes displayed a high level of tolerance to human-induced land changes, and 98% of territories at Ukulinga encompassed either roads, buildings or fence lines. Unlike most animals, which employ territorial strategies to protect food or reproductive resources, fiscal shrikes defended the resource of perch sites. Perch sites were important determinants of territory size in that they allowed otherwise unused areas of the territory to be foraged in. Territory size was inversely proportional to the density of tall trees, which were used as perches for locating prey. Territories contracted when perch density was artificially increased and expanded when perch density was reduced. The addition of artificial perches into suitable habitats may be a valuable conservation tool for declining shrike populations by increasing territory density, and thus, increasing population size.

INTRODUCTION.

A territory is an area defended from conspecifics (Davies & Houston 1984; Stamps 1994), and functions to allow the owner exclusive access to some critical resource within it (Brown 1964; Krebs & Davies 1993). The resource that is defended varies from species to species. For example spotted hyaenas *Crocuta crocuta* in the Serengeti hold territories to protect limited den sites (Hoffer & East 1993); male fallow deer *Dama dama* defend lekking territories to obtain matings from females (Langbein & Thirgood 1989); and European badgers *Meles meles* defend discrete patches of *Lumbricus* prey (Kruuk & Parish 1982). The concept of the economic defendability of a resource (Brown 1964) is influenced by the following three factors: (1) resource quality and spatial distribution, (2) resource temporal distribution, and (3) competition for the resource (Davies & Houston 1984). Territoriality is favoured when resources are of a high quality and are clumped temporally and spatially as individuals can monopolise the resource by holding territories (Davies & Houston 1984). As resources are usually limiting, competition can be high. Differences in the competitive ability of individuals (e.g. because of age or size) will lead to the adoption of alternative territorial strategies (e.g. defended core areas with shared home range, floaters) or varying territory sizes within a population (Davies & Houston 1984). Territoriality will be employed only when its benefits are greater than its costs (Brown 1964).

The benefits of territorial defence are usually assumed to involve exclusive access to a limited resource, although territorial spacing might itself be a benefit if territoriality is also affected by predation or parasitism (Stamps 1994). Costs are usually measured in terms of the behaviour patterns used to defend and maintain the territory (Stamps 1994). Territorial maintenance can take the form of acoustic signalling (e.g. singing in birds), olfactory signalling (e.g. scent marking), visual signalling (e.g. flight displays, colour) and boundary patrols, all of which reduce the time available to perform other activities and may be energetically costly to perform. The removal of intruders can be costly, not just in terms of time loss, but also in terms of injury and mortality.

The benefits of territorial defence outweigh the costs in golden-winged sunbirds *Nectarinia reichenowi* defending a food source. Although territorial defence requires three times more energy than foraging, individuals make an energetic profit when they defended territories containing *Leotonis* flowers (Gill & Wolf 1975). Nectar levels are higher in territories than in

surrounding areas because territorial defence excludes other nectar consumers, reducing nectar depletion, and this is sufficient to outweigh the costs of defence. Energy demands are satisfied more quickly in territories and spare time is spent conserving energy by perching.

Territory size is not always static, but can vary with resource abundance. Rufous hummingbirds *Selasphorus rufus* establish and defend feeding territories along their summer southward migration route, and adjust territory size daily in relation to flower abundance. Birds defend larger territories when flowers are less abundant (Carpenter et al. 1983). The cue used for modifying territory size appears to be weight gain, and territory size is altered to maximise the rate of energy gain (Carpenter et al. 1983). Pied wagtails *Motacilla alba* also hold territories to ensure the renewal of food resources by excluding conspecifics (Davies & Houston 1984). Territorial birds hold linear territories along river banks in southern England, which are walked as a regular circuit to avoid depleting any one area and to harvest insect prey at profitable renewal times (Davies & Houston 1984). However, unlike hummingbirds, pied wagtails do not adjust their territory size in relation to the abundance of resources (Davies & Houston 1984). Instead they adjust their territorial behaviour, becoming non-territorial when resource abundance is low, and allowing a satellite to share the territory when resources are over-abundant. Although sharing a territory reduces the food supply to the owner, the territory holder benefits from halved defence costs. The wagtail's satellite territorial strategy is, in effect, a reduction in territory size (Davies & Houston 1984). However, by maintaining initial territory boundaries wagtails reduce conflict when resource abundance declines, as instead of expanding the territory it evicts the satellite. When resources became super-abundant the territorial strategy is dropped altogether, as further benefits accrued from prey access do not outweigh the exaggerated defence costs from increased competition (Davies & Houston 1984).

There are several hypotheses that attempt to explain the relationship between resource abundance and territory size. (1) The sufficient resource hypothesis (Myers et al. 1979) states that territories function to ensure an adequate supply of resources for the owner. Territory size is adjusted as resources fluctuate, being smaller where resources are greater and vice versa. (2) Alternatively holders could always defend large territories, but territory size could be constrained by competition (Myers et al. 1979), here referred to as the intrusion pressure hypothesis. As resources become more abundant intruder pressure increases. Territories become more costly to defend and as a result reduce in size. It is difficult to separate these two hypotheses as food abundance and intruder pressure usually covary. However, the proximate

cause for a correlation between sanderling *Calidris alba* territory size and the abundance of their prey was intrusion pressure rather than prey density (Myers et al. 1979). Applicable only to facultative polygynous species in which mating opportunities increase with territory size is (3) the polygyny threshold model (MacLean & Seastedt 1979). Females become a limiting resource for male reproductive success, and therefore territory size should be proportional to female abundance.

The true shrikes (genus *Lanius*) are small to medium sized passerines. Shrikes are predatory and carnivorous in habit, feeding mostly on insects, although larger species take small reptiles, mammals and birds (Cramp & Perrins 1993). Shrikes are sit-and-wait foragers and hunt almost exclusively from prominent perches. Most hold breeding territories as pairs, and are usually solitary and territorial outside the breeding season (Cramp & Perrins 1993). Territory size has important implications for shrikes in general. Many of the world's 26 species are in decline, are threatened, or have suffered local extinctions (Yosef 1994; Harris 1998). Loss of suitable wintering or breeding habitats have been implicated as important factors in this decline. As shrikes hunt from perches (e.g. trees, shrubs) and as numbers have declined with changing habitats, perches may be a resource limiting shrike abundance. If territory size is inversely related to resource abundance and resource abundance can be manipulated, then it should be possible to reduce territory size by increasing resource abundance. If perches are a limiting resource this could be achieved by the addition of artificial perches into established territories. As land becomes vacant when territories contract in size, more territories could be established within a given area, thereby increasing the population. This could serve as a possible conservation strategy for diminishing populations.

Fiscal shrikes *Lanius collaris* hold territories throughout the year in South Africa, as individuals and as pairs (Harris & Arnott 1988). They are monogamous and typically hunt from prominent perches such as trees, fence lines, and overhead cables. During an initial descriptive study I noticed that territory size in fiscal shrikes appeared to vary with tree density. After mapping these territories an inverse correlation was observed between territory size and tree density. A correlation is not causal and does not prove that tree density is directly effecting territory size, so in order to test the hypothesis that fiscal shrikes are defending the resource of perch sites I performed an experimental manipulation. I erected artificial perches in fiscal shrike territories where perch sites were limited. According to both the sufficient resource and the intrusion pressure hypotheses, resource abundance is inversely proportional to territory size.

The addition of artificial perches in fiscal shrike territories should reduce territory size, and the removal of perches should increase territory size.

METHODS.

Study area.

Most of this study was performed at Ukulinga Research Farm, 5 km south-east of Pietermaritzburg, South Africa (30°24'E, 29°40'S, elevation 775 m). Ukulinga consisted of Dohne sourveld (Acocks type 44b), characterised by *Acacia karoo*, *A. nilotica* and *A. sieberiana* bushveld, and *Themida triandra* dominated grasslands (Acocks 1988). Most of the land was used for cattle, sheep and goat grazing by animal science and range and forage resources research, with the remainder of the farm partitioned between horticulture, poultry and pig science, plant breeding, crop production, agricultural engineering, and private residences. In addition, three game reserves in KwaZulu-Natal (Weenen Game Reserve (28°48'S, 30°07'E), Itala Game Reserve (27°35'S, 31°07'E), and Hluhluwe-Umfolozi Game Reserve (28°22'S, 32°25'E)) were used as study areas for behavioural experiments. The major habitats in all three reserves were *Acacia* bushveld and grassland, and the reserves were administered for the purpose of conservation and eco-tourism by Natal Parks Board.

Territorial behaviour.

The behaviour of adult fiscal shrikes was monitored with a combination of approximately 15 min and 2 h observation sessions in 1995, and approximately one hour observation sessions in 1996 and 1997 (total session length: $\bar{X} \pm SE = 1.14 \pm 0.11$ h, $N=56$). Fifteen minute sessions focused entirely on the behaviour of males in order to determine activity budgets (see Chapter 2). One and 2 h sessions concentrated on female behaviour although it was usually possible to follow and record the behaviour of both sexes. However, it is possible that the occurrence of territorial behaviour has been underestimated if activity occurred during periods when the other sex was being observed. Males and females were easily discernible in the field as *L. c. vigilans* is sexually dimorphic; the female has chestnut-coloured flanks, and has duller plumage than the male. Birds were observed using 10x25 binoculars from within the territory or near to its boundary. A hide was not necessary for observations as fiscal shrikes were tolerant of humans and quickly habituated to my presence.

All territorial and agonistic behaviour was recorded onto audio cassette and classified as follows: static marking (perching in a prominent location with an upright position and scapulars exposed, without singing, foraging or scanning for prey); territorial song for

advertisement and defence (call types 5 & 11 (Harris 1995)), sometimes accompanied by exaggerated bowing); physical attack (chasing or being chased by a conspecific or heterospecific, occasionally terminating with physical contact).

Fiscal shrikes were subjected to playback experiments in order to establish the existence and intensity of a vocal territorial response to conspecific song, as part of a larger experiment on geographical variation in fiscal shrike song (C. Devereux & R. Slotow, unpublished data). Territorial song for stimulus tapes was elicited from ten male fiscal shrikes at four locations (Ukulinga, Weenen Game Reserve, Itala Game Reserve & Hluhluwe-Umfolozi Game reserve) by broadcasting Gibbon's (1996) fiscal shrike song from a loudspeaker placed inside the territory. Any vocal response was recorded using a Tect UEM83R unidirectional microphone connected to a Sony TC5 cassette recorder. A 30 s burst of each male's response (males: Ukulinga $N=4$, Weenen Game Reserve $N=3$, Itala Game Reserve $N=2$, Hluhluwe-Umfolozi Game Reserve $N=1$) was compiled onto separate playback tapes to the following format:

0-30 s	song
30-60 s	silence
60-90 s	song
90-120 s	silence
120-150 s	song
150-180 s	silence
180-360 s	long silence

A song was classified as the shortest repeated vocal unit, and the 30 s burst of each male's response contained on average 14 songs to increase external validity (i.e. the 30 s burst was not composed of one song looped 14 times). The 360 s (6 min) sequence was repeated four times so the total duration of an experiment was 24 min. The format of short, repeated bursts of song was designed to minimise adverse effects of (ASAB 1998), whilst the interspersed periods of silence allowed quality recording of the subject's response.

The conspecific song of local but non-neighbouring males was broadcast to 15 additional males (Ukulinga $N=7$, Weenen Game Reserve $N=5$, Itala Game Reserve $N=2$, Hluhluwe-Umfolozi Game Reserve $N=1$) between 0700 and 1200 hours from November 1996 to June 1997.

Subjects were chosen when sighted from a road vehicle and playback only occurred if the

subject was not singing on arrival and did not sing during the two minute period before the experiment began. During this time the loudspeaker was placed in an elevated position within 10 m of the vehicle (e.g. on a rock) or on the roof of the vehicle if no such location was available. The number of songs uttered by each male in response to the playback were counted for the duration of the experiment.

Territory mapping.

Fiscal shrike territories were surveyed throughout the year at Ukulinga and were assigned a number for identification purposes. The boundaries of all territories were determined by observing the territory holder for a period of 3 h or more and recording the outermost points defended or hunted from. If the fiscal shrike was inactive or did not use part of its suspected territory during this period the bird was displaced by repeatedly moving towards where it perched, until it turned back on itself at a boundary or was chased from an adjacent territory.

In 1994, 1995 and 1996 territory maps were drawn by hand, by connecting the outermost perches used, and areas were calculated using a grid system of known areas. In 1997 territory boundaries were overlaid onto a 1:2500 map of Ukulinga using landmarks (e.g. fence lines) as references, and digitised and measured using Geographical Information Systems software (Bentley Workstation). Digitised fiscal shrike territories were superimposed onto Ukulinga's vegetation features (estimated) and man-made structures that had previously been mapped by the Department of Agricultural Economics, University of Natal, to assess their effects on territory distribution and size.

For 17 fiscal shrike territories every tree, shrub, forb (>0.5 m above grass height), fence line and overhead cable were mapped by measuring bearings and distances to the object from a known point. All trees and shrubs within 13 of these were identified to the species level where possible, and heights were estimated to the nearest 0.5 m using a metre rule as a guide. The position of every tree and other object used for perching was therefore measured accurately rather than estimated. Densities of woody plants were calculated (overall, and into the following height classes: <1.49 m; 1.50-2.99 m; >3 m) by dividing the number found in a territory by territory size.

Experimental manipulation testing for the effect of perch density on territory size.

In July 1997 ten non-breeding fiscal shrike territories in open habitats at Ukulinga were mapped according to the above methods. Six 3 m high bamboo perches were erected in the centre of each territory, away from other elevated structures and at least 20 m apart from each other. Perches consisted of a bamboo upright (60-120 mm diameter) with two 1.8 m x 9 mm doweling cross-poles secured at 1.75 m and 3 m by garden wire. Perches were attached by wire to a 1.4 m fencing standard sunk 0.5-0.75 m vertically into the ground. The cross-poles were aligned east-west in all territories for another experiment (see Chapter 4). The perches were erected for ten days, after which the boundaries of each territory were mapped and perches were removed from the fencing standard. The utilisation of perches as observation posts was determined during the ten day period by observation, and on perch removal by the presence of faecal accumulation and pellets on and underneath perches. After a further ten days with no additional perches the boundaries of all territories were re-mapped.

Statistical analysis.

Unless otherwise stated all statistical tests are two-tailed with $\alpha=0.05$. Raw data were subjected to the Kolmogorov-Smirnov test for normality (Steele & Torie 1980) prior to further analysis and transformed if necessary for parametric analyses (all transformations are stated). Normally distributed data are described as mean \pm one standard error of the mean ($\bar{X} \pm SE$). Sample sizes are denoted by N . Statistical analyses followed Sokal & Rohlf (1995) or Siegal & Castellan (1988). Linear regression was performed to test for causal relationships between continuously distributed variables. Wilcoxon paired signed-ranks test was employed to compare individuals' behaviour between treatments. Analysis of variance (ANOVA) was used to test for differences amongst sample means. Where ANOVA was appropriate residuals were subjected to Komogorov-Smirnov tests for residual normality, and Barlett's test for homogeneity of variance was performed (Sokal & Rohlf 1995).

The population of fiscal shrikes at Ukulinga was not colour-banded so individual recognition was not possible. This study does not focus on long term territory dynamics, associations, dispersal, or inter-territory movements. It was therefore decided unnecessary to stress individuals by capture and ringing (ASAB 1998). Once incubation began it is unlikely that a pair bond was broken, and pairs are assumed to have remained together for the duration of a

nesting attempt. Therefore, as almost all pairs were observed during the same time periods it is unlikely that any one individual was sampled excessively, reducing the occurrence of pseudoreplication (Hurlbert 1984). The same individual may have been re-sampled in different years by repeated sampling of a territory. However, fiscal shrikes appear to have a large population turnover, in that following fledging some individuals at Ukulinga contained just one parent tending offspring. In Kenya fiscal shrikes are known to divorce following unsuccessful nesting attempts, and 26% of a population of 19 fiscal shrikes changed territory at least once during a two and a half year study (Zack 1986). Furthermore, fiscal shrikes residing in the same territory for more than a year were subject to different climatic and land-use conditions between years (Fig. 1.2, 1.3 & 1.4, Chapter 1).

RESULTS.

Territorial behaviour.

Fiscal shrikes held exclusive territories throughout the year at Ukulinga. Territory boundaries were advertised by static marking and vocal displays. Conspecific intruders were actively chased from the territory, often through adjacent territories, although physical contact was rare. After intrusions both parties perched prominently at the boundary of their respective territories, singing, accompanied by the counter-song of neighbours. On one occasion an adult male intruder landed at the boundary between two pair-held territories during the breeding season and performed an exaggerated bowing display to both pairs, similar to that described for excited great grey shrikes *Lanius excubitor* (Cramp & Perrins 1993). One of the pairs watched for 30 s as the male performed the bowing display to the male and female occupants, after which, initiated by the other male territory holder, both pairs attacked and chased the intruder for 400 m. One pair broke off and returned to their territory where the male sang, whilst the other pair continued the chase, doubling back on themselves and flying a further 550 m before returning to sing.

Territorial song was used by both sexes of fiscal shrikes at Ukulinga, although most frequently by males, in response to actual and perceived intrusion threats, playback, and as an advertisement. Fiscal shrikes responded to the broadcast (playback) of a local non-neighbouring fiscal shrike by counter-singing (Fig. 3.1). Eleven out of 12 males who were exposed to the song responded by singing on average 150 songs ($\bar{X} \pm \text{SE} = 151.0 \pm 37.7$ songs, $N=12$). In addition, the subjects approached the loudspeaker during the playback and two males from Weenen Game Reserve and one from Ukulinga landed on the playback apparatus whilst singing and performed an exaggerated bowing display. Territorial song was exhibited during and outside the breeding season at the four study sites, and subjects responded to playback throughout the period November to June. There was no difference in the intensity of male territorial behaviour during early and late stages in the breeding season (Fig. 2.14, Chapter 2).

Fiscal shrikes were not only aggressive to conspecifics, but also attacked similar-sized and smaller heterospecifics. Twenty-two interspecific and two intraspecific agonistic interactions involving fiscal shrikes were recorded in 27 study sessions (length of session: $\bar{X} \pm \text{SE} = 1.14 \pm 0.11$ h, $N=56$). Fiscal shrikes attacked black-eyed bulbuls *Pyconotus barbatus* significantly

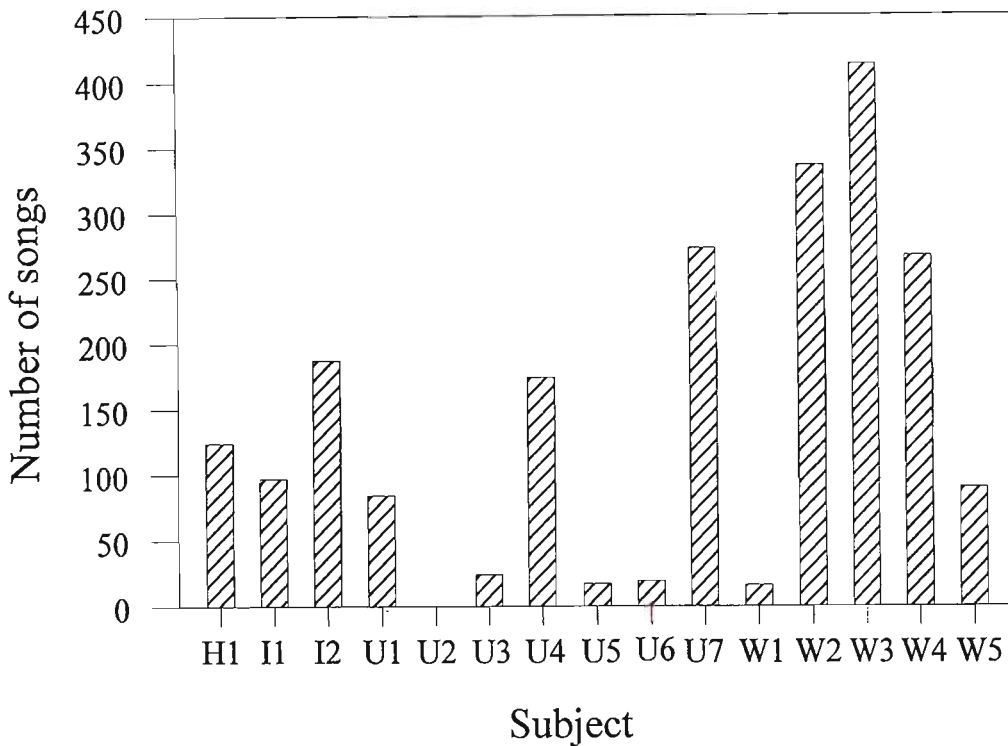


Figure 3.1. The counter-singing response of 15 male fiscal shrikes from four locations in KwaZulu-Natal, in reply to playback of the territorial song of a local, non-neighbouring individual. A song was defined as the shortest repeated vocal unit, and the sum of songs is presented for each 24 minute experimental playback. H=Hluhluwe-Umfolozi Game Reserve, I=Itala Game Reserve, U=Ukulinga Research Farm and W=Weenen Game Reserve.

more often than other fiscal shrikes, yelloweye canaries *Serinus mozambicus*, red bishops *Euplectes orix*, and spotted-backed weavers *Ploceus cucullatus* (G-test: $G_3=22.8$, $P<0.001$) (Fig. 3.2). There was no difference in the outcome (i.e. the probability of winning) between intraspecific and interspecific interactions ($G_1=0.28$, *NS*). However, the sample size of intraspecific interactions is low resulting in low power for this test.

After successful interspecific encounters (i.e. ones in which the fiscal shrike chased its opponent out of the territory) fiscal shrikes usually continued with non-territorial behaviour, whereas after unsuccessful encounters (i.e. ones in which the fiscal shrike was chased by its opponent) fiscal shrikes always performed static and vocal displays (Fig. 3.3). This trend was reversed for intraspecific encounters, and was statistically significant (G-test: $G_1=5.17$, $P<0.05$). However, it lost significance after William's correction was applied (G-test: $G_{adj}=1.99$, *NS*), which again might be a biologically significant result but not statistically significant due to low power.

Territory organisation.

Territories were held by individuals or pairs of fiscal shrikes at Ukulinga, and although boundaries fluctuated slightly the location of territories remained similar throughout the study. Territories were exclusive and did not overlap during or outside the breeding season. Sixty-three fiscal shrike territories were described at Ukulinga in 1997 (Fig. 3.4). Territories ranged in size from 0.27 Ha to 6.31 Ha ($\bar{X} \pm SE = 2.15 \pm 0.16$ Ha, $N=61$) (Fig. 3.5). Not all territories were used for breeding; eleven out of 47 territories for which territory ownership was fully known did not contain a nest during the period 1994-1997 (Fig. 2.1, Chapter 2). Territories that contained a nest during the study are termed breeding territories, and those that did not contain a nest are termed non-breeding territories. Breeding territories were significantly smaller than non-breeding territories (ANOVA: $F_{1,45}=11.37$, $P<0.01$) (Fig. 3.6). In addition breeding territories were occupied throughout the year in all cases ($N=36$), whereas six non-breeding territories (55%) were only occupied during winter periods, four (36%) were occupied throughout the year, and the occupancy of one territory was not known ($N=11$).

Fiscal shrike territories were located around man-made structures as well as in natural habitats at Ukulinga (Fig. 3.7). Buildings and sheds were located in 21 territories, tared roads ran through ten territories, and a further 13 were traversed by a main dirt road. Fence lines intersected 61 territories (97%) (Fig. 3.8). Overall, only one of 63 territories contained no

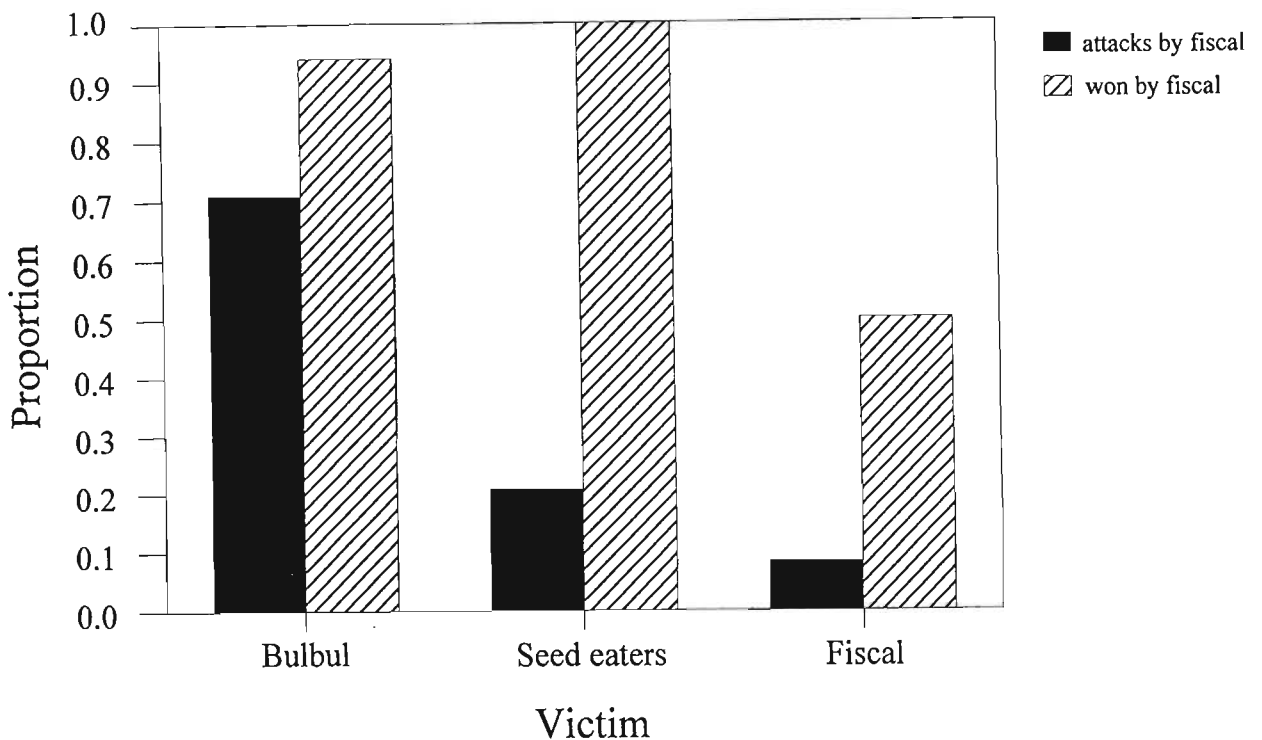


Figure 3.2. Agonistic behaviour of fiscal shrikes. Attacks and chases initiated by fiscal shrikes on conspecifics and heterospecifics during 48 h of observation at Ukulinga Research Farm, and the proportion of attacks and chases in which the initiating fiscal shrike was dominant.

‘Bulbul’=black eyed bulbul *Pyconotus barbatus* ($N=17$); ‘Seed eaters’=yelloweye canary *Serinus mozambicus*, red bishop *Euplectes orix* and spotted-backed weaver *Ploceus cucullatus* ($N=5$); ‘Fiscal’=fiscal shrike *Lanus collaris* ($N=2$).

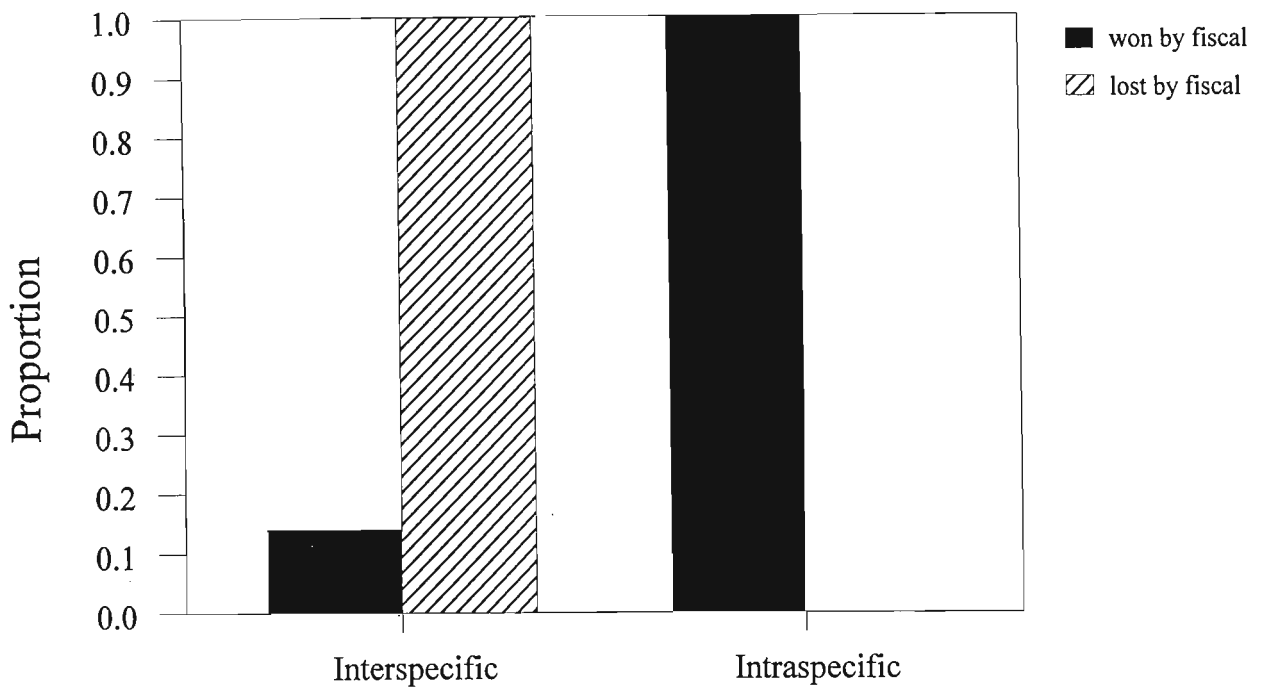


Figure 3.3. Proportion of fiscal shrikes exhibiting territorial behaviour following successful (where the initiator was victorious) and unsuccessful (where the initiator was defeated) interspecific ($N=22$) and intraspecific ($N=2$) agonistic interactions. Territorial behaviour included static marking and singing.

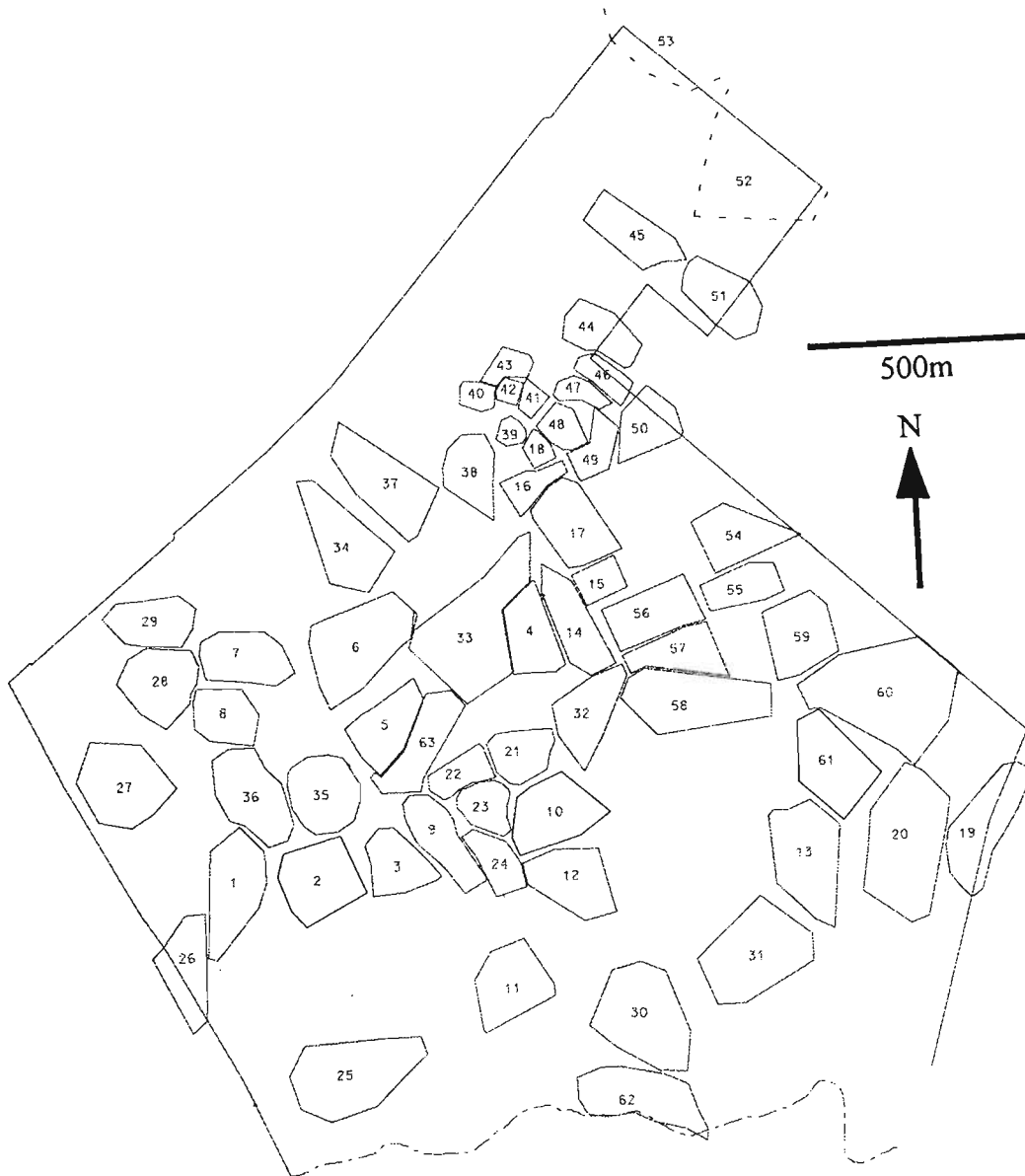


Figure 3.4. Organisation and numbering of fiscal shrike territories at Ukulinga Research Farm. Territories for which all boundaries are known are bounded by a solid line, whereas dotted lines indicate estimated boundaries. The boundaries of fiscal shrike territories were charted between 1994 and 1997. During this period boundaries shifted slightly but locations remained the same. This map represents territory boundaries during July 1997.

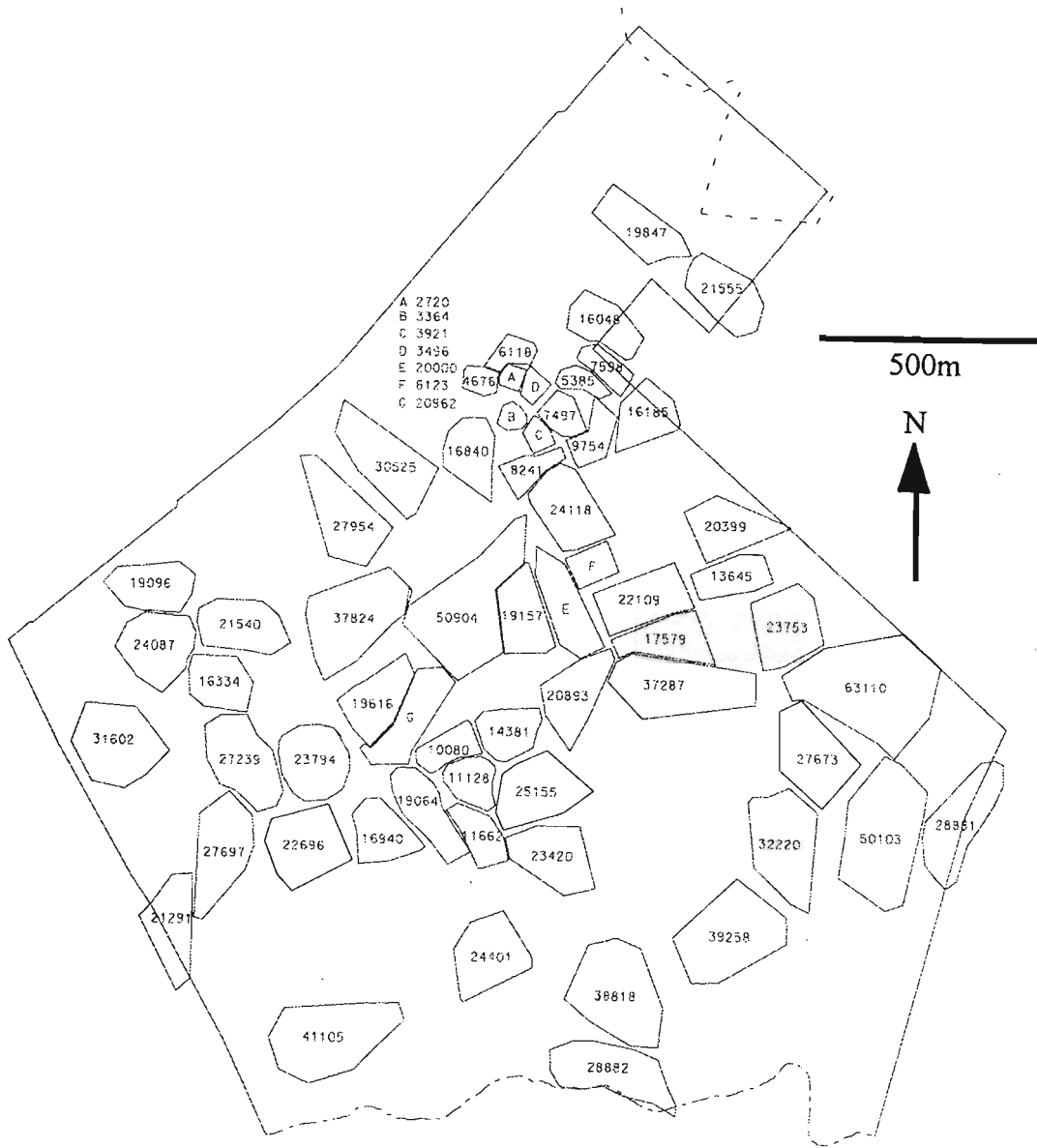


Figure 3.5. Areas (Ha) of fiscal shrike territories at Ukulinga Research Farm during July 1997.

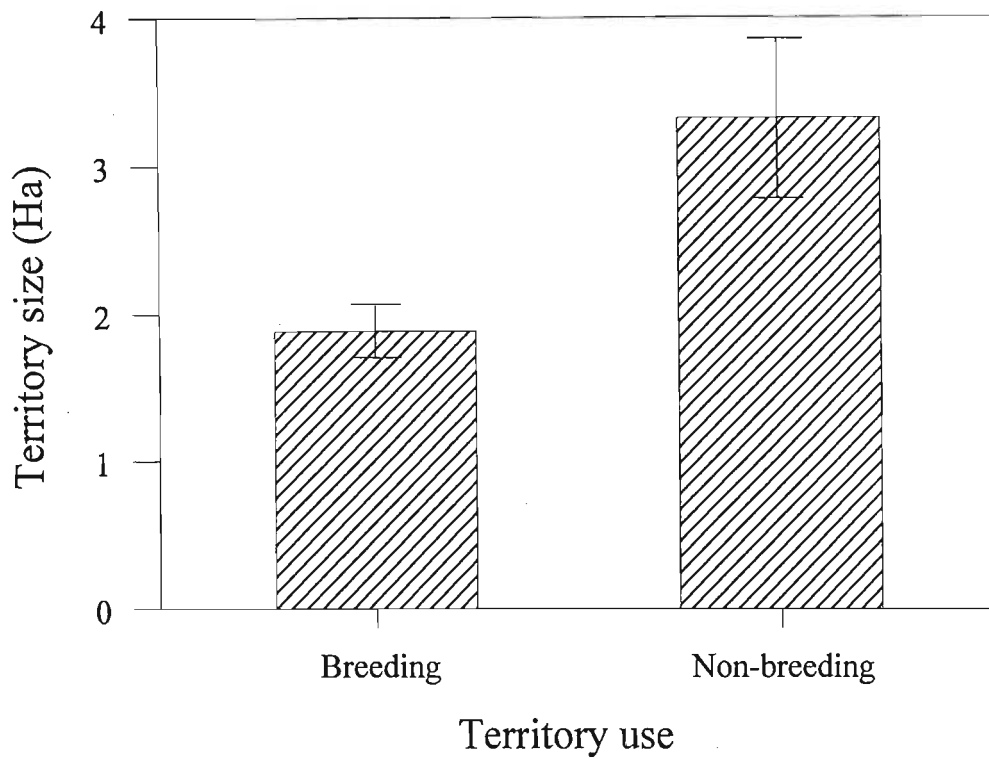


Figure 3.6. Mean area (Ha) of 47 breeding and ten non-breeding territories at Ukulinga Research Farm. Breeding territories were classified as territories that contained one or more nests during the period December 1994-November 1997, whereas non-breeding territories did not contain any nests during this period. Whiskers above and below the bars indicate \pm one standard error of the mean.

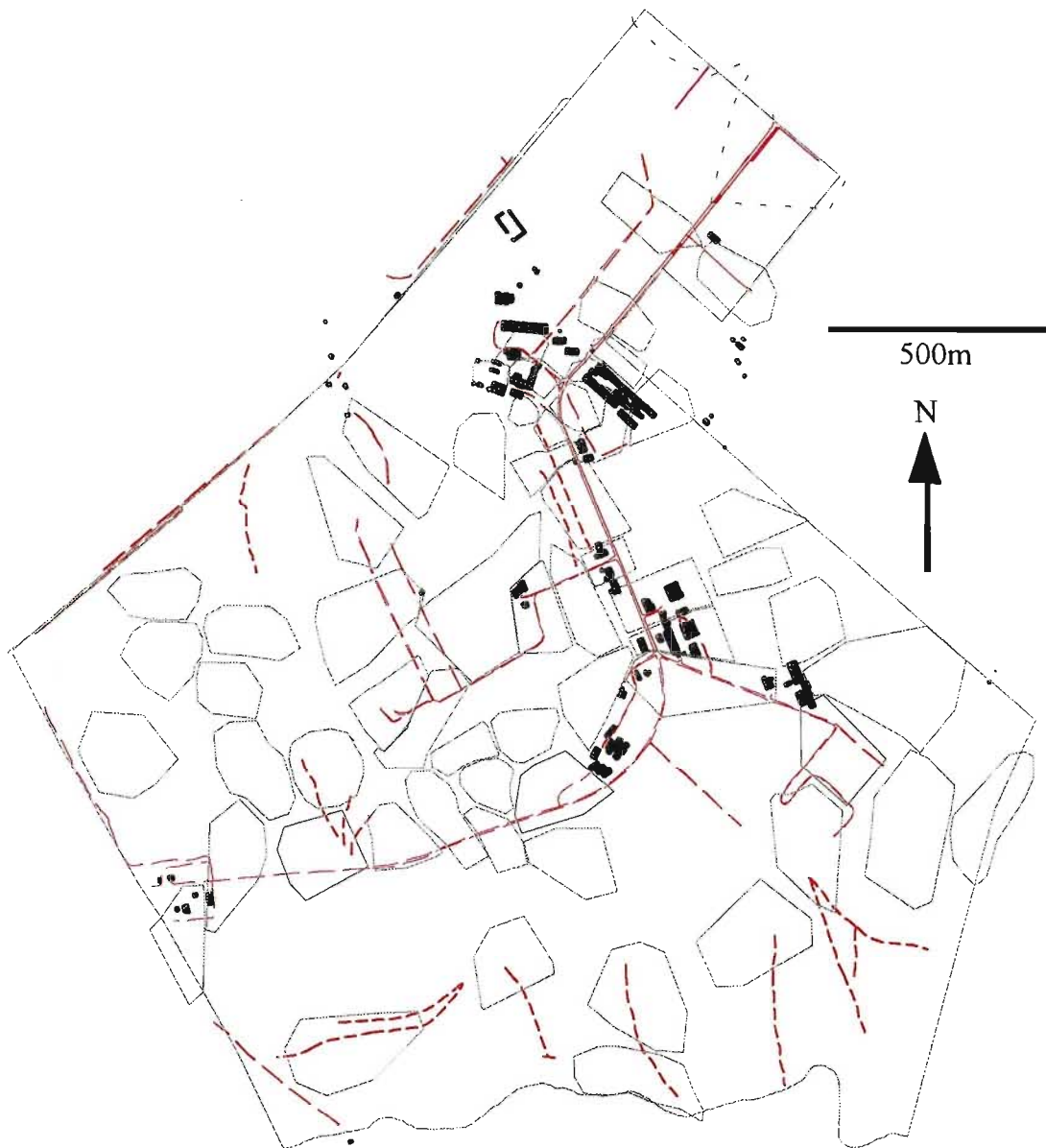


Figure 3.7. Arrangement of fiscal shrike territories at Ukulinga Research Farm during July 1997 in relation to tarred roads (solid red lines), dirt roads, tracks and paths (dashed red lines), and buildings (black polygons). The mapping and digitising of features at Ukulinga was performed by the Department of Agricultural Economics, University of Natal, Pietermaritzburg, South Africa.

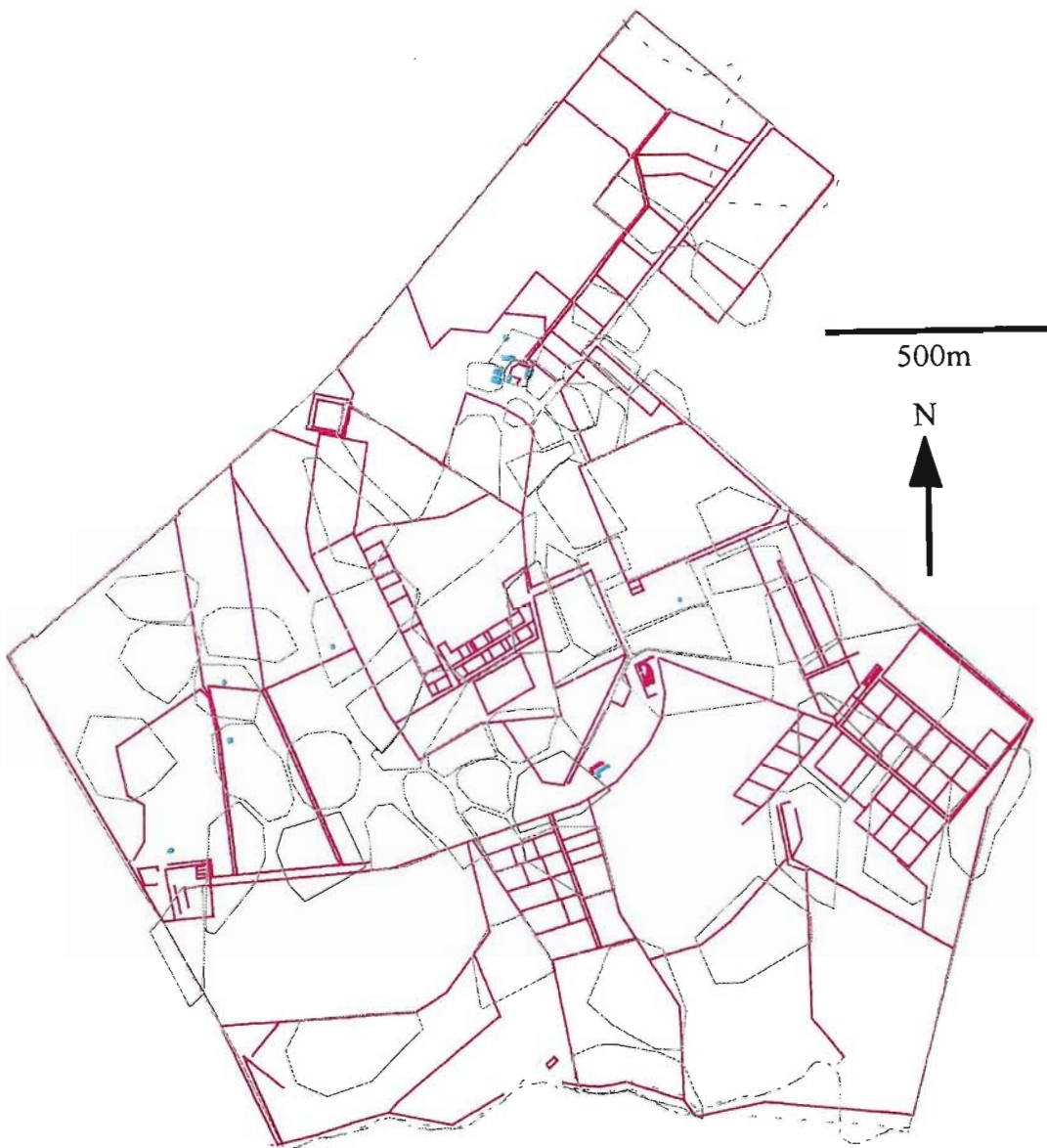


Figure 3.8. Arrangement of fiscal shrike territories at Ukulinga Research Farm during July 1997 in relation to fence lines (pink). Blue areas indicate the position of water troughs. The mapping and digitising of features at Ukulinga was performed by the Department of Agricultural Economics, University of Natal, Pietermaritzburg, South Africa.

roads, buildings, or fence lines (territory 23).

Fiscal shrike territories were not confined to riverine habitats or areas containing open water (Fig. 3.9). Territories were found in areas of grassland with and without scattered trees, and in areas of open and semi-open bush (Fig. 3.9). No territories were located in areas of thick bush where tree densities exceeded 1200/Ha. Territory 60 contained only two trees but was transected by numerous fence lines, whereas the area south of territories 20 and 31 contained slightly more trees, but no fence lines, and was devoid of fiscal shrike territories. Fence lines are therefore a valuable resource and offer alternative observations posts to trees and shrubs. Areas of Ukulinga used for crop, silage and hay production were characterised by very low densities of trees and shrubs. Fiscal shrikes did not hold territories wholly within these areas (Fig. 3.10), although a few territories encompassed small parts of them.

Fifty species of trees and large shrubs were found in mapped fiscal shrike territories at Ukulinga (Table 3.1). Twenty per cent of all trees (by number) were not indigenous to the region, however, these contributed to 28 of the 50 recorded species. Territory size decreased significantly with increasing density of tall trees (>2.99 m) (Regression: $R^2=0.505$, $F_{1,12}=12.24$, $P<0.01$) (Fig. 3.11). Territory 2 (1997) contained a high density of trees for its size due to recent bush encroachment, and this had a large influence on the relationship between the density of all trees and territory size (Table 3.2). When this data point was removed there was a significant relationship between overall tree density and territory size (Regression: $R^2=0.353$, $F_{1,11}=5.99$, $P<0.05$). Large territories contained a lower total density of trees, and a lower density of tall trees, than smaller territories (Table 3.2).

The effects of perch density on territory size.

Artificial perches were erected in ten non-breeding fiscal shrike territories to assess the effects of perch density on territory size. All experimental subjects used the artificial perches (>92% of perches used). Territory size significantly reduced with perch addition (Wilcoxon paired signed ranks test: $T=28$, $N=7$, $P<0.01$); seven territories reduced in size with perch addition and two showed no change (Fig. 3.12). One male vacated his territory after perches were erected and was dropped from the analysis. When perches were removed the seven territories that had decreased in area with perch addition increased to near-former proportions or larger; two again showed no change. Furthermore a new territory was established in the study area. A male fiscal shrike moved into an area vacated by an

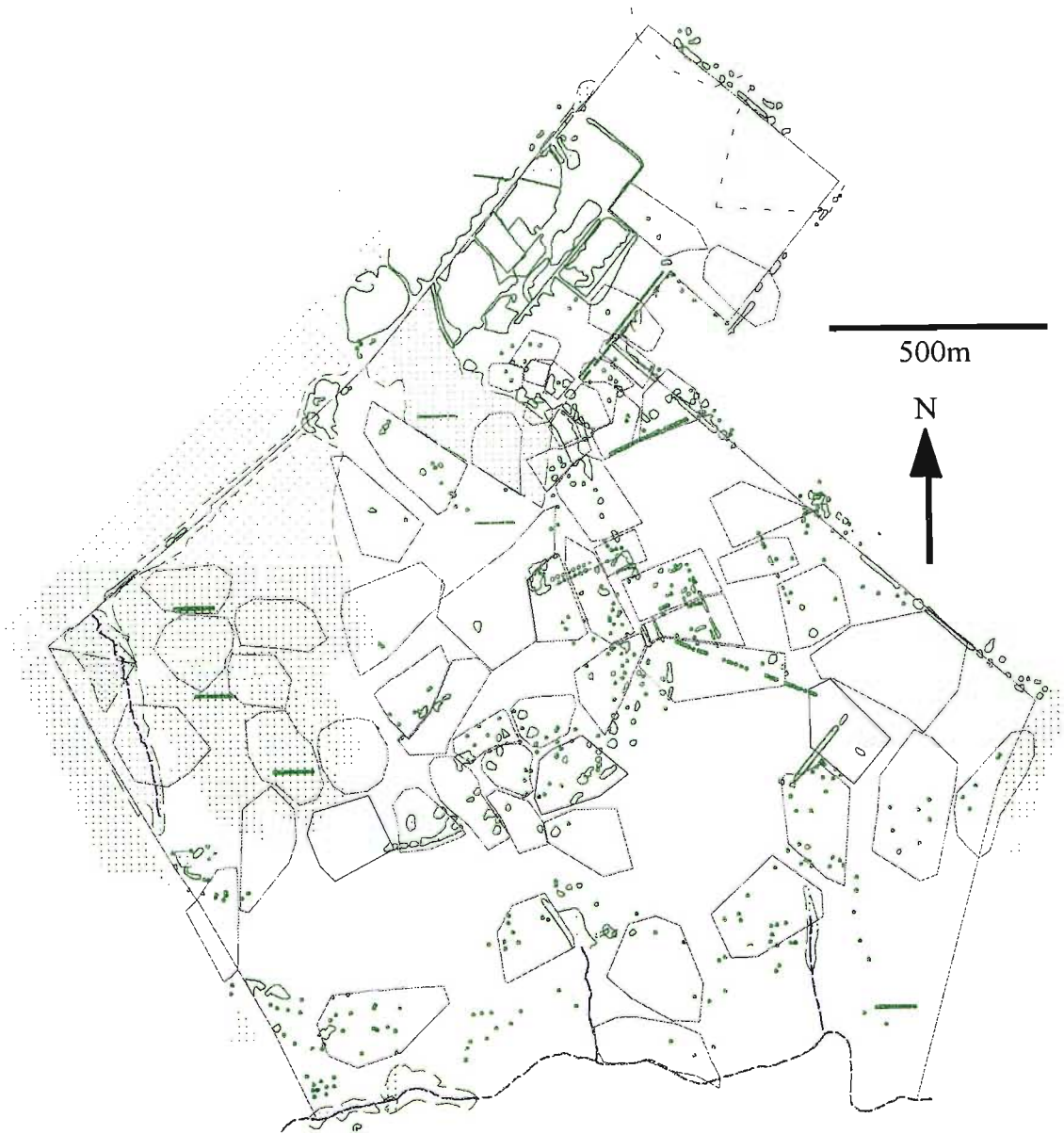


Figure 3.9. Arrangement of fiscal shrike territories at Ukulinga Research Farm during July 1997 in relation to tree and bush density. Green lines indicate the approximate position of scattered trees, light stippling indicates dense bush, and heavy stippling indicates open bush. Rivers and streams are shown as purple dashed lines. Note that the mapping and digitising of features at Ukulinga was performed by the Department of Agricultural Economics, University of Natal, Pietermaritzburg, South Africa, and is approximate. All calculations in this thesis refer to actual measurements and data collected during the fiscal shrike study, and not to these maps.

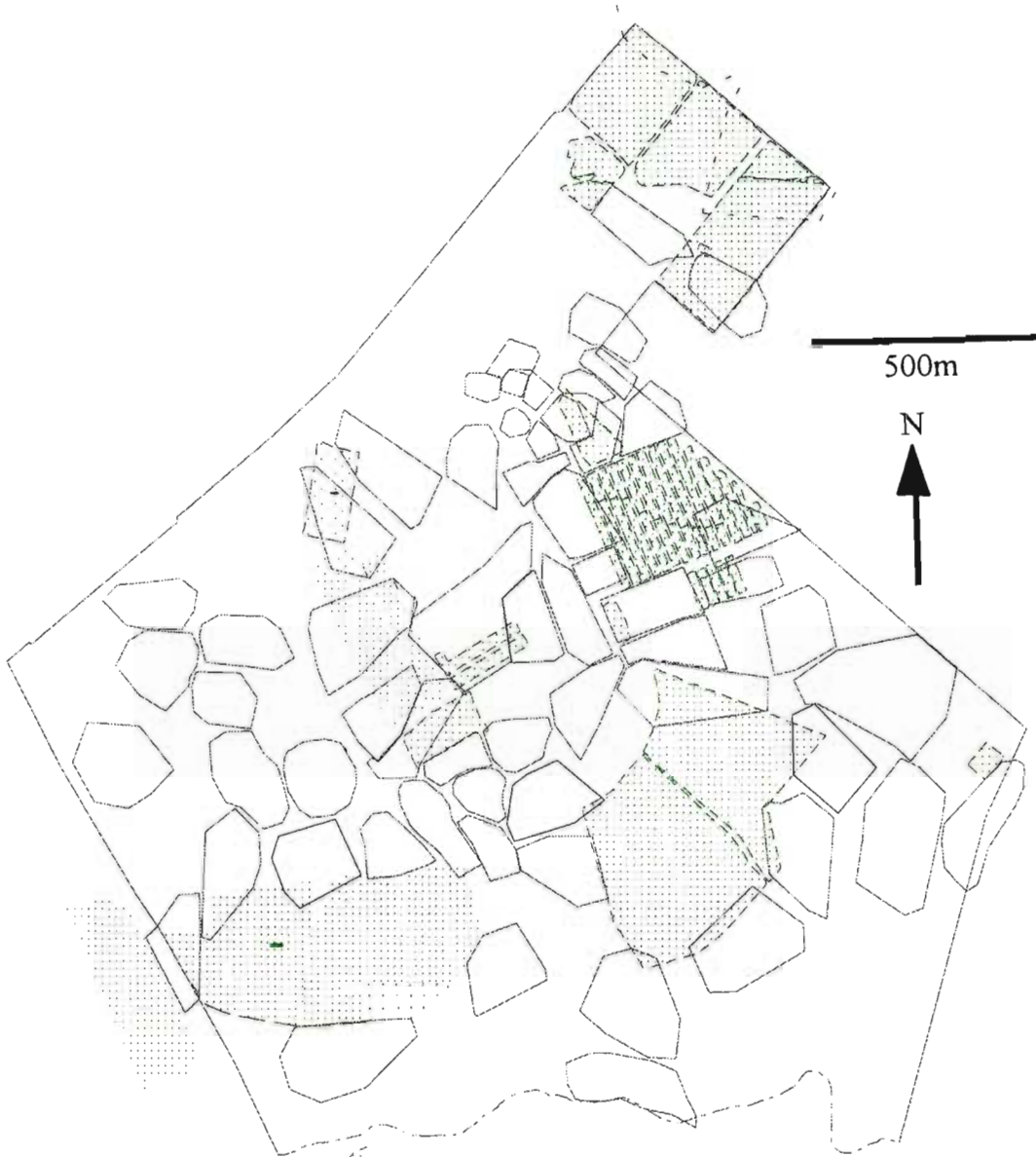


Figure 3.10. Arrangement of fiscal shrike territories at Ukulinga Research Farm during July 1997 in relation to land used for annual crops, hay and silage (green stippling), areas where all trees and bushes had been removed. The mapping and digitising of features at Ukulinga was performed by the Department of Agricultural Economics, University of Natal, Pietermaritzburg, South Africa.

Table 3.1. Names and densities of trees and large shrubs occurring in fiscal shrike territories at Ukulinga Research Farm.

Scientific name	English name	Origin ^a	Number ^b
Five species	Unidentified	exotic	5
<i>Acacia karoo</i>	Sweet thorn	indigenous	3
<i>Acacia mearansii</i>	Black wattle	exotic	59 (3%)
<i>Acacia nilotica</i>	Sweet thorn	indigenous	90 (4%)
<i>Acacia sieberiana</i>	Paperbark tree	indigenous	1581 (71%)
<i>Albizia spp.</i>	Albizia	indigenous	2
<i>Aloe barberai</i>	Tree aloe	indigenous	2
<i>Aloe ferox</i>	Candelabra aloe	indigenous	2
<i>Aracula spp.</i>	Norfolk pine	exotic	4
<i>Bauhenia petersiana</i>	White bauhenia	indigenous	2
<i>Bougainvillea buttiana X^c</i>	Bougainvillea	exotic	12
<i>Brachylaena elliptica</i>	Bitterleaf	indigenous	1
<i>Calodendrum capense</i>	Cape chestnut	indigenous	8
<i>Canthium mundianum</i>	Rock alder	indigenous	13
<i>Carya pecan</i>	Pecan tree	exotic	2
<i>Citrus limon</i>	Lemon tree	exotic	4
<i>Coddia rudis</i>	Small bone apple	indigenous	22 (1%)
<i>Crataegus spp.</i>	Hawthorn	exotic	1
<i>Cussonia spicata</i>	Cabbage tree	indigenous	2
<i>Dalbergia obovata</i>	Climbing flat-bean	indigenous	2
<i>Dichrostachys cinera</i>	Sickle bush	indigenous	9
<i>Eucalyptus spp.</i>	Blue gum	exotic	215 (10%)
<i>Ficus carica</i>	Cultivated fig	exotic	3
<i>Gylitzia</i>	Gylitzia	exotic	9
<i>Jacaranda mimosifolia</i>	Jacaranda	exotic	16
<i>Koelreuteria paniculata</i>	Rainbow tree	exotic	8
<i>Lantana camara</i>	Lantana	exotic	16
<i>Liptona japonica</i>	Fevertea	indigenous	4
<i>Magnolia liliflora X^c</i>	Magnolia	exotic	3
<i>Maytenus heterophyllia</i>	Common spike thorn	indigenous	2
<i>Melia azadarach</i>	Syringa	exotic	18
<i>Morus alba</i>	Mulberry	exotic	11
<i>Olea europea</i>	Olive	indigenous	1
<i>Optunia europea</i>	Prickly pear cactus	exotic	1
<i>Persia americanum</i>	Avocado tree	exotic	1
<i>Phoenix reclinata</i>	Wild date palm	indigenous	2
<i>Pinus spp.</i>	Pine	exotic	20
<i>Podocarpus latifolius</i>	Real yellowwood	indigenous	10
<i>Portulaca afra</i>	Spekboom	indigenous	1
<i>Prunus persica</i>	Peach tree	exotic	2
<i>Quercus robur</i>	Oak	exotic	10
<i>Rhus pentheri</i>	Common crow-berry	indigenous	2
<i>Salix babylonica</i>	Weeping willow	exotic	6
<i>Solanum mauritianum</i>	Bug weed	exotic	24 (1%)
<i>Toona cilata</i>	Cedril / Toon tree	exotic	1
<i>Ziziphus mucronata</i>	Buffalo thorn	indigenous	17

^a Indigenous species are those occurring naturally within KwaZulu-Natal, whereas exotic species are not naturally found in the region or have been brought into the region by Man (e.g. naturalised plantation species, garden shrubs and plants).

^b Number of individuals of the species located in fiscal shrike territories at Ukulinga, and percentage (for species constituting one per cent or more) of total number of individuals.

^c X indicates a hybrid species.

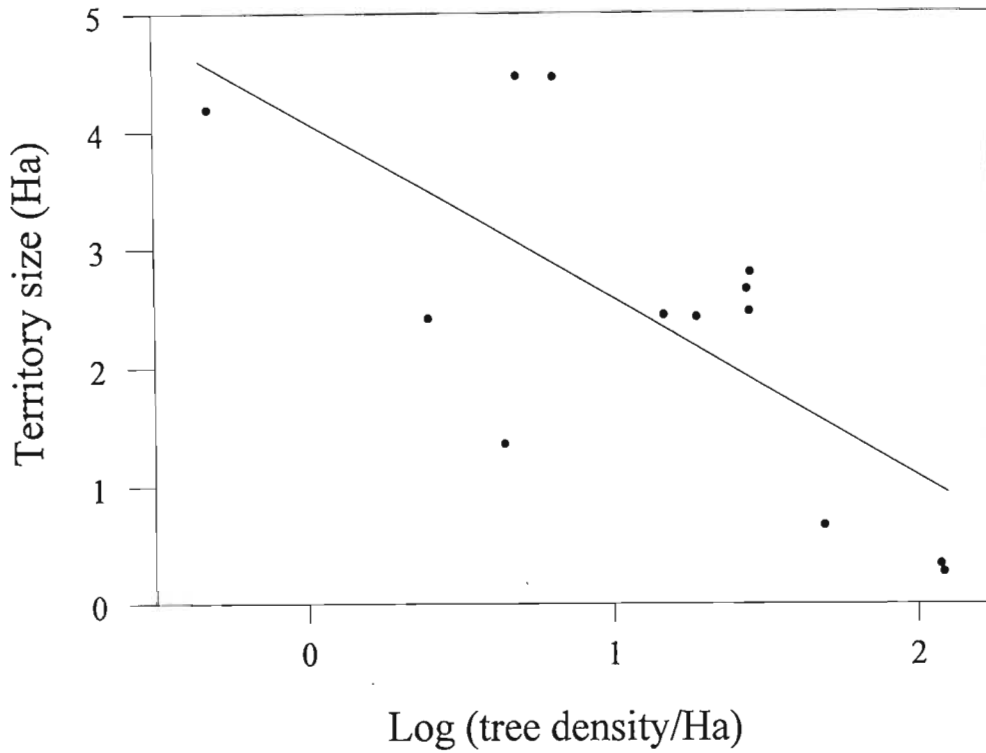


Figure 3.11. Relationship between the density of tall trees (>2.99 m) and territory size of fiscal shrikes at Ukulinga Research Farm. As tall tree density increased, territory size decreased. Tree density was logarithmically transformed to achieve data normality.

Table 3.2. The size of, and density of trees within, 13 fiscal shrike territories at Ukulinga Research Farm.

Territory & Year ^a	Tree height class ^b (m)			Overall # of trees	Overall tree density (Ha)	Territory size (Ha)
	< 1.49	1.49-2.99	> 3			
2 (1995)	157	290	74	521	196.1	2.7
10 (1997)	13	69	70	152	61.6	2.5
13 (1995)	0	3	36	39	41.4	2.4
16 (1995)	0	0	40	40	118.9	0.3
17 (1995)	0	0	33	33	49.3	0.7
17 (1997)	47	126	46	219	90.4	2.4
18 (1995)	0	0	33	33	121.3	0.3
30 (1997)	111	85	29	225	50.4	4.5
33 (1997)	0	0	22	22	4.9	4.5
34 (1997)	0	3	80	83	29.7	2.8
55 (1997)	0	0	6	6	4.4	1.4
59 (1997)	0	0	6	6	2.5	2.4
60 (1997)	0	0	2	2	0.5	4.2

^a Territory number (see Fig. 3.1) and year in which data were recorded. Data were recorded prior to any experimental manipulations on territory size.

^b Number of trees in each height class.

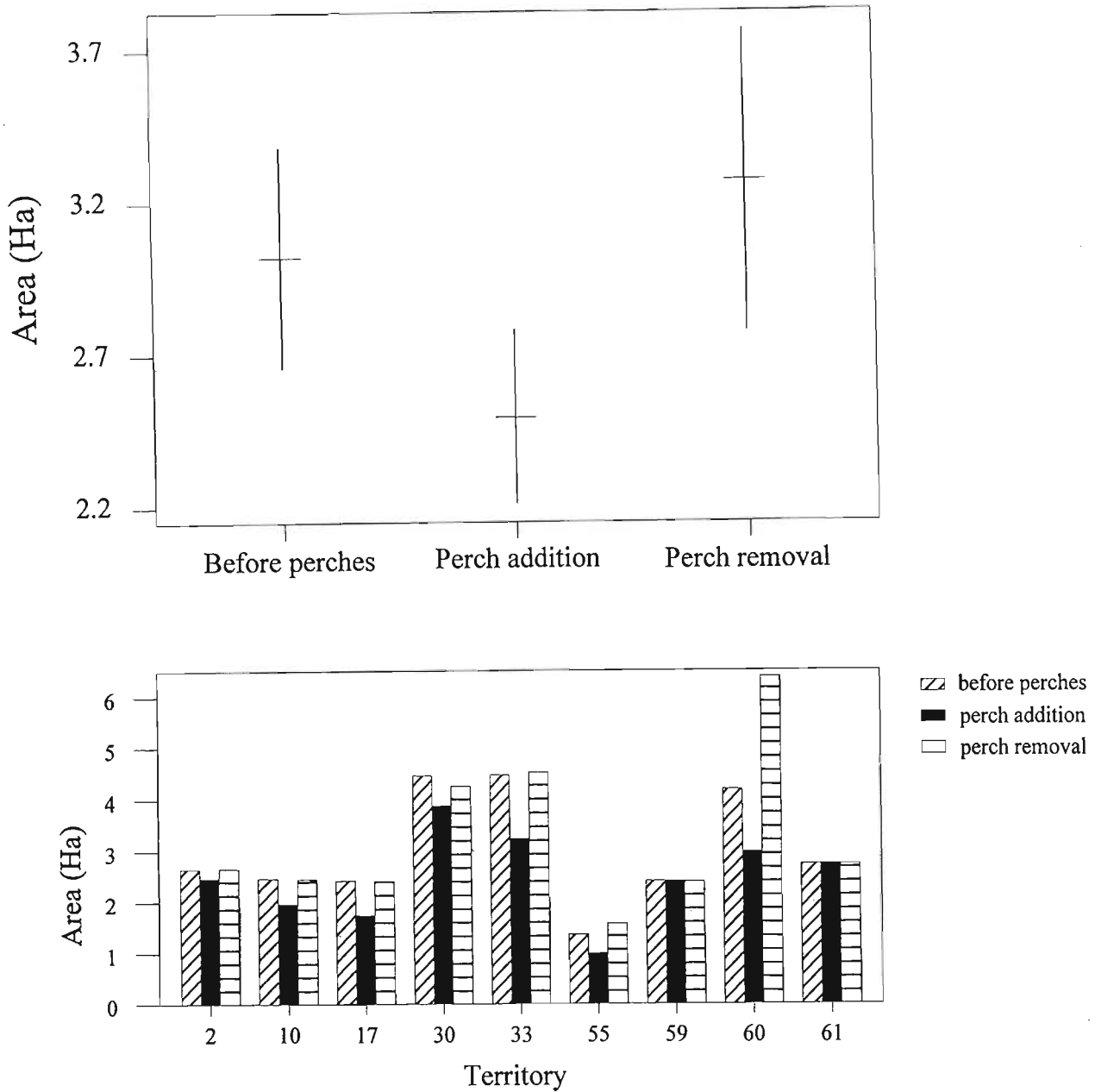


Figure 3.12. The effect of the addition and removal of six 3 m high perches on the size of nine fiscal shrike territories at Ukulinga Research Farm. Areas were determined before perches were erected, ten days after erection, and ten days after removal. Territory size significantly reduced with perch addition (Wilcoxon paired signed ranks test: $T=28$, $N=7$, $P<0.01$), and significantly increased with perch removal (Wilcoxon paired signed ranks test: $T=28$, $N=7$, $P<0.01$).

experimental subject when the subject contracted his territory after the addition of perches. When perches were removed the experimental subject was unable to displace the male who had established the new territory, and instead expanded into an uninhabited area.

DISCUSSION.

Fiscal shrikes held exclusive territories at Ukulinga Research Farm that were defended using active combat and passive visual and vocal displays. Interspecific attacks on bulbuls were the most common form of aggression, and interspecific attacks averaged one every 2 h. Fiscal shrike territories were distributed throughout Ukulinga and were not restricted by human disturbance. Territories functioned as both breeding and wintering grounds, and breeding territories were significantly smaller than non-breeding territories. Territory size was inversely proportional to tree density, although territories were not found where the density of woody vegetation exceeded 1200/Ha or where trees were absent or scarce. Fiscal shrikes defended perch sites, and the addition of perches into a territory significantly reduced its area.

Territorial behaviour.

Visual and vocal signals can reduce the occurrence of intraspecific antagonistic interactions which could result in injury, as injury may reduce reproductive success by reducing parental care or mating effort. Static marking and singing were common behaviours exhibited by male fiscal shrikes and, although less commonly, by females. Playback of just 30 s of local song caused a strong counter-singing response in male fiscal shrikes. As at Ukulinga fiscal shrikes in Pretoria used a loud grated “jert” call during territorial defence and advertisement, which was usually given from an exposed or prominent position, and accompanied by exposed scapulars in the male or concealed chestnut flanks in the female (Harris 1995). Territorial advertisement by static marking and song is common in *Lanius*; great grey shrikes sang from treetops in a manner suggesting territorial advertisement (Tye 1984), and red-backed shrikes *Lanius collurio* and lesser grey shrikes *Lanius minor* used song as a territorial signal (Harris & Arnott 1988). The low occurrence of intraspecific antagonistic encounters relative to interspecific conflicts observed in fiscal shrikes at Ukulinga is an indication that song and static marking reduce the occurrence of intraspecific territorial conflicts.

Interspecific territorialism occurs in species with overlapping ecology, when the territory holder of one species exhibits behaviour usually associated with intraspecific encounters to an intruder of a second species (Simmons 1951; Krebs & Davies 1993). Interspecific encounters initiated by fiscal shrikes were almost always won by the initiator, and were directed at species of a similar size or smaller, most frequently at black-eyed bulbuls. Black-eyed bulbuls pose no

threat to fiscal shrikes in terms of reduced breeding opportunities as they are not brood parasites nor will they raid nests. However, the feeding requirements of the black-eyed bulbul overlap with the fiscal shrike, although the bulbul's diet also incorporates a large proportion of fruit (Maclean 1993). Aggressive interactions have been observed between members of the Laniinae with overlapping diets. Occasionally at Ukulinga and more commonly at Weenen Game Reserve red-backed shrikes established winter territories, but these did not overlap with fiscal shrike territories despite both species occupying similar habitats. Great grey shrikes, in addition to displacing conspecifics from hunting perches and chasing conspecific intruders, also displaced woodchat shrikes *Lanius senator* (Tye 1984), and sympatric red-backed shrikes and masked shrikes *Lanius nubicus* displayed intra- and interspecific aggression (Simmons 1951).

Territory organisation.

It is generally accepted that animals hold territories to gain access to limited resources, and only do so when the benefits of holding a territory outweigh the costs (Brown 1964; Davies & Houston 1984; Krebs & Davies 1993). Birds employ a variety of territorial strategies with varying degrees of territoriality, for example, mating territories, feeding territories, and defended home ranges. In addition, territorial strategies are flexible and can change with resource abundance and time, and different populations of the same species often employ different territorial strategies.

The Laniinae are territorial and pairs usually defend exclusive, non-overlapping territories during the breeding season (Cramp & Perrins 1993), although Italian populations of the red-backed shrike employ the alternative strategy of a defended core area and shared home range (Fornasari et al. 1994, Massa et al. 1995). Most palaeartic and North American species of *Lanius*, for which most of the information on the genus has been acquired, are migratory. Wintering individuals either hold territories, which are usually smaller than pair-held breeding territories, or are non-territorial (Harris & Arnott 1988). Populations of great grey shrikes in south-western Germany have larger wintering territories (single birds) than breeding territories (pairs), both of which are smaller than resident territories held by pairs throughout the year (Schon 1995). Resident populations of loggerhead shrikes *Lanius ludovicianus* in California, USA, held territories as pairs during the breeding season, but afterwards territories split and males and females defended exclusive adjacent territories (Craig 1978).

Fiscal shrike populations at Ukulinga and in South Africa were stable throughout the year, indicating that they were non-migratory (Parker 1997). Over half of territories at Ukulinga were held by pairs throughout the year. Breeding territories, in contrast to most species of shrike, were smaller than non-breeding territories. However, non-breeding fiscal shrike territories were often held by pairs, in contrast to the individual-held wintering territories of the other Laniinae, and so would require more resources and hence would be larger. Non-breeding territories were often located in areas where observation posts were scarce; if the resource that fiscal shrikes were defending was perch sites, territories would be large in such areas to encompass sufficient quantities of the resource. Pairs occupying such large territories might have failed to reproduce because the increased energetic costs incurred by reproduction offset the balance of costs and benefits associated with holding territories, so that although resources were sufficient for maintaining a pair, they were insufficient for reproduction. By remaining paired and holding territories throughout the year, fiscal shrikes would benefit from increased opportunities to reproduce, should favourable conditions prevail, as fiscal shrikes are known to breed opportunistically throughout the year in South Africa (see Chapter 2).

Many of the 26 species of Laniinae are suffering a global decline in population numbers, and changes in breeding or wintering habitats are believed to be a major causal factor (Yosef 1994). Many other raptorial species are affected by land-use systems. Black-shouldered kite *Elanus caeruleus* and black kite *Milvus migrans* numbers were enhanced by human activities, whereas most other raptors in southern Africa, especially eagles and hawks, were detrimentally effected by human induced habitat destruction (Brandl et al. 1985b). Red-backed shrikes, woodchat shrikes, and lesser grey shrikes exhibited decreasing degrees of urban tolerance respectively, with the lesser grey shrike only present in areas without urbanisation (Guerrieri et al. 1995). Following this, human induced urbanisation and land-use changes could adversely affect the future of these species. Fiscal shrikes, however, maintain high densities in commercial land use systems in South Africa (Brandl et al. 1985a). Fiscal shrikes were found in areas of human disturbance at Ukulinga, and 97% of all territories encompassed some form of man-made construction. Fiscal shrikes therefore exhibit a high degree of urban tolerance. Exotic species of tree are often found associated with human induced land changes (e.g. urbanisation, forestry). Fiscal shrike territories also contained many non-indigenous species of woody plants, which did not appear detrimental to their abundance. Therefore, it would appear that fiscal shrikes are not as threatened by urbanisation as other members of the Laniinae.

Sufficient resources or intrusion pressure?

According to the sufficient resources hypothesis (Myers et al. 1979) territory size is inversely proportional to resource abundance, whereas the intrusion pressure hypothesis (Myers et al. 1979) states birds should always hold large territories, but increased competition associated with increased resources reduces territory size. Therefore the outcome of each hypothesis is the same and it is difficult to distinguish between them. However, if territory size is inversely proportional to resource abundance, holders of small territories should be in a better nutritional condition than those in larger territories. Conversely, according to the intrusion pressure hypothesis, large territories should maximise fitness. Note that the currency being optimised is nutritional condition. Although other factors such as reproductive success could be important, these are directly related to nutritional condition (e.g. food supplementation experiments show increased reproductive success, see Chapter 2) and so nutritional condition is a valid currency. The technique of ptilochronology can be used to assess the nutritional condition of birds (Grubb & Yosef 1994). It determines nutritional condition by measuring the width of daily growth bars on a feather removed from an adult bird's tail (R4). Daily growth bar width in loggerhead shrikes was compared with territory size and activity budgets, and it was discovered that shrikes living in larger territories had a poorer nutritional condition than those in smaller territories and spent more of their time on the wing. Furthermore, large territories contained more dead space and the cost:benefit ratio for holding large territories was worse.

The influence of perch sites on territory size.

Traditionally food has been the resource most often considered to determine territory size (Stamps 1994), but perch sites are an important determinant of territory size in fiscal shrikes. In areas where observation posts are dispersed territories are large, and where the resource is more concentrated territories are smaller. As fiscal shrikes are sit-and-wait hunters, perches offer a structure to scan for prey items. The area within the field of view around the base of an observation perch can be termed 'usable area'. When perch density is low, much of the territory cannot be scanned due to lack of hunting perches, and this unavailable area unavailable for hunting can be termed 'dead area'. Large territories with a low density of perches will therefore contain a high ratio of dead area to usable area compared to territories with higher densities of trees (Fig. 3.13). When perch density is very high there is a large degree of overlap in usable areas of a territory (Fig. 3.13). Perches can become obstacles, reducing scanning ability (Fig. 3.14), and together with competition from woodland birds (e.g. southern boubou *Laniarius feringous*) may prevent fiscal shrikes from exploiting such habitats (Eason & Stamps 1992).

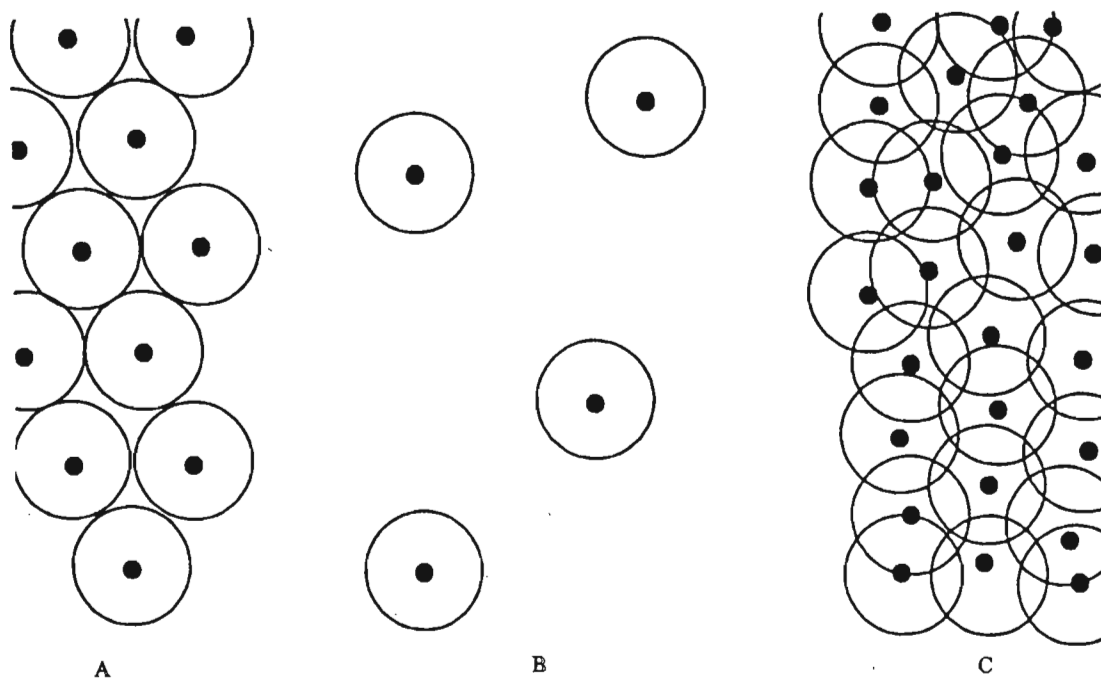


Figure 3.13. The effects of perch density on usable area in a fiscal shrike territory. When there is approximately one field of vision diameter between perches (A) most of the ground can be used for foraging. When perch density decreases (B) much of the territory becomes unusable due to lack of suitable observation sites. At high perch densities (C) all of the territory is available for foraging, but there is a large degree of overlap in the fields of vision. Solid dots indicate perch sites and circles indicate the field of vision (usable area) around the perch base.

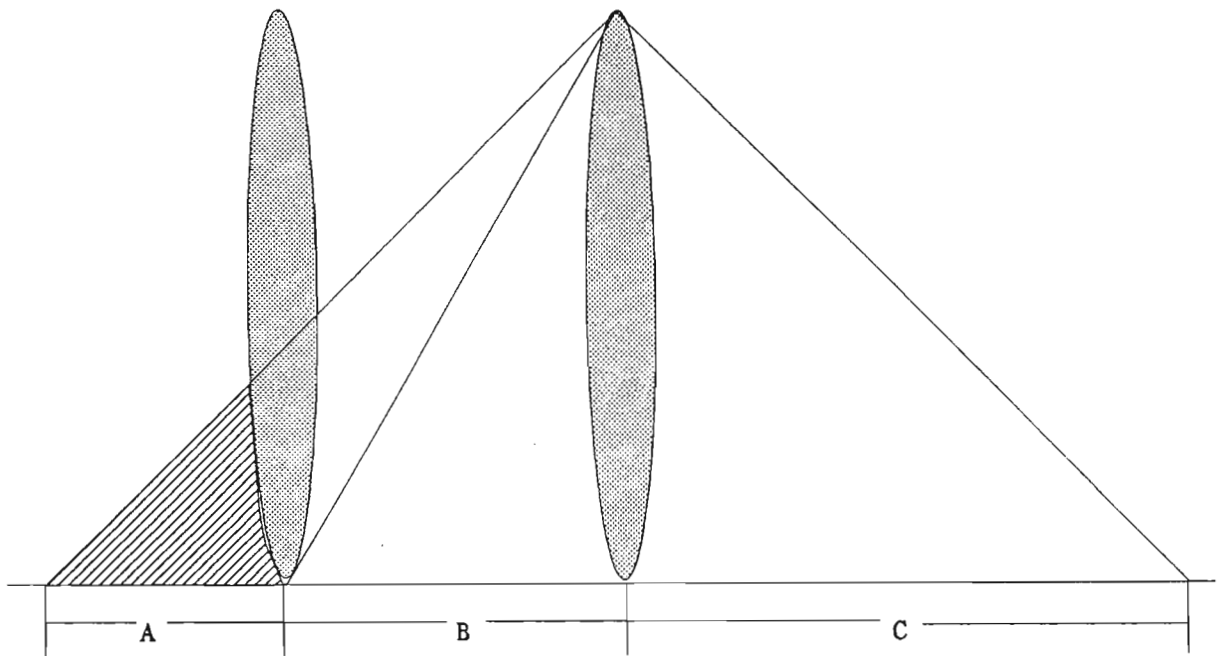


Figure 3.14. The effect of high perch density on obstruction of the field of vision around a perch base. Usable area is reduced by A to B, compared to the unobstructed area C when inter-perch spacing is closer than one field of vision diameter.

Territory size at Ukulinga was inversely related to tree density, and tall perch sites (>2.99 m) were the most important factor in assessing territory size. Great grey shrikes used 3-10 m high perches significantly more than expected, and their home range was negatively correlated to perch density (Rothhaupt 1995). Both great grey shrikes (Yosef 1993) and loggerhead shrikes (Yosef & Grubb 1994) responded to the addition of perches to their territory by reducing territory area. Great grey shrikes territories reduced in area by 3.7-15.3% with perch addition, and when perches were removed territories reverted to approximately their original size. Territory size in fiscal shrikes decreased significantly when perches were added and increased when these were removed.

The height of perches has an important influence on prey detection. Taller perches allow a larger area of ground to be scanned as the radius of the field of vision increases with perch height, increasing usable area. In addition interference from low vegetation is reduced (Fig. 3.15). The amount of interference from low vegetation can be termed the vision reducing distance. This is equivalent to the part of the hypotenuse the of the right-angled triangle embedded in low vegetation, whose other two sides are the perch and the ground (Fig. 3.15). As perch height increases, the angle the hypotenuse makes with the ground increases, and the vision reducing distance decreases. Red-backed shrikes increased their probability of prey detection when they hunted from higher perches (Carlson 1985). There will be an optimum perch height for a species in a given habitat, after which a further height increase will decrease resolution and small prey objects will become indiscernible (Andersson 1981).

The quality of perch sites and habitat can also affect foraging ability. Artificial perch sites (e.g. overhead cables, fence posts) offer less obscured views than most trees and shrubs, as there is less interference from foliage. Tall grass or herbaceous layers will increase vision reducing distances (i.e. the amount of low vegetation interference) (Fig. 3.15) and reduce foraging ability, and in some cases may render perches obsolete. Grass height has an important influence on territory dynamics in many of the Laniinae. Red-backed shrikes wintering in the Kalahari basin and resident populations of loggerhead shrikes in South Carolina avoided areas with tall grass (Gawlik & Bildstein 1993; Herremans 1997). Red-backed shrikes living in pastures had a greater reproductive success than those living in meadows or fallow land, because although there was no difference in prey abundance, pastures offered more accessible prey through increased detection because of shorter vegetation (Brandl et al. 1986). Vegetation height also effects hunting behaviour.

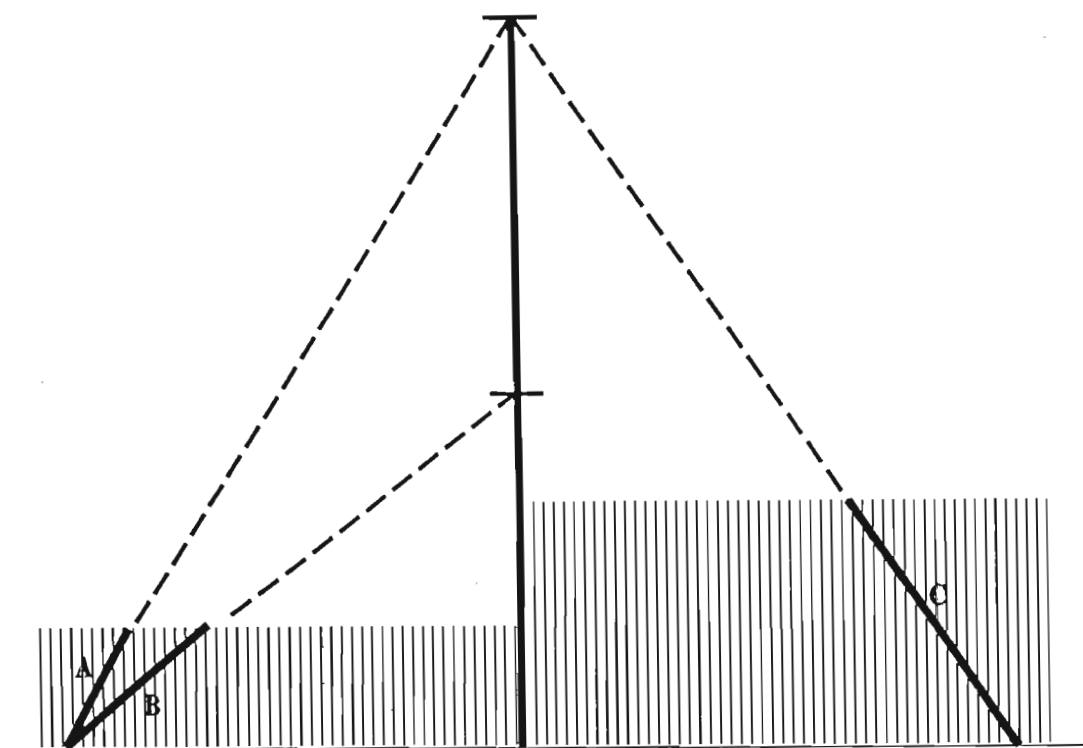


Figure 3.15. The effects of perch height and grass height on the ability of a sit-and-wait forager to detect ground-dwelling prey. The distance that must be viewed through grass to see prey (i.e. A, B & C) can be termed the vision reducing distance. As perch height increases the vision reducing distance decreases (A compared to B). As grass height increases the vision reducing distance increases (A compared to C).

Loggerhead shrikes spent significantly more time in flight performing energetically expensive aerial forays when the herbaceous layer was high, and more time perched scanning for prey and performing ground hunts when vegetation height was reduced by mowing (Yosef & Grubb 1993). Territory 2 at Ukulinga, which had a high density of trees for its size, had not been grazed for six months prior to mapping. Although data were not collected on vision reducing distances this territory had taller grass than others which could have reduced perch quality and in combination with a high density of short perches may consequently explain its large size.

In summary, fiscal shrikes were able to hold territories at Ukulinga by monopolising the limited resource of perch sites, which were important for foraging and nutritional condition.

Ultimately, territory size will also be influenced by the distribution of other resources. For example, an area saturated with, but containing only artificial perches would offer fiscal shrikes optimal foraging sites, but as territories are multipurpose and used for breeding in addition to foraging, an area would also need to encompass at least one nest site. Trees were also used by fiscal shrikes as a refuge from overhead predators. However, in areas already populated by shrikes, habitat suitability may be enhanced by introducing perches where perch sites are limited, thereby allowing shrikes to forage in previously unsuitable areas. Perch addition could be used as a future tool for conservation, as by decreasing the size of territories more can be established in an area, and hence, increase the population

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CHAPTER 4: FORAGING STRATEGY OF A SIT-AND-WAIT PREDATOR: FISCAL SHRIKES HUNTING FROM PERCHES.

ABSTRACT.

Factors affecting the foraging behaviour of fiscal shrikes *Lanius collaris* were investigated during a three year study at Ukulinga Research Farm, near Pietermaritzburg, South Africa. Fiscal shrikes were sit-and-wait foragers that primarily used elevated perch sites to scan for ground-dwelling prey. Forty per cent of all search attempts terminated in a successful prey capture. In accordance with optimal foraging theory, fiscal shrikes adjusted their foraging method according to the strength of the wind, employing perch-to-air foraging in light winds and perch-to-ground foraging in stronger winds. Surface gleaning was only observed during very strong winds. Birds perched at lower heights and in less exposed positions during windy conditions. During sunny periods fiscal shrikes faced into the direction of the sun (north) significantly more often than during cloudy periods. Search duration and subsequent movement distance increased with perch height, which is a reflection of search area increasing with perch height. Movement distances were also affected by the outcome of the previous hunting attempt. Following successful hunts fiscal shrikes moved greater distances before foraging compared with unsuccessful hunts, possibly to avoid patch depletion. Most of the prey captured by fiscal shrikes were invertebrates between 18-55 mm long. Males consumed 36% of the prey they caught, delivered 61% to offspring or a partner, and cached the remaining 3%. Cached prey were significantly longer than consumed prey, and caches contained a higher proportion of vertebrates and annelids. In accordance with optimal foraging theory fiscal shrikes concentrated their search effort in patches close to the nest. Prey size only increased with distance from the central place in patches further than 35 m from the nest. This was in agreement with a modification of the single prey loader hypothesis for central place foraging. The only differences observed between the foraging behaviour of male and female fiscal shrikes were that females had shorter search durations than males, and unlike males, females did not feed their partner.

INTRODUCTION.

Natural selection has resulted in the shaping of phenotypes by changing environmental conditions, leading to adaptations that maximise fitness. Selection can act on an organisms morphology, for example, on body mass and bill size. Following a drought in 1977 on Daphne Major, Galapagos Islands, Darwin's ground finches *Geospiza fortis* had significantly greater masses and larger, narrower bills than in 1976 (Boag & Grant 1981). Large, narrow bills were favoured as they were able to crack and twist open the large *Tribulus* seeds that were more abundant following the drought. This selection for larger mass and changing bill shape was recurrent, occurring after other periods of drought (Price et al. 1984), but oscillated to favour smaller masses following years with heavy rainfall when there was an excess of small soft seeds (Gibbs & Grant 1987). Natural selection also operates on an organism's behaviour. Since 1950 blackcaps *Sylvia atricapilla* that were previously summer migrants began overwintering in the British Isles. By comparing the migration direction of populations from continental Europe with young and adult British birds it was discovered that British overwintering blackcaps were not summer visitors that became resident, but were continental birds that had evolved a novel migration route (Berthold et al. 1992).

Optimal foraging theory was developed to explain how natural selection can shape behaviours that maximise the rate of energy intake within the constraints imposed by the environment (Maurer 1996; Perry & Pianka 1997). Optimality modelling considers the best way of making a decision such as when to begin reproducing, or how long to search a food patch before leaving. It constructs testable hypotheses and dissects their components to discover the relationships between them, and is tested by comparing predictions from its hypotheses and predictions from alternative models to observed phenomena (Stephens & Krebs 1986). Optimality models can be applied to many behavioural and ecological strategies (e.g. territoriality, reproduction), but most approaches have been in foraging due to the necessity of obtaining energy for survival and reproduction (Perry & Pianka 1997). Most optimal foraging models fall into two broad categories, those that explain optimum diets and those that explain patch exploitation (MacArthur & Pianka 1966), where a patch is a clump of prey. An extension of the patch model to incorporate an animal returning to a nest or den to feed offspring is known as central place foraging theory (Orians & Pearson 1979).

Although much work had been done on optimal foraging (Emlen 1966; MacArthur & Pianka 1966; Pyke 1984; Krebs et al. 1983; Krebs & McCleery 1984; Stephens & Krebs 1986), most focuses on experimental circumstances (Stephens & Krebs 1986). The vogue has moved from such studies to more holistic approaches that consider the forager's environment, internal state, and the effects of phylogenetic factors (e.g. stochastic dynamic modelling). These evaluate how short term behavioural decisions contribute to lifetime fitness, integrating foraging theory into the natural circumstances of individuals (Krebs & Kacelnik 1991; Perry & Pianka 1997).

Sit-and-wait foragers have been the focus of some optimality work (e.g. Carlson 1985a, b), although an integrated picture of this strategy is lacking. The fiscal shrike *Lanius collaris* is a medium sized passerine occurring in sub-Saharan Africa, and like other members of its genus it primarily uses the characteristic sit-and-wait foraging method. Ground-dwelling prey are spotted from a elevated perch site and captured after gliding or flying to the ground. Fiscal shrikes are ideal subjects for studying optimal foraging questions as they are common and easy to view, and prey type and size, patch residence times, and travel distances can be recorded easily. I describe in detail fiscal shrike hunting behaviour, assessing several aspects when alternative methods are available. I assess how such methods change in response to physical and environmental conditions. I end by revisiting optimal foraging theory, and offer a perspective as to how it can be applied in a modern integrative manner.

I tested the following predictions derived from optimal foraging theory (Fig. 4.1). The specific currencies of fitness that I use include searching and hunting success, prey size and prey type. Foraging theory is well covered in many general texts (e.g. Stephens & Krebs 1986), and so is described here only briefly. (1) Foraging method should depend on wind strength due to the cost of flight (Mendelsohn & Jaksic 1989), and on perch height and structure through their influence on prey detection (Andersson 1981; Carlson 1985a). In strong winds birds should use foraging methods that rely less on flight, perch in lower and less exposed positions, and utilise shelter from vegetation perches. (2) Shrikes should spend longer on higher perches and longer hunting from structures that offer an unobscured view of the surrounding area, in order to search the larger patch more thoroughly. (3) The decision of whether to attack prey should depend upon prey size and the distance from the central place. Large prey should always be attacked but small prey should be ignored in patches far from the nest. (4) Shrikes should leave a patch after prey capture to avoid patch depletion, but remain following an unsuccessful hunting attempt. (5) Small prey should be consumed and intermediate-sized prey should be

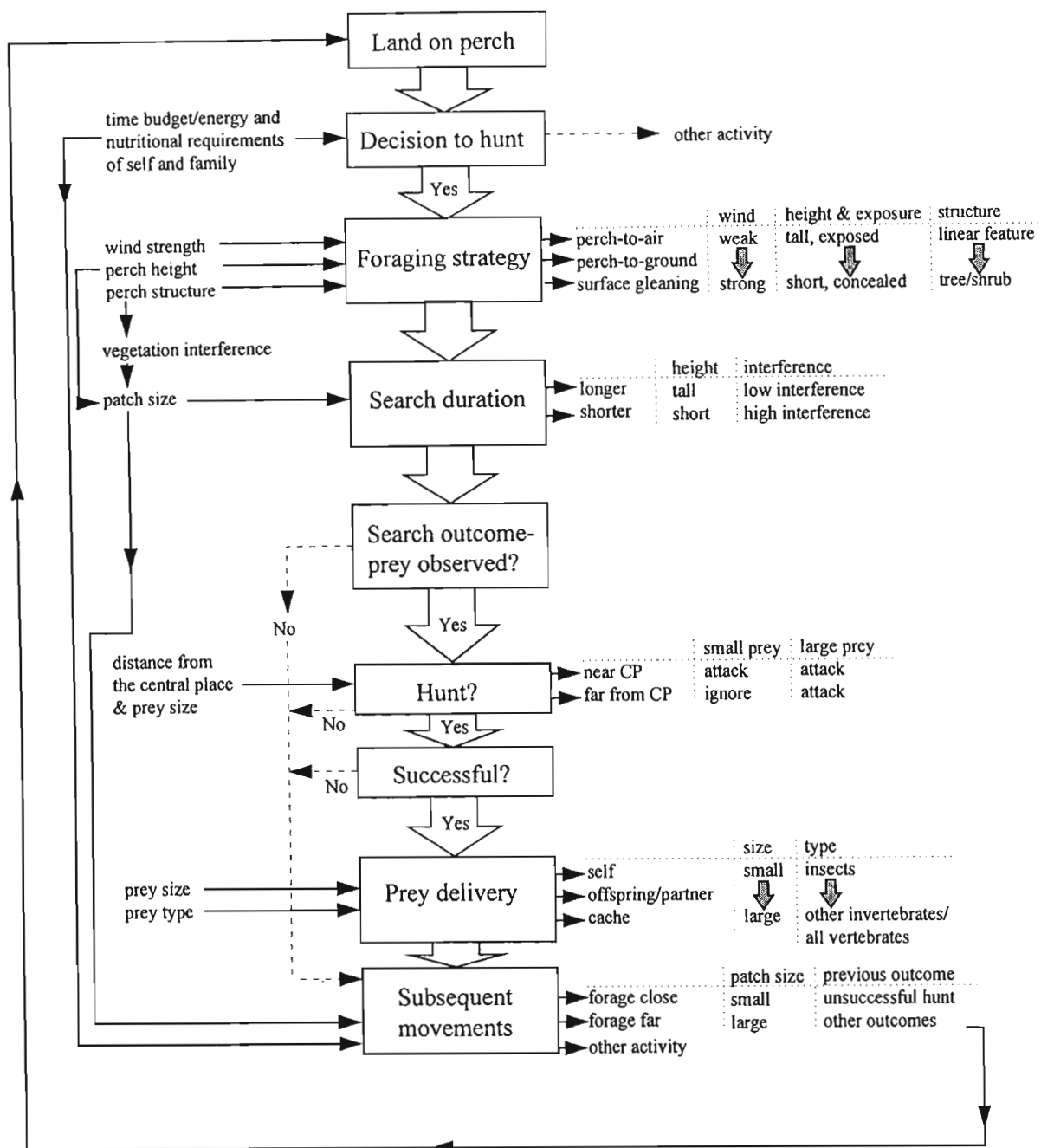


Figure 4.1. Factors affecting foraging decisions of breeding fiscal shrikes. Foraging decisions are enclosed in boxes. Factors affecting decisions are located to the left of boxes, and predictions arising from these factors are to the right, connected by solid small arrows. Foraging decisions follow sequentially through large open arrows descending the flow chart, with alternative outcomes represented by dashed lines.

delivered to offspring or a partner, to offset travel costs (Orians & Pearson 1979). Large prey, especially vertebrates, should be cached to aid prey manipulation and act as an indicator of male and/or territory quality (Yosef & Pinshow 1989). Noxious prey should also be cached to aid the breakdown of toxins into harmless substances (Yosef & Whitman 1992). In addition, from noticing that fiscal shrikes appeared to face into the sun when foraging, I test whether this is true, and assess how solar radiation, time of day, and temperature affect posture when searching for prey.

METHODS.

Study area.

This study was conducted during October-November 1995 ($N=16$, 17 breeding attempts), August-December 1996 ($N=4$, eight breeding attempts), and August-October 1997 ($N=3$, three breeding attempts), at Ukulinga Research farm, situated 5 km south-east of Pietermaritzburg, South Africa ($30^{\circ}24'E$, $29^{\circ}40'S$, elevation 775 m). Fiscal shrikes were socially monogamous and highly territorial, and at least 36 pairs bred at Ukulinga each year. Ukulinga consisted of Dohne sourveld (Acocks type 44b), characterised by *Acacia karoo*, *A. nilotica* and *A. sieberiana* bushveld, and *Themida triandra* dominated grasslands (Acocks 1988). Most of the land was used for grazing by animal science and range and forage resources research, and the remainder was partitioned between horticulture, poultry and pig science, plant breeding, crop production, agricultural engineering, and private residences.

Behavioural observations.

Territories were chosen for observation based on accessibility, visibility, an understanding of territory boundaries (see Chapter 3), knowledge of the breeding stage of the owners (see Chapter 2), and where applicable, position of the nest. All individuals were observed between courtship (determined by presence of courtship feeding, see Chapter 2) and fledgling dispersal, which occurred up to several months after hatching. Observations took place at least one hour after dawn and one hour before dusk, although most occurred between 0800-1200 h. Birds were observed using 10x25 binoculars, and notes were taped for later transcription. A hide was not necessary for observations as fiscal shrikes were tolerant of humans and quickly habituated to my presence, foraging within 15 m of where I sat.

The foraging behaviour of adult fiscal shrikes was monitored with a combination of 15 min and 2 h observation sessions in 1995, and 1 h observation sessions in 1996 and 1997 (total session length: $\bar{X} \pm SE = 1.14 \pm 0.11$ h, $N=56$). Fifteen minute sessions focused entirely on the behaviour of males to determine activity budgets. One and two hour sessions concentrated on female behaviour although it was usually possible to follow and record the behaviour of both sexes. In addition, six nests in six territories were video taped on two to four occasions each using a Sony 8 mm camera (video session length: $\bar{X} \pm SE = 1.06 \pm 0.09$ h, $N=17$), to observe chick feeding behaviour, prey sizes and types fed to offspring, and nest maintenance.

The following foraging parameters were determined from observation notes: height of perch structure, height perched whilst searching (height of bird in tree), orientation, perch type (e.g. tree, fence line, overhead cable, artificial perch), duration perched, perching outcome (either prey attack or give-up), hunt type (perch-to-air, perch-to-ground, or surface gleaning), hunt success, prey size, prey type (broadly classified into Orthoptera, Coleoptera, Hymenoptera, other winged insects, insect larvae (e.g. grubs, caterpillars), Annelida, other invertebrates, Amphibia, Reptilia, Aves, and Mammalia), prey destination (self, partner, offspring, or cache), distance flown to the perch, distance flown from the perch, and round trip distance. Prey size was recorded as a multiple of beak lengths after being compared to the size of the fiscal shrike's beak. Beak length of fiscal shrikes inhabiting the Midlands region of KwaZulu-Natal averaged 18 mm ($\bar{X} \pm SE = 18.2 \pm 0.3$ mm, $N=12$). The success of hunting forays in long grass were difficult to determine as prey items were sometimes consumed on the ground, although it was usually possible to record the size and type of prey caught if the prey was consumed on a perch, or transported to the nest, to a partner, or to fledglings. For this reason, the number of prey captured for self-forays could be underestimated.

Temperature was recorded on an hourly basis by the Institute of Soils, Climate, and Water (Pretoria) at the weather station at Ukulinga. Wind conditions were ranked 1 to 2 for none/light wind and moderate/strong wind, respectively. The amount of cloud cover was ranked 1, 2 or 3 for complete cloud cover, partial cloud cover, and no cloud cover, respectively.

In territories studied for foraging behaviour every possible perch (e.g. trees, shrubs, fence lines, artificial perches, overhead cables) within the territory was mapped by measuring distances (to the nearest 0.5 m) and compass bearings (to the nearest degree) to the object from a known point. The height of all trees and other objects used to scan for prey were estimated using a 1 m rule as a guide. Territory maps showing the location of every perch were drawn by hand. It was therefore possible to calculate the distance flown to the nearest metre between any two perch sites within a territory.

In order to study foraging behaviour without the confounding effects of perch structure (e.g. vegetation interference from trees, availability of suitable branches for perching) artificial perches were erected in seven territories. Perches consisted of a 3 m bamboo upright (diameter 60-90 mm), with 1.8 m x 9 mm doweling cross-poles secured horizontally at 3 m and at

1.75 m. They were attached by wire to a 1.4 m fencing standard sunk 0.5–0.65 m vertically into the ground. The cross-poles were aligned east-west in every territory to determine perching orientation preference between facing into the sun (north) and facing away from the sun (south). Each territory in 1996 received eight perches, erected in a V formation (acute angle approximately 60°) at the following distances radiating from the nest: 4 m, 16 m, 32 m, and 64 m. The V formation was chosen as it allowed all perches to be observed for usage, but following concern that aerial predators could use the formation to locate nests the design was modified for the following season. In 1997 six perches were erected randomly in the centre of each of ten territories prior to nest construction as part of a study on the effects of perch density on territory size (see Chapter 3). In all cases artificial perches were erected at least 20 m from other perch sites over 1.5 m in height to avoid overcrowding and reduce visual disruption arising from surrounding vegetation.

Male and female fiscal shrikes (*L. c. vigilans*) were sexually dimorphic and easily discernible in the field, as the female's plumage was duller than the male's and only the female had chestnut coloured flanks. Adult fiscal shrikes have pied plumage, whereas juveniles are cryptic brown (Maclean 1993). The population of fiscal shrikes at Ukulinga was not colour-banded so individual recognition was not possible. This study does not focus on long term territory dynamics, associations, dispersal or inter-territory movements. It was therefore decided unnecessary to stress individuals by capture and ringing (ASAB 1998). Once incubation began it is unlikely that the pair bond was broken, and pairs are assumed to have remained together for the duration of a nesting attempt. Therefore, as almost all pairs were observed during the same time periods it is unlikely that any one individual was resampled, reducing the possibility of pseudoreplication (Hurlbert 1984). The same individual may have been sampled in different years by repeated sampling of a territory. However, fiscal shrikes have a large population turnover, and following fledging some territories at Ukulinga contained one-parent families. In Kenya fiscal shrikes are known to divorce following unsuccessful nesting attempts, and 26% of a population of 19 fiscal shrikes changed territory at least once during a two and a half year study (Zack 1986). Furthermore, fiscal shrikes residing in one territory for more than a year were subject to different climatic and land-use conditions (Fig. 1.2, 1.3 & 1.4, Chapter 1). In total, males were sampled from 18 different territories and females were sampled from 19 different territories.

Statistical analysis.

Unless otherwise stated, all statistical analysis are two-tailed with $\alpha=0.05$. Raw data were subjected to Kolmogorov-Smirnov one-sample test for normality (Steele & Torie 1980) prior to further analysis. Data which were normally distributed are described as mean \pm one standard error of the mean. Data which were not normally distributed or could not be transformed to achieve normality were subject to non-parametric analyses, and medians and interquartile ranges are quoted when describing such data. Methods used for choosing an appropriate statistical test followed Sokal & Rohlf (1995) and Siegal & Castellan (1988). Associations were tested using the G-test, comparisons of distributions were tested with the Kolmogorov-Smirnov test, differences between categories were tested with Kruskal-Wallis tests, and correlations were tested using Spearman's correlation.

RESULTS.

All recorded parameters were analysed to determine differences in foraging between male and female fiscal shrikes. However, with two exceptions, no significant differences were found between the sexes. The two exceptions were, firstly, that males spent longer searching from perches (median: 60 s (males), 48 s (females)) (Kruskal-Wallis test: $H_1=4.26$, $P<0.05$).

Secondly, there was a difference in prey allocation between the sexes, because males fed their partners during courtship, incubation and brooding, but females did not feed males (G-test: $G_3=45.52$, $P<0.001$). Unless otherwise stated, all calculations below refer to male and female fiscal shrikes.

Frequency of hunting attempts and prey captures.

Fiscal shrikes were observed foraging throughout the day during the breeding season, from one hour after dawn to one hour before dusk. On average vigilance contributed to 63% ($\bar{X} \pm SE=63.1 \pm 2.7\%$) and foraging to 11% ($\bar{X} \pm SE=11.2 \pm 1.7\%$) of the activity budget of male fiscal shrikes. In total nearly three-quarters of a male's day was devoted to finding food and feeding, similar to the sympatric buffstreaked chat *Oenanthe bifasciata* (71.9% foraging) which uses similar methods of prey capture (Tye 1988). There was no significant difference between the proportion of time devoted to either vigilance or foraging during the courtship, incubation, brooding or fledging stages of breeding (for a definition of stages see Chapter 2) (Kruskal-Wallis test: vigilance $H_3=3.6$, *NS*; foraging $H_3=6.7$, *NS*). For a summary of the entire daily time budget of male fiscal shrikes see Fig. 2.12, Chapter 2.

Eight hundred and seventy-two searching attempts were observed during 79.16 h observation of 20 fiscal shrike territories. Seventy-two per cent (632) terminated when prey was attacked. The remainder of perchings (245) terminated when the forager left for another perch, and are termed give-ups. In total, fiscal shrikes perched on average 1.4 times for each prey attack. The percentage of prey attacks that ended in capture (i.e. the capture rate) averaged 56%. This is similar to capture rates of the loggerhead shrike *Lanius ludovicianus* (64% (Morrison 1980), 65% (Craig 1978)), less than buffstreaked chats (80% (Tye 1988)), but greater than wheatears *Oenanthe oenanthe*, stonechats *Saxicola torquata* (41% and 45% respectively (Moreno 1984)) and hawk owls *Surmia ulula* (36% (Sonerud 1992)). When every search attempt is considered, fiscal shrikes perched on average 2.5 times per successful capture.

Foraging method.

Fiscal shrikes employed three foraging methods during observation sessions at Ukulinga. The most common method employed was perch-to-ground sallying, which was used for 90% (566) of hunting attempts. This is almost identical to the brown shrike *Lanius cristatus* which uses perch-to-ground sallies for 89.1% of hunts (Severunghaus & Liang 1995). After locating terrestrial prey from an elevated perch fiscal shrikes flew, glided, or hopped to the ground and attempted to capture the prey. Occasionally they hovered over the prey before attacking, or appeared to flush prey from undergrowth by flapping their wings. Most prey were captured on landing but some that escaped were pursued on the ground. Prey were either consumed on the ground or on returning to a perch, or transported in the beak to a mate, offspring or a cache. Fiscal shrikes transport large prey items such as rodents and birds in their feet (Ade 1978; Harris & Arnott 1988), as this may stabilise flight when prey mass approaches the mass of the forager (Yosef 1993).

Fiscal shrikes used perch-to-air sallying (hawking) for 9% of hunts. Prey were located from an elevated vantage point and pursued and captured in flight. On one occasion outside the observation sessions at Ukulinga, fiscals were observed hunting almost exclusively by perch-to-air sallies in response to alate termites swarming. Surface gleaning (perch gleaning (Fitzpatrick 1980)) was uncommon (1% of hunts) and was characterised by searches within tree canopies where prey were picked off foliage whilst the fiscal perched.

The foraging method employed by fiscal shrikes was significantly related to wind conditions (G-test: $G_1=9.25$, $P<0.01$) (Fig. 4.2a). Ground and aerial foraging were employed less often in moderate to strong winds than in less windy conditions. Surface gleaning was rare and was only observed during moderate and strong winds. As predicted, fiscal shrikes perched lower (Kruskal-Wallis test: $H_2=10.19$, $P<0.01$) (Fig. 4.2b) and in less exposed positions (Kruskal-Wallis test: $H_2=13.97$, $P<0.001$) when searching for prey during strong winds than in less windy conditions. Hunting success was significantly related to foraging mode (G-test: $G_1=3.98$, $P<0.05$). All surface gleaning hunts were successful. Although aerial foraging is energetically more expensive than ground foraging due to the increased expenditure on flight, aerial hunts were more successful than ground hunts (G-test: $G_1=3.98$, $P<0.05$). Therefore fiscal shrikes adjusted their method of foraging according to the probability of prey capture under prevailing climatic conditions.

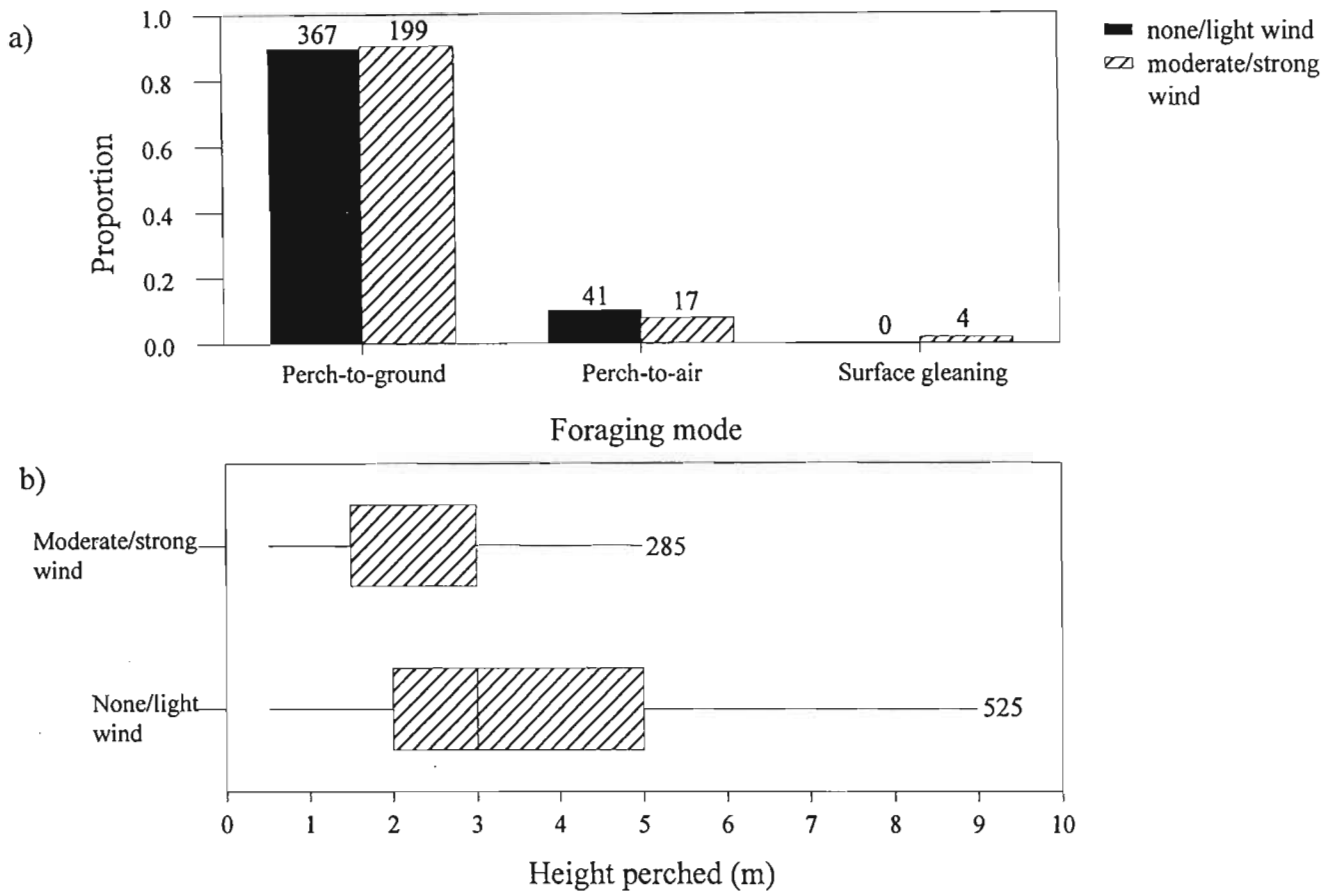


Figure 4.2. The effect of wind on fiscal shrike hunting behaviour. (a) Foraging strategy. The foraging mode employed was significantly related to wind condition (G-test: $G_1=9.25$, $P<0.01$). Fiscal shrikes performed significantly more perch-to-air hunts when wind was light compared with stronger wind conditions and surface gleaning was only employed in moderate and strong winds. (b) Perch height. Fiscal shrikes perched significantly higher above ground level during still conditions than in moderate or strong winds (Kruskal-Wallis test: $H_1=9.82$, $P<0.01$). Box-and-whisker plot vertical line represents median, box encloses 1st to 3rd quartiles, and horizontal line connects the lowest and highest observations defined by the lower limit $Q1-1.5(Q3-Q1)$ and the upper limit $Q1+1.5(Q3-Q1)$ (Minitab Inc.). Wind strength was subjectively ranked none/light (wind speed <3.5 m/s) or moderate/strong (wind speed >3.5 m/s). Numbers above bars and adjacent to whiskers indicate sample sizes.

Perch site characteristics.

Fiscal shrikes used a variety of elevated structures from which to hunt. Trees were used as perch sites for 53% (462) of searches, and linear features and artificial perches were used for the remaining 47% (423). Perch structure effects the search area available to sit-and-wait foragers through perch height and vision disruption by vegetation interference. Linear features and artificial perches offer an unobstructed view of the surrounding ground that is often impeded by foliage when the forager perches on a tree or shrub. Because of this, searches from trees were more likely to occur lower in the canopy compared to searches from artificial perches and linear features, which always occurred from the apex (note that almost all linear features and all artificial perches offered more than one perch height) (Kruskal-Wallis test: $H_1=288.79$, $P<0.001$). Compared to linear features and artificial perches, searches from trees were significantly more likely to terminate with a give-up than a hunt, possibly because of vision disruption (G-test: $G_1=43.22$, $P<0.001$) (Fig. 4.3a). However, when prey was spotted, hunting attempts from trees were significantly more successful than from other elevated structures ($G_1=4.30$, $P<0.05$) (Fig. 4.3b). Overall, a fiscal had to perch on average 2.6 times per successful hunt from a tree, and on average 2.3 times per successful hunt from linear features and artificial perches.

Fiscal shrikes should employ more ground hunts from artificial perches and linear features than from vegetation because of the uninterrupted field of vision around the base of the perch. Significantly more ground hunts occurred from artificial perches and linear features and more aerial hunts were performed from trees (G-test: $G_1=38.84$, $P<0.001$) (Fig. 4.3c). Trees may have been favoured for aerial hunting as aerial hunts occurred more frequently from taller perches (Kruskal-Wallis test: $H_1=4.86$, $P<0.05$) (Fig. 4.4). Trees offered taller observation posts (Kruskal-Wallis test: $H_1=240.11$, $P<0.001$) and fiscal shrikes perched significantly higher on trees than on linear features and artificial perches (Kruskal-Wallis test: $H_1=33.03$, $P<0.001$). Alternatively, flying insect densities could have been greater near trees than other perch sites, due to vegetation offering flying insects a food source or refuge. Buffstreaked chats switched from perch-to-ground to aerial foraging as perch height increased, but it was unclear whether this was because of a preference for air-borne prey, or a consequence of perch height and prey visibility (Tye 1988).

The height at which a predator perches whilst searching for prey has important implications for prey detection. As height increases there is an increase in the area within which prey can be

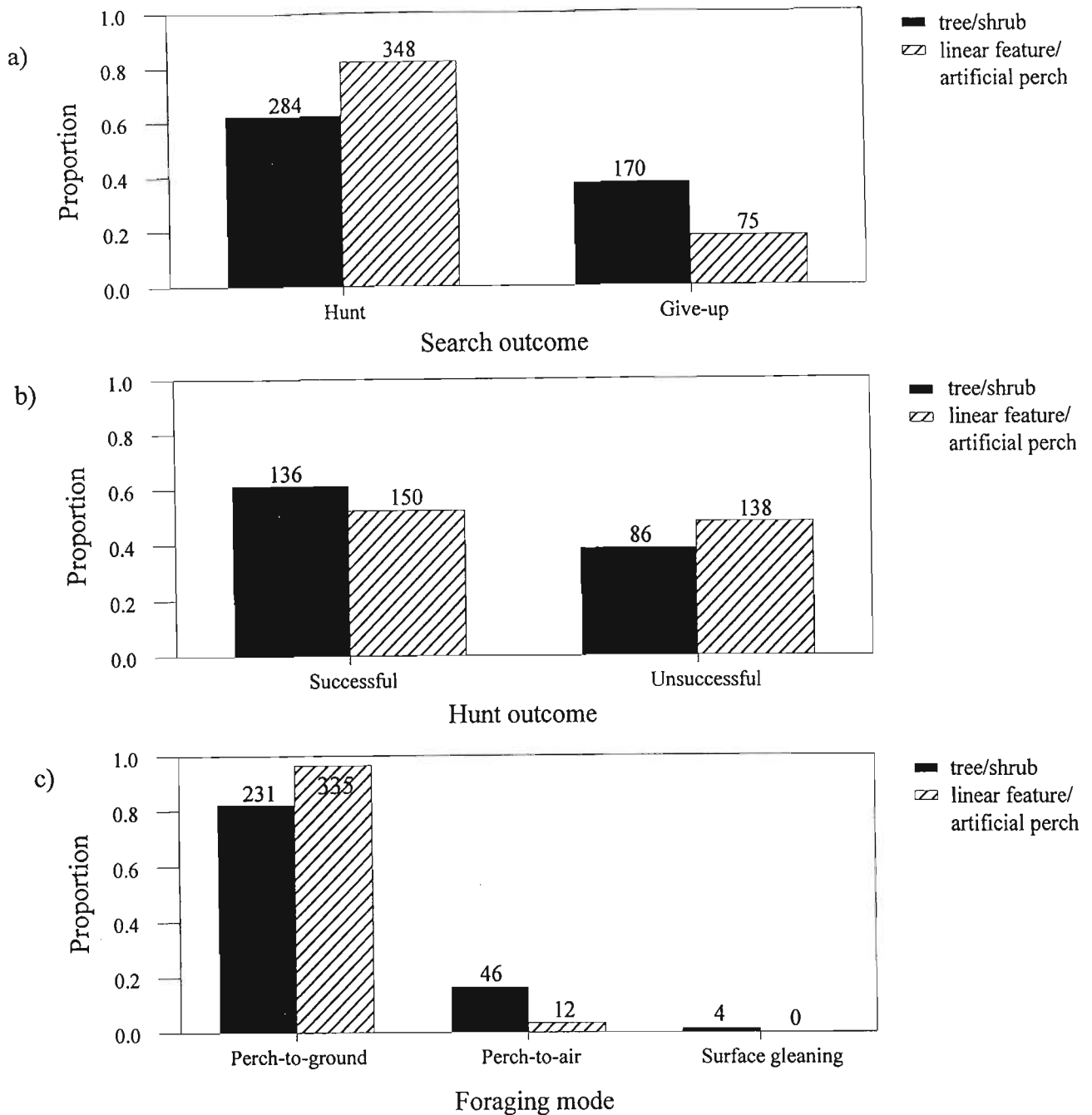


Figure 4.3. Effect of visual disruption on hunting success. (a) Give-ups. A significantly higher proportion of searches from trees and shrubs terminated when the perch was vacated (give-ups), compared to searches from linear features (fence lines and overhead cables) and artificial perches, which were more likely to terminate in a hunt attempt (G-test: $G_1=43.22$, $P<0.001$). (b) Hunting success. The proportion of successful hunts from trees and shrubs was significantly higher than from linear features and artificial perches (G-test: $G_1=4.30$, $P<0.05$). (c) Foraging mode. The foraging mode employed by fiscal shrikes was significantly related to perch structure (G-test: $G_1=38.84$, $P<0.001$). More ground forays occurred from artificial perches and linear features, and more aerial forays occurred from trees and shrubs. Surface gleaning was only observed in trees and shrubs. Numbers above bars indicate sample sizes.

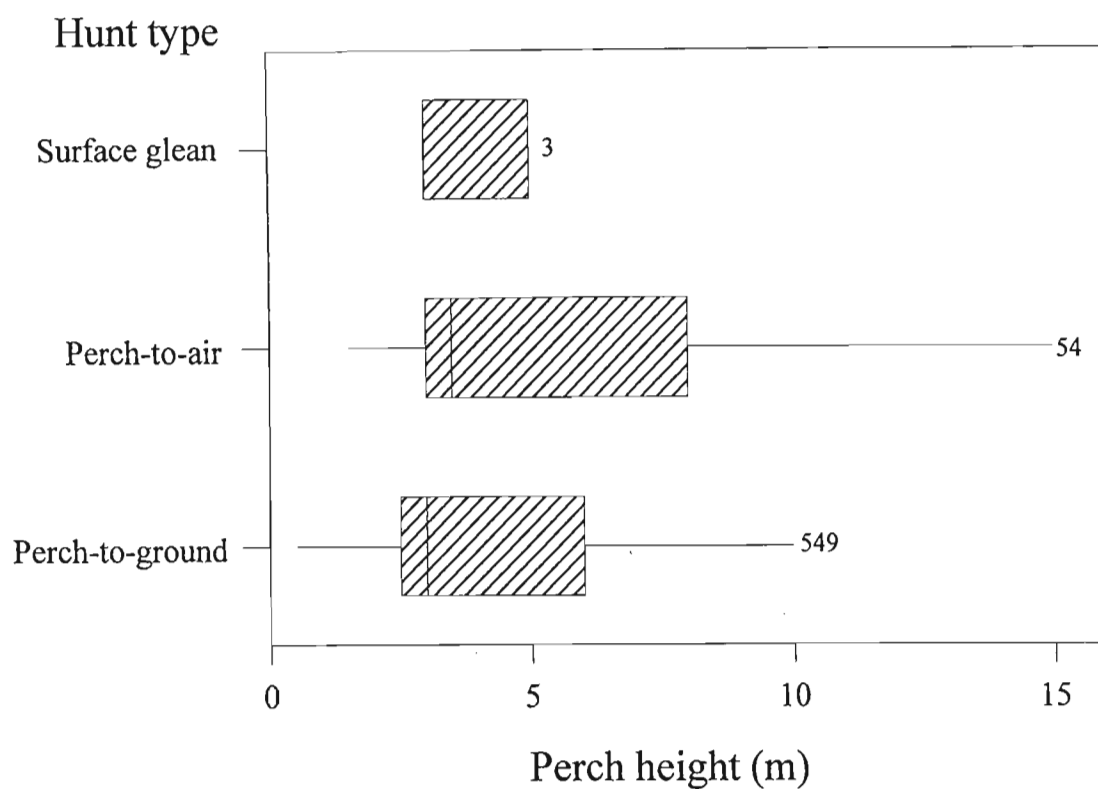


Figure 4.4. The effect of perch height on foraging mode. The foraging mode employed by fiscal shrikes was significantly related to the height above ground level at which they perched (Kruskal-Wallis test: $H_1=4.86$, $P<0.05$). Aerial forays occurred at greater heights than ground forays or surface gleaning. Numbers indicate sample sizes. For a description of box-and-whisker plots please refer to Fig. 4.2.

detected (the field of vision), but as the distance to prey increases, the probability prey detection declines (Andersson 1981). There should exist an optimum search height for a predator foraging in a given habitat where the benefits of field of vision size balance the costs of reduced prey discrimination. I expect the distribution of perch heights to be significantly different to the distribution of heights used by fiscal shrikes to search for prey, because the height selected will reflect the best search height rather than the top of the perch. Fewer searches should occur from very short perches as the field of vision decreases with perch height, or from very tall perches as prey detection decreases with increasing perch height (Andersson 1981; Carlson 1985a). When fiscal shrikes are presented with the option of 1.75 m or 3 m high perches I expect one to be favoured over the other, and this should be the one closest to their natural choice of perch height. The perch sites used by fiscal shrikes at Ukulinga Research Farm for foraging ranged from 0.5 m to 25 m in height, greater than fiscal shrikes in Ghana which only used perches up to ten metres in height (Macdonald 1980). Fiscal shrikes perched between 0.5 m and 18 m above ground level at Ukulinga, although most perchings were below ten metres (median, Q1-Q3=3 m, 2.5-6 m). The distribution of heights at which fiscal shrikes perched in trees was significantly different to the distribution of available perch sites (linear features and artificial perch sites were omitted from the analysis as fiscal shrikes always perched at the top of these structures) (Kolmogorov-Smirnov two sample test: $D=0.167$, $P<0.001$) (Fig. 4.5). Fiscal shrikes perched on the top of trees less than 3 m in height, but relatively lower in taller trees. Three metre high artificial perches were used significantly more often than 1.75 m artificial perches (173 of 176 observed searches) (G-test: $G_1=195.6$, $P<0.001$), as predicted by their favoured natural perch height in trees.

Perching orientation.

A relationship was observed between the direction a fiscal shrike faced whilst perching, and the presence or absence of direct sunlight (Fig. 4.6). On sunny days fiscal shrikes faced into the direction of the sun (north) significantly more often than on cloudy and partly cloudy days (G-test: $G_1=28.67$, $P<0.001$). This relationship was not an artefact of wind strength, which had no effect on perch direction (G-test: $G_1=0.34$, *NS*). If this behaviour has prey or predator detection roles there should be a difference between search duration or hunting success and orientation, but if it functions in thermoregulation there should be a relationship between temperature and orientation preference. There was no significant difference in either search duration (Kruskal-Wallis test: $H_1=0.16$, *NS*) or hunting success (G-test: $G_3=3.38$, *NS*) with search orientation. However, there was a significant relationship between temperature and orientation preference.

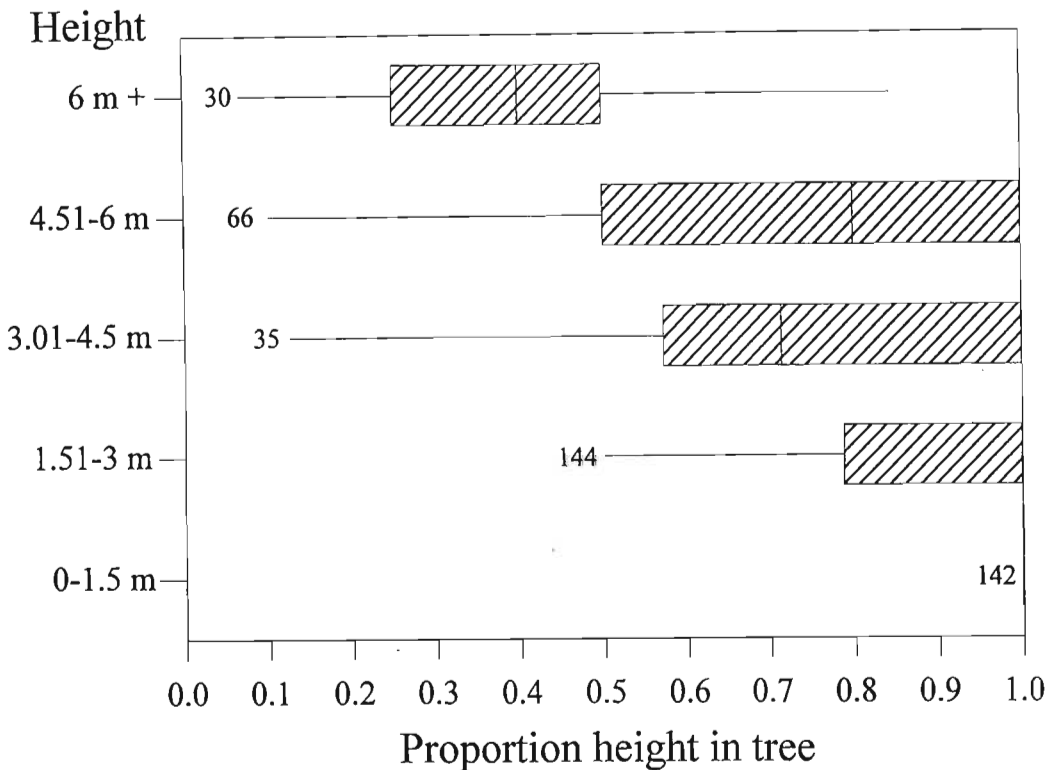


Figure 4.5. The distribution of perch heights and the height above ground at which fiscal shrikes perch whilst searching for prey. Trees and shrubs offers significantly taller perch sites than linear features and artificial perches (Kruskal-Wallis test: $H_1=240.11$, $P<0.001$), and fiscal shrikes perched significantly higher above ground level on trees and shrubs than on linear features and artificial perches (Kruskal-Wallis test: $H_1=33.03$, $P<0.001$). The term linear feature includes fence lines and overhead cables. Numbers indicate sample sizes. For an explanation of box-and-whisker plots please refer to Fig. 4.2.

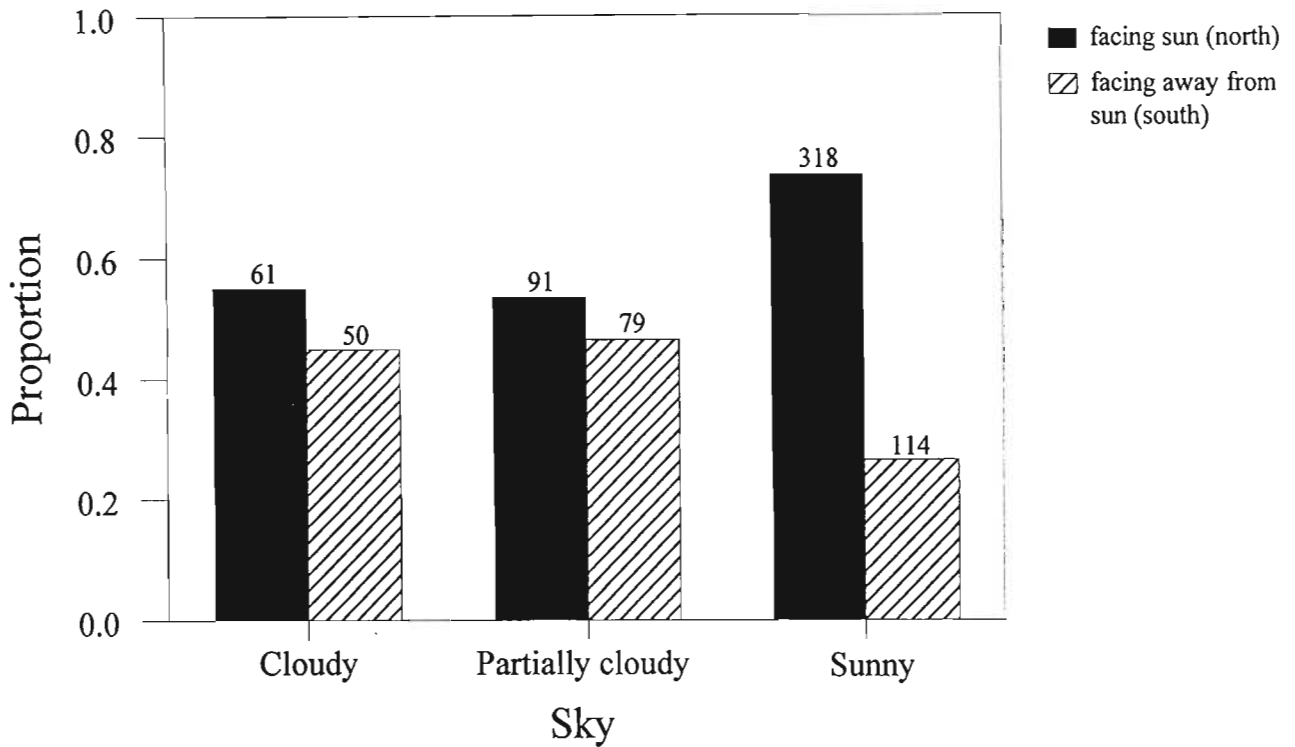


Figure 4.6. Orientation of shrikes relative to the sun. Fiscal shrikes faced into the direction of the sun (or where sun would be if obscured by cloud) significantly more often during sunny periods than during cloudy or partially cloudy periods (G-test: $G_1=28.67$, $P<0.001$). Numbers above bars indicate sample sizes.

Shrikes orientated towards the sun at temperatures between 16-30.5°C, but outside this range they orientated away from the sun (G-test: $G_4 = 42.28$, $P < 0.001$).

Prey captured.

Fiscal shrikes captured on average 3.1-6.2 prey items an hour at Ukulinga during the breeding season, which was at the lower range of delivery rates reported for loggerhead shrikes (4.8/hr (Craig 1978); 6.3-8.4/hr (Morrison 1980); 5.4/hr (Scott & Morrison 1995). All of the prey caught by fiscal shrikes during observation sessions were invertebrates, like the diet of brown shrikes (Severinghaus & Liang 1995), although fiscal shrikes were observed killing and transporting three mice at other times at Ukulinga. Two of the mice were *Mus musculus*, whilst the third was *Mastomys spp.*, and all were killed by repeated pecking to the head and neck region. Two of the mice were cached on barbed wire (*M. musculus*) and one was cached on *Acacia sieberiana* thorns (*Mastomys spp.*). Ninety four per cent of the invertebrates killed by fiscal shrikes were insects and arachnids, and the remaining six per cent were annelids (Fig. 4.7a). Prey ranged in size from half to five beak lengths long (approximately 9-91 mm), with over 85% were between one and three beak lengths long (approximately 18-55 mm) (Fig. 4.7b). Sixty-one per cent of prey captured by fiscal shrikes during the breeding season in southern Africa were fed to either a partner or offspring, and 36% were consumed by the forager. This reflects the division of labour in breeding fiscal shrikes, where the female devotes 80% of her time to incubating (see Chapter 2) during which time the male supplements her diet.

Instances where prey were not consumed but were cached on barbed wire or a thorn were only observed eight times during the observation sessions (3% of prey captures). However, a further 47 prey items were discovered cached in four fiscal territories at Ukulinga. Most cached prey were found between 0.75-1.5 m above ground level, and one was discovered 2.25 m high, wedged inbetween two branches of a tree. Cached items were significantly longer than consumed prey (caches found and prey observed being cached) (G-test: $G_{10} = 39.66$, $P < 0.001$) (Fig. 4.7c), and more vertebrates and annelids were cached than eaten (G-test: $G_5 = 45.52$, $P < 0.001$) (Fig. 4.7d). Brown shrikes impaled less than one per cent of their prey at heights between 0.65-2.5 m above ground level, and impaled prey were larger than those that were consumed (Severinghaus & Liang 1995). Over a third of brown shrike caches were lizards, and over half of all impaled prey were consumed at a later date (Severinghaus & Liang 1995).

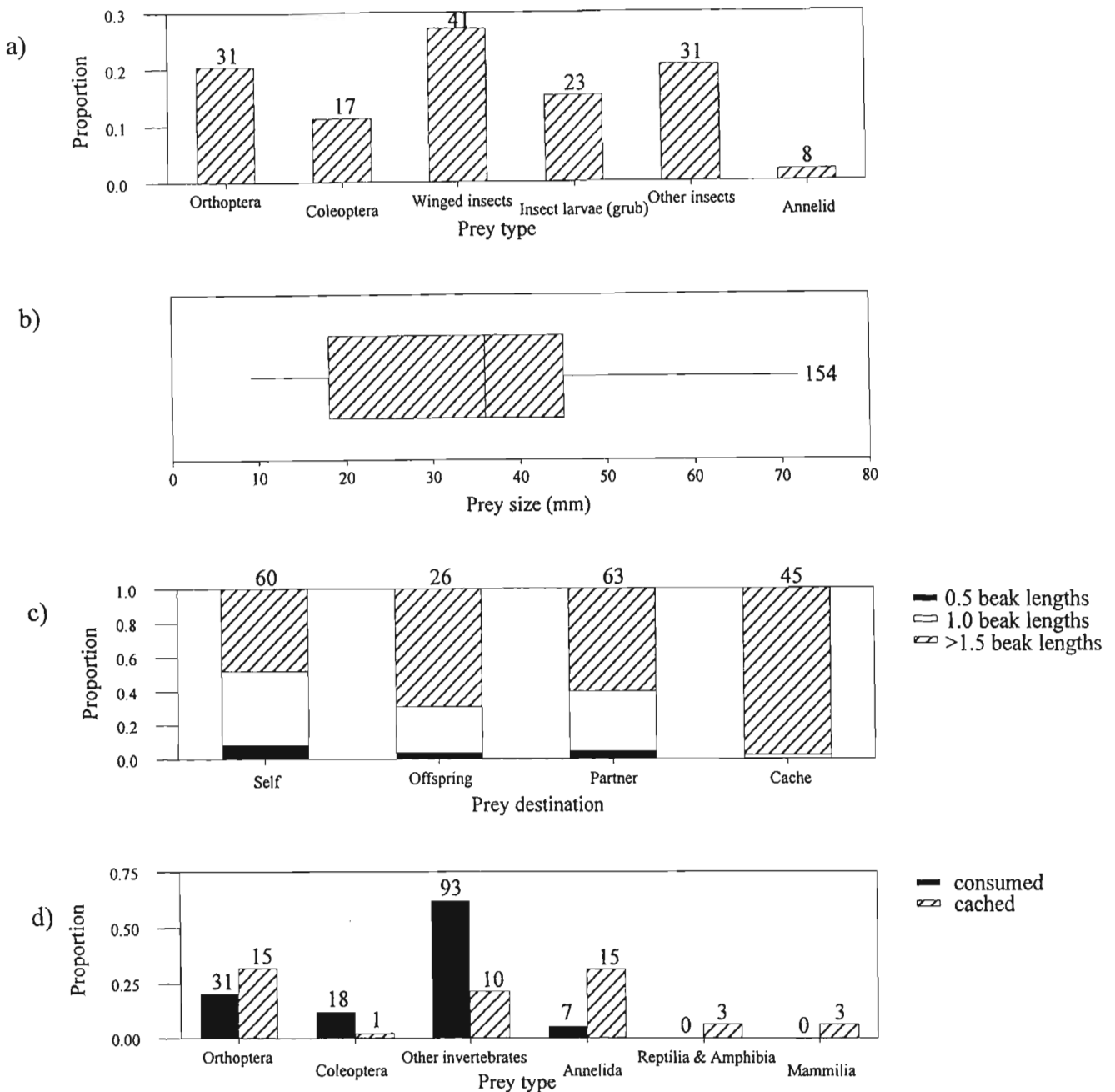


Figure 4.7. Prey captured by breeding fiscal shrikes. (a) Prey type (see text for details of prey categories). (b) Prey size. Prey size was estimated by comparing it to the fiscal shrike's beak (18 mm long). (c) End user - prey size. Cached prey were significantly larger than consumed prey (all caches considered) (Kolmogorov-Smirnov two sample test: $D=0.3925$, $P<0.001$). (d) End user - prey type. A larger proportion of Coleoptera and other insects were consumed and vertebrates, Orthoptera and Annelida were cached (G-test: $G_5=45.52$, $P<0.001$). For a description of box-and-whisker plots refer to Fig. 4.2. Numbers above bars indicate sample sizes.

Search duration and subsequent movements.

The average duration spent searching for prey from a perch was approximately one minute (median, Q1-Q3=60 s, 28-120 s). Fiscal shrikes remained on a perch for significantly longer when the search terminated in a give-up than a hunting attempt (Kruskal-Wallis test: $H_1=29.23$, $P<0.001$). This suggests that fiscal shrikes were prepared to remain searching from each perch for a set length of time, but searches were often terminated before this occurred when prey were observed and attacked. Search times for American kestrels were significantly longer if the search ended in a give-up compared to a hunting attempt (Rudolph 1982), but there was no difference between the duration of successful and unsuccessful searches in wheatears and stonechats (Moreno 1984).

Search duration significantly increased with perch height for foraging fiscal shrikes (Spearman's correlation: $r_s=0.066$, $N=809$, $P<0.05$), which suggests that the larger field of vision from taller perches required longer to search. Search duration was positively correlated with the distance flown to the perch (Spearman's correlation: $r_s=0.092$, $N=711$, $P<0.05$), and the distance flown on leaving the perch (Spearman's rank correlation: $r_s=0.075$, $N=746$, $P<0.05$). This could be interpreted as greater search efforts being employed at greater distances from the previous search patch to avoid scanning depleted or previously searched areas. Also, as flight effort increases search effort should increase. Shrikes are familiar with the availability of perches in their territories and only fly far if they know there is a patch worth investigating. To offset the costs of flying to and from the perch they should remain searching the patch for longer. Insectivorous wheatears and stonechats and rodentivorous hawk owls spent longer searching for prey from tall perches than from short perches (Moreno 1984; Sonerud 1992). In addition, move distance was positively correlated with perch height in all three species (Moreno 1984; Sonerud 1992).

The distance moved between perches by fiscal shrikes should depend on the outcome of the search. Following an unsuccessful search or successful hunt fiscal shrikes should move further from the initial patch to avoid scanning an area where prey density was low or reduced. However, if prey was detected but a capture was unsuccessful, fiscal shrikes should remain in the patch to recapture the prey item. The distance moved by a fiscal shrike from a perch was dependant on the outcome of the previous search (Kruskal-Wallis test: $H_3=14.73$, $P<0.05$) (Fig. 4.8a). Fiscal shrikes flew shorter distances following unsuccessful hunting attempts, than after successful hunts, give-ups, or non-hunt activities.

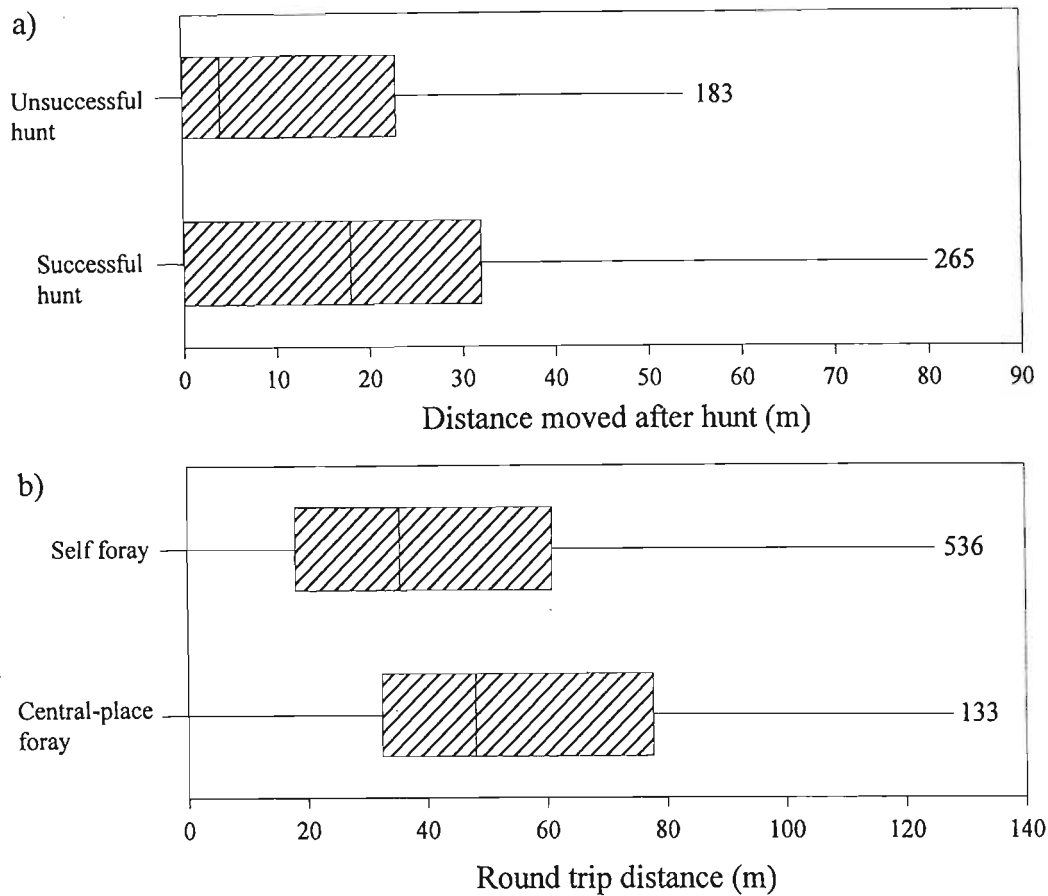


Figure 4.8. Foraging flight distances of fiscal shrikes. (a) Search outcome. The distance moved by fiscal shrikes following successful hunts was significantly greater than following unsuccessful hunts (Kruskal-Wallis test: $H_1=19.65$, $P<0.001$). (b) Foray type. Round trip distance was significantly greater for central place forays than self forays (Kruskal-Wallis test: $H_1=7.83$, $P<0.01$). For a description of box-and-whisker plots please refer to Fig. 4.2. Numbers indicate sample sizes.

Optimal Foraging Theory & Central Place Foraging.

In its simplest form, central-place foraging theory predicts that prey size and size selectivity should increase with distances from the nest, and the forager should spend more time searching patches further from the central place than patches closer to the nest. There was no significant size-distance relationship overall for fiscal shrikes foraging from a central place (Spearman's correlation: $r_s=0.033$, $N=78$, *NS*). However, a positive correlation was observed between prey size and distance for patches over 35 m from the nest (Spearman's correlation: $r_s=0.465$, $N=22$, $P<0.05$). Prey size was not subject to less variation from patches within 35 m of the nest compared to more distant patches (Coefficient of Variation: <35 m, $C=51\%$; >35 m, $C=53\%$). This suggests that as distance increased, small prey were dropped from the diet but only from patches over a threshold distance from the central place.

The mean duration of time spent searching a patch did not depend on its distance from the central place when all patches were considered (Spearman's correlation: $r_s=-0.021$, $N=148$, *NS*), nor when patches further than 35 m from the central place were considered ($r_s=0.216$, $N=44$, *NS*). This may be because other factors, such as perch height, influence search duration (Andersson 1981; Rice 1983; Sonerud 1992). However, search effort did decline with distance from the central place, i.e. the total duration of time spent at distances over 40 m from the central place was less than between 20-40 m, which in turn was less than the duration of time spent searching for prey within 20 m of the nest. This was due to fewer forays occurring at greater distances from the central place. The size of prey consumed by adult fiscal shrikes was significantly smaller than the size of prey fed to their nestlings (G-test: $G_6=40.88$, $P<0.001$). In addition, central place forays covered a significantly greater distance than self forays (Kruskal-Wallis test: $H_2=18.68$, $P<0.001$) (Fig. 4.8b).

DISCUSSION.

Optimal Foraging Theory and Central Place Foraging.

When applied to foraging theory, optimal foraging models attempt to explain and predict the behaviour of foraging animals using mathematical and economic principles (MacArthur & Pianka 1966; Emlen 1966; Charnov 1976). Initially optimal foraging theory was intended to develop more mechanistic ways of thinking about population and community dynamics by integrating evolutionary biology and community ecology (Schmitz 1997). However, because it generated more questions than answers, optimal foraging theory quickly became restricted to focusing purely on foraging decisions (Schmitz 1997). Optimal foraging theory developed into two fields, one used to understand the general rules deciding prey choice and the other used to understand patch exploitation (Charnov 1976; Stephens & Krebs 1986). Organisms were assumed to either minimise the time spent foraging (time minimisers) or maximise the rate of energy intake (energy maximisers) (Schoener 1971). Since then the theory has extended to movement patterns of animals foraging for occupants of a central place (e.g. a nest, den or cache), thereby linking reproduction and foraging disciplines (Orians & Pearson 1979).

Optimal foraging theory generated a considerable amount of interest initially as it conferred testable hypotheses and predictions in what can be a subjective field of science (Perry and Pianka 1997). However, observations from many initial empirical studies of optimal foraging did not agree with theoretical predictions, or only did so partially (Stephens & Krebs 1986; Perry & Pianka 1997). A negative result in an optimality model test indicates that the constraints and/or currency assumptions are not adequate to explain observed behaviour (Krebs & Kacelnik 1991), and one of the main criticisms of optimal foraging theory is that models were too simple and contained untestable assumptions (Perry & Pianka 1997). The relative contribution of optimal foraging to studying foraging has declined in recent years, and although this is in part to criticisms about untestable assumptions it is also a reflection of the growing awareness of the complex demands placed on an organism (Perry & Pianka 1997). By initially concentrating exclusively on foraging questions, optimal foraging research neglected to consider other factors such as reproduction, predator avoidance and nutrient requirements.

The vogue in foraging theory is changing from questions regarding feeding alone to ones that incorporate other activities, and so return to the original intentions of optimality modelling

(MacArthur & Pianka 1966; Emlen 1966; Perry & Pianka 1997; Schmitz 1997). Instead of considering untestable models whose goals lead to maximal fitness, Perry & Pianka (1997) suggest defining the goal of optimal foraging theory in terms of finding the optimal foraging strategy (i.e. the one that maximises foraging success). Below I describe the factors affecting foraging methods and foraging success, discuss how fiscal shrike foraging behaviour fits into previous optimal foraging models, and offer insight into how foraging and another factor, behavioural thermoregulation, integrate in shaping searching behaviour.

Foraging mode.

The foraging modes of many animals, including birds, have long been viewed as bimodal (Perry & Pianka 1997). Predators have either been thought of as widely foraging active predators, or as sedentary sit-and-wait foragers (Jaskic' & Carothers 1985). As a result of adaptation to foraging modes sedentary and active foragers should differ in their biology, including their morphology, physiology, metabolic rate and sensory mode in addition to prey type and capture rate (Huey & Pianka 1981; Perry & Pianka 1997). One way of defining foraging mode is to measure the number of patches a predator visits before attacking prey (Fitzpatrick 1978). For sedentary foragers this should be low, and prey should be attacked in at least 70% of the patches visited (Fitzpatrick 1978). Active predators should move quickly between patches and only forage in 40% or less of the patches visited. Although many animals fit neatly into these brackets, some, such as buteonines, falcons and accipters, are mixed mode hunters and use both active searching and sit-and-wait techniques (Jaskic' & Carothers 1985). Fiscal shrikes at Ukulinga attacked prey in 72% of the patches they visited, classifying them as sedentary sit-and-wait foragers. The loggerhead shrike of North America, which has a similar mass to the fiscal shrike, has an attack rate of 30% (Morrison 1980), classifying it as an active searcher. Therefore the true shrikes use both foraging modes and do not appear to be constrained to either by their phylogeny.

Foraging methods.

Fiscal shrikes display a variety of foraging methods and, like other members of their genus, show a remarkable convergence with raptors in their hunting behaviour (Harris & Arnott 1988). During this study fiscal shrikes employed perch-to-air foraging, perch-to-ground foraging and surface gleaning methods of prey capture. Fiscal shrikes have also been recorded plunge-diving into water to capture *Xenopus laevis* tadpoles in the Western Cape, South Africa (Ryan 1992). Foraging sallies were carried out from a perch close to one metre deep water, and

after a head-first dive the fiscal rested on its belly in the water before returning to its perch. Fiscals raid nests to eat nestlings (Moreau & Moreau 1941) and adults can be kleptoparasites of similar-sized and larger birds (Moreau & Moreau 1941; Elliot 1998). The wide array of foraging methods used by fiscal shrikes is evidence for the behavioural plasticity of the species. Other members of the genus *Lanius* hover in front of plants, gleaning prey for foliage (Severunghaus & Liang 1995), scavenge for carrion (Brent 1950), and acoustically lure prey (Atkinson 1997).

The method of hunting employed by fiscal shrikes should depend on the associated costs and benefits of each method according to prevailing conditions (Fig. 4.1). Flight, which is an energetically expensive strategy (Rudolph 1982; Norberg 1996), increases in cost with wind speed as the cost of maintaining a position increases. Active cruising predators incur greater costs for foraging than sedentary sit-and-wait predators (Jaskic' & Carothers 1985). Ground and aerial foraging methods of fiscal shrikes employ flight and, therefore, these methods should be the most affected by wind condition. Sit-and-wait foraging is less strenuous than aerial foraging (Collopy & Koplín 1983), and hovering is the most energetic flight mode used by birds (Collopy & Koplín 1983; Norberg 1996). Blackshouldered kites *Elanus caeruleus* avoided hovering in very strong winds (Mendelsohn & Jaksic 1989). In accordance with predictions (Fig. 4.1) fiscal shrikes adjusted their foraging method to prevailing climatic conditions. Flight was employed less frequently in foraging as wind strength increased. Surface gleaning was the least affected by wind speed as it did not depend on flight and occurred in the shelter of a tree canopy in adverse weather. However, as it was only employed when other methods were not viable it should have fewer benefits than other methods, possibly because of fewer prey encounters. Flapping flight required six to eight times more energy than sitting in American kestrels *Falco sparverius*, but energy intake was significantly greater for hovering birds than perching birds, because more prey were encountered and captured when hovering (Rudolph 1982).

Optimal foraging theory: the influence of patch size on foraging.

The duration of time a sit-and-wait forager should scan for prey from a perch and the subsequent distance it should move to its next observation site may depend on the size of the area it can scan, which in turn may depend on the height at which it is perched (Sonerud 1992) and vision interference (Fig. 4.1). The optimum perch height for a predator depends largely on the sensory modes it primarily uses to detect prey. For a visual predator the field of vision

around the base of a perch increases quadratically as perch height increases (Rice 1983). However, as the distance between predator and prey increases, visual acuity will decrease and the increased delay in reaching prey once detected will eventually counterbalance the advantage of the increased field of view. For a predator relying on visual cues to find prey this will result in an intermediate optimum perch height (Andersson 1981; Rice 1983). The relationship reverses for a predator relying on acoustic cues to detect and catch prey. As perch height increases the sonic field of detection declines quadratically, so acoustical predators should favour increasingly lower elevations at which to forage (Rice 1983). As search duration increased with perch height fiscal shrikes rely primarily on visual cues to detect and capture prey.

Caching

Traditionally, the function of impaling prey by birds such as shrikes has been considered as either an aid for prey manipulation or as a store or larder (Bevan & England 1969) that is provisioned when prey density is high and utilised when prey density falls (Hernández 1995; Oksanen et al. 1985). Caching has also been viewed as a division of labour between the sexes (Applegate 1977). The female alone incubates eggs in most species of shrike (Cramp & Perrins 1993), reducing her time available for foraging. Males who provision their partner via a cache, leaving the female to butcher prey and deliver it to the young, reduce the energetic expenditure of their mate whilst increasing the time available to themselves for foraging. More recently mate choice and reproductive success have been forwarded as possible functions of caching behaviour (Yosef & Pinshow 1989). Male great grey shrikes with larger caches mated first and sired more offspring than those with small caches. Impaling prey may also be a method of degrading toxic prey to render them edible, as toxins break down after death (Yosef & Whitman 1992). Fiscal shrikes cache prey like other members of their genus, but they do not cache to the same extent as some of their northern hemisphere counterparts (Harris & Arnott 1986).

The temporal and spatial pattern of caching varies between different species of shrike. Red-backed shrikes *Lanius collurio* in Iberia cache prey during the breeding season, whereas in the same area northern shrikes *Lanius excubitor* cache during the winter (Hernández 1995). Not all cached prey are eaten (Hernández 1995). Although detailed records of cache utilisation were not kept during the present study, approximately half of fiscal shrike impaled prey items were dried and appeared to be at least one week old. Unused caches may demonstrate territory

occupation or have a role in sexual selection (Yosef & Pinshow 1989; Hernández 1995). At Ukulinga caches were observed during and outside the breeding season, but caches containing live or freshly killed prey were only found around the time of nest building, suggesting that these were used during reproduction. All items observed being cached and most freshly impaled items discovered were located close to the nest site at Ukulinga. By storing food close to the central place fiscal shrikes were foraging optimally, minimising the travel costs of the sedentary consumers when retrieving prey (Orians & Pearson 1979; Carlson 1985b).

Patch use and central place foraging.

Central Place foraging theory (CPF) deals with foraging animals that must return to a central place, such as a nest, den or cache, and is actually a special case of optimal foraging incorporating travel (Orians & Pearson 1979). The basic unit of CPF is the round trip, consisting of an outbound trip, the foraging period, and a return trip. Energy is expended in all three phases but only acquired during the foraging period. Given the cost of the round trip it is normally advantageous for a predator to return with as large a load as possible, which could be multiple small prey (multiple prey loaders) or a large single prey item (single prey loaders). Some single prey loaders may be constrained by morphology to carrying just one item, such as hawks and owls, which carry their prey in their feet (Orians & Pearson 1979). Fiscal shrikes, which are raptorial in their foraging methods, are single prey loaders, carrying small prey in their beaks and large prey in their feet (Harris & Arnott 1988).

The marginal value theorem (Charnov 1976) predicts that when handling time is neglected a predator should only take prey above a certain energetic value (size) from patches greater than some threshold distance from the central place (Orians & Pearson 1979). When handling time is incorporated into the model the foraging tactics for short travel times hinge on energy per unit handling time, whereas for long travelling times large prey are always superior, regardless of handling times. Small prey only should be selected from patches close to the nest and large prey only should be delivered from patches far from the nest. The Orians & Pearson single prey loader model could account for the observed pattern of prey size selectivity in fiscal shrikes when handling times were neglected. There is reason to believe that handling times for foraging fiscal shrikes may be unimportant, although prey availability and manipulation times were not assessed in this study. Firstly, during most foraging episodes prey size variation was just three-fold and the larger regular prey items were proportionally small compared to the mass of the forager. Secondly, when large items, such as vertebrates and annelids, were captured they were

cached. Caching aids prey manipulation and is a division of labour between the sexes (Bevan & England 1969; Applegate 1977). Caches were often located close to the nest and so allowed travel times for the sedentary consumers to be minimised (Orians & Pearson 1979; Carlson 1985b). Water pipits *Anthus s. spinoletta*, white-fronted bee-eaters *Merops bullockoides*, European bee-eaters *M. apiaster*, red-backed shrikes, sand martins *Riparia riparia* and house martins *Delichon urbica* all transport larger items of prey to the central place as distance from the central place increases (Frey-Roos et al. 1995; Hegner 1982; Krebs & Avery 1985; Carlson 1983; Bryant & Turner 1982). However, breeding barn swallows *Hirundo rustica* did not show a size-distance relationship (Bryant & Turner 1982). Because of the cost of round trips, search effort should be concentrated close the central place, and fiscal shrikes reduced their search effort as distance from the central place increased. Search effort decreased with increasing distance from the central place in loggerhead shrikes, whinchat *Saxicola ruberta*, and water pipits (Morrison 1980; Andersson 1981; Frey-Roos et al. 1995), and wheatears began their searches close to nest, working away until prey was captured (Carlson & Moreno 1985). By concentrating searches close to the nest males are able to minimise travel costs and perform other activities such as protecting their partners and offspring (Andersson 1981; Frey-Roos et al. 1995).

Differences in the diets of adult and dependent young have been documented for a variety of species of bird (e.g. Davies 1977; Rudolph 1982; Sonerud 1989; Baird 1991), which could be due to a variety of factors. Nutritional requirements may differ between birds of different ages (Davies 1977; Baird 1991), resulting in different prey type or size selectivity, or adults may feed their offspring larger prey items as nestlings have larger gapes than adults (Davies 1977). Alternatively, large prey could be selected for offspring to offset the costs of longer foray distances when returning to the central place (Davies 1977; Orians & Pearson 1979; Lessells & Stephens 1983; Krebs & Avery 1985; Sonerud 1989), i.e. consistent with optimal foraging theory (MacArthur & Pianka 1966; Charvov 1976; Stephens & Krebs 1986). Natural selection favours the parental foraging strategy that maximises fitness. Survival of the young, aided by parental provisioning, increases fitness because more young survive to fledge and reproduce (Baird 1991).

In summary, optimal foraging theory was able to predict the size discrepancy between adult and nestling diets, and Orians & Pearsons single prey loader model (1979) predicted the size-distance relationship in central place foraging fiscal shrikes. However, size selectivity did not vary between patches close to or far from the central place, and there was no patch residence-

distance relationship. Like many other investigations (see reviews by Stephens & Krebs 1986; Maurer 1996) this study has demonstrated a partial qualitative agreement with optimal foraging models. Without testing the assumptions of the models and considering other non-optimality models it should be concluded that optimal foraging models provide only approximations to the problems faced by foraging birds.

Integrating foraging and other behaviours: factors affecting the searching orientation of fiscal shrikes.

Fiscal shrikes at Ukulinga orientated into the sun when scanning the ground for prey. Although birds may face the sun for warmth (Cramp & Perrins 1993) or to dry feathers (e.g. cormorants, darters), I can find no other account of an orientation preference for any other bird when it is foraging. One possible explanation for this phenomena is that facing the sun conferred some advantage in prey capture. This could be because the white breast of a fiscal shrike was less conspicuous to prey on the ground and so increased hunting success, either through simple counter-shading or because more UV radiation is reflected from white surfaces, blending the bird into the UV-rich sky. There would be less benefit to facing into the direction of the sun of cloudy days as cloud scatters UV radiation. However, there was no increase in hunting success between fiscal shrikes facing into or out of the sun on sunny days. Fiscal shrikes could be facing into the sun whilst searching for prey because of increased prey detection (e.g. increased visibility), and this should show by reducing prey detection time when facing the sun. Again, however, there was no significant difference between search durations into the sun or out of the sun on sunny days.

Alternatively, fiscal shrikes may orientate towards the sun because of needs unrelated to foraging. Although fiscal shrikes are homeotherms, the countershading pattern of a fiscal shrike's plumage could function in thermoregulation. White surfaces reflect more radiation than dark surfaces as so should reduce heat transfer to surfaces below (Hamilton & Heppner 1967; Heppner 1970; Lustick et al. 1980; but see Walsberg 1983). Heat gain could be important in the hot climate of South Africa. Black-dyed zebra finches *Poephila castanotis* in sunlight at low temperatures had a reduced metabolic economy of 22.9% compared to white birds, indicating the importance of colour and sun in homeotherms (Hamilton & Heppner 1967; Heppner 1970). The grey backs of adult herring gulls *Larus argentatus* have a heat transfer of 50%, whereas the white breast have a heat transfer of just 15% (Lustick et al. 1980). Herring gulls orientate towards the sun during the breeding season when they are exposed during

incubation and brooding, and rotate their bodies throughout the day so that the sun always falls on their white breasts (Lustick et al. 1978). Fiscal shrike orientation preferences were significantly related to temperature, suggesting a possible thermoregulatory role for the behaviour. As the day progressed fiscal shrikes orientated significantly more often into the sun. Time of day and temperature were positively correlated, suggesting that as temperature increased fiscal shrikes adjusted their posture to minimise heat gain. This declined during the middle of the day, possibly because at this time the sun was directly overhead so the benefits of orientation in reducing thermal heat gain were minimised. Various other behaviour patterns in response to thermal stress have been observed. For example, fiscal shrikes raise their bodies, shading their eggs, and pant when incubating and brooding in high temperatures (This Study). Hummingbirds build their nests under overhanging vegetation to avoid radiation loss during the night (Calder 1973).

To conclude, this study has demonstrated the importance of ecological factors on the foraging behaviour of fiscal shrikes. The climate influenced foraging method (wind), search position (wind), and search orientation (sun and temperature). Perch structure influenced foraging method, search position, search duration and subsequent movements. Perch height and structure determined the area around the base of a perch in which fiscal shrikes could search for prey. Search area increased with perch height but reduced with visual interference from surrounding vegetation. Fiscal shrikes foraged optimally, taking larger prey items to their sedentary partner, offspring or cache, which acted as a division of labour between the sexes. This freed the male to forage and the female to incubate, which is important when so much of a female's time budget is devoted to incubation (see Chapter 2). Foraging, or any other behaviour, cannot be studied in isolation from other activities as has happened previously (e.g. Stephens & Krebs 1986; Perry & Pianka 1997; Schmitz 1997). I have demonstrated how many aspects of foraging are influenced by outside factors, e.g. the climate, perch structure. In addition, search orientation of fiscal shrikes is not a direct response to foraging, but to thermoregulation. In order to fully understand an organism's behaviour we must take an integrated approach, assessing all activities, rather than concentrating our efforts in obtaining answers to specific questions.

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CHAPTER 5: CONCLUDING REMARKS.

The initial aim of this project was to document the behavioural ecology of the fiscal shrike in South Africa, as it had not been subject to detailed study elsewhere. Two field investigations describe equatorial populations (MacDonald 1980; Zack 1986) and Cooper (1971), Marshall & Cooper (1969) & Hargrove et al. (1972) describe some aspects of the biology of tropical populations of fiscal shrikes. Information about temperate populations exists only in general textbooks (e.g. Harris & Arnott 1988; Ginn et al. 1989; Maclean 1993). This thesis describes three major areas of fiscal shrike behavioural ecology from detailed field investigations - reproductive ecology and life history strategies, territoriality, and foraging behaviour.

In addition to contributing to the ornithological database on shrike biology, I have been able to identify ecological and physical factors that affect the behavioural and life history strategies of birds. The vogue in behavioural ecology is changing from narrow to wider fields, incorporating many aspects of an organisms behaviour to provide a more balanced overall picture (e.g. Perry & Pianka 1997). Below I describe briefly one of the main findings from this study, suggesting how various aspects of behaviour integrate to provide a fuller picture of the behavioural ecology of the fiscal shrike. I end this chapter by reviewing the current global decline in true shrikes and suggest why it appears that the fiscal shrike is not undergoing range or population reductions.

Integrating foraging behaviour and territoriality: the importance of perch sites for fiscal shrikes.

The true shrikes are sit-and-wait foragers that use elevated perch sites as vantage points from which to search for prey (Harris & Arnott 1988). Perch structure has important implications for foraging fiscal shrikes. Hunts from vegetation structures (e.g. trees) were more likely to be aerial in nature and more successful, but searches from trees were more likely to terminate without a hunt compared to searches from other structures such as fence lines and overhead cables. Perch structure affects the field of vision for prey detection (Andersson 1981). Fiscal shrikes use visual cues to spot prey, and as perch height increases the field of vision around the base of the perch increases in area. However, as resolution declines with increasing height there will be an optimum perch height for a fiscal shrike foraging for certain prey in a given habitat (*sensu* Andersson 1981).

The field of vision around the base of a perch varies in both quality and quantity (area), depending on surrounding and underlying vegetation. The length of the grass or herbaceous layer has important implications for prey detection. As grass height increases, the probability of locating prey decreases, and foraging strategies may change (Yosef & Grubb 1993). Territories having very tall grass layers may be inferior in quality to those with shorter stratum. Interference from surrounding vegetation, or from the canopy of vegetation perches, will affect the area available to a shrike to scan for prey. At high perch densities much of the field of vision around the base of a perch is obscured and sit-and-wait foraging techniques may be unsuitable. Therefore, habitats with a high density of perch sites may be inferior to those with a lower density of perch sites.

Perch density was found to vary enormously in fiscal shrike territories in KwaZulu-Natal. Fiscal shrikes were not found in closed woodland habitats or in dense thickets, nor were they found where there was an absence of suitable perch sites, such as trees or fence lines. However, in habitats with an intermediate density of trees, territory size was found to correlate with perch (tree) density. Tall trees were the most important perch sites in controlling for territory size. When perch density was artificially increased territories shrank in area, and when density was reduced they expanded.

This relationship between perch density and territory size is a reflection of the importance of perches as a foraging resource. By manipulating resource abundance I was able to alter territory area. On a larger scale, increasing perch density by erecting artificial perches in suitable shrike habitats may increase the local density of shrikes as new territories are established in areas vacated by others, and as such could be used as a conservation technique.

Conservation status of true shrikes: current knowledge, the cause of declines, and possible future conservation measures.

There are 30 species of true shrikes, 26 of which are members of the genus *Lanius* (Table 5.1) (Sibley & Monroe 1990, 1993). Few have been studied in any great detail (see Cramp & Perrins 1993; Yosef 1994; Safriel 1995; Temple 1995a; Marcum & Yosef 1998) and those that have generally occupy first world areas where there is and has been a strong research interest in ornithology, namely Europe and North America

Table 5.1. The true shrikes: nomenclature, residency, geographical range, status, and population size and trends.

Species	English common name	Resident/migratory ^a	Range ^b	Status ^c	Population size and trends ^c	References
<i>Lanius tigrinus</i>	Tiger shrike	M	NE Asia (B); SE Asia (W)	?	?	
<i>L. bucephalus</i>	Bull-headed shrike	M	NE Asia, Japan (B); E & NE Asia (W)	?	Declining	Haas & Ogawa 1995
<i>L. collurio</i>	Red-backed shrike	M	Europe, W Asia (B); E & S Africa (W)	Unknown	Declining (B)	Cramp & Perrins 1993; Yosef 1994; Bassin 1995; Busse 1995; Holan 1995; Kurlavicius 1995; Malik 1995; Olsson 1995; Peakall 1995; Lebedeva 1998; Lemaire et al. 1998
<i>L. isabellinus</i>	Rufous-tailed shrike	M	W Asia (B); Middle East, E & C Africa (W)	Unknown	?	
<i>L. cristatus</i>	Brown shrike	M	N & C Asia; Indonesia, S Asia, Middle East, NE Africa	Unknown	<100000 in Africa, Declining (B)	Haas & Ogawa 1995
<i>L. collurioides</i>	Burmese shrike	R	SE Asia	?	?	
<i>L. gubernator</i>	Emin's shrike	R	C & W Africa	Unknown	<70000	Harris 1998
<i>L. souze</i>	Souza's shrike	R	C & S Africa	Unknown	<10000	Harris 1998
<i>L. vittatus</i>	Bay-baked shrike	R	S Asia	?	?	
<i>L. schach</i>	Long-tailed shrike	R	S & E Asia	?	?	Galushin & Polozov 1998
<i>L. tephronotus</i>	Grey-backed shrike	R	C Asia	?	?	
<i>L. validirostris</i>	Mountain shrike	R	Indonesia	?	?	
<i>L. minor</i>	Lesser grey shrike	M	Europe, W Asia (B); S Africa (W)	Unknown	Declining (B)	Stastny et al. 1998; Kristin 1998; Holan 1998
<i>L. ludovicianus</i>	Loggerhead shrike	R/M	C & N America (B); N America (W)	Unknown	Declining (B)	Peterjohn & Sauer 1995; Mundy & Woodruff 1998; Laporte & Robert 1995

<i>L. excubator</i>	Great grey/northern shrike	R/M	N America, Europe, Asia, N Africa (B & W)	Unknown	Declining (B)	Atkinson 1995; Bassin 1995; Kristin 1998; Stastny et al. 1998
<i>L. sphenocercus</i>	Chinese grey shrike	R/M	NE Asia (B); NE & E Asia (W)	?	?	
<i>L. excubitoroides</i>	Grey-backed fiscal	R	C Africa	Secure	>Million, stable	Zack 1986
<i>L. cabanisi</i>	Long-tailed fiscal	R	E Africa	Secure	<100000	
<i>L. dorsalis</i>	Teita fiscal	R	E Africa	Unknown	<100000	
<i>L. somalicus</i>	Somali fiscal	R	E Africa	Unknown	<100000	
<i>L. mackinnoni</i>	Mackinnon's shrike	R	E Africa	Unknown	<100000	Harris 1998
<i>L. collaris</i>	Common fiscal	R	SW, S, E & C Africa	Stable/ increasing	>Million, stable	Harris & Arnott 1988; Parker 1997
<i>L. newtoni</i>	Newton's fiscal	R	W Africa	Critical/ex tinct	<50, declining/ extinct	Harris 1998
<i>L. marwitzi</i>	Uhehe fiscal	R	C Africa	Unknown	<10000	
<i>L. senator</i>	Woodchat shrike	M	Europe, Middle East (B); E, C & W Africa (W)	Unknown	Declining (B)	Stastny et al. 1998; Kristin 1998; Holan 1998
<i>L. nubicus</i>	Masked shrike	M	E Europe (B); E & C Africa (W)	Vulnerable	<10000 in Africa, declining (B)	Harris 1998
<i>Corvinella corvinella</i>	Yellow-billed shrike	R	C, SW & SE Africa	Secure	>Million, stable	
<i>C. melanoleuca</i>	Magpie shrike	R	S & SE Africa	Secure	>Million, stable	Harris & Arnott 1988
<i>Eurocephalus rueppelli</i>	White-rumped shrike	R	S Africa	Unknown	>Million, stable	
<i>E. anguitemens</i>	White-crowned shrike	R	E Africa	Secure	>Million, stable	Harris & Arnott 1988

^a R/M: resident (R), migratory (M). (Temple 1995b, c)

^b Breeding grounds (B), wintering grounds (W). (Temple 1995c).

^c Declining (B) means declining in all or part of breeding range. (Harris 1998)

As a group shrikes are similar in many aspects of their biology (Temple 1995a). Most favour open woodland habitats, with the exceptions residing in closed woodlands and forest (Marcum & Yosef 1998). They are sit-and-wait opportunistic predators that take large invertebrates and small vertebrates, which may be consumed or impaled. The sexes are similar in mass and plumage and are primarily monogamous, the exceptions being two species that occasionally adopt a polygynous mating system and four species that are known to breed communally (Yosef & Pinshow 1989; Marcum & Yosef 1998). At their breeding grounds shrikes hold exclusive territories and are not social, although at other times they may form small aggregations. Shrike species differ in their migration tendencies, being resident, short and long distant migrants, and within a species one population may be resident whilst another may be migrant, depending on the conditions of the surrounding habitat (Marcum & Yosef 1998). Most resident species occupy tropical and sub-tropical latitudes, whilst migrant species occupy more northern climates.

There has been a global decline in the true shrikes during the latter half of the twentieth century (Yosef 1994) (Table 5.1). Most central European countries have lost 50% of their breeding populations in the past 15 years (Rothhaupt 1995) and at a continental level North American populations are declining at 3.5% per annum (Yosef 1994). However, although the global decline in the true shrikes is generally accepted, many species have not been studied in enough detail to draw accurate conclusions (Safriel 1995; Harris 1998). Most studies reporting a decline in shrike populations have been on a local or regional scale (Safriel 1995). Without knowledge of long-term trends over large parts of a species range and a species minimum viable population size, it is difficult to confidently classify shrikes as threatened or endangered.

Of the thirty species of true shrike, reports of only one, the fiscal shrike, indicate population increases but no declines (Table 5.1) (Harris 1998). Several other species, notably resident species of Africa and some eastern European populations, remain stable, and although as a whole most species are declining, some populations show local increases. Three major causes for the decline in shrike populations have been suggested. (a) Anthropomorphic land changes, especially decreased environmental heterogeneity. (b) Diminished prey diversity caused by these changes and by pesticide use. (c) Climatic variation (Yosef 1994). In addition, migrating shrikes may be falling prey to human hunters, as most shrikes are known to be poor flyers and suffer out of proportion in migratory bottlenecks (Haas & Ogawa 1995). On reviewing the proceedings of the First and Second International Shrike Symposia (*Proc. West. Found.*

Vert. Zool., 6, 1-343; International Birdwatching Centre in Eliat Technical Publication 7, 1-119). I discovered that out of 26 papers describing changes in shrike populations, two reported increases whilst the remaining 24 recounted declines in numbers. Both increases were put down to local climatic fluctuations, whilst suggested causes for the declines were as follows: 20 suggested habitat alteration, usually by man, two were attributed to pesticide misuse, four proposed climate changes and one credited road kills as a major cause of shrike mortality.

I suggest that the reason fiscal shrikes are showing a range expansion when so many of their congeners are declining is due to their tolerance of human activity and the availability of suitable habitat. Like other species of shrike, fiscals are sensitive to certain anthropomorphic habitat changes, especially vegetation clearance (Parker 1997). However, they flourish around man and utilise fence lines and overhead cables as foraging perches, expanding their range with the expansion of more intensive agricultural techniques (see Chapters 3 & 4).

The importance of perch sites in controlling territory size has been demonstrated for northern shrikes (Yosef 1993) and for loggerhead shrikes (Yosef & Grubb 1994). Territory size influences the nutritional condition of loggerhead shrikes. Smaller territories are easier to patrol, and time saved on territorial defence can be used for foraging, thereby increasing the nutritional condition of the territory holders (Yosef & Grubb 1992).

This study has shown that perch sites also determine territory size for fiscal shrikes. It also demonstrates why perches are so important. Perches are a limiting resource and by increasing their density territory size can decrease. Perches are used primarily as lookout posts for foraging, and the structure and height of a perch has important determinants for foraging methods and success. Not only did territory size decrease with perch addition, presumably increasing the nutritional condition of the owners, but also a new territory was established in the area vacated by one pair.

Habitat suitability for other species of shrike residing in open woodlands, especially those in decline, may be enhanced by manipulating perch density (Yosef 1993; Yosef & Grubb 1994). Within an already colonised area the local population can be increased if the territory size of those already residing decreases. New territories can be established on land made available when previous territories decrease in size, thereby increasing the local population.

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