

ASPECTS OF THE FORAGING AND BREEDING ECOLOGY OF THE  
SOUTHERN AFRICAN KESTREL, *Falco tinnunculus rupicolus*

by

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*To my parents, Danie and Helmine,  
for all the love and support they have given me*

*"Utebe-thebana ngumdlobisi wabantwana. Ithi xa ive ingoma ime inanazelise amaphiko, kutfho ebantwaneni kube mnandi bakuyibona."*

[The kestrel rejoices the hearts of the children. When it hears the singing, it stands fixed in the sky fluttering its wings. To the children it is very pleasant when they see the bird.]

Xhosa school pupil at St. Cuthberts

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## ABSTRACT

van Zyl, Anthony J. 1993. *Aspects of the foraging and breeding ecology of the Southern African Kestrel, Falco tinnunculus rupicolus*. M.Sc. Thesis, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700, South Africa.

A study of the ecology of the Southern African Kestrel was made in two areas of differing topography in the Eastern Cape Province (32°S) of South Africa. The main objectives of the study were to describe foraging parameters (behaviour-time budgets, hunting success and diet) and breeding parameters (clutch size, hatching and fledging success, nestling, fledging and post-fledging periods) of the Southern African Kestrel. These parameters were compared to those from studies made on the European Kestrel (*Falco tinnunculus tinnunculus*) in western Europe (53°N) in an environment which fluctuates relatively more than the South African study sites.

Predictions concerning foraging and breeding ecology made by life-history theory in stable and fluctuating environments prompted the erection of the following hypotheses which were examined in this study.

1. Common Kestrels (*Falco tinnunculus*) in relatively stable environments have a more consistent but lower foraging yield than those breeding in fluctuating environments.

2. Common Kestrels in relatively stable environments have lower reproductive rates (longer incubation, nestling and post-fledgling dependence periods, later age at first breeding and longer life-span) than those in fluctuating environments.

Southern African Kestrels spent different proportions of time of the two main hunting methods used, perch- and hover-hunting, than the European Kestrel. Perch-hunting was the predominant hunting method used by the Southern African Kestrel compared to hover-hunting in the European Kestrel. Southern African Kestrels had a higher prey-capture success for both hunting techniques. However, daily food intake was lower in Southern African Kestrels because a high proportion of the diet consisted of small invertebrates.

Average clutch size was smaller in the Southern African Kestrel than that of the European Kestrel and Southern African Kestrels fledged on average fewer young. However, incubation, nestling and post-fledging periods were within the range recorded for the European Kestrel.

The hypothesis that Common Kestrels in relatively stable environments have lower foraging yields is supported by this study. Although results from this study suggest that food yields are more consistent in stable environments, it was unable to

evaluate this adequately. The hypothesis that reproductive rates are lower in relatively stable environments is partly supported in this study, but more data are required for parameters such as incubation and nestling periods to confirm such trends.

## CHAPTER 1

AN INTRODUCTION TO STUDYING THE ECOLOGY OF THE SOUTHERN  
AFRICAN KESTREL IN THE EASTERN CAPE PROVINCE, SOUTH AFRICA

## GENERAL INTRODUCTION

Animals are capable of inhabiting most environments found on earth. This has prompted the fundamental ecological question "why do animals differ in distribution and abundance?" (Krebs 1972). Study of the life histories of animals and development of life-history theory can possibly best explain why animals differ in abundance in different environments.

For instance, general trends in life-history traits in birds have been shown over latitudinal and rainfall gradients in southern Africa (Siegfried and Brooke 1989). Such trends have been shown elsewhere to correlate with proximate factors, for example, food supply in raptors (Newton 1979). However, Western and Ssemakula (1982) have suggested that environmental factors influence life-history traits less than previously proposed, and that scaling to body size is able to explain a significant amount of the life-history variation.

The aim of this study was to document the life-history traits of a single bird species and to examine whether its life-history traits correlate with different environmental conditions.

The Common Kestrel (*Falco tinnunculus*) is particularly well suited to test certain predictions of life-history theory. It is found in a variety of environments, including tundras, grasslands, high mountains and urban areas over a wide range of latitudes (Village 1990). Predatory birds at the tops of food chains are sensitive to fluctuations in food supply and are useful species in which to investigate how this factor influences life-history parameters. An abundance of comparative data are available for the Common Kestrel from several studies made in the temperate regions of the northern hemisphere (Village 1990).

## DISSERTATION OUTLINE

In this dissertation, I document the life-history parameters, such as incubation, nestling (period that the chicks are in the nest) and post-fledging period (period from when the chick leaves the nest until it becomes independent of its parents), clutch and brood size and nesting success of the southern African Common Kestrel (referred to as the Southern African Kestrel in this dissertation, see discussion on nomenclature on pg. 4). I then examine the following hypotheses which might explain latitudinal trends in life-history traits in the Common Kestrel.

1. Common Kestrels in relatively stable environments have a more consistent but lower foraging yield throughout the year than those breeding in fluctuating environments.

2. Common Kestrels in relatively stable environments have lower reproductive rates (longer incubation, nestling and post-fledgling dependence periods, later age at first breeding and longer life-span) than those in fluctuating environments.

Traditionally, once body size has been corrected for, life-history traits have been correlated to latitudinal or rainfall gradients (Siegfried and Brooke 1989). However, these are not necessarily the true gradients with which life-history traits covary but rather effects of true correlations. Food supply is known to influence life-history traits (Martin 1987) and it is probable that food supply correlates to latitudinal and rainfall gradients in the same way as life-history traits correlate to these gradients. Throughout this dissertation, the terms stable and fluctuating will be used to describe different environments, referring ultimately to stable *versus* fluctuating food supply available to the Common Kestrel. Food supply fluctuations could be due a number of reasons, including variation in the climate or land carrying capacities. The terms stable and fluctuating are synonymous with terms used often in the literature such as tropical and temperate regions, low and high latitude, low and high altitude and high and low rainfall.

In this chapter, I offer a general introduction to life-history theory, the study animal and the study areas. Chapter 2 describes the diurnal behaviour-time budget of the Southern African Kestrel and compares the results to a model based on data from European Kestrels in the Netherlands. Chapter 3 documents the various hunting parameters and daily food intake rates of the Southern African Kestrel. These hunting parameters are compared to the results of studies done in Europe with the aim of examining the first hypothesis. Chapter 4 describes the Southern African Kestrel's diet and how it differs from that of the European Kestrel. Chapter 5 summarizes the breeding data, to examine the second hypothesis. Chapter 6 provides a synthesis of the results and a discussion on the validity of the hypotheses in explaining variation in life-history traits in different environments.

The results of this study are presented as a sequence of discrete papers. This approach allows the rapid communication of results, but inevitably results in some repetition, particularly in the methods used.

Unfortunately, the review of life-history evolution by Stearns (1992) was not available until after this dissertation had been written, and therefore has not been referenced.

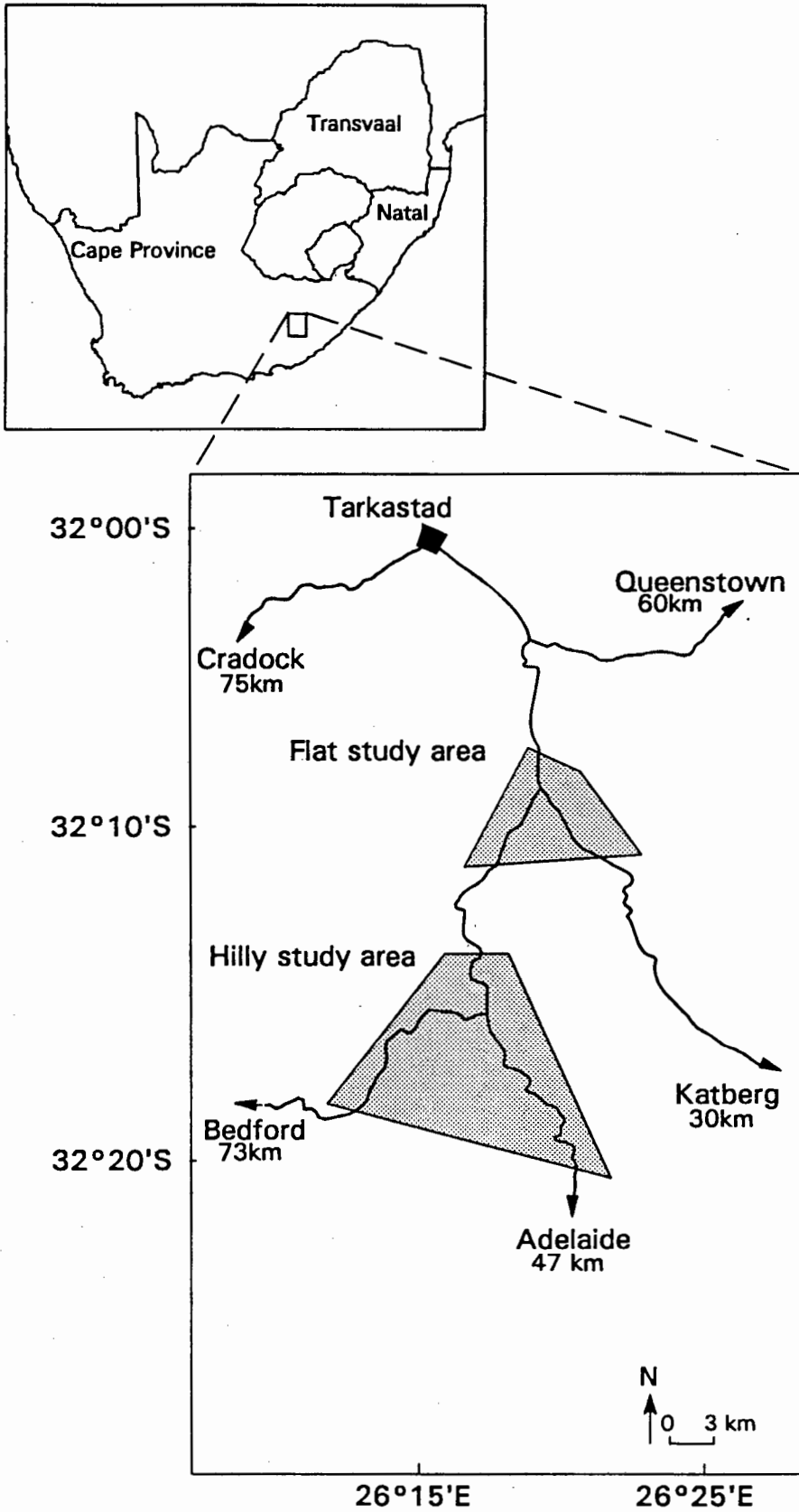


FIG. 1.1. Map of South Africa showing the location of the study areas in the eastern Cape Province.

#### A GENERAL DESCRIPTION OF THE COMMON KESTREL

The kestrels are a group of small falcons belonging to the genus *Falco* of the avian order Falconiformes. They are a truly cosmopolitan group with different species of kestrels found on all the continents except Antarctica and living in a variety of environments, excluding only extreme deserts, dense forests and areas of permanent snow cover.

The Common Kestrel (*Falco tinnunculus*) is believed to be the ancestor of the kestrel group (Boyce and White 1987). It is found over most of Europe, Africa, the middle East and eastern Asia and has been divided into eleven races. The precise status of each race as a species or subspecies is unclear as taxonomic work has been restricted to plumage comparisons (Village 1990). For this reason, the races compared in this dissertation have been given separate names, to aid the reader when comparisons are made and to provide possible names should subspecies be found to be separate species after a more thorough taxonomic investigation. Common Kestrel (*Falco tinnunculus*) will be used when referring to all the races, European Kestrel (*Falco tinnunculus tinnunculus*) will be used when referring to the race in Europe (as used by Village 1990), and Southern African Kestrel (*Falco tinnunculus rupicolus*) will be used when referring to the race found in southern Africa. This name is different from the locally used name, Rock Kestrel (MacLean 1987), which has little meaning as they are not only confined to rocky areas (they also breed in trees, see Chapter 5) and the name is rarely used outside southern Africa. The European Kestrel is the nominate species and the Southern African Kestrel is, apart from two races on the equator, the only race of the Common Kestrel in the southern hemisphere.

Adult Common Kestrels show varying degrees of sexual plumage dimorphism depending on the race. The male European Kestrel differs from the female by having a blue head, a brown body with black tear-shaped spots and a plain blue tail. The female has a brown head with fine dark streaks, a brown body with black barring and a brown tail with black bars. Females of the other races have varying degrees of male plumage features of which the female Southern African Kestrel is the most extreme. While male Southern African Kestrels are generally a little darker than the European Kestrel with barring on the blue tail, the females also have blue heads, a spotted back and chest and a blue tail with black bars. Females can easily be misidentified as males by inexperienced field workers. Immature Common Kestrels all have the typical brown barred plumage of European Kestrel females and are difficult to sex in all the races unless in the hand (Village *et al.* 1980).

There is a vast literature on the biology of the Common Kestrel and this has been reviewed by Village (1990). The Common Kestrel is an annual seasonal breeder

but in this study, over half of the population did not breed during a severe drought year. This provided the unique opportunity to study non-breeding and breeding Southern African Kestrels during the summer when under normal circumstances, they all would breed.

In his monograph, Village (1990) emphasizes that "despite their wide distribution, nearly everything we know about kestrels comes from studies done either in Europe or in North America." This study is an attempt to fill in some of the gaps in our knowledge of the Common Kestrel from one other part of the world.

## STUDY AREAS

### Location

The study area is located in the Tarkastad magisterial district of the eastern Cape Province, South Africa, between 32°06' and 32°23' S and 26°13' and 26°24' E (Fig. 1.1). Two study areas of differing topography were selected, an open flat study area 15 km south of Tarkastad, and a hilly study area 30 km south of Tarkastad.

### Topography

The main difference between the two study areas was the topography. The study area closest to Tarkastad was on a relatively flat region of land surrounded by hills. Small shale cliffs occurred on the northern edge and the rest of the flats were surrounded by steep slopes.

The other study area, in contrast, was characterized by mountains with an elevation ranging from 1400 m to more than 2000 m a.s.l. and was situated in the foothills of the Great Winterberg range. This study area embraced mountain ranges and shallow valleys, with shelves of sedimentary substrata on the lower slopes and igneous substrata along the very high ridges.

### Climate

The climate was cold in winter and hot in summer. It snows irregularly in winter (0.9 days.year<sup>-1</sup>,  $N = 111$ ), but snow does not cover the ground for more than a few days. Frost is often recorded during winter (25.5 days.year<sup>-1</sup>,  $N = 60$ ). Mean daily minimum and maximum temperatures were measured in Queenstown (53 km north-east of the flat study area, Fig. 1.2), and ranged from an average minimum of 9.2°C to an average maximum of 24.5°C. Rain falls mostly during the summer months (November to March, Fig. 1.3) and average annual rainfall measured at Tarkastad is 426.4 mm ( $N = 29$  years). Total rainfall measured during the drought year (1990) was 245 mm and 539 mm was measured the following year. Wind speed measured at Queenstown is given in Fig. 1.4.

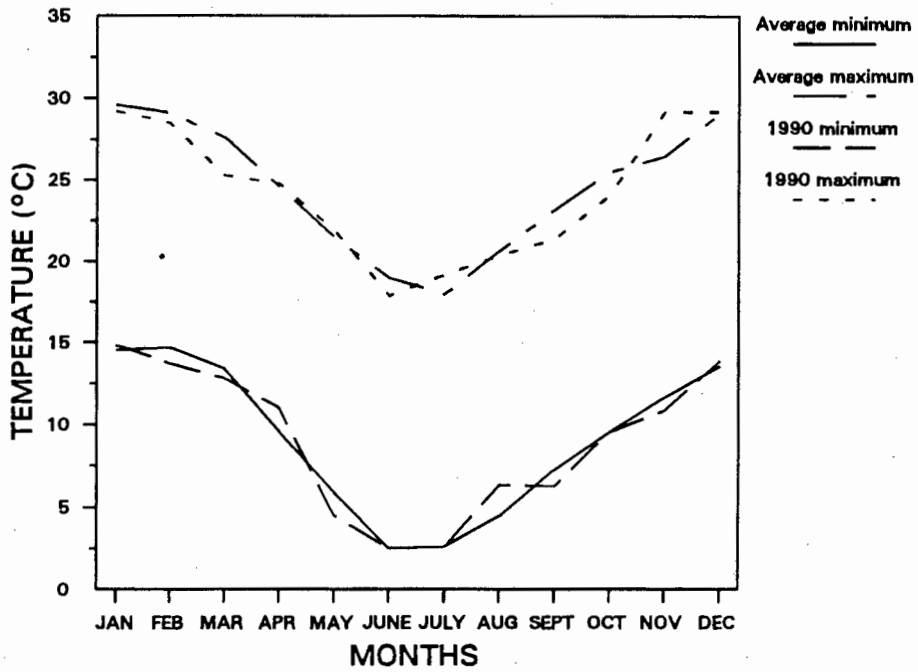


FIG. 1.2. Average daily minimum and maximum temperatures measured in Queenstown (53 km NE of the flat study area) between 1973 and 1950. Average daily minimum and maximum temperatures are also given for 1990.

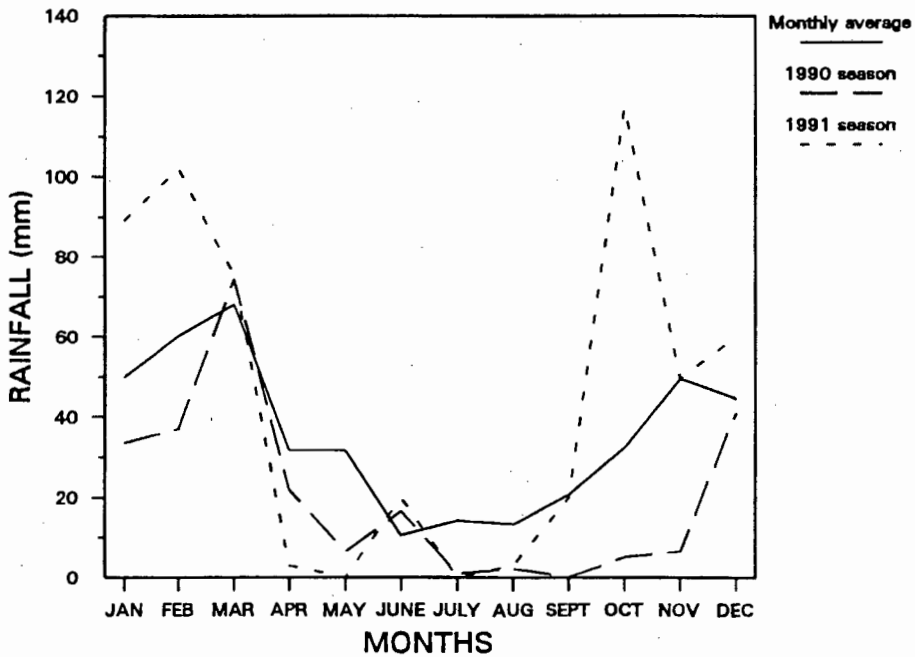


FIG. 1.3. Average monthly rainfall measured in Tarkastad (15 km N of the flat study area) during 1921 to 1950. Average monthly rainfall is also given for the drought year (1990) and the following relatively wet year.

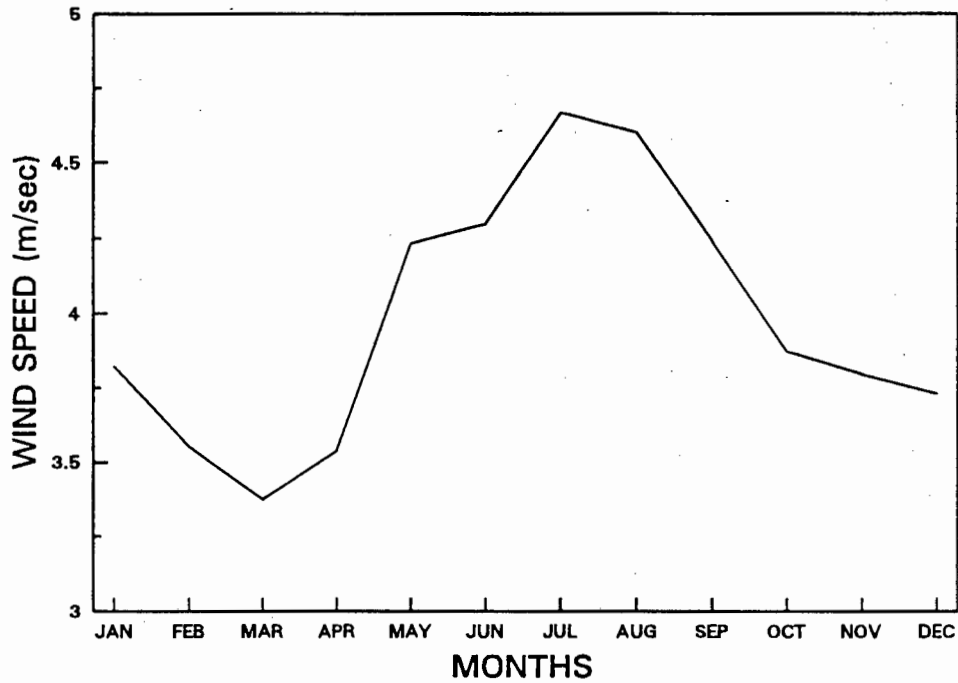


FIG. 1.4. Average daily wind speed measured in Queenstown (53 km NE of the study area) during 1959 to 1988. The average daily wind speed is based on readings taken at 8h00, 14h00 and 20h00.

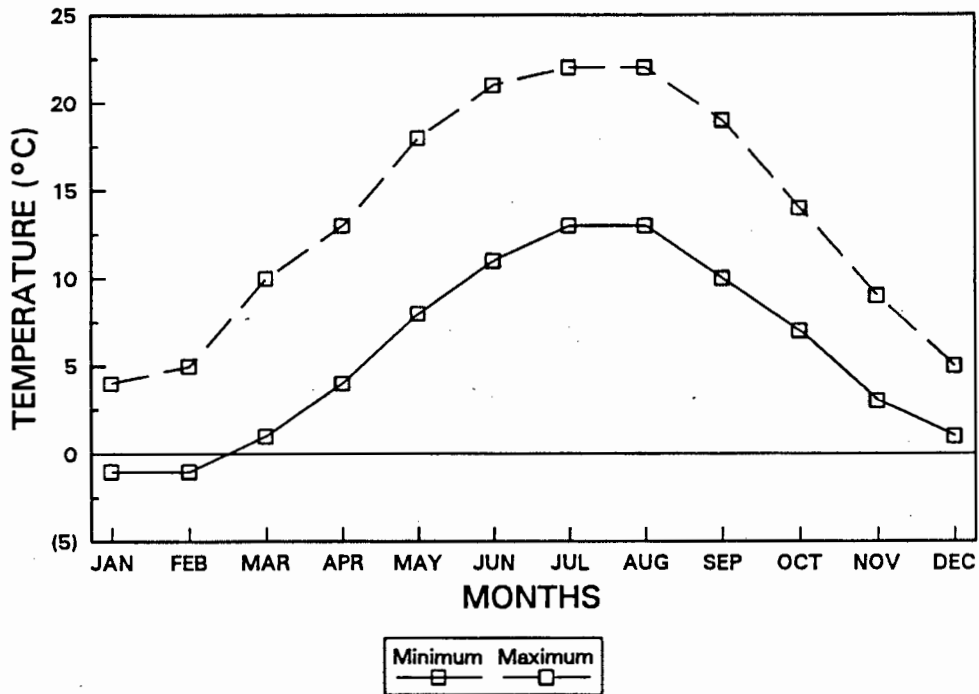


FIG. 1.5. Average daily temperature for De Bilt ( $52^{\circ}06'N$ ,  $5^{\circ}11'E$ ), Netherlands, as an example of the annual monthly temperatures in a northern high latitude region.

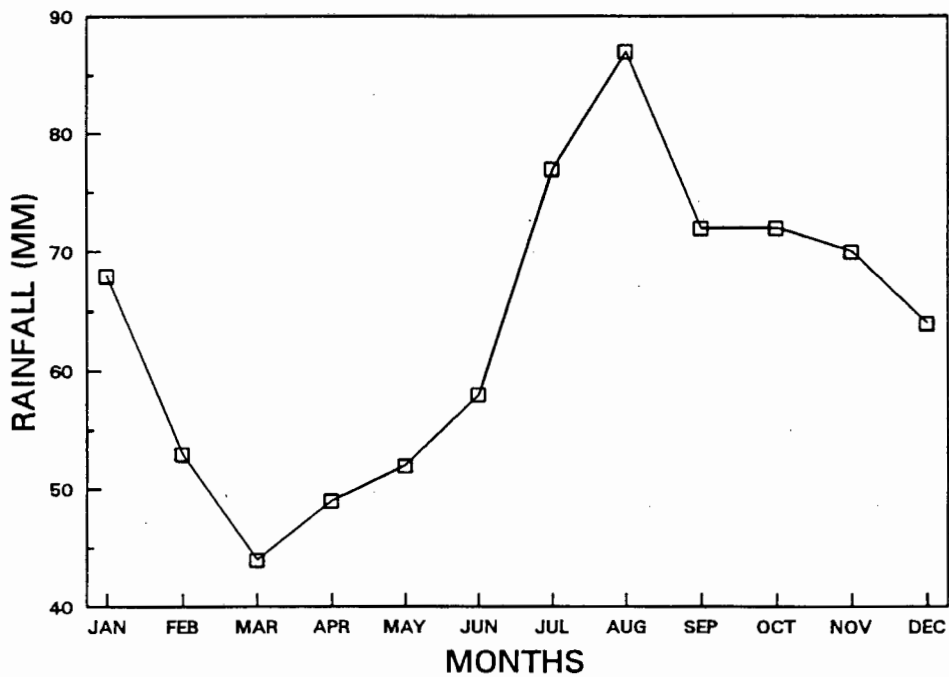


FIG. 1.6. Average monthly rainfall for De Bilt ( $52^{\circ}06'N$ ,  $5^{\circ}11'E$ ), Netherlands, as an example of monthly rainfall in a northern high latitude region.

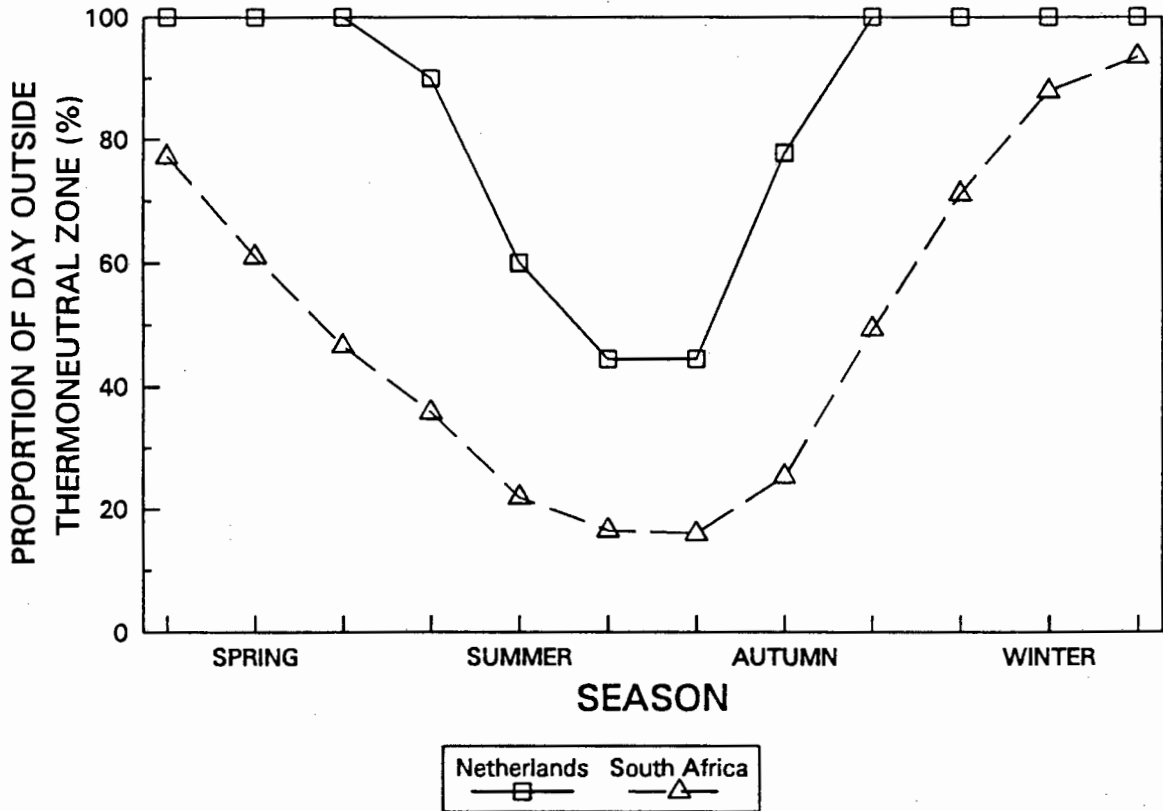


FIG. 1.7. The proportion of time of the day for which a Common Kestrel in the Netherlands and in South Africa has to actively increase its metabolic rate to maintain a constant body temperature during the year. Lower critical temperature was taken to be  $18^{\circ}\text{C}$  (calculated for the Grey Plover (*Pluvialis squatarola*), a similar-sized bird to the Common Kestrel).

### Vegetation

The vegetation of both study areas is classified as karroid *Merxmuellera* mountain veld (Acocks 1975) with *Merxmuellera disticha* the dominant grass. Small clumps of alien trees such as pines (*Pinus* spp.) and poplars (*Populus* spp.) had been planted in the flat study area for shade. Alien trees are also found around homesteads and along the rivers in the hilly study area.

### Land use

Sheep and cattle farming is the primary agricultural practice in the study area.

Fodder crops such as lucerne and oats are cultivated in the valleys along the annual river system. A few lands are irrigated, but most lie fallow during the dry winter.

### A comparison with the Netherlands study area

The account of study areas would not be complete without a very brief description of the Lauwersmeers study area (53°20'N, 6°16'E) in the Netherlands from which much of the comparative data comes. Data on minimum and maximum temperatures and rainfall in the Netherlands are given in Figs 1.5 and 1.6 (Pierce and Smith 1984). Average temperatures in the Netherlands are lower than in South Africa while the rainfall was higher in the Netherlands than in the study areas in South Africa. Although a study of the climatic differences and measuring variability of the environmental conditions in South Africa and the Netherlands would be a study of their own, the Netherlands is known to have a highly changeable climate from day to day (Pierce and Smith 1984). Furthermore, although temperature and rainfall extremes are probably greater in the Tarkastad study area, seasonal variation in temperature is more extreme in the Netherlands subjecting Common Kestrels to low survival conditions during winter. Rain also falls more frequently in the Netherlands which makes hunting conditions less favourable for Common Kestrels. Tarkastad can be considered a seasonally stable environment compared to De Bilt although temperatures and rainfall vary more from month to month.

The Netherlands study site was in the reclaimed polders of Lauwersmeer. European Kestrels nested in nest boxes provided for them and hunted mostly for voles in the surrounding flat area which was covered with short grass.

Different environmental conditions probably have a major effect on animals in their environments. For instance, ambient temperature possibly influences the basal metabolic rate of Common Kestrels in different areas, depending on how long they have to endure temperatures out of their thermoneutral zone. The amount of time a Common Kestrel would be out of its thermoneutral zone is considerably longer in

the Netherlands than in South Africa (Fig. 1.7). The thermoneutral zone was estimated using a lower critical temperature (18°C) available for a similarly-sized bird, the Grey Plover (*Pluvialis squatarola*) (Kersten and Piersma 1987). Although this figure is probably not exactly the same as for the Common Kestrel, it was preferred to the lower critical temperature measured for the smaller American Kestrel (*Falco sparverius*) of 23.0°C (Wasser 1986) because of the similar body size of Grey Plovers and Common Kestrels and the fact that they both breed in Europe. It provides a good indication of the difference in the environments that Common Kestrels in the Netherlands and in South Africa have to endure.

#### LITERATURE CITED

- Acocks, J.P.H. 1975. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 40:1-98.
- Boyce, D.A. and C.W. White. 1987. Evolutionary aspects of Kestrel systematics: a scenario. Pages 1-21 in D.M Bird and R. Bowman, editors. *The Ancestral Kestrel*. Raptor Research Foundation, Quebec.
- Kersten, M. and T. Piersma. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* 75:175-187.
- Krebs, C.J. 1972. *Ecology: the experimental analysis of distribution and abundance*. Harper and Row, Publishers, New York.
- Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecological Systems* 18:453-487.
- MacLean, G.L. *Robert's Birds of southern Africa*. John Voelcker Bird Book Fund, Cape Town.
- Newton, I. 1979. *Population ecology of raptors*. T & AD Poyser, Berkhamsted.
- Pierce, E.A. and C.G. Smith. 1984. *The world weather guide*. Hutchinson & Co., London.
- Siegfried, W.R. and R.K. Brooke. 1989. Alternative life-history styles of South African birds. Pages 385-420 in M.N. Bruton, editor. *alternative life-history styles of animals*. Kluwer Academic Press, Dordrecht.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, New York.
- Village, A., M. Marquiss and D.C. Cook. 1980. Moults, ageing and sexing of kestrels. *Ringings and migration* 3:53-59.
- . 1990. *The Kestrel*. T & AD Poyser, London.
- Wasser, J.S. 1986. The relationship of energetics of falconiform birds to body mass and climate. *Condor* 88:57-62.

Western, D. and Ssemakula, J. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia* 54:281-290.

## CHAPTER 2

A FIELD STUDY OF THE DIURNAL BEHAVIOUR-TIME BUDGET  
IN THE SOUTHERN AFRICAN KESTREL

## ABSTRACT

Diurnal behaviour-time budgets of 14 non-breeding Southern African Kestrels (*Falco tinnunculus rupicolus*) in both a hilly and flat study area were compiled for the period April 1990 to June 1991. Behaviour was classified into 11 categories during 478 hours of observations. Southern African Kestrels perch-hunted for the largest proportion of the day, with a maximum of 83.2% of their time spent perch-hunting during the austral summer and a minimum of 55.2% of their time spent perch-hunting during spring. There were no significant differences in the time budget between seasons or between sexes. Time allocated to different behaviour correlated best with topography and weather. Southern African Kestrels hover-hunted more frequently on slopes but less so in still conditions. Southern African Kestrels mostly preened during the early morning. Peaks in perch-hunting occurred in the morning and afternoon for the Southern African Kestrels on the flats. Southern African Kestrels in the hills perch-hunted during the morning and hover-hunted during the afternoon. Reproductive activity was seen during spring and summer. Interactions between conspecifics and other animals were noted throughout the year. The large proportion of perch-hunting was the major difference in time allocation in the Southern African Kestrel compared to the time budget of the western European Kestrel (*Falco tinnunculus tinnunculus*). It is proposed that the difference in allocation of time to different hunting methods is due to a lower food availability, but relatively consistent food supply, for the Southern African Kestrel than the western European Kestrel.

## INTRODUCTION

The allocation of time and, hence, energy, to different behaviour is central to the discipline of behavioural ecology. An organism must balance its energetic costs and benefits by allocating different proportions of time to different behaviour. For instance, energy flow in an organism can be partitioned conceptually between the requirements of self-maintenance and reproduction.

Considering the importance of time budgets to behavioural ecology, it is surprising how little attention has been given to a general theoretical and empirical framework for understanding how much time animals devote to various activities (Herbers 1981). Time allocated to foraging has, however, received special attention

within this time-budget framework. This has resulted in several models (Norberg 1977; Pyke *et al.* 1977; Herbers 1981; Masman, Daan and Dijkstra 1988).

These models predict different time budgets, depending on whether the animal optimizes the energetic costs and benefits of each behaviour or rather just satisfies its needs. Masman, Daan and Dijkstra (1988) suggest that more than one strategy may be employed. The European Kestrel (*Falco tinnunculus tinnunculus*), for example, minimizes energy expenditure during winter and maximizes daily energy gain during summer. Present models, however, remain limited to specific situations. To further complicate time-budget theory, time budgets are also influenced by other factors such as innate temporal programmes (for example, the circannual rhythms of migratory birds) or adjustment to an individual's circumstances (Drent and Daan 1980; Gwinner 1981).

A shortage of accurate time-budget data has prevented further development of time-budget theory (Masman, Daan and Dijkstra 1988 with references). Although time budgets and energetics are intricately linked, improvement in the ease and accuracy of energy expenditure measurements has meant that time-budget theory has been neglected. Calculation of overall energy-turnover rate remains inadequate, because it often neglects the contribution of the different energy-turnover rates for different behaviour. Thus, time-energy budget analysis has merits beyond the determination of daily energy expenditure as it takes the energetic contribution of each behaviour into consideration (Weathers *et al.* 1984; Masman, Daan and Beldhuis 1988).

Animals alter their behaviour according to the environment in which they live. Comparison of time budgets in single species will not only add to time-budget theory but also aid our understanding of differences, such as life-history parameters, between populations in different environments.

The aim of this chapter is to examine adaptations to the environment of Southern African and European Kestrels by investigating their time budgets. I contribute to time-budget data sets by providing a diurnal behaviour-time budget for the Southern African Kestrel (*Falco tinnunculus rupicolus*). I report on time budgets according to season, time of day, sex, habitat and weather conditions. I then compare these results with the time budget for the European Kestrel (*F. t. tinnunculus*) and propose possible explanations for the differences.

#### STUDY AREAS

Southern African Kestrels were studied in a hilly and flat area 15 km apart in the Tarkastad (32°00'S, 26°15'E) District, eastern Cape Province, South Africa. The hilly study area was characterised by hills and valleys with dolerite cliffs and the

flat study area had no cliffs except along the edges. Telephone and power lines criss-crossed both areas.

Average annual summer (October to March) rainfall measured in Tarkastad 15 km north of the flat study area was 426.4 mm ( $N = 29$  years). Mean average rainfall during 1990 was 245 mm. Low rainfall during this year was the possible reason for none of the observed Southern African Kestrels breeding. This situation provided the unique opportunity to study non-breeding Southern African Kestrels during the breeding season when they would normally all breed. Mean daily minimum and maximum temperatures were measured in Queenstown (53 km north-east of the flat study area) and ranged from an average minimum of 9.2°C to an average maximum of 24.5°C.

The habitat of both study areas is classified as karroid *Merxmuellera* mountain veld (Acocks 1975). Small clumps of alien trees such as pines (*Pinus* spp.) and poplars (*Populus* spp.) were found in the flat study area and around homesteads and along the rivers in the hilly study area.

#### METHODS

Fourteen non-breeding Southern African Kestrels (6 males and 8 females) were observed from April 1990 to June 1991, using focal-animal sampling (Altmann 1974). All focal birds were caught using a bal-chatri trap baited with mice (Berger and Mueller 1959), and were colour ringed and measured according to the protocol of Biggs *et al.* (1978).

Southern African Kestrels were observed using a car as a hide, 10X binoculars and a 30X telescope. Behaviour was recorded in a notebook except when the Southern African Kestrel was in flight when a tape recorder was used.

The total observation time for each Southern African Kestrel differed, because I was unable to follow an individual for a full day. The behaviour-time budgets of the 14 individuals covered at least 70% of the daytime and a total number of hours greater than 75% of daytime. Using these criteria, 362 hr of data were accumulated in the flat study area and 116 hr of data in the hilly study area. Average observation period length was  $57 \pm 70$  min ( $X \pm SD$ ,  $N = 501$ ). These data were used to compare the behaviour-time budgets under different weather conditions, between sexes and study areas. When the data were categorised by season, not all individuals met the requirements for inclusion for each season. Therefore, only 302 hr of data were accumulated for the flat study area and 82 hr of data for the hilly study area for seasonal behaviour-time budget comparisons. Average observation period for these data were  $58 \pm 72$  min ( $X \pm SD$ ,  $N = 398$ ). The duration of hovering, flying, soaring, perching, sitting and maintenance behaviour were calculated for each using customized computer program routines. Duration of a

behaviour for the individuals was calculated as percentages of the total time that an individual was observed. Overall time budgets were calculated by averaging these percentages. Daily time budgets in hours for each season were calculated by dividing the season's average day length by the proportion of each behaviour observed for that season.

Observations were spread over all hours of daylight. Once a focal bird had been located, it was observed until lost from sight. Temperature was recorded every 30 min using a thermometer placed in the shade 1 m above the ground. Wind speed was estimated according to the Beaufort Scale. Cloud cover was estimated on a scale of one to eight, and nine represented rain.

Eleven categories of behaviour were distinguished (Table 2.1) based on behaviours defined in time-budget studies of European Kestrels in the Netherlands (Masman, Daan and Dijkstra 1988). Durations of six behaviour were recorded and only frequencies were recorded for the remaining five behaviour, because their durations were normally very short (< 1 min). Frequencies for prey-strikes and caching are not included in this analysis (see Chapter 3). Durations of the following six behaviour were used for time-budget analysis.

**Hovering:** The kestrel hunted by hovering when it remained in a stationary position on the wing and scanned the ground below (*sensu Videler et al.* 1983). It normally flapped to maintain such a position, although above slopes it could 'hang' in updrafts without flapping. This category included the time spent flying between hovers.

**Soaring:** Soaring was recorded when the kestrel spread its tail, did not flap its wings and circled in updrafts.

**Flying:** Flying included all activity when on the wing except hovering and soaring.

**Perch-hunting:** Perch-hunting was recorded when the kestrel sat at a height of 1 m or more and had a clear view (> 180°) of the ground around the perch. Short flights between perches are included in this category. When kestrels spent time on the ground catching termites, it was also incorporated as perch-hunting. It was not possible to distinguish whether the kestrel was actively hunting from the perch. It was assumed that most perching was equivalent to perch-hunting. This might not be so for periods early in the morning and late in the evening when very few strikes were made or directly following a large meal although some strikes did occur at these times. Maintenance behaviour while perched was subtracted from the time spent perching and the remainder was considered perch-hunting. There may also be a seasonal difference with more time spent hunting when perched in winter than summer (Masman, Daan and Dijkstra 1988).

TABLE 2.1. Behavioural categories of Southern African Kestrels distinguished in the observation protocol.

Behavioural category	Type of information collected
1. Hover	Duration
2. Fly	Duration
3. Soar	Duration
4. Perch	Duration
5. Sit	Duration
6. Maintenance	Duration
7. Interaction	Frequency
8. Reproductive behaviour	Frequency
9. Food transfer	Frequency
10. Strike	Frequency
11. Cache	Frequency

**Sitting:** Sitting was recorded when a kestrel was on a perch less than 1 m from the ground or in a sheltered position (view  $< 180^\circ$  of the ground). Sitting was not considered a hunting behaviour, although strikes were occasionally recorded from sitting positions.

**Maintenance behaviour:** Two types of maintenance behaviour were distinguished, preening and dust bathing. Kestrels preened while perched or sitting, and dust-bathed while sitting.

Frequencies only were recorded for the remaining behaviour.

**Interactions:** This category included bowing (except before copulation), chasing and calling to mates, other kestrels and other birds and animals.

**Food transfers:** The male kestrel was observed giving the female food at the start of the breeding season. This was only seen twice, as the time-budget data were collected throughout the year only for non-breeding kestrels.

**Reproductive behaviour:** Several displays were interpreted as reproductive behaviour, although they may also have a territorial function. Kestrels were seen flying into the nest site with wings held in a vee above their backs, or flying over their territories in a zig-zag pattern (Village 1990). Bowing before copulation was also included in this category.

The year was divided into four seasons with months of equinox and solstice taken as the middle of the season. Although seasons were not defined according to

rainfall or temperature, summer (November to January) can be considered as hot and dry, winter (May to July) as cold and dry, spring (August to October) as cold and wet and autumn (February to April) as warm and wet. The average day length for each season was taken as the civil twilight day length (CTDL) of the 15th day of the equinox and solstice months.

$$\text{CTDL} = 25 \text{ min before sunrise to } 25 \text{ min after sunset}$$

Civil twilight period, which remains constant throughout the year in South Africa, is equal to 25 min for 32°S (Astronomical Data, HM Nautical Almanac Office). This has been found to be a good representation of the daylight hours available to European Kestrels (Masman, Daan and Dijkstra 1988).

Non-parametric statistical tests (Mann-Whitney *U* and Kruskal-Wallis) were used to test for differences in duration of behaviour (STSC 1984). Tukey tests were performed to identify which were the significantly different conditions in the case of multiple-sample tests (Zar 1984).

## RESULTS

### Daily time budgets

Southern African Kestrels followed a typical behaviour pattern over the diurnal hours (Figs 2.1 and 2.2). Early mornings were spent preening followed by an increase in perch-hunting and hovering. There was a slight drop in perch-hunting during mid-day accompanied by an increase in sitting. Southern African Kestrels on the flats showed a second peak in perch-hunting during the afternoon while Southern African Kestrels in the hills perch-hunted less and hover-hunted more. A large proportion of time in the late afternoon was spent sitting for the Southern African Kestrels in the hills. Roost perches in the hills were all in sheltered positions such as under vegetation on cliffs.

### Seasonal time allocation

There were no significant seasonal differences in the time allocated to flying, soaring, perch-hunting, sitting or maintenance behaviour (Fig. 2.3). Southern African Kestrels hovered significantly more during spring than autumn (Kruskal-Wallis,  $H = 11.425$ ,  $P < 0.01$ ). Little time was allocated to flying and soaring. There were insignificant decreases in perch-hunting from summer to spring, and during summer for the time spent sitting.

### Topography and time budgets

Although relatively more time was allocated to hovering in the hills, the difference was not statistically significant (Fig. 2.4). The small amounts of time

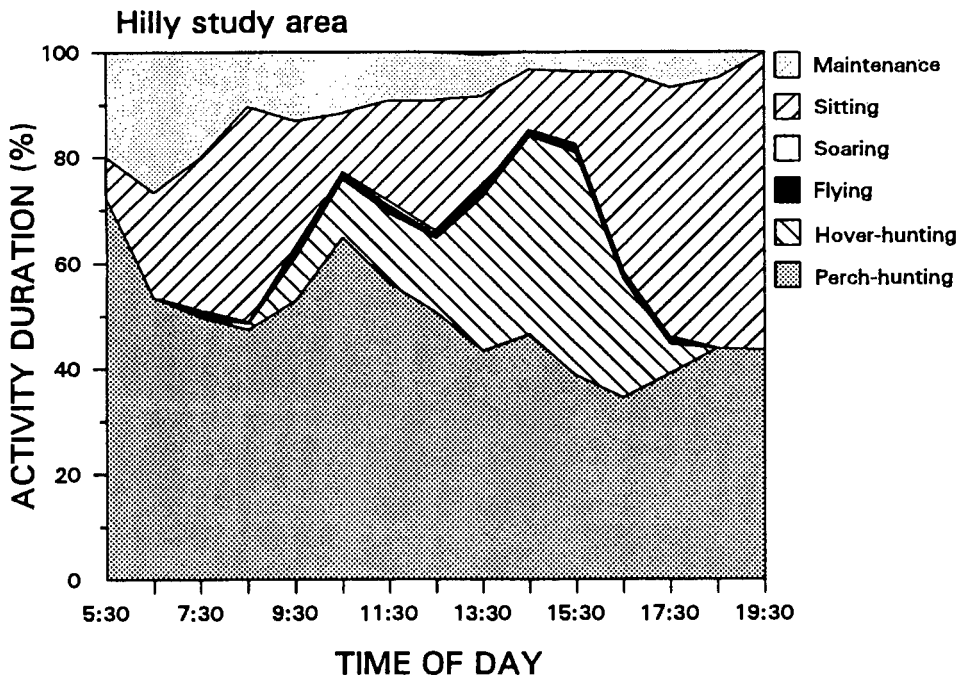


FIG. 2.1. Daily diurnal activity budget for the hilly study area based on 116 hours of observations. Activity durations are given as a percentage of the total activity duration for each hour.

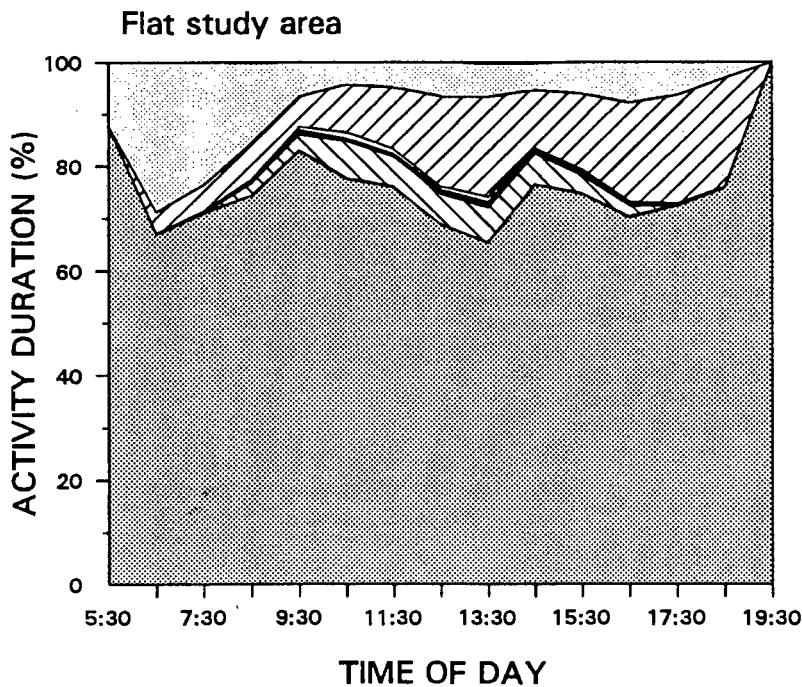


FIG. 2.2. Daily diurnal activity budget for the flat study area based on 363 hours of observations. Activity durations are given as a percentage of the total activity duration for each hour.

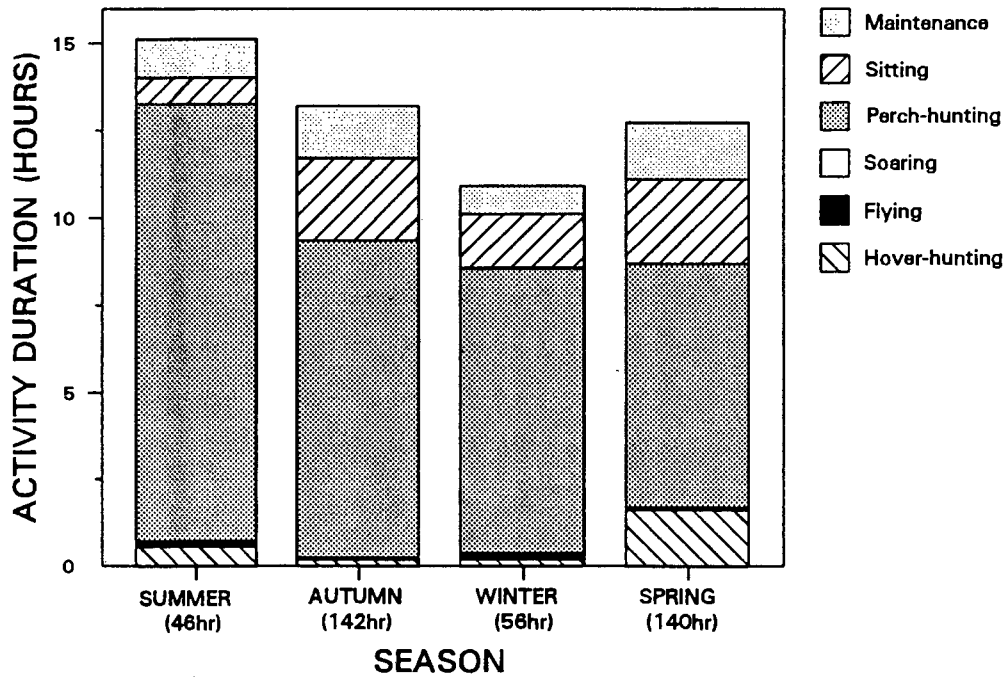


FIG. 2.3. Combined seasonal daily diurnal activity budget of Southern African Kestrels for the two study areas. Behaviours for which only frequencies were recorded are excluded. Number of hours observations for each season is given in brackets. Summer is defined as November to January, autumn as February to April, winter as May to July and spring from August to October.

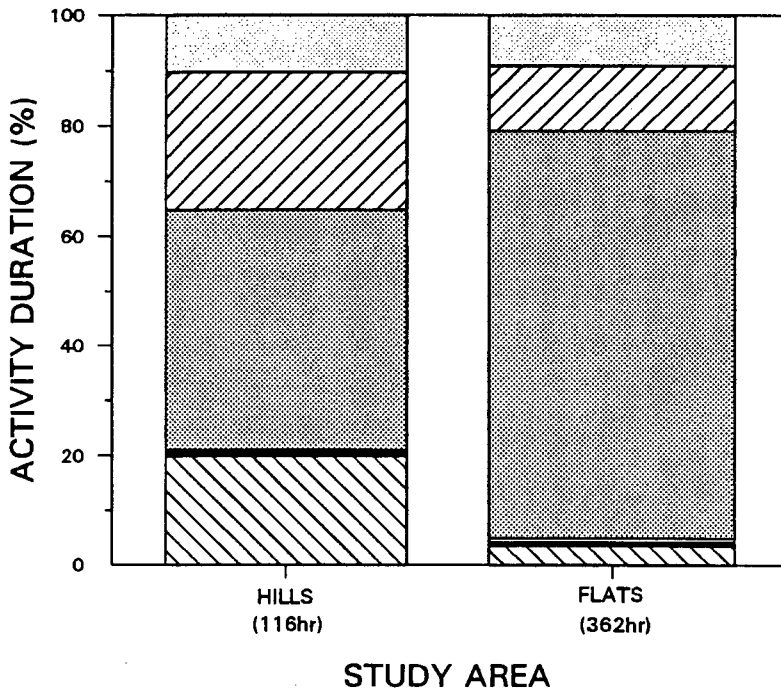


FIG. 2.4. Daily diurnal activity budget of Southern African Kestrels in the hilly and in the flat study areas. Activity duration is presented as a percentage of the total daytime period. The number of hours of observation for each area is given in brackets.

spent flying, soaring and on maintenance behaviour were similar in the two areas. Southern African Kestrels on the flats spent significantly more time perch-hunting than in the hills (Mann-Whitney  $U$ ,  $Z = -2.647$ ,  $P < 0.01$ ), and less time sitting.

#### Difference in time allocation between the sexes

There was no significant difference in time allocated to the six behaviour categories for males and females (Fig. 2.5). Females spent slightly more time flying and sitting than males and less time hovering, perching and on self-maintenance.

#### Weather and time budgets

The correlation between the weather categories and time of day was poor (Table 2.2). The best correlations were of temperature and wind with time of day, and this was slightly better for the flats than the hills.

There was a weak correlation between temperature and the behaviour of the Southern African Kestrels (Fig. 2.6). Most time was spent on maintenance activity during colder periods in the hills (Kruskal-Wallis,  $H = 6.974$ ,  $P = 0.03$ ). This, however, is difficult to separate from the major proportion of time allocated to preening during the early morning when temperatures were at their lowest (see Daily time budgets). Although Southern African Kestrels in the hills hovered more as temperature increased, this was not statistically significant. Southern African Kestrels in the hills perch-hunted significantly less than those on the flats for low (Mann-Whitney  $U$ -test,  $Z = 2.388$ ,  $P = 0.02$ ) and mild temperatures (Mann-Whitney  $U$ -test,  $Z = 2.775$ ,  $P = 0.005$ ). Southern African Kestrels in the hills sat in concealed positions for longer (Mann-Whitney  $U$ -test,  $Z = -2.51$ ,  $P = 0.01$ ) during mild temperatures.

There was a good correlation between wind and the time budgets of the Southern African Kestrels (Fig. 2.7). Southern African Kestrels on the flats hovered significantly less in low winds (Kruskal-Wallis,  $H = 9.275$ ,  $P = 0.01$ ). They also perch-hunted significantly less in strong winds (Kruskal-Wallis,  $H = 9.298$ ,  $P = 0.01$ ) which was accompanied by a significant increase in sitting (Kruskal-Wallis,  $H = 7.588$ ,  $P = 0.02$ ). Maintenance activity occurred during light winds in the hills and flats (Kruskal-Wallis,  $H = 7.436$ ,  $P = 0.006$  and  $H = 9.693$ ,  $P = 0.008$ , respectively). This could be due to the time of day, as most maintenance activity was recorded early in the morning (see Daily time budgets) when wind speeds were low.

Correlations between cloud cover and rain, and the Southern African Kestrel's behaviour were poor (Fig. 2.8). There was an insignificant trend for Southern African Kestrels in the hills to hunt less (perch-hunting and hovering) and sit more with an increase in cloud cover. Southern African Kestrels in the hills perch-hunted

TABLE 2.2. Correlation co-efficients and significance value in brackets between weather conditions and time of day for the two study areas. In the hilly study area, 443 weather records were collected and 440 in the flat study area and analysed using Statgraphics (STSC 1984).

Study area		Temperature	Wind	Cloud
Hilly study area	Wind	0.13 (0.008)		
	Cloud	-0.06 (0.201)	0.09 (0.379)	
	Time of day	0.42 (0.001)	0.33 (0.001)	0.02 (0.626)
Flat study area	Wind	0.43 (0.001)		
	Cloud	-0.15 (0.002)	0.16 (0.001)	
	Time of day	0.50 (0.001)	0.55 (0.001)	0.10 (0.626)

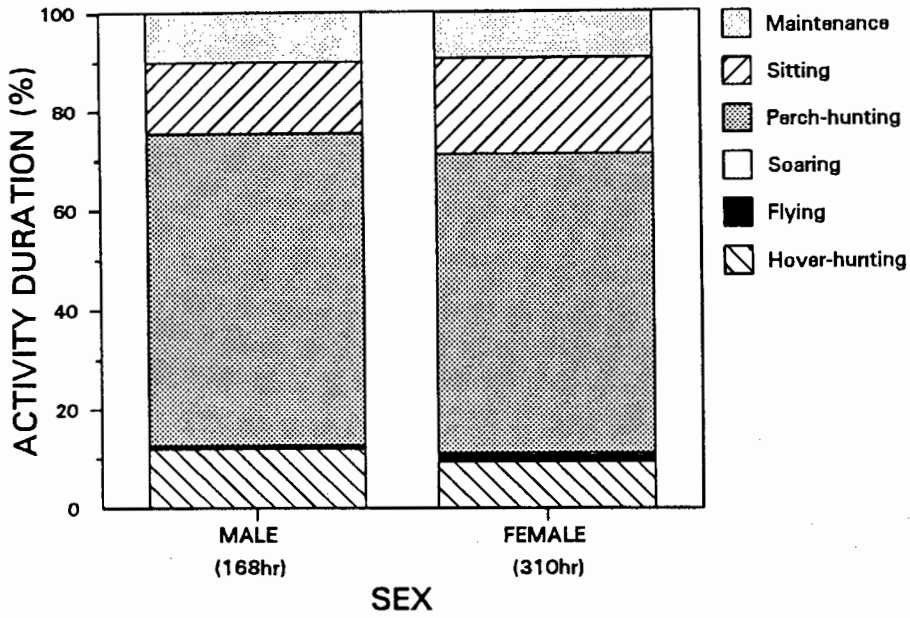


FIG. 2.5. Daily diurnal activity budgets of male and female Southern African Kestrels. Activity duration is given as a percentage of the total activity during the diurnal period. The number of hours observation for each sex is given in brackets.

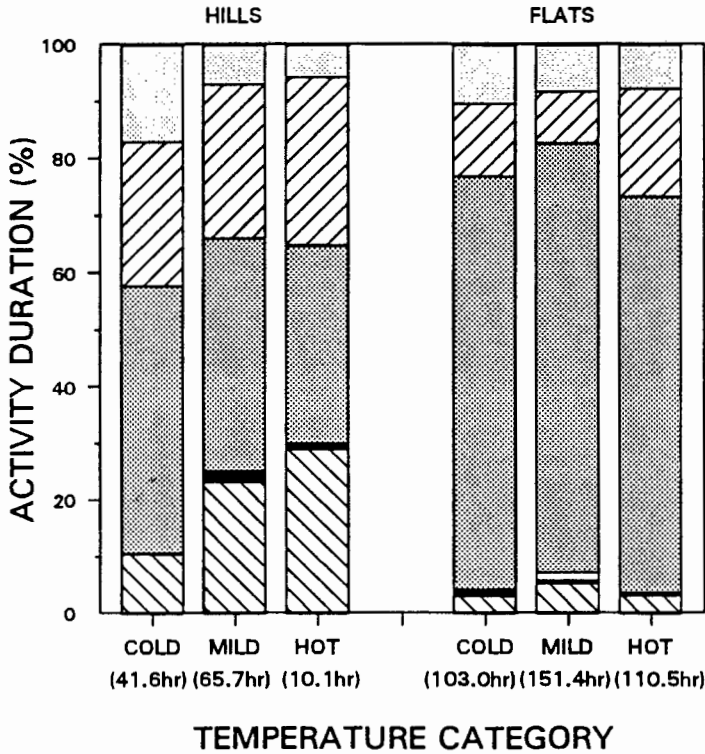


FIG. 2.6. Daily diurnal activity budgets of Southern African Kestrels during cold (-9° - 15°C), mild (15° - 24°C) and hot (25°C+) temperatures for the hilly and flat study areas.

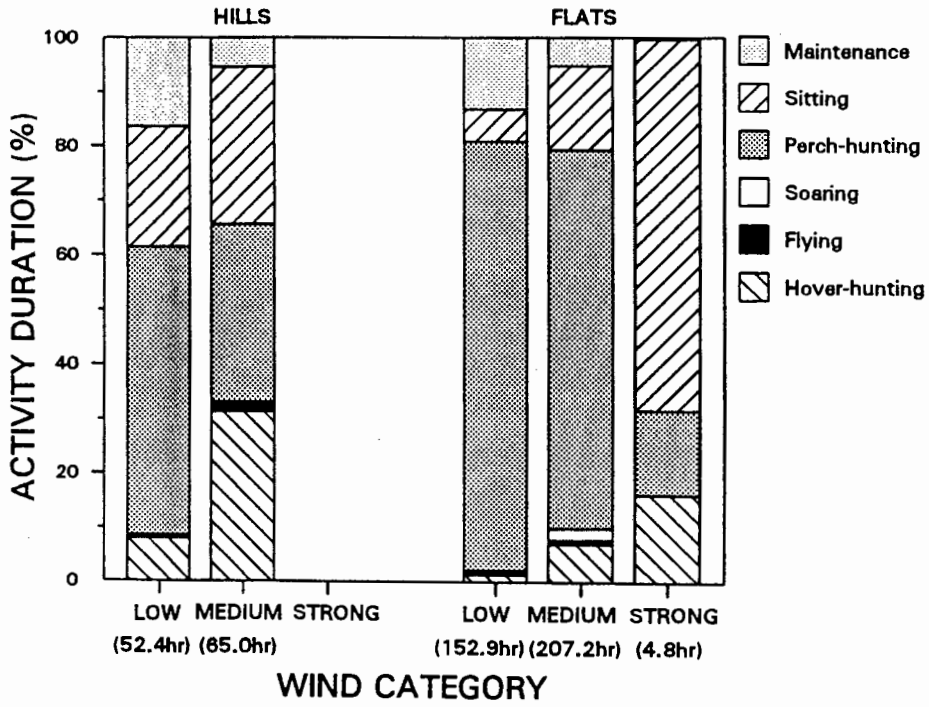


FIG. 2.7. Daily diurnal activity budgets of Southern African Kestrels during low (0 - 1.7 m.s<sup>-1</sup>), medium (1.8 - 5.2 m.s<sup>-1</sup>) and strong (5.3 m.s<sup>-1</sup>+) winds for the hilly and flat study areas.

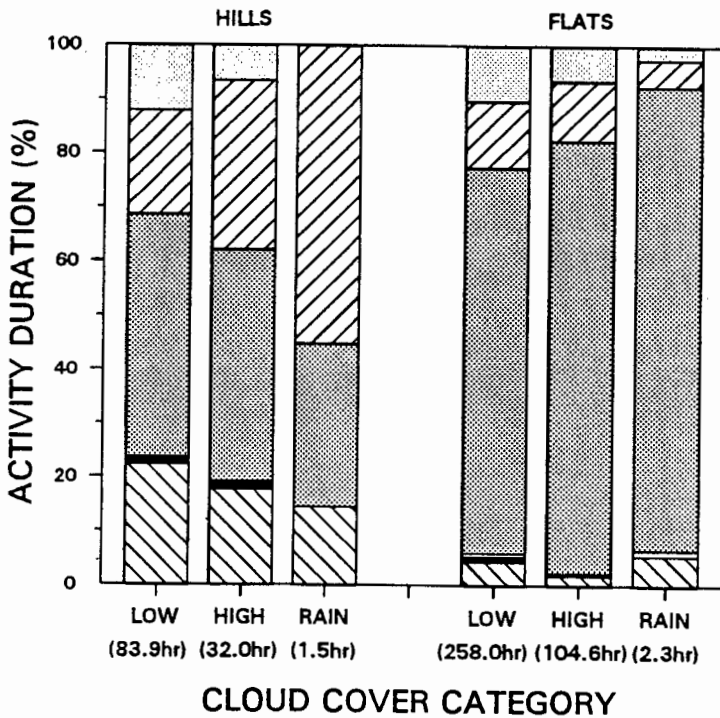


FIG. 2.8. Daily diurnal activity budgets of Southern African Kestrels during low (up to half of the sky) and high (half to all the sky) cloud cover and rain for the hilly and flat study areas.

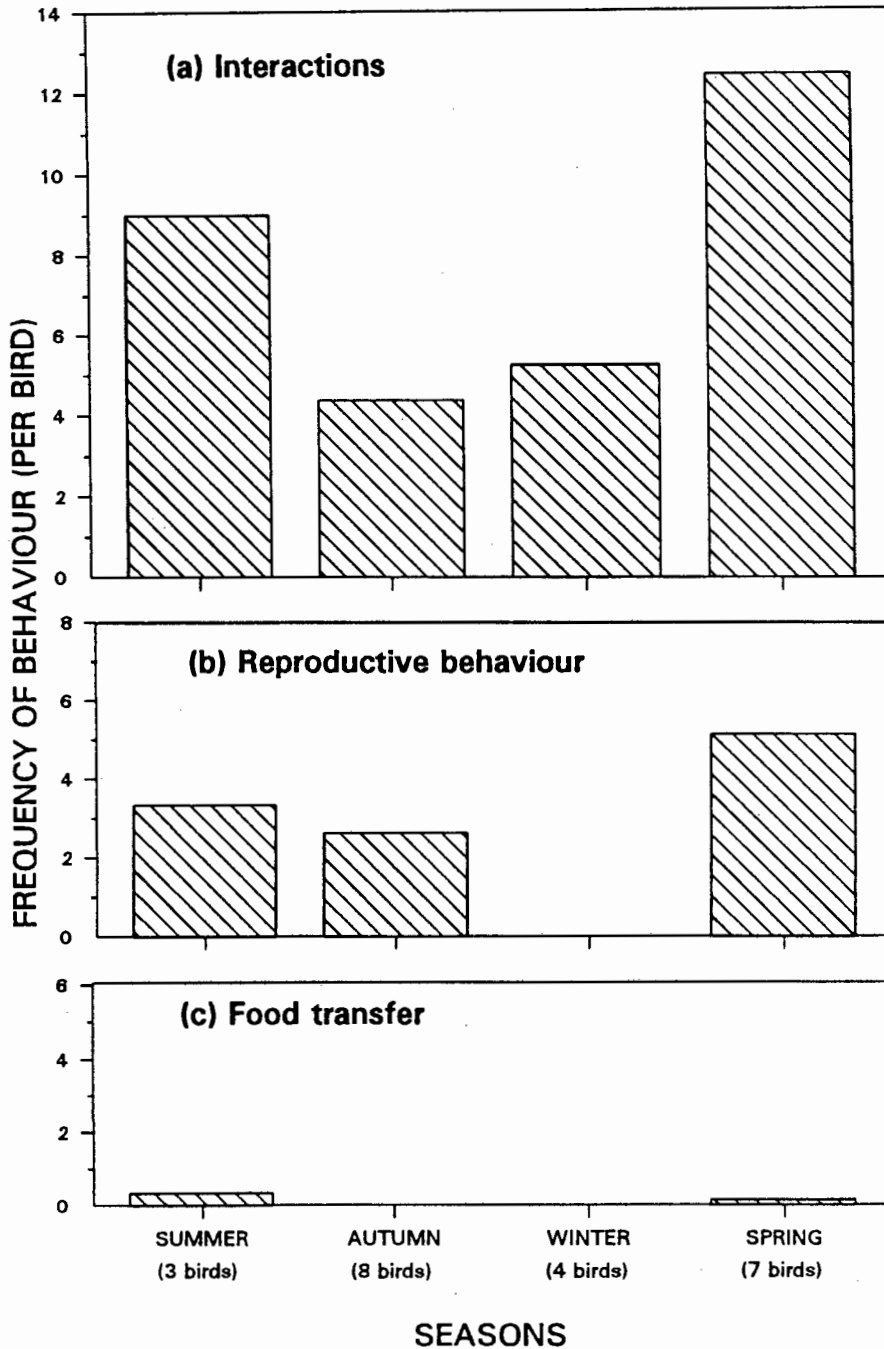


FIG. 2.9. Frequency of (a) interactive behaviour with mates, other kestrels and other animals, (b) reproductive behaviour (flying displays, bowing displays with the mate and copulation) and (c) food transfers from the male to the female. Data from both study areas were pooled for each season and frequencies are given per bird.

significantly less than those on the flats when it was not raining (Mann-Whitney *U*-test,  $Z = 2.13$ ,  $P = 0.03$  for low cloud cover and  $Z = 2.64$ ,  $P = 0.008$  for high cloud cover).

#### Frequencies of interactions, reproductive behaviour and food transfers

Most interactions with a mate, other kestrels or other animals such as crows and mongooses were recorded during spring and summer (Fig. 2.9a). Reproductive behaviour was recorded in all seasons except winter and was highest in spring (Fig. 2.9b). Food transfers were recorded only twice, during spring and summer (Fig. 2.9c). The peaks in these behaviour coincide with the breeding season (spring and summer). Southern African Kestrels over-wintering in the study areas interacted with other animals relatively less than during spring and summer.

#### DISCUSSION

The Southern African Kestrel allocates similar time to various behaviour as European Kestrels in other studies (Pettifor 1983; Masman, Daan and Dijkstra 1988; Village 1990). This study differs from others in that non-breeding birds were observed during the breeding season. There are no other published studies on time budgets of non-breeding Common Kestrels during the breeding season, and this makes comparison of summer results between studies difficult.

#### Hover-hunting and time budget differences between the sexes

The major differences from other studies are the relatively small amount of time spent hover-hunting (Fig. 2.3), and the similar time budgets between the sexes (Fig. 2.5).

These differences can be explained by the fact that the time budgets recorded were for non-breeding birds. Masman, Daan and Dijkstra (1988) observed an increase in hovering by male European Kestrels providing food for females or young. Females, in turn, spent most of their time at the nest sites. This led to an increase in time spent hover-hunting during summer by males, as well as a difference in time budgets between males and females. Their study also showed that in winter, males and females had similar time budgets and much lower hover-hunting durations. The amount of food provided for the female by the male also determined the date of laying of the clutch which in turn determined the size of the clutch in European Kestrels (Meijer, Daan and Hall 1990). In this study, none of the observed Southern African Kestrel pairs reached the stage of egg-laying in the breeding cycle and males only provided food to females in the early part of the breeding season. This was probably due to a low food availability during a year of poor rainfall. Male Southern African Kestrels may have been unable to increase

their hunting yield to provide the female with enough energy reserves to form a clutch of eggs. Females had to hunt for themselves during the stage when they were normally fed by the male. Without the increased demand for food by chicks, adult male and female Southern African Kestrels probably adopted similar behaviour roles between sexes and seasons.

The increase in time spent hover-hunting during spring, however, diverges from the winter pattern. Food availability was possibly at its lowest during spring and Southern African Kestrels could be expected to change to the more profitable hover-hunting method (see Chapter 3) to increase their daily food intake. Alternatively, the increase in hover-hunting during spring could be the start in reproductive activity early in the season which was later aborted because of poor food availability (Fig. 2.9). Male European Kestrels provide food to the females at the start of the breeding season by increasing their hover-hunting time and prey capture rate (food yield) (Masman, Daan and Dijkstra 1988). Food provisioning to female Southern African Kestrels, however, was rarely recorded and it appears that males were unable to catch enough food for themselves and their mates, even after an increase in hover-hunting. In this study, the food-intake threshold for breeding of the female Southern African Kestrel was probably not reached due to low prey availability in a severe drought situation during which they did not breed.

#### Weather and time budgets

Rain caused a decrease in time spent hunting in European Kestrels (Masman, Daan and Dijkstra 1988) but had little effect in this study for the few days where rain was recorded. Wind, as in other studies (Village 1983; Masman, Daan and Dijkstra 1988), affected behaviour more than other weather conditions. Southern African Kestrels preferred to hover in medium to strong wind speeds (Beaufort scale 3 to 4, 3 to 7 m.s<sup>-1</sup>). Hovering was infrequent in low wind conditions, when it is energetically more costly (Village 1983), or in very strong winds when the Southern African Kestrels preferred to sit in a sheltered position.

Hovering Common Kestrels obtain more food per hour than when perch-hunting (Masman, Daan and Dijkstra 1988; Chapter 3) but it is energetically much more expensive (Masman and Klaassen 1987). There is, therefore, a "trade-off" between hover-hunting and perch-hunting, depending on which is energetically more efficient. Village (1983) demonstrated the effect of slope, wind speed and wind direction on the European Kestrel's choice to perch- or hover-hunt. In his study, European Kestrels chose slopes facing the wind where they could preferably 'hang' (where the bird hardly flaps but relies on the wind updraft to maintain its position) in the wind. In a study in the mountainous Natal Drakensberg of South Africa, Barnard (1986) showed that Southern African Kestrels would vary the amount of

flapping while hovering, depending on the updraft. Videler *et al.* (1991) calculated that 'hanging' European Kestrels saved two-thirds of the energy used during normal hovering.

Thus, the minimum wind speed required for efficient hovering in a hilly area with many slopes is probably much lower than in a flat area. The low proportion of perch-hunting and greater proportion of hovering in the hills compared with the flats probably reflects differences in topography and resultant wind conditions. The higher food yield per unit time for hover-hunting *versus* perch-hunting would result in less time spent hunting which could explain the larger proportion of time spent sitting in the hilly study area (Fig. 2.4).

#### Modelling perch- and hover-hunting trade-offs

Masman, Daan and Dijkstra (1988) have modelled the trade-off between perch-hunting and hovering for European Kestrels in their Lauwersmeer study area in the Netherlands. Using energetic values for different behaviour measured in the field and laboratory, they calculated the energetic costs associated with each combination of perch- and hover-hunting. These iso-expenditure lines join all combinations of perch- and hover-hunting with equal energy expenditure (Fig. 2.10). By calculating the energy intake for each hunting method, they were able to calculate the iso-gain lines joining all combinations of time spent perch and hover-hunting with an equal level of energy gain. The line,  $G = 0$  in Fig 2.10, represents the line where energy intake was equal to energy expenditure.

From the winter results presented in this study, the Masman, Daan and Dijkstra (1988) winter model can be used to predict the proportion of perch-hunting to hover-hunting. Their model predicts a series of hunting-behaviour combinations for the situation where energy intake balances energetic cost (Fig. 2.10,  $G = 0$ ). According to the model, European Kestrels that minimize the total time spent foraging would select the lowest point on the  $G = 0$  line (0 hr perch-hunting, 2 hr hover-hunting). European Kestrels that minimize energy expenditure would choose the left most point on the  $G = 0$  line where energy expenditure is low but food intake is low as well (14.5 hr perch-hunting, 0 hr hover-hunting). This last option is not available to the European Kestrel due to a restricted day length. The best solution within the day light available is 10.2 hr perch-hunting and 0.8 hr hover-hunting.

Southern African Kestrels spend a large proportion of their time perch-hunting, which, like the European Kestrels in winter, suggests that they minimize energy expenditure. While European Kestrels selected an average solution of 4.6 hr perch-hunting and 1.1 hr hover-hunting, Southern African Kestrels spent much more time

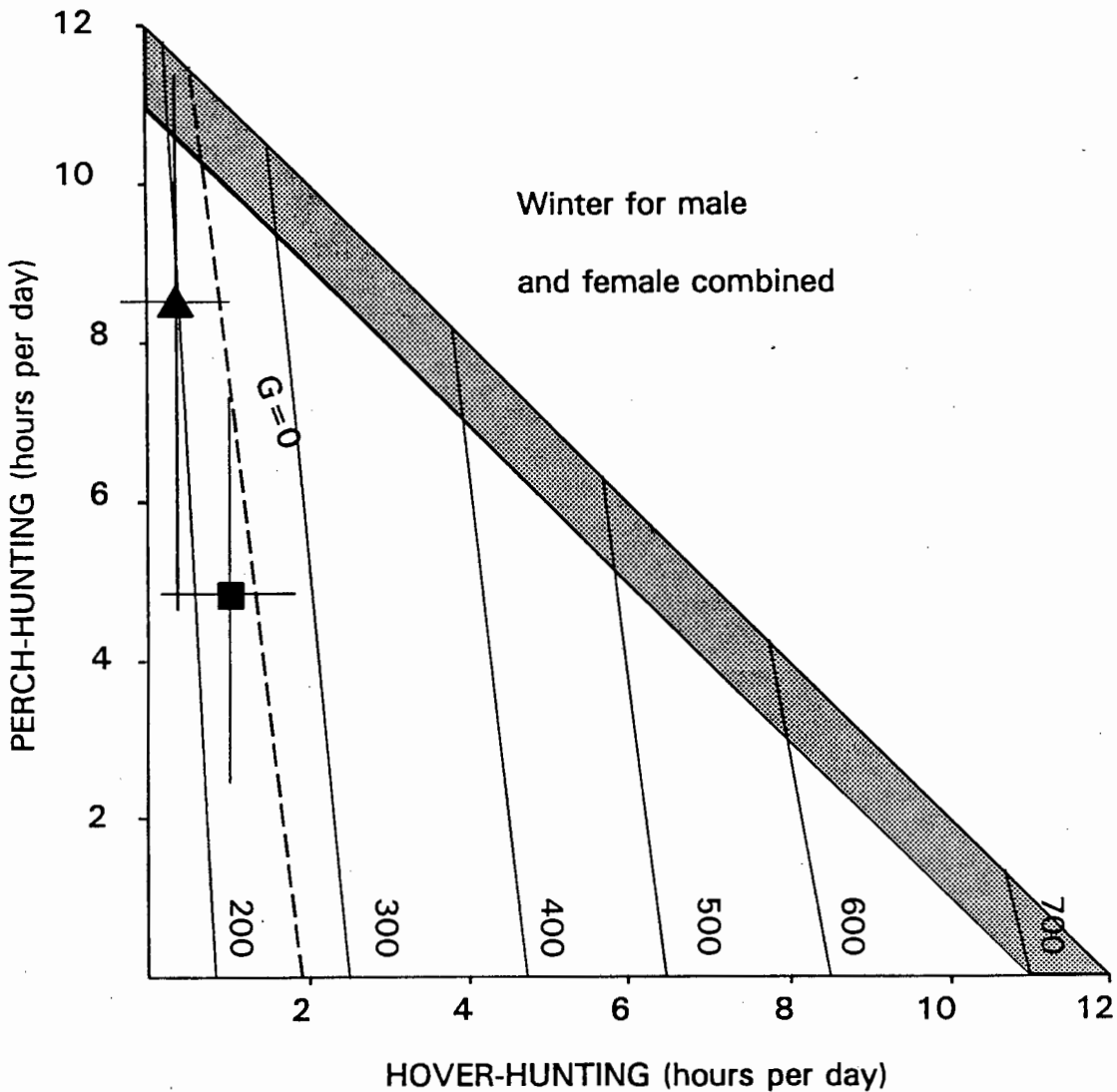


FIG. 2.10. Energetic consequences of the choice between perch-hunting and hover-hunting, and the daily foraging time for the European Kestrel in winter in the Netherlands. Shaded area = combinations of perching and flight-hunting exceeding daylength. Solid lines = iso-expenditure lines, indicating all combinations with the same estimated daily energy expenditure ( $\text{kJ}\cdot\text{day}^{-1}$ ). Dashed line = iso-gain line, indicating all combinations of daily perch-hunting and flight-hunting times with equal gain. The line,  $G = 0$ , is where daily metabolizable energy intake is equivalent to daily energy expenditure.

■ - average choice of the European Kestrels

▲ - average choice of the Southern African Kestrels

The horizontal and vertical lines are 2 s.d. long. This model was taken from Masman, Daan and Dijkstra (1988) and applies to the European Kestrel in the Netherlands.

perch-hunting (8.2 hr perch-hunting and 0.2 hr hover-hunting). Masman and his colleagues concluded that the European Kestrels were minimizing energy expenditure and suggested that the deviation from a more optimal situation (spending more time perch-hunting than what they did) was to allow for day to day variation in food yield. In days of low food intake, they were able to perch-hunt for longer, as they still had several hours of daylight available. Southern African Kestrels clearly adopt a different hunting strategy than the European Kestrels (Fig. 2.10). It would appear that variation in the food intake rates in South Africa are lower than in Europe and this constrained the Southern African Kestrels to perch-hunt for even longer and flight-hunt less than the European Kestrels. Southern African Kestrels are closer to the predicted optimal solution for the minimization of energy expenditure with little extra time available to perch hunt should hunting yields be low.

#### Comparison problems with the model

Although the Masman, Daan and Dijkstra model is useful to understand the hunting options available to European Kestrels, caution must be exercised when it is used for Southern African Kestrels. Several shortcomings must be considered before any conclusions can be made.

First, the model was designed using data from European Kestrels under European conditions. As will be shown in subsequent chapters, Southern African Kestrels differ from European Kestrels in their food yields (Chapter 3) and diet (Chapter 4). Thus, when we compare Southern African Kestrels with European Kestrels, we assume that energetic values calculated for different behaviour are the same for both races. This might not be so, especially in different environments. We would expect Common Kestrels in colder climates to spend more energy to maintain their body temperature. European Kestrels were below the lower limit thermoneutrality for seven months of the year compared to no months in Southern African Kestrels (see Chapter 1, A comparison with the Netherlands study area). This would result in an increase in basic metabolic rate and hence an increase in energy demand in the colder climates. If a model such as the Masman, Daan Dijkstra (1988) model was built for South African conditions, the iso-expenditure lines would lie to the left of the European Kestrel's iso-expenditure lines. Thus, the plotted point for Southern African Kestrels on the Netherlands model might not be as far on the negative side of the  $G = 0$  line as it appears in Fig. 2.10.

Energy expenditure during hunting may also be different. For instance, Southern African Kestrels made frequent use of slopes to 'hang' rather than hovering. The flapping style of hovering adopted by European Kestrels in the flat Netherland study area is energetically more expensive (Videler *et al.* 1991). In a

South African model, the energetically more expensive hovering method of the European Kestrel would mean that its iso-expenditure lines would be further to the right than the Southern African Kestrel's iso-expenditure lines. This source of error further supports the idea that the plotted point for Southern African Kestrels is closer to the  $G = 0$  line or even on its positive side than what the direct comparison suggests.

A second major difference is the energy intake rates for the two hunting methods. Because Southern African Kestrels eat primarily invertebrates (Chapter 4), the amount of energy gained during one hour of perch- and flight-hunting is less than half that gained by the vole-eating European Kestrels (Chapter 3). This difference would influence the ratio of the gross energy gain of the two hunting methods. Such problems make the comparison of European and Southern African Kestrel time budgets difficult and will influence the slope and position of the iso-expenditure and iso-gain lines in a model.

Thirdly, time-budget data were collected using a slightly different protocol in the South African study to that used in the Netherlands. Differences in the time budgets might reflect differences in protocols, especially as an under-estimation of flying time in the Southern African Kestrel. Masman, Daan and Dijkstra (1988) found that, in spite of collecting data from dawn-to-dusk watches, the proportion of time devoted to flight-hunting for males feeding broods was still significantly lower for males that were in sight longer. European Kestrels were lost from sight more often when on the wing than when sitting or perching. It is therefore likely that the birds spent more time on the wing than this study suggests, as data were summarized from bouts of various length as opposed to dawn-to-dusk watches.

Although the Masman, Daan and Dijkstra (1988) model must be interpreted with caution, it does illustrate that Southern African Kestrels use a different strategy to the European Kestrel. This preliminary comparison provides a foundation for future research to investigate the exact extent of these differences.

Difference in time budgets between Southern African and European Kestrels probably reflect differences in adaptation of the Common Kestrel to its environment. Topography, weather conditions and reproductive activity are shown here to influence time budgets. Southern African Kestrels minimize energy expenditure, which is the predicted strategy when food availability is low (Norberg 1977). They are also closer to the predicted optimum situation than the European Kestrel. Divergence from this optimum has been suggested by Masman, Daan and Dijkstra (1988) to be due to the variation in food yield in European Kestrel. Thus, although food availability is lower for the Southern African Kestrel, day to day variation in food yield may be less than for the European Kestrel.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

- Acocks, J.P.H. 1975. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* **40**:1-98.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* **49**:227-267.
- Barnard, P. 1986. Windhovering patterns of three African raptors in montane conditions. *Ardea* **74**:151-158.
- Berger, D.D., and H.C. Mueller. 1959. The bal-chatri: a trap for the birds of prey. *Bird-Banding* **30**:18-26.
- Biggs, H.C., R. Biggs, and A.C. Kemp. 1978. Measurement of raptors. Pages 77-82 in J. Mendelsohn, and C.W. Sapsford, editors. *Proceedings of the Symposium of African Predatory Birds, Northern Transvaal Ornithological Society, Pretoria.*
- Drent, R.H. and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**:225-252.
- Gwinner, E. 1981. Circannual systems. Pages 391-408 in J. Aschoff, editor. *Handbook of behavioural neurobiology Vol. 4. Biological rhythms.* Plenum, New York.
- Herbers, J.M. 1981. Time resources and laziness in animals. *Oecologia (Berlin)* **49**:252-262.
- Masman, D., S. Daan, and H.J.A. Beldhuis. 1988. Ecological energetics of the Kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labelled water methods. *Ardea* **76**:64-81.
- Masman, D., S. Daan, and C. Dijkstra. 1988. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. *Journal of Animal Ecology* **57**:411-432.
- Masman, D., and M. Klaassen. 1987. Energy expenditure during flight in trained and free-living Kestrels, *Falco tinnunculus*. *Auk* **104**:603-616.
- Meijer, T., S. Daan, and M. Hall. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. *Behaviour* **114**:117-136.
- Norberg, R.A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology* **46**:511-529.

- Pettifor, R.A. 1983. Seasonal variation and associated energetic implications in the hunting behaviour of the Kestrel. *Bird Study* **30**:201-206.
- Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**:137-154.
- STSC, Inc. 1984. Statgraphics Version 4.00.
- Videler, J., and A. Groenewold. 1991. Field measurements of hanging flight aerodynamics in the Kestrel *Falco tinnunculus*. *Journal of Experimental Biology* **155**:519-530.
- Videler, J., D. Weihs, and S. Daan. 1983. Intermittent gliding in the hunting flight of the Kestrel, *Falco tinnunculus*. *Journal of Experimental Biology* **102**:1-12.
- Village, A. 1983. Seasonal changes in the hunting behaviour of Kestrels. *Ardea* **71**:117-124.
- . 1990. *The Kestrel*. T. & A.D. Poyser, London.
- Weathers, W.W., W. A. Buttemer, A.M. Hayworth, and K.A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* **101**:459-472.
- Zar, J.H. 1984. *Biostatistical Analysis*. Prentice-Hall International, New Jersey.

## CHAPTER 3

ENVIRONMENTAL EFFECTS ON THE HUNTING BEHAVIOUR  
OF THE SOUTHERN AFRICAN KESTREL

## ABSTRACT

Twenty-eight marked and an unknown number of unmarked Southern African Kestrels (*Falco tinnunculus rupicolus*) were observed for a total of 727 hours from May 1990 to May 1991 in an open flat and hilly area in South Africa. Food yield was highest during the summer and was higher for all times of the year except early winter for the Southern African Kestrels on the flats. Southern African Kestrels on the flats spent relatively little time hover-hunting, whereas hover-hunting was extensively used in the hills during winter. Prey-strike rates were higher for hover-hunting than perch-hunting. Hover-hunting prey-strike rates were higher in the hills than the flats, whereas perch-hunting prey-strike rates were highest on the flats. Prey-capture success was higher for perch-hunting than hover-hunting. The Southern African Kestrels on the flats were more successful at catching prey than the those in the hills for both hunting techniques. Southern African Kestrels on the flats caught on average larger prey than those in the hills. Daily food intake was probably under-estimated for the Southern African Kestrels in the hills. Daily food intake was relatively constant during winter, increasing in summer and autumn. Average daily food intake was lower in this study than for European Kestrels (*Falco tinnunculus tinnunculus*), and it is proposed that fluctuations in daily food intake are larger for Common Kestrels at higher latitudes.

## INTRODUCTION

Food availability is known to influence clutch size in birds (Dijkstra *et al.* 1982; Hornfeldt and Eklund 1990). Foraging in animals has been widely studied and several general theories have been proposed to explain how animals get their food (for a review, see Stephens and Krebs 1986).

Many aspects of foraging have been studied for the Common Kestrel (*Falco tinnunculus*) and the American Kestrel (*Falco sparverius*). These include time allocated to various hunting methods (Rudolph 1982; Shrubbs 1982), prey-strike rates and prey-capture success (Collopy and Koplun 1983; Masman *et al.* 1988), seasonal changes in hunting (Pettifor 1983; Village 1983), daily habits (Rijnsdorp *et al.* 1981) and choice of hunting habitats (Shrubbs 1980; Barnard 1987). Except for a study on the use of different hunting methods and habitat use (Barnard 1986, 1987),

there are no published data on the foraging of the Common Kestrel in the southern hemisphere.

The aim of this chapter is to describe the hunting methods used by the Southern African Kestrel (*Falco tinnunculus rupicolus*), an African subspecies of the Common Kestrel, and to document the various parameters associated with hunting such as hunting-time budgets, prey-strike rates and prey-capture success, and daily food yields. Using this information, I examine the hypothesis that Common Kestrels at low latitudes have a lower foraging yield than Common Kestrels at relatively high latitudes, but that fluctuations in daily food yield are smaller for Common Kestrels living at low latitudes than for those at relatively high latitudes.

#### STUDY AREAS

Southern African Kestrels were studied in a hilly and open flat area 15 km apart in the Tarkastad (32°00'S, 26°15'E) District, eastern Cape Province, South Africa. The hilly study area was characterized by hills and valleys with dolerite cliffs and the flat study area had no cliffs except along the edges. Telephone and power lines criss-crossed both areas.

Average annual summer rainfall measured in Tarkastad 15 km north of the flat study area was 426.4 mm ( $N = 29$  years). Mean average rainfall during 1990 was 245 mm. Low rainfall during this year was the possible reason for none of the observed Southern African Kestrels breeding during the 1990 breeding season. Mean daily minimum and maximum temperatures were measured in Queenstown (53 km north-east of the flat study area) and ranged from an average minimum of 9.2°C to an average maximum of 24.5°C.

The habitat of both study areas is classified as karroid *Merxmuellera* mountain veld (Acocks 1975).

#### METHODS

Observations were made on twenty-eight marked and an unknown number of unmarked Southern African Kestrels from May 1990 to May 1991 in both study areas. A total of 727 hours was spent observing Southern African Kestrel behaviour, using focal animal sampling (Altmann 1974). All behaviour (defined in Chapter 2) and weather conditions were recorded in a notebook, but flying and hovering were recorded using a portable tape recorder and later transcribed. Measures of weather conditions included cloud cover (estimated 1/8th's of sky covered), wind speed (Beaufort scale), wind direction (estimated) and temperature (thermometer held 1 m above the ground in the shade).

All observations for each marked Southern African Kestrel were pooled and analysed on a monthly basis as no full-day observations were made on an individual

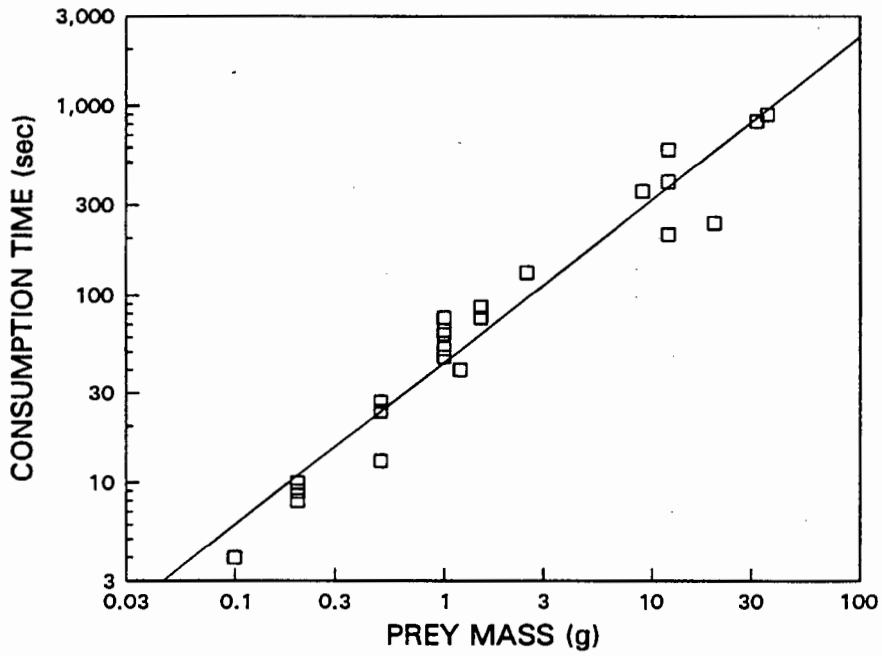


FIG. 3.1. Regression of the time spent eating prey and prey mass based on a sample 17 invertebrates and 4 vertebrates collected in the study areas. The regression formula is  $Y = 43.51X^{0.8632}$  ( $r = 0.97$ ,  $N = 24$ ,  $P < 0.001$ ).

Southern African Kestrel. Data for unmarked or unidentified Southern African Kestrels were pooled and considered as one kestrel. Southern African Kestrel hunting time budgets for the two areas were calculated by pooling all observations for the month. Observations with fewer than 8 min of perch-hunting or fewer than 2 min of hovering were excluded from the strike-rate analysis, because very short observation periods provided erroneous results (for example, prey-capture success of 0%). Data collected for the Southern African Kestrels in the hills during December and January were not sufficient to calculate hunting parameters, except for hover-hunting prey-strike rate during January. Because of the low proportion of time spent hunting using techniques other than perch and hover-hunting (Chapter 2), all other modes of hunting were excluded from the analysis.

Estimates of prey size were made by recording the consumption time for each prey item as captured prey was not seen in all cases. Consumption time has been shown to correlate well with prey mass (Masman *et al.* 1986). A captive Southern African Kestrel was fed prey of known mass and consumption time was measured using a stop watch. Consumption time correlated well with prey mass (consumption time =  $43.51M^{0.8632}$ ,  $r = 0.97$ ,  $N = 24$ ,  $P < 0.001$ , Fig. 3.1). The regression was used to estimate mass of prey eaten.

## RESULTS

Based on a total of 3351 observed prey-strikes, perch-hunting (47.3%) and hover-hunting (50.7%) were the two most used methods of hunting. Other methods used less frequently were attacks launched from high flying (0.2%) or soaring positions (0.1%), and while perched low down or in a concealed position (1.7%).

### Description of hunting methods

Hover-hunting. - The kestrel remained in a stationary position in the air by flapping its wings or 'hanging' in updrafts off slopes or cliffs (Videler *et al.* 1983; Videler and Groenewold 1991). In this study, Southern African Kestrels in the hilly area often made use of updrafts off hill slopes. Those on the flats seldom hovered in slow wind speeds. Captured prey was often very small and was mostly eaten on the wing.

Perch-hunting. - A large variety of perches, both natural (e.g. trees and cliffs) and artificial (e.g. pylons and poles for electricity and telephone lines), were freely available on the flat and hilly areas. The kestrel scanned the area around these perches from which it launched attacks on its prey. Attacks were sometimes launched from positions with poor visibility ( $< 180^\circ$  vision) of the surrounding area or while perched low down ( $< 1$  m from ground). The frequency of use and average height of different perch sites for the two areas is given in Table 3.1.

TABLE 3.1. Perches and their average heights used by Southern African Kestrels in the hills and on the flats.

Perch Type	Hills (%)	Flats (%)	Average height in metres (SD)
Aerial	3 (0.3)		2.0 (-.-)
Cliff	229 (21.7)	1 (0.04)	19.7(15.3)
Double electricity pole	79 (7.5)	70 (3.0)	11.5(0.9)
Fencepost	82 (7.8)	211 (9.1)	1.0(0.0)
Nest	6 (0.6)		5.3(3.6)
Electricity line	48 (4.6)	71 (3.0)	12.5(6.4)
Post	2 (0.2)		5.0 (-.-)
Electricity pole	74 (7.0)	627 (26.9)	10.0(0.0)
Rock	11 (1.0)	4 (0.2)	1.8(0.6)
Telephone line	4 (0.4)	2 (0.1)	5.8(0.4)
Telephone pole	421 (40.0)	977 (41.9)	6.0(0.0)
Tree	94 (8.9)	351 (15.1)	10.5(6.5)
Building		2 (0.1)	4.5(0.7)
Sand heap		11 (0.5)	2.5(0.5)
Windmill		3 (0.1)	9.3(1.1)
Total for perches	1053	2330	

Southern African Kestrels in the hills perch-hunted mainly from cliffs and telephone poles, and to a lesser extent from electricity lines and poles and fence posts. The Southern African Kestrels on the flats hunted most often from electricity and telephone poles, and to a lesser extent from trees and fence posts.

Prey capture from high flying and soaring. - Occasionally a kestrel flew up high (over 200 m above the ground) and then made long vertical stoops at prey. These attacks were often at small birds (2 of 4 successful prey-strikes). Similar attacks were made after soaring.

Robbing nests for young birds. - On one occasion, a Southern African Kestrel tried to rob Rock Martin (*Hirundo fuligula*) nests under an overhang on a cliff (van Zyl 1991).

Hunting termites on the ground. - During winter, the Southern African Kestrels spent time on the ground, picking up harvester termites (*Microhodotermes* sp.). After making the initial strike from a perch or hover, the kestrel would run to a

termite, pick it up in its beak and swallow it. During summer, when termite alates emerged from their nests, Southern African Kestrels would catch these in the air using their feet (cf. Rudolph 1983), and eat them while flying, discarding the wings.

#### Seasonal pattern of foraging parameters

**Time budgets.** - The time allocated to the two main modes of hunting is shown in Fig. 3.2. Perch-hunting is the most frequently used mode of hunting in the Southern African Kestrels on the flats (58%); only 3% of the time being devoted to hovering. Less time was spent in summer on hunting. The Southern African Kestrels in the hills spent a greater proportion of their time hover-hunting (34% perch-hunting and 16% hover-hunting) than those on the flats. Most hover-hunting occurred during winter in the hills. Perch-hunting, as on the flats, was the main mode of hunting during the rest of the year. Relatively more time was spent hunting during winter and early spring.

**Prey-strike rate.** - Prey-strike rate for the flats and hills is given in Fig. 3.3. Prey-strike rate was significantly higher for hovering than for perch-hunting (mean perch-hunting prey-strike rate =  $3.4 \text{ str.hr}^{-1}$ , mean hover-hunting prey-strike rate =  $26.7 \text{ str.hr}^{-1}$ , Student's *t*-test  $t = -17.8$ ,  $P < 0.001$ ,  $N = 221$ ). Prey-strike rate for perch-hunting was insignificantly higher on the flats than for the Southern African Kestrels in the hills for all months except August and April (mean for hills =  $3.2 \text{ str.hr}^{-1}$ , mean for flats =  $3.5 \text{ str.hr}^{-1}$ , Student's *t*-test  $t = -0.45$ ,  $P = 0.64$ ,  $N = 132$ ). The Southern African Kestrels in the hills, however, had a significantly higher prey-strike rate for hover-hunting than those on the flats (mean for hills =  $30.5 \text{ str.hr}^{-1}$ , mean for flats =  $23.8 \text{ str.hr}^{-1}$ , Student's *t*-test  $t = 2.19$ ,  $P = 0.03$ ,  $N = 89$ ).

**Prey-capture success.** - The average monthly prey-capture success is given in Fig. 3.4. While prey-capture success increased from winter to summer and autumn for perch-hunting, prey-capture success was highest during early summer and early winter for hover-hunting. The prey-capture success was significantly higher for perch-hunting than hover-hunting (61.3% vs 49.2%, Mann-Whitney *U*-test  $Z = -2.94$ ,  $P = 0.003$ ). Although not significant, prey-capture success was marginally higher for the Southern African Kestrels on the flats for perch-hunting (65.4% vs 57.4%, Mann-Whitney *U*-test  $Z = 0.73$ ,  $P = 0.46$ ). Prey-capture success was significantly higher for the Southern African Kestrels in the hills for hovering (56.9% vs 41.5%, Mann-Whitney *U*-test  $Z = -2.02$ ,  $P = 0.04$ ).

**Prey size.** - Prey size based on consumption time is given in Fig. 3.5. Prey was significantly larger for prey-strikes from perches, as opposed to prey-strikes from hovers (44 sec from perches and 14 sec from hovers, Student's *t*-test  $t = 10.45$ ,

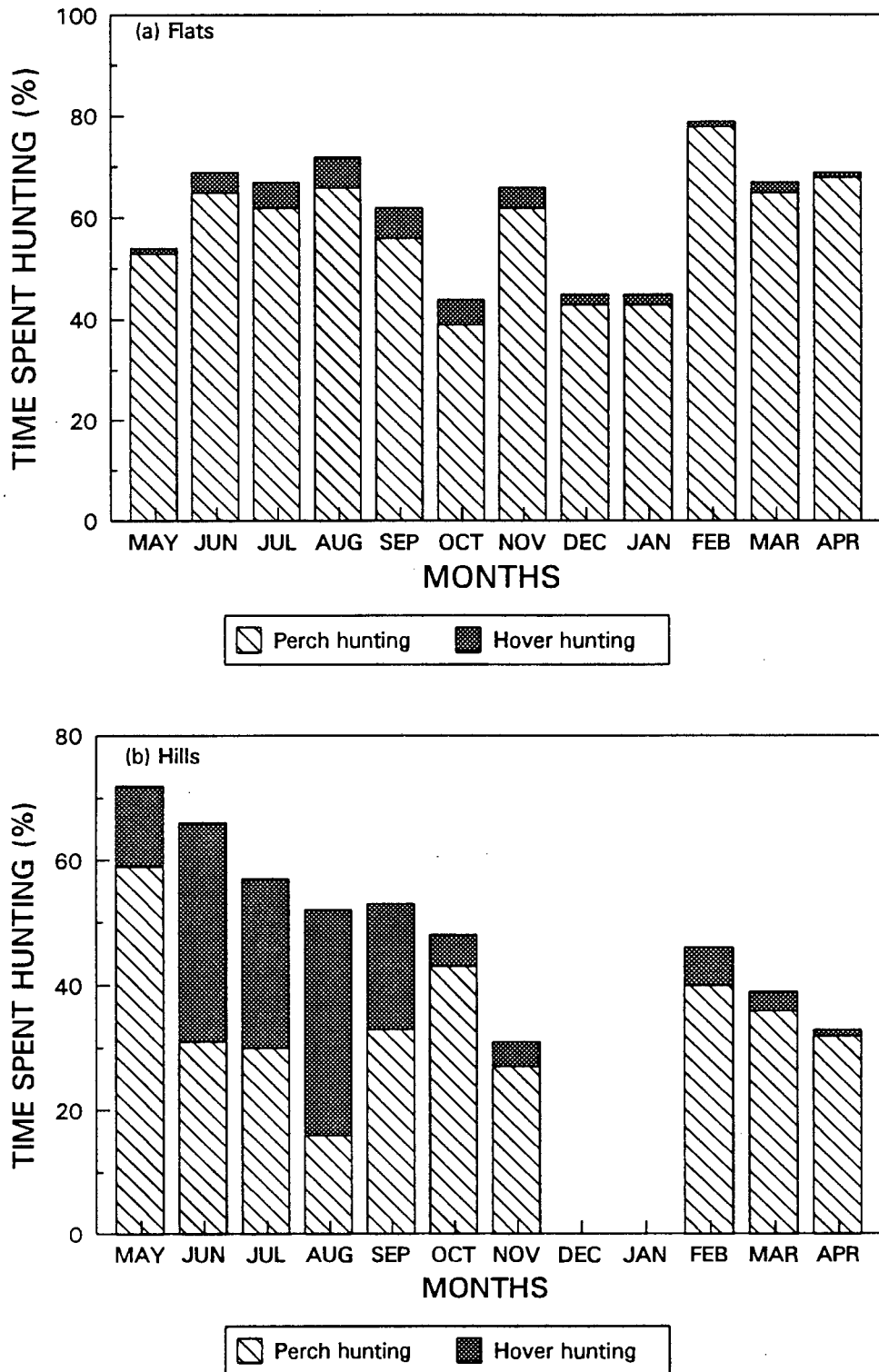


FIG. 3.2. Proportion of monthly daytime activity spent perch and hover hunting (a) in the flat and (b) in the hilly study areas. Observations started in May (beginning of autumn).

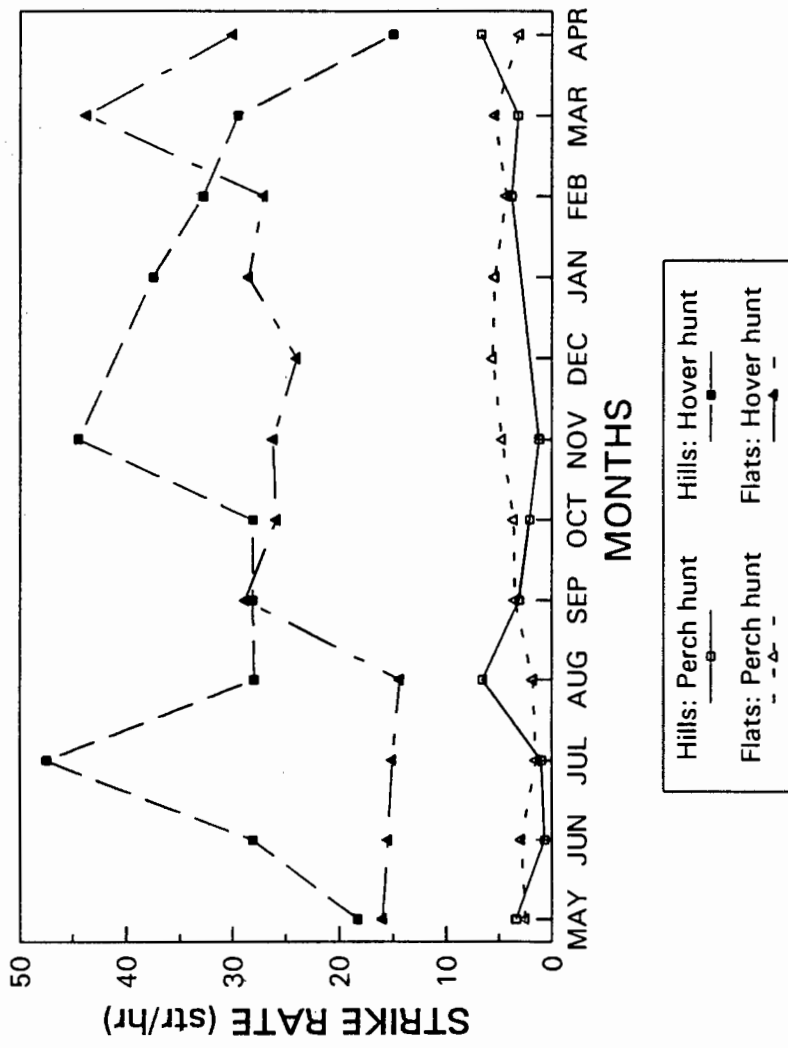


FIG. 3.3. Monthly strike rate for perch and hover hunting in the flat and hilly study areas.

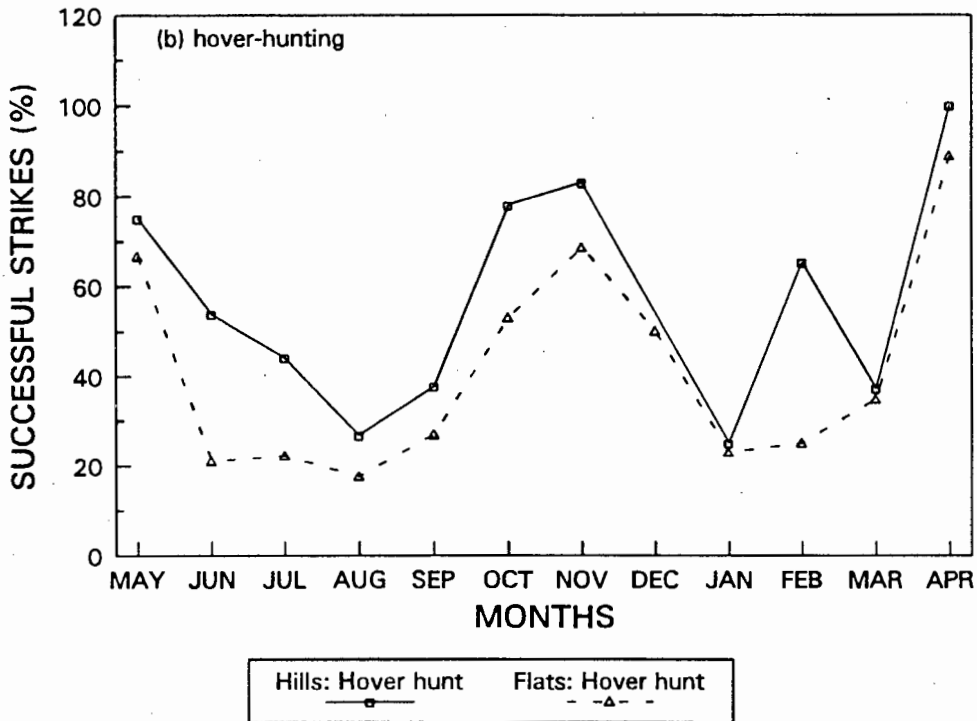
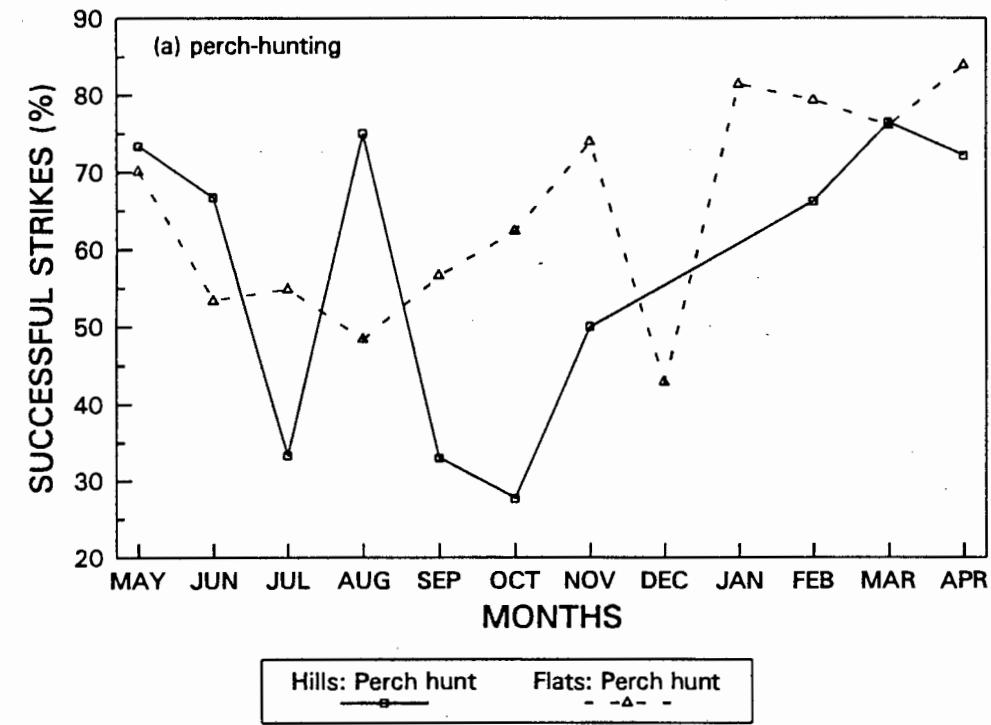


FIG. 3.4. Monthly percentage of strikes that ended in a successful capture of prey for (a) perch hunting and (b) hover hunting in the flat and hilly study areas.

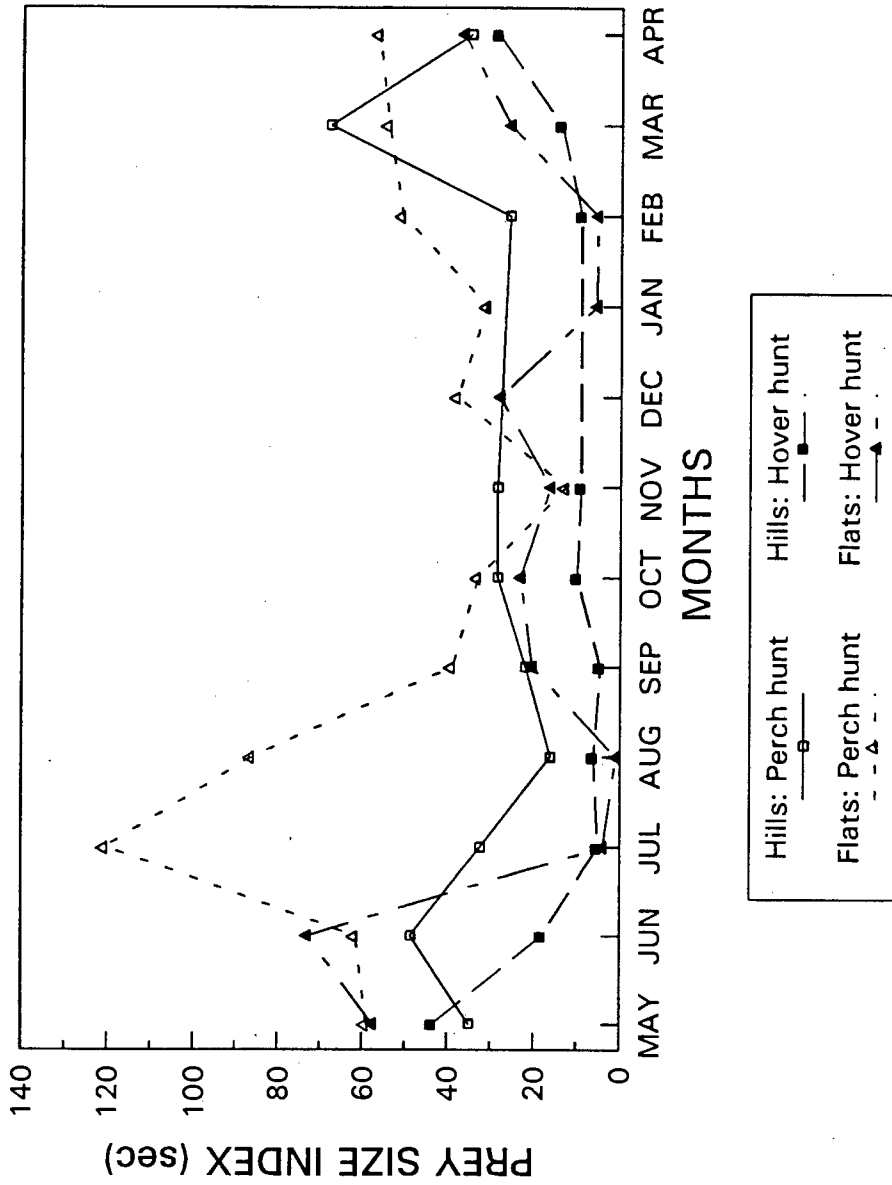


FIG. 3.5. The monthly size of prey captured by Southern African Kestrels perch- and hover-hunting in the flat and hilly study areas. An index of prey size was determined by measuring the average duration of meal consumption.

$P < 0.001$ ,  $N = 1336$ ). Southern African Kestrels on the flats caught on average larger prey than those in the hills (perch-hunting: 46 vs 37 sec, hover-hunting 23 vs 12 sec) but this was only statistically significant for prey caught by hover-hunting (Student's  $t$ -test  $t = -4.74$ ,  $P < 0.001$ ,  $N = 546$ ). Prey size showed no obvious trends through the season except for an increase in prey size for the Southern African Kestrels on the flats during winter.

Food yield. - Average daily food yield in grams of prey captured per day is given in Fig. 3.6. Daily food yield was lower for the Southern African Kestrels in the hills than those on the flats for the whole year except early winter. The very low daily food yield for the Southern African Kestrels in the hills is possibly under-estimated, whereas food yield for the birds on the flats probably reflects their actual food intake. This is due to an underestimate of time spent hover-hunting in the hilly area, because of the topography of the area and the large distances that the Southern African Kestrel could travel in a relatively short time. Southern African Kestrels perch-hunting were lost from view less easily than those hover-hunting, and hover-hunting was relatively easier to follow on the flats. Food yield was lowest in both areas during late winter with a peak in late summer. Average daily food yield for each month varied little from late winter to mid-summer.

Caching of prey. - Prey caching was recorded for all the months of the year except March and December. Most items were cached and retrieved during winter and spring. Mostly large prey were cached (Table 3.2).

TABLE 3.2. Prey size for prey cached or retrieved from caches. Prey was either categorized as above or below an estimated mass of 5 g.

	Mass category		Unknown mass	Total
	< 5 g	> 5 g		
Prey cached	3	4	4	11
Prey retrieved	2	3	1	6

#### The effect of weather on hunting

There was no strong correlation between the weather parameters (Chapter 2). The highest correlations were between temperature and time of day ( $r = 0.50$ ) and wind and time of day ( $r = 0.55$ ).

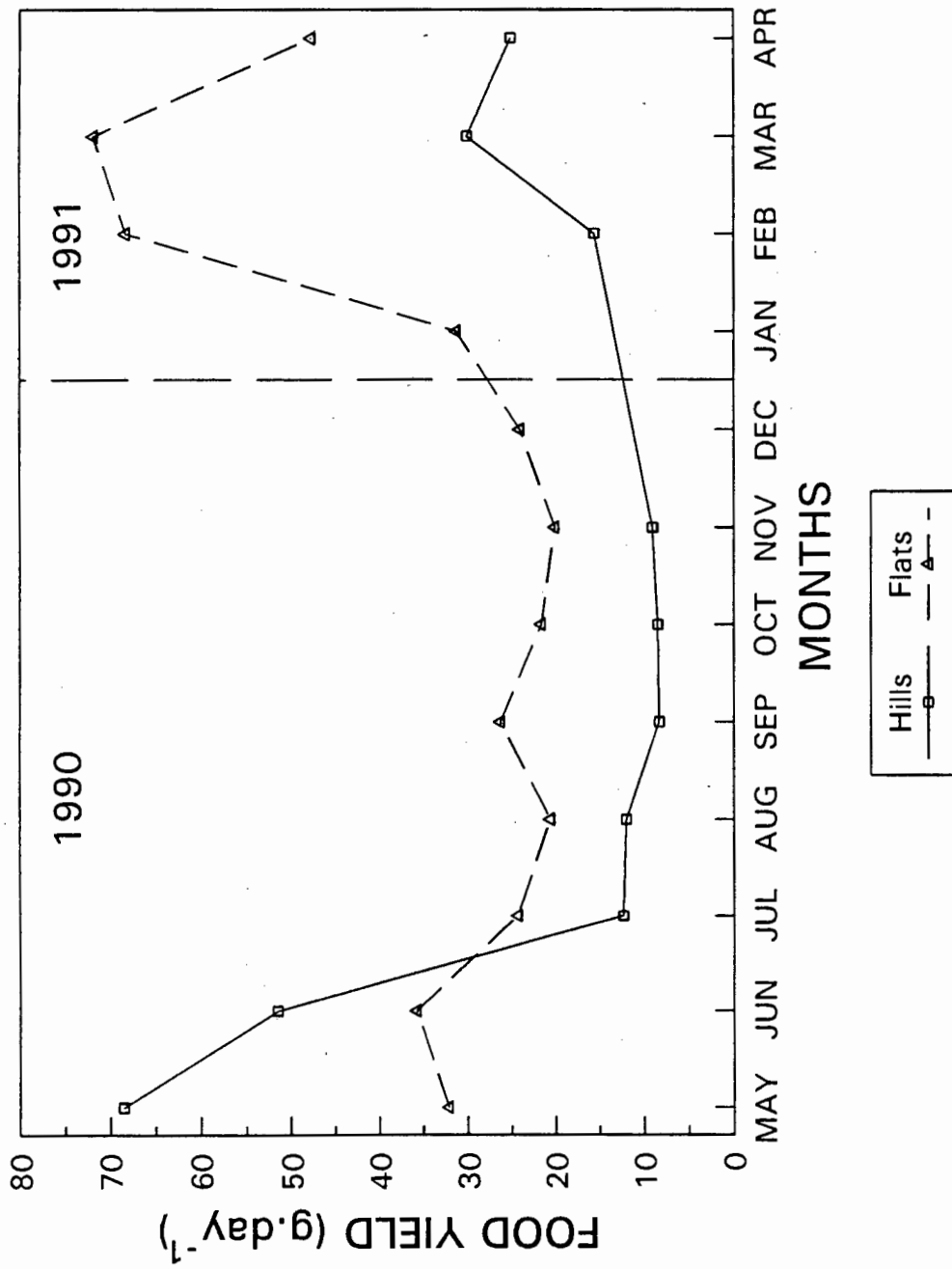


FIG. 3.6. Average food yield for individual Southern African Kestrels in the flat and hilly study areas during the observation period. Average food yield was calculated by averaging the amount of time spent eating per day per bird and converting this consumption time using a previously determined regression (see Methods in text).

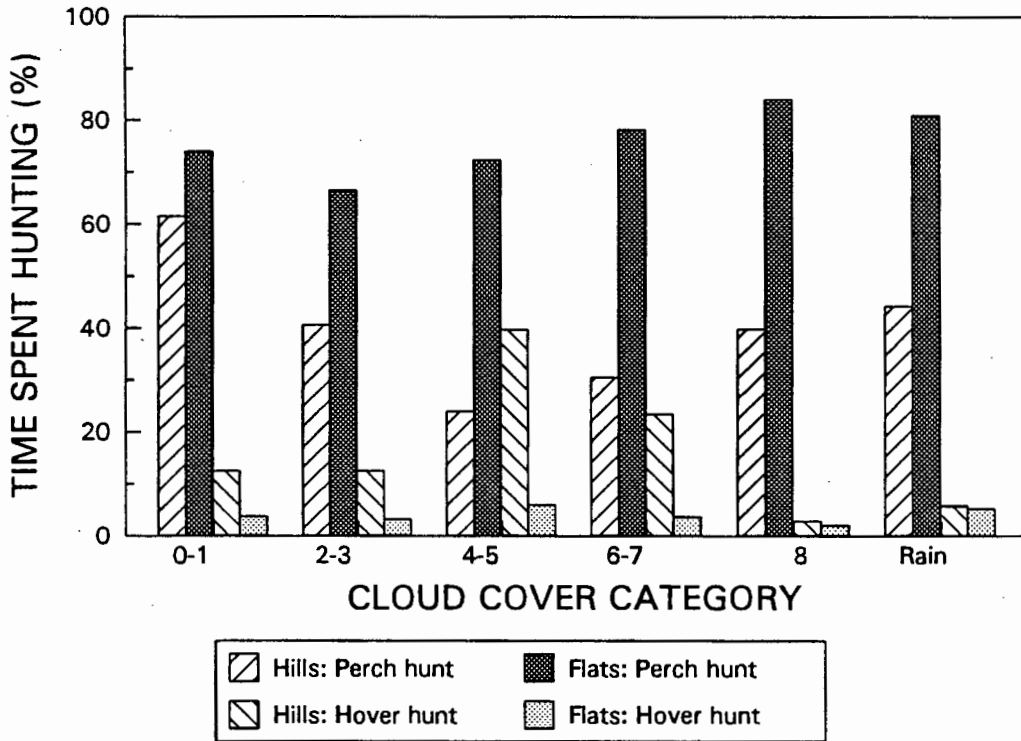


FIG. 3.7. The relationship between different cloud and rain conditions in the flat and hilly study areas and the proportion of time spent perch and hover hunting. Cloud cover categories are on a scale of 1 to 8 parts of the sky covered by cloud.

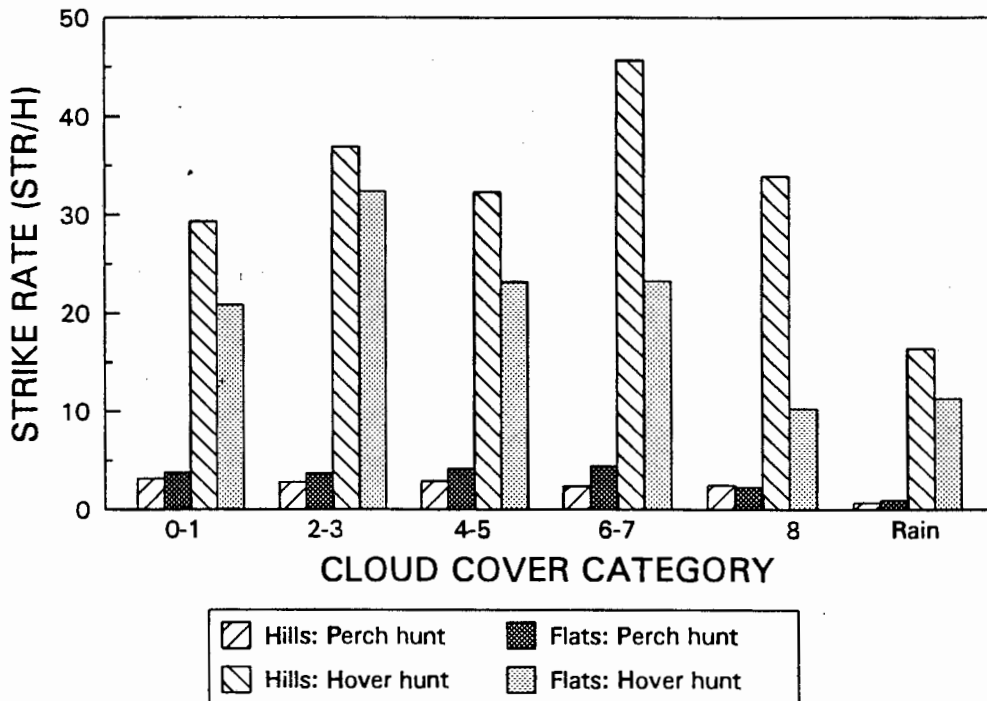


FIG. 3.8. The relationship between different cloud and rain conditions in the flat and hilly study areas and the average strike rate while perch and hover hunting. Cloud cover categories are on a scale of 1 to 8 parts of the sky covered by cloud.

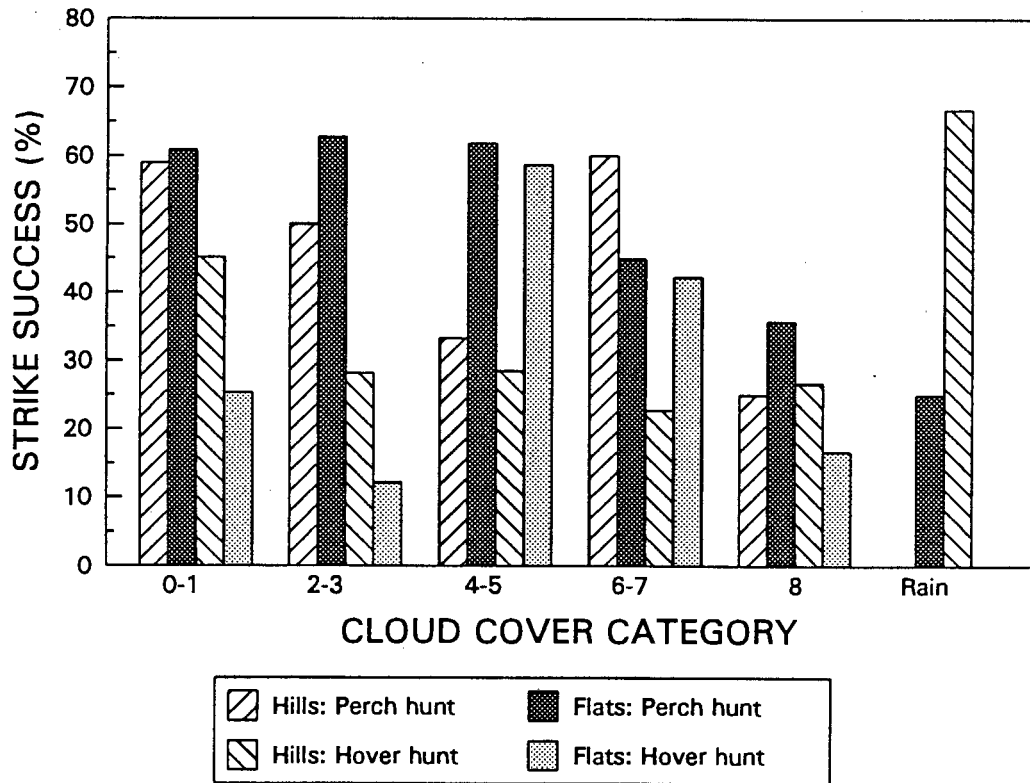


FIG. 3.9. The relationship between different cloud and rain conditions in the flat and hilly study areas and the percentage of successful strikes (prey-capture attempts) while perch and hover hunting. Cloud cover categories are on a scale of 1 to 8 parts of the sky covered by cloud.

Cloud cover and rain. - Cloud cover did not correlate with the time spent hunting by Southern African Kestrels on the flats (Fig. 3.7). In the hills, however, the Southern African Kestrels spent most time hover-hunting for periods with some cloud cover.

There was a decrease in the hover-hunting prey-strike rate when it was overcast or raining while there was no obvious trend for perch-hunting prey-strike rate (Fig. 3.8).

There was a decrease in prey-capture success with an increase in cloud cover for perch- and hover-hunting Southern African Kestrels on the flats (Fig. 3.9). There were no obvious correlations between cloud cover and prey-capture success of the Southern African Kestrels in the hills.

Temperature. - Temperature did not correlate with the time spent hunting in the two areas (Fig. 3.10).

There was a marked increase in prey-strike rate for all the hunting modes with an increase in temperature (Fig. 3.11).

There was a slight increase in prey-capture success with an increase in temperature for perch-hunting Southern African Kestrels (Fig. 3.12). There were no obvious correlations between hover-hunting prey-capture success and temperature.

Wind. - There was a decrease in the time spent perch-hunting in the hills with an increase in wind speed (Fig. 3.13). Southern African Kestrels hover-hunted in medium- to high-speed winds. The proportion of time spent hover-hunting increased with an increase in wind speed. The Southern African Kestrels in the hills allocated more time to hover-hunting than those on the flats.

The lowest perch-hunting prey-strike rates were recorded during slow wind speeds (Fig. 3.14). Prey-strike rate was high at very slow and high wind speeds for hover-hunting Southern African Kestrels on the flats.

While perch-hunting prey-capture success was unaffected by wind speed, prey-capture success of hover-hunting Southern African Kestrels on the flats increased with an increase in wind speed (Fig. 3.15).

#### DISCUSSION

Hunting methods, as observed in this study, are well described for the Common Kestrel (Village 1990). The Common Kestrel is a generalist hunter with a wide range of hunting techniques which it uses over a large range of different food conditions (Cramp and Simmons 1980).

Common Kestrels are able to live in different habitats and environmental conditions by adjusting their hunting time budgets, strike rates, prey-capture success and prey size. This was apparent for the two areas in this study. The Southern

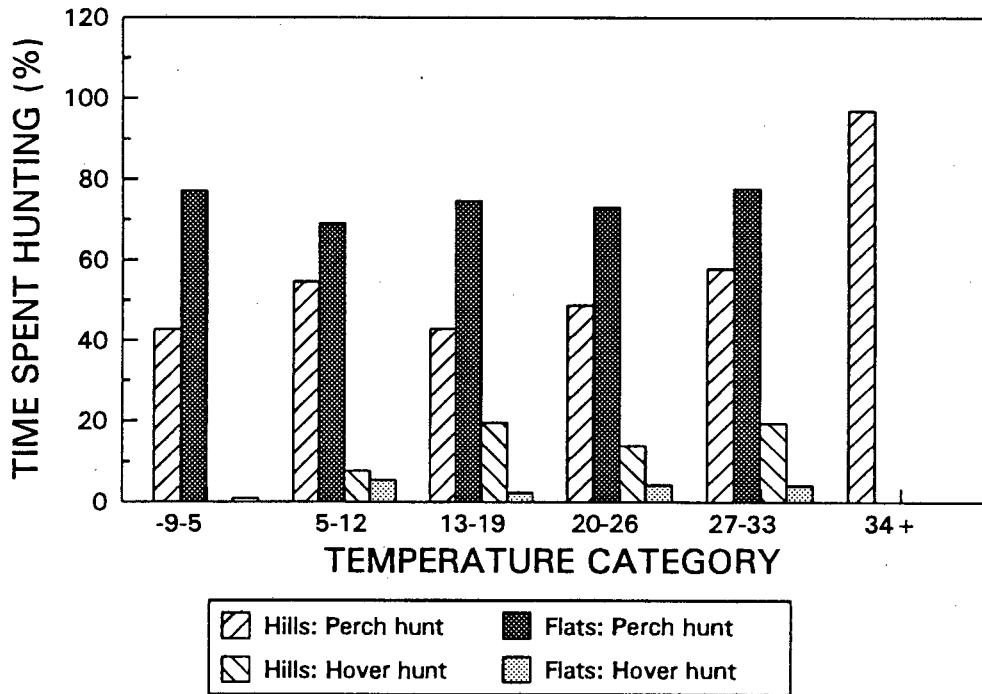


FIG. 3.10. The relationship between temperature in the flat and hilly study areas and the proportion of time spent perch and hover hunting. Temperature is in °C.

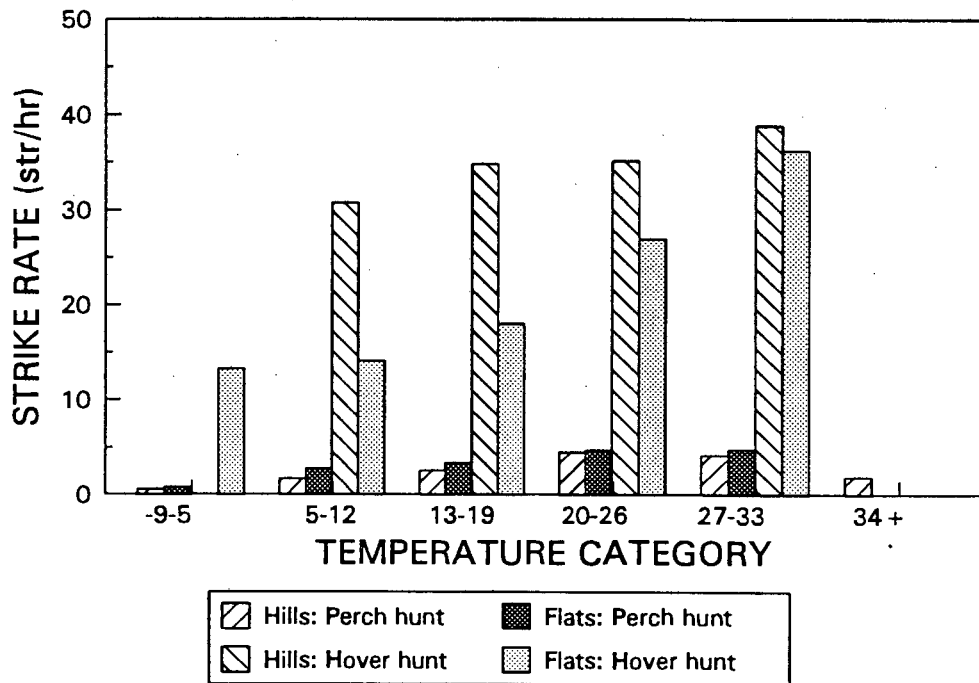


FIG. 3.11. The relationship between temperature in the flat and hilly study areas and the average strike rate while perch and hover hunting. Temperature is in °C.

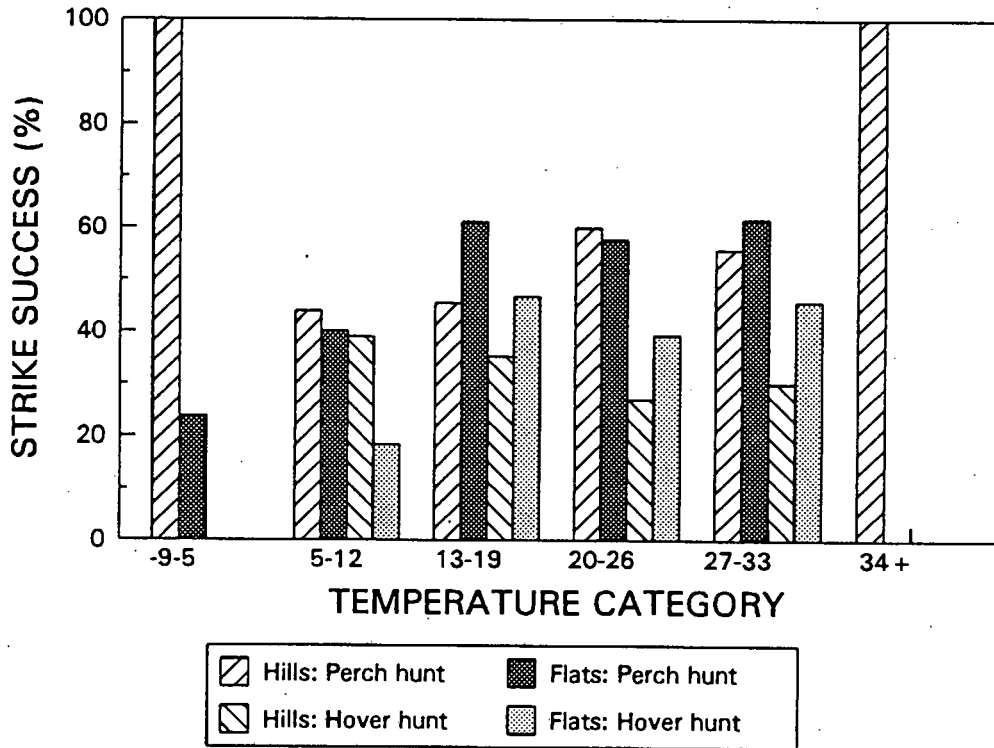


FIG. 3.12. The relationship between temperature in the flat and hilly study areas and the percentage of successful strikes (prey-capture attempts) from perch and hover hunting. Temperature is in °C.

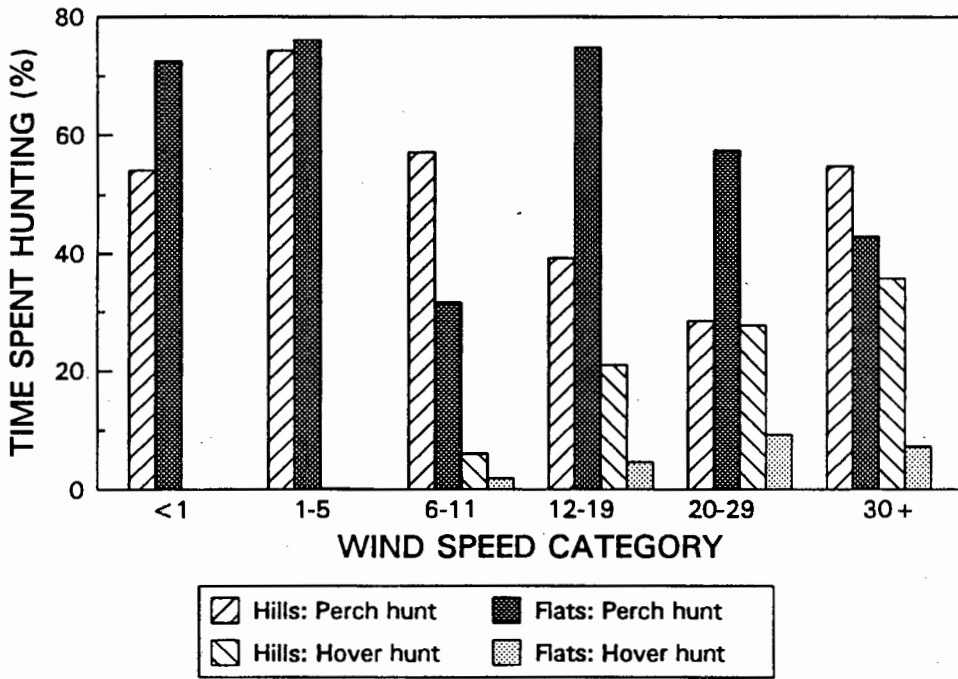


FIG. 3.13. The relationship between wind speed in the flat and hilly study areas and the proportion of time spent perch and hover hunting. Wind speed is in km.hr<sup>-1</sup>.

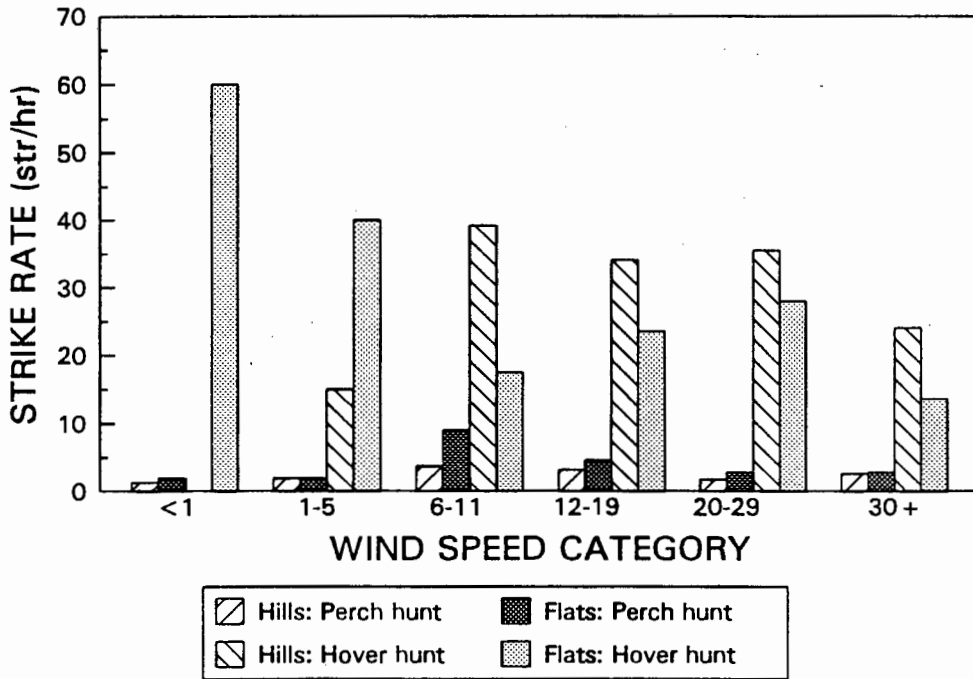


FIG. 3.14. The relationship between wind speed in the flat and hilly study areas and the average strike rate while perch and hover hunting. Wind speed is in km.hr<sup>-1</sup>.

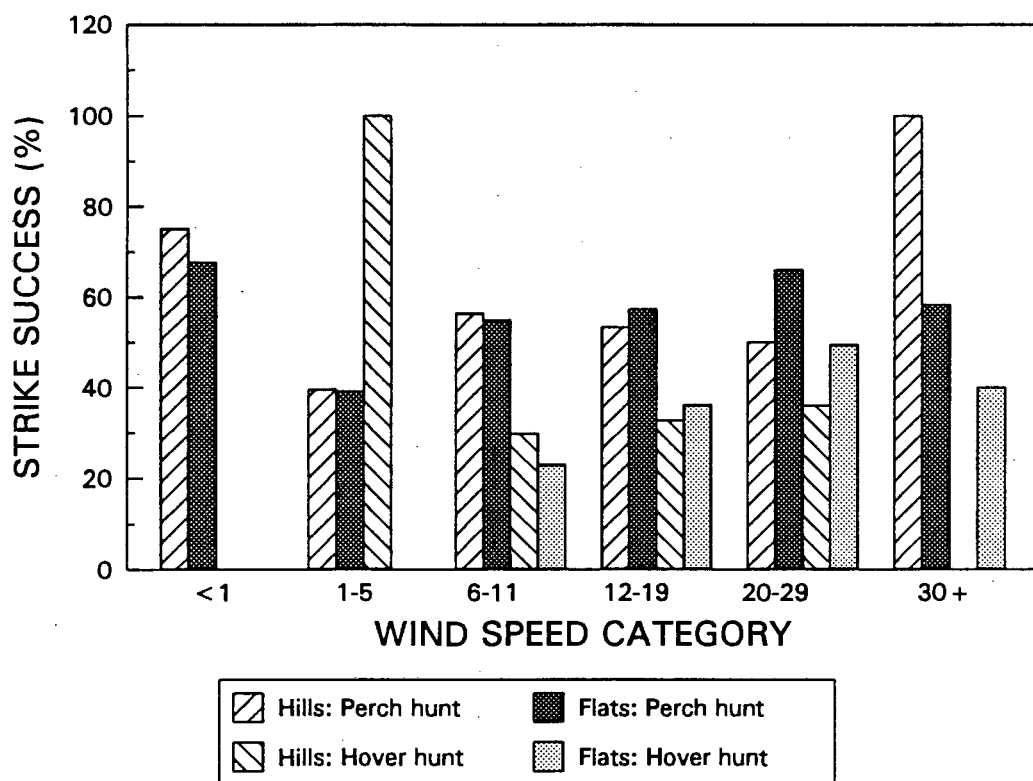


FIG. 3.15. The relationship between wind speed in the flat and hilly study areas and the percentage of successful strikes (prey-capture attempts) from perch and hover hunting. Wind speed is in km.hr<sup>-1</sup>.

African Kestrels in the hilly study area spent more time hovering and thus had an accompanying higher prey-strike rate; the Southern African Kestrels on the flats had a higher prey-capture success and caught larger prey by perch-hunting.

#### Seasonal trends in daily food yield

The average daily yield of the Southern African Kestrel was lower during winter than summer, as found for the European Kestrel (Masman *et al.* 1986). This was probably due to a drop in arthropod availability. The greater proportion of vertebrates taken by the Southern African Kestrels on the flats during winter (Chapter 4) could be due to an increase in vertebrate availability or because of a drop in invertebrate availability. Although the Southern African Kestrels in the hills had a higher prey-strike rate than the birds on the flats, their food yield was lower for the whole year except early winter. The difference in prey size for perch- and hover-hunting can explain these results. Despite a high prey-strike rate for Southern African Kestrels hover-hunting in the hills, gross daily intake was low because of the small prey obtained from hover-hunting. A large proportion of the time of Southern African Kestrels in the hills was spent hunting during May and June and this, accompanied by higher prey-strike rates and prey-capture success compared to the Southern African Kestrels on the flats, explains the higher daily food yield for these months.

A number of hypotheses have been proposed to explain why animals cache food (Stanback 1991). It has been suggested that American Kestrels cache prey to eat just before roosting (Collopy 1977). This provides a source of extra energy needed to maintain body temperature during cold nights. Although caching behaviour recorded in this study supports this hypothesis in that food was cached most often during winter and spring and was often eaten just before roosting, caching was recorded throughout the year. This suggests that body-temperature maintenance during the night was not the only reason for caching prey, but that food might have also been stored in times of increased food abundance when several large prey items were caught.

#### The influence of weather on hunting

Weather had two major influences on the foraging behaviour of the Southern African Kestrel. Wind apparently played an important role in determining whether the Southern African Kestrels should hunt from a perch or by hovering. In both areas, an increase in wind was accompanied by an increase in the proportion of time spent hovering. Although the Southern African Kestrels on the flats spent less time hovering than the those in the hills, this can be explained by the effect that slopes have on wind speeds. The wind speed was recorded at the base of a slope on which the Southern African Kestrels were hovering. Wind speed, however, was often

much higher on the slopes than at the base. High wind speeds on the slopes favoured hover-hunting. Village (1983) showed that European Kestrels selected slopes with updrafts to aid hovering and hovered more on windy days than still days. Temperature also correlated well to certain foraging parameters. Prey-strike rates for all the hunting modes increased with an increase in temperature. High temperatures are favourable for insect activity, and insects formed the major component of the Southern African Kestrel's diet (Chapter 4).

#### Food yield comparisons with the European Kestrel

The monthly food yield was lower in the Southern African Kestrel than the European Kestrel. European Kestrels were found to obtain a large proportion of their daily yield from hover-hunting (Masman *et al.* 1988). Prey-strike rates and prey-capture success of European Kestrels were not as high as recorded in this study. Prey size was much larger for European Kestrels, as they preyed mostly on small mammals such as the vole (*Microtus arvalis*), and average daily food yields were higher than in this study. The lowest daily food yield for the European Kestrel was approximately 40 g.day<sup>-1</sup> (Masman *et al.* 1988). This figure was exceeded in this study only during the summer. Southern African Kestrels on the flats had a daily food intake of around 30 g.day<sup>-1</sup> for nine months of the year, while the intake of Southern African Kestrels in the hills at 10 g.day<sup>-1</sup> for most of the year was probably under-estimated.

Daily intake rate varied widely for European Kestrels (Masman *et al.* 1988). This study was unable to gauge fluctuations in food intake rates. However, as the prey-strike and capture-success rates for catching small prey was high, I suggest that fluctuations would be much less than in high latitude regions. A decrease in hunting performance is less likely to influence daily food intake significantly when small prey are taken than if the kestrel relied mainly on large prey, as does the European Kestrel. Furthermore, the diverse preybase available to the Southern African Kestrel (Chapter 4) would allow the birds to change food sources should one particular type become scarce. This option is probably not available to European Kestrels with a diet limited to only a few prey species. The high diversity of prey would further reduce fluctuations in daily food intake in the Southern African Kestrel.

European Kestrels probably have greater energetic requirements compared to Southern African Kestrels because temperatures are below the kestrel's critical temperature (the temperature at which a bird has to actively increase its metabolic rate to maintain a constant body temperature) for a large proportion of the year in Europe (Chapter 1). Common Kestrels at relatively high latitudes probably have

greater food intake rates than Common Kestrels at lower latitudes because of this increased basal metabolic rate during extreme weather conditions.

This study supports the hypothesis that Common Kestrels at high latitudes have greater food intake rates than Common Kestrels at lower latitudes. It further suggests that day-to-day food intake fluctuates less at lower latitudes because of the diverse preybase and small size of prey eaten.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- Acocks, J.P.H. 1975. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 40:1-98.
- Altmann, J. 1974. Observational study of behaviour: Sampling methods. *Behaviour* 49:227-267.
- Barnard, P. 1986. Windhovering patterns of three African raptors in montane conditions. *Ardea* 74:151-158.
- . 1987. Foraging diet selection by three raptors in relation to grassland burning in a montane habitat. *African Journal of Ecology* 25:35-45.
- Collopy, M.W. 1977. Food caching by female American Kestrels in winter. *Condor* 79:63-68.
- Collopy, M.W. and J.R. Koplin. 1983. Diet, capture success, and mode of hunting by female American Kestrels in winter. *Condor* 85:369-371.
- Cramp, S. and K.E.L. Simmons. 1980. *Handbook of the birds of Europe, the Middle East and North Africa. Vol. 2. Hawks to Bustards.* London: Oxford University Press. pg 289-200.
- Dijkstra, C., L. Vuursteen, S. Daan, and D. Masman. 1982. Clutch size and laying date in the Kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis* 124:210-213.
- Hornfeldt, B., and U. Eklund. 1990. The effect of food on laying date and clutch-size in Tengmalm's Owl *Aegolius funereus*. *Ibis* 132:395-406.
- Masman, D., M. Gordijn, S. Daan, and C. Dijkstra. 1986. Ecological energetics of the Kestrel: field estimates of energy intake throughout the year. *Ardea* 74:24-39.
- Masman, D., S. Daan, and C. Dijkstra. 1988. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. *Journal Animal Ecology* 57:411-432.

- Pettifor, R.A. 1983. Seasonal variation, and associated energetic implications, in the hunting behaviour of the Kestrel. *Bird Study* **30**:201-206.
- Rijnsdorp, A., S. Daan, and C. Dijkstra. 1981. Hunting in the Kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. *Oecologia* **50**:391-406.
- Rudolph, S.G. 1982. Foraging strategies of American Kestrels during breeding. *Ecology* **63**:1268-1276.
- . 1983. Aerial insect-catching by American Kestrels. *Condor* **85**:368-369.
- Shrubb, M. 1980. Farming influences on the food and hunting of Kestrels. *Bird Study* **27**:109-115.
- . 1982. The hunting behaviour of some farmland Kestrels. *Bird Study* **29**:121-128.
- Stanback, M.T. 1991. A reassessment of avian food caching. *Bird Behaviour* **9**:1-6.
- Stevens, D.W., and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.
- van Zyl, A.J. 1991. Unusual falcon hunting behaviour. *Gabar* **6**:68.
- Videler, J., D. Weihs, and S. Daan. 1983. Intermittent gliding in the hunting flight of the Kestrel, *Falco tinnunculus* L. *Journal of Experimental Biology* **102**:1-12.
- Videler, J., and A. Groenewold. 1991. Field measurements of hanging flight aerodynamics in the Kestrel *Falco tinnunculus*. *Journal of Experimental Biology* **155**:519-530.
- Village, A. 1983. Seasonal changes in the hunting behaviour of Kestrels. *Ardea* **71**:117-124.

## CHAPTER 4

THE DIET OF THE SOUTHERN AFRICAN KESTREL  
IN THE EASTERN CAPE PROVINCE, SOUTH AFRICA

## ABSTRACT

The diet of the Southern African Kestrel (*Falco tinnunculus rupicolus*) was studied in both a flat and a hilly area in the eastern Cape Province, South Africa. Diet was determined by direct observation of prey captured, prey brought to nests and an analysis of pellets collected on a monthly basis throughout the year. The main component of the diet consisted of arthropods, primarily Orthoptera and Arachnida, while the few vertebrates eaten included birds and lizards. The diet differed in the two study areas. Southern African Kestrels on the flats ate more vertebrate prey than Southern African Kestrels in the hills. Arthropods were taken throughout the year, whereas vertebrates were taken mainly during winter by Southern African Kestrels on the flats. Vertebrates were taken more often during flight-hunting on the flats, and by perch-hunting in the hills. Males brought vertebrates to the females during incubation, whereas the chicks were fed vertebrates and arthropods during nestling and post-fledging dependence periods. Diet differed from that of western European Kestrels by having a large invertebrate component for both breeding and non-breeding birds.

## INTRODUCTION

The breeding performance of many raptors can be related to food intake rates and diet quality (Newton 1979). The importance of voles (Mammalia: Rodentia) in the diet of the European Kestrel (*Falco tinnunculus tinnunculus*) has been shown in several studies (Cavé 1968; Dijkstra *et al.* 1982; Village 1982; Korpimäki 1985, 1986). Although small mammals form a substantial part of the diet of European Kestrels, several studies have found that large numbers of insects are taken throughout the year (Yalden and Walburton 1979; Shrubbs 1982; Itämielä and Korpimäki 1987). Small mammals, however, remain the principal component on a biomass basis. Village (1990) found that kestrels closer to the equator ate a large number of invertebrates, but emphasized the paucity of information from low latitudes. Steyn (1982) was unable to give any quantification of the Southern African Kestrel's diet.

The aim of this chapter is to describe the diet of the Southern African Kestrel (*Falco tinnunculus rupicolus*), a subspecies of the Common Kestrel, at a relatively low latitude (32°S). The seasonal variation at two study areas of vertebrates and arthropods in the Southern African Kestrel diet will be shown. Seasonal variation

in diet was recorded for breeding and non-breeding Southern African Kestrels during spring and summer and non-breeding Southern African Kestrels during autumn and winter.

#### METHODS

Hunting behaviour of the Southern African Kestrel was observed from May 1990 to May 1991 in the Tarkastad (32°00'S, 26°15'E) district, South Africa, in both a flat and a hilly area. Average annual summer (October to March) rainfall measured in Tarkastad 15 km north of the flat study area was 426.4 mm ( $N = 29$  years). The low rainfall during 1990 (245 mm) was the possible reason for none of the observed Southern African Kestrels breeding which provided the unique opportunity to study non-breeding Southern African Kestrels during the normal breeding season. The habitat of both areas is classified as karroid *Merxmuellera* mountain veld (Acocks 1975) with *Merxmuellera disticha* the dominant grass.

Prey caught or retrieved from caches was identified where possible, while most prey was categorized as either vertebrate or arthropod. The proportion of vertebrate and arthropod prey in the diet was calculated by comparing the frequency of capture attempts (prey-strikes) for each prey type. It was possible to categorize prey as vertebrate or invertebrate by the type of strike made at the prey. Southern African Kestrels flew hard and fast into the vegetation when trying to catch vertebrates and when these strikes were at birds, they were often made over relatively large distances. Strikes at invertebrates were characterized by their relatively slower strike and were most often not further than 60 m away. Unidentified prey caught (5.9% of 1370 successful strikes) was categorized as vertebrate or arthropod based on the proportion of vertebrate to arthropod for known successful prey-strikes. Three nests in the hilly study area were observed for 324 hours and prey brought to the nest was identified where possible.

No estimation of prey mass could be made during observations. Average masses of vertebrate and invertebrate prey were therefore estimated by randomly collecting and weighing as small sample of similar-sized prey in the area. Average mass for invertebrates was  $0.6 \pm 0.6$  g ( $X \pm SD$ ,  $N = 43$ ) and  $22.8 \pm 16.3$  g ( $X \pm SD$ ,  $N = 9$ ) for vertebrates (Table 4.1). The proportion of each prey species collected influences these averages considerably but the main difference in average mass between invertebrates and vertebrates remains large.

Regurgitated pellets were collected on a monthly basis from under roosts and hunting perches. These pellets were dried in an oven at 60°C for 48 hours and then weighed. Pellets were dissected in water and prey items were identified to at least ordinal level. Diet was estimated from the percentage of pellets containing various prey items (Village 1990). Soft-bodied invertebrates such as earthworms could

have been missed (Yalden and Yalden 1985) but the proportion of such invertebrates was probably low since none were taken during 727 hours of direct observations on hunting. There might also have been a bias towards rodents in the pellets. Based on observations at the nest, many more reptiles were provisioned than what the pellets suggest. Invertebrates, however, seemed to be well represented by the pellet analysis.

TABLE 4.1. Average prey mass for invertebrate and vertebrate prey species collected in the hilly study area.

Prey type	Average	SD	<i>N</i>
Invertebrates			
Orthoptera	0.6	0.5	41
Coleoptera	0.25		1
Solifugidae	3.0		1
Invertebrate average	0.6	0.6	43
Vertebrates			
Aves	22.3	13.7	4
Lacertilia	13.0	1.4	2
Rodentia	30.0	24.6	3
Vertebrate average	22.8	16.3	9

## RESULTS

### Diet based on observations

Seventy-four prey items were identified during foraging observations (Table 4.2). No birds were taken by the Southern African Kestrels in the hills and the proportion of small mammals taken was less than on the flats.

Precise identification of prey was difficult, and often it was only possible to distinguish whether prey were vertebrates or arthropods (Table 4.3). Southern African Kestrels on the flats made a higher proportion of prey-strikes at vertebrates while flight-hunting (Table 4.4). In contrast, the Southern African Kestrels in the hills made more hunts at vertebrates from a perch. Perch-hunting Southern African Kestrels in the two study areas caught similar ratios of vertebrates to invertebrates. Overall, the Southern African Kestrels on the flats took more vertebrates than those in the hilly area. Similar results were found for successful prey-strikes (Table 4.4).

TABLE 4.2. Prey items identified during field observations of breeding and non-breeding Southern African Kestrels.

Prey	Number caught
Isoptera	17
Coleoptera	2
Unidentified arthropods	21
Common Longtailed Seps <i>Tetradactylus tetradactylus</i>	1
Gekkonidae sp.	1
Scincidae sp.	1
Unidentified lizards	9
Unidentified snakes	2
Unidentified small mammals	10
Neddicky <i>Cisticola fulvicapilla</i>	1
Greybacked Finchlark <i>Eremopterix verticalis</i>	1
Unidentified birds	2
Carrion (Ant-eating Chat <i>Myrmecocichla formicivora</i> )	1
Prey cached at Southern African Kestrel nest sites	
<i>Agama</i> spp.	3
Sand Lizard <i>Pedioplanis</i> sp.	1
Cape Girdled Lizard <i>Cordylus cordylus</i>	1

Results from perch-hunting were almost identical but prey taken while flight-hunting differed considerably. Flight-hunting Southern African Kestrels in the hills caught no vertebrates while a greater proportion of vertebrates caught by Southern African Kestrels on the flats were taken while flight-hunting.

Based on prey mass, invertebrate prey formed the bulk of the Southern African Kestrel's diet in the hilly study area while vertebrates contributed 55.1% to the total prey mass for those on the flats (Table 4.5).

Prey provisioned to the nest and to fledged chicks in the hilly study area are given in Table 4.6. Male Southern African Kestrels brought mainly large prey such as lizards to the incubating female. During the nestling and post-fledging periods, both large and small prey were provisioned to the chicks. Lizards still formed the bulk of the vertebrate food provisioned, but a high proportion of the prey provisioned during this period were arthropods.

TABLE 4.3: Monthly prey-capture success for perch and flight hunting in the hilly and flat study areas. Prey-capture success in percent is given for arthropod and vertebrate strikes and sample sizes are given in brackets.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.Total(%)
<b>Flat study area</b>												
Vert. from perch	50 (2)	66 (6)	100 (6)	58 (12)	50 (4)	50 (2)	29 (7)	50 (4)	100 (1)	0 (1)	0 (1)	0 (1) 55.3 (47)
Vert. from flight	0 (2)	- (0)	0 (1)	- (0)	100 (3)	100 (1)	0 (1)	0 (2)	0 (9)	100 (1)	0 (0)	100 (1) 33.0 (21)
Arth. from perch	73 (137)	82 (188)	78 (136)	78 (153)	70 (77)	53 (59)	73 (51)	36 (50)	56 (108)	77 (64)	76 (136)	80 (10) 71.6 (1169)
Arth. from flight	41 (27)	20 (20)	61 (33)	81 (16)	75 (8)	25 (24)	38 (16)	27 (30)	52 (60)	61 (62)	83 (46)	50 (2) 53.5 (344)
<b>Hilly study area</b>												
Vert. from perch	- (0)	100 (2)	100 (5)	0 (1)	0 (1)	- (0)	0 (1)	- (0)	0 (1)	33 (3)	- (0)	- (0) 57.1 (14)
Vert. from flight	- (0)	- (0)	- (0)	- (0)	- (0)	- (0)	- (0)	- (0)	0 (4)	0 (1)	- (0)	0 (0) 0.0 (5)
Arth. from perch	100 (1)	72 (99)	73 (56)	77 (56)	73 (59)	75 (8)	40 (5)	68 (19)	12 (25)	59 (61)	91 (11)	- (0) 67.5 (400)
Arth. from flight	46 (13)	67 (178)	53 (43)	100 (3)	68 (77)	54 (138)	38 (228)	37 (332)	35 (247)	61 (64)	88 (33)	- (0) 41.1 (1356)

TABLE 4.4. Proportions of vertebrate to arthropod prey (vertebrate : arthropod) for perch- and flight-hunting in the two study areas. The proportion of vertebrates of the total number of prey-strikes is expressed as a percentage in brackets.

	Perch-hunting		Flight-hunting	
Total prey-strikes				
Flats	47	:1169 (3.87%)	21	: 344 (5.75%)
Hills	14	:400 (3.38%)	5	: 1356 (0.37%)
Successful prey-strikes				
Flats	26	:837 (3.01%)	7	: 184 (3.66%)
Hills	8	:270 (2.88%)	0	: 630 (0.00%)

TABLE 4.5. Total prey mass captured by Southern African Kestrels during 727 hours of field observations in the flat and hilly study areas. Sample size is given in brackets. Total prey mass was calculated using the average mass of similar-sized prey in the study area ( $X = 0.6$  g for invertebrates and  $X = 22.8$  g for vertebrates). The proportion of the vertebrate mass to the total mass of prey is given as a percentage.

	Total vertebrate mass		Total invertebrate mass		Proportion of vertebrate mass
Flats	752	(33)	613	(1021)	55.1%
Hills	182	(8)	540	(900)	25.2%

#### Diet based on pellet analysis

The percentage of pellets containing ten food categories is given in Table 4.7. Orthoptera, solifugids and Coleoptera were the preferred prey types, with at least one of these prey types found in 65 out of 68 pellets in the hills and 142 out of 146 pellets in the flats. Arthropods from the orders Hymenoptera, Isoptera, Odonata and Arachnida were also found in the pellets. Vertebrates were not found often, with rodents being the most numerous followed by birds and reptiles.

TABLE 4.6: Number of prey provisioned during incubation, nestling and post-fledging periods to three nest sites in the hilly study area during the 1990/91 breeding season.

Prey type	Number of objects delivered		
	Incubation	Nestling	Post-fledging
Orthoptera	11	45	42
Coleoptera	1	6	-
Lepidoptera	1	-	-
Odonata	-	-	1
Unidentified arthropods	16	134	137
Centipede	1	5	-
Scincidae spp.	2	13	8
<i>Agama</i> spp.	2	8	3
Unidentified lizards	16	16	1
Unidentified snakes	1	5	1
<i>Falco tinnunculus</i> chick	-	1	-
<i>Elephantulus</i> sp.	1	-	-
Unidentified small mammals	1	4	1
Unidentified vertebrates	-	-	1
Unidentified prey	3	80	121
Total prey	56	317	316
Hours observation (hours)	127	126	70

#### Seasonal variation in the diet

Invertebrate prey occurred frequently in the diet of the Southern African Kestrels in the hills during winter and late summer. The analysis of pellets revealed a high intake of arthropods throughout the year with a peak in spring and summer for Coleoptera and in summer and autumn for solifugids. This is in contrast to a peak in arthropods in the diet of the birds on the flats during summer and a depression during winter according to the observations, a trend only reflected by the solifugids in the pellets. Many pellets contained Orthoptera during autumn and winter, while there was little seasonal variation in Coleoptera and Hymenoptera present in the

pellets. According to the pellet analysis, Isoptera formed an important part of the diet during spring for Southern African Kestrels on the flats.

TABLE 4.7. Percentage of pellets containing the 10 main categories of prey for the two study areas. Pellets were collected from roost and hunting perches on a monthly basis and lumped for seasonal analysis.

	Autumn	Winter	Spring	Summer	<i>N</i>
<b>Hilly study area</b>					
<i>N</i>	12	16	28	12	68
Orthoptera	91.7	100.0	82.1	91.7	61
Solifugidae	66.7	50.0	57.1	91.7	43
Coleoptera	16.7	37.5	57.1	58.3	31
Isoptera	8.3	12.5	10.7	16.7	8
Hymenoptera	16.7	18.8	28.6	16.7	15
Odonata	0.0	0.0	0.0	0.0	0
Aves	0.0	0.0	3.6	8.3	2
Rodentia	0.0	50.0	17.9	8.3	19
Reptilia	0.0	0.0	0.0	0.0	0
Arachnida	33.3	0.0	0.0	0.0	4
<b>Flat study area</b>					
<i>N</i>	33	33	40	39	145
Orthoptera	84.8	87.9	52.5	59.0	101
Solifugidae	60.6	30.3	67.5	84.6	90
Coleoptera	48.5	54.5	55.0	59.0	79
Isoptera	9.1	6.1	35.0	15.4	25
Hymenoptera	30.3	36.4	22.5	25.6	41
Odonata	3.0	0.0	0.0	0.0	1
Aves	3.0	12.1	10.0	0.0	9
Rodentia	6.1	30.3	30.0	5.1	26
Reptilia	0.0	0.0	2.5	0.0	1
Arachnida	18.2	0.0	0.0	0.0	6

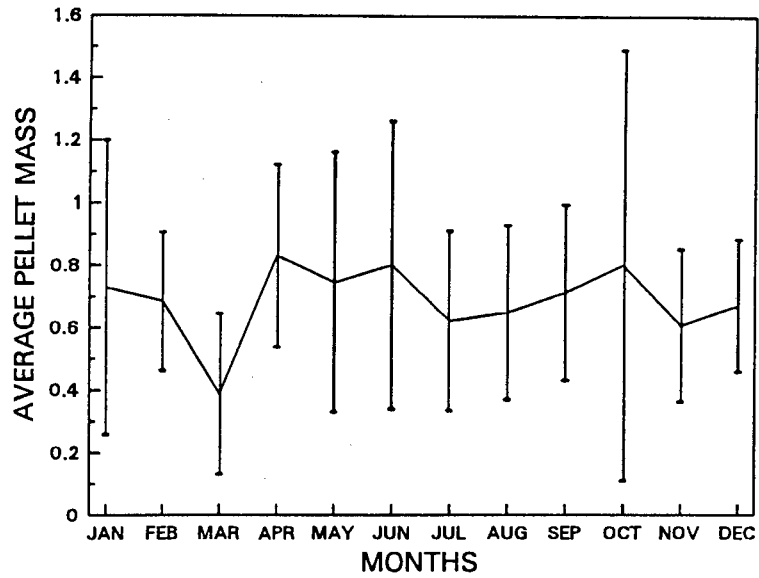


FIG. 4.1: Average monthly pellet mass for both study areas combined. Vertical lines indicate standard deviation.

The majority of pellets did not contain vertebrates in either area. Vertebrates were more prevalent in the diet of the Southern African Kestrels on the flats during winter. The presence of vertebrates in the pellets increased during winter and spring in both areas. This was not reflected in the observations on Southern African Kestrels in the hills during winter when no successful vertebrate prey-strikes were recorded. Rodents were the predominant vertebrate found in pellets.

Average monthly pellet mass for the year is given in Fig. 4.1. Although pellet mass has been correlated to intake rates (Yalden & Yalden 1985), there was no obvious seasonal trend in this study.

#### DISCUSSION

The proportion of arthropods in the diet of Southern African Kestrels in this study is in contrast to the high proportion of mammals in the diet of European Kestrels. Based on numbers, arthropods formed the bulk of the diet of the Southern African Kestrel, especially in the flat study area. There was only a slight increase in vertebrates eaten during winter and during provisioning of food to the incubating female by the male. Orthoptera was the major component of the diet, with Coleoptera, Isoptera and solifugid spiders forming varying proportions depending on the season. Breeding Southern African Kestrels brought relatively large numbers of invertebrates to chicks in the nest, in contrast to other studies of the Southern African Kestrel (Mendelsohn 1990) and the European Kestrel (Village 1990). When vertebrates were brought to the nest, lizards formed the bulk provisioned, as in other studies at low latitudes (Mendelsohn 1990, Village 1990).

Southern African Kestrels in the hills caught most of their invertebrate prey when hover-hunting. This was unusual as several other studies have found that kestrels using the energetically more expensive technique of windhovering caught more vertebrates than perch-hunting kestrels (Masman *et al.* 1988, Collopy and Koplín 1983). Southern African Kestrels on the flats caught more vertebrates while windhovering as reported in other studies.

The correlation of diet and variation in life-history traits is well-known (Blondel *et al.* 1991). Village (1990) demonstrated an increase in invertebrates in the diet of kestrels living at relatively low latitudes. Village (1990) generalised that Common Kestrel diets in the relatively high latitudes seemed to comprise small mammals, birds and beetles, whereas those at lower latitudes were based more on lizards, birds and grasshoppers. He was unable, however, to obtain a significant trend for the proportion of invertebrates in the diet at low latitudes, and he suggested that this was because of the increase in the proportion of reptiles taken during the breeding season. This study provides data during the breeding season for Southern African Kestrels that bred and those that did not breed, that strongly supports Village's diet

trend over latitudes. Southern African Kestrels in this study balanced their effort of catching many small prey items by using the low-energy perch-hunting technique (Chapter 2 and 3). Flight-hunting in the hills was characterized by hanging in updrafts, the energetically least expensive form of flight-hunting (Videler *et al.* 1991). Thus, positive energetic budgets were probably maintained, being balanced by the high intake rates associated with flight-hunting.

Vertebrates have an equivalent energetic value per gram dry mass to invertebrates (21.4 kJ.g<sup>-1</sup> for voles, Masman *et al.* 1986; 18.9 - 23.0 kJ.g<sup>-1</sup> for invertebrates, Whittow 1986, R.M. Little unpubl. data). Common Kestrels living primarily on invertebrates have to catch many small prey to equal the energetic content of a single vertebrate. Southern African Kestrels in this study had to hunt longer (Chapter 2) using energetically less expensive hunting techniques to catch less food (Chapter 3) than vole-eating European Kestrels (Masman *et al.* 1988). These data support the current idea that life-history traits are correlated with diet (Blondel *et al.* 1991). Furthermore, trends in life-history traits in kestrels over latitude and rainfall gradients can be explained by the proportion of arthropods in the diet of breeding kestrels.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- Acocks, J.P.H. 1975. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 40:1-98.
- Blondel, J., A. Dervieux, M. Maistre, and P. Perret. 1991. Feeding ecology and life history variation of the blue tit in Mediterranean deciduous and sclerophyllous habitats. *Oecologia (Berlin)* 88:9-14.
- Cavé, A.J. 1968. The breeding of the Kestrel (*Falco tinnunculus*) in the reclaimed area Oostelijk Flevoland. *Netherlands Journal of Zoology* 18:313-407.
- Collopy, M.W., and Koplín, J.R. 1983. Diet, capture success and mode of hunting by female American Kestrels in winter. *Condor* 85:369-371.
- Dijkstra, C., L. Vuursteen, S. Daan, and D. Masman. 1982. Clutch size and laying date in the Kestrel *Falco tinnunculus*: Effect of supplementary food. *Ibis* 124:210-213.
- Itämies, J., and E. Korpimäki. 1987. Insect food of the Kestrel, *Falco tinnunculus*, during breeding in western Finland. *Aquilo Ser Zoologica* 25:21-31.

- Korpimäki, E. 1985. Diet of the Kestrel *Falco tinnunculus* in the breeding season. *Ornis Fennica* **62**:130-137.
- . 1986. Diet variation, hunting habitat and reproductive output of the Kestrel *Falco tinnunculus* in the light of the optimal diet theory. *Ornis Fennica* **63**:84-90.
- Masman, D., M. Gordijn, S. Daan, and C. Dijkstra. 1986. Ecological energetics of the European Kestrel: The variability of natural intake rates. *Ardea* **74**:24-39.
- Masman, D., S. Daan, and C. Dijkstra. 1988. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. *Journal of Animal Ecology* **57**:411-432.
- Mendelsohn, J.M. 1990. Observations on the breeding of Rock Kestrels in Windhoek, Namibia. *Gabar* **5**:5-10.
- Newton, I. 1979. Population ecology of raptors. T. & A.D. Poyser, London.
- Shrubb, M. 1982. The hunting behaviour of some farmland Kestrels. *Bird Study* **29**:121-128.
- Steyn, P. 1982. Birds of prey of southern Africa. Their identification and life histories. David Philip, Cape Town.
- Videler, J., and A. Groenewold. 1991. Field measurements of hanging flight aerodynamics in the Kestrel *Falco tinnunculus*. *Journal of Experimental Biology* **155**:519-530.
- Village, A. 1982. The diet of Kestrels in relation to vole abundance. *Bird Study* **29**:129-138.
- . 1990. The Kestrel. T. & A.D. Poyser, London.
- Whittow, G.C. 1986. Energy metabolism. Pages 253-268 in P.D. Sturkie, editor. *Avian Physiology*. Springer-Verlag, New York.
- Yalden, D.W., and A.B. Walburton. 1979. The diet of the Kestrel in the Lake District. *Bird Study* **26**:163-170.
- Yalden, D.W., and P.E. Yalden. 1985. An experimental investigation of examining Kestrel diet by pellet analysis. *Bird Study* **32**:50- 55.

## CHAPTER 5

THE INFLUENCE OF FOOD ON THE BREEDING BIOLOGY OF THE  
SOUTHERN AFRICAN KESTREL *Falco tinnunculus rupicolus*

## ABSTRACT

The breeding biology of 23 pairs of Southern African Kestrels (*Falco tinnunculus rupicolus*) were studied over two seasons in the Tarkastad District (32°S), South Africa, and compared to studies of the western European Kestrel (*Falco tinnunculus tinnunculus*; 53°N). In this study, most Southern African Kestrels bred in old stick nests and on cliffs at densities comparable with average densities of European Kestrels. Average clutch size was smaller than in Europe (3.47 eggs for the Southern African Kestrel, 4.4 eggs for the European Kestrel) while incubation period for one nest was 27 days, within the range for European Kestrels. Nestling period (30-31 days) and post-fledging period (32-39 days) were within the range recorded for the European Kestrel. There was a decrease in the number of chicks fledged with an increase in laying date. Chick feather-growth rate was slow compared to European Kestrels, and it is suggested that food-intake rate relates directly to feather-growth rate. Provisioning rates to the nestlings were higher than in Europe but the amount of food delivered per day was lower. It is suggested that low food-intake rates limit the clutch size, the number of young produced and the growth rates of chicks.

## INTRODUCTION

Breeding rates in birds are influenced by egg and clutch size, laying date, the duration of incubation, nestling and post-fledging periods, the age of first breeding and the frequency of breeding attempts (Newton 1979). These features are inter-related with one another, and with environmental factors such as food (Drent and Daan 1980). The respective influences of clutch size, number of clutches per season, and age of maturity contribute to the overall long-term survival of the species (Bennett and Harvey 1988).

Trends in breeding rates over latitudinal gradients are well known (Ricklefs 1972; Slagsvold 1982; Möller 1984) although there remains speculation concerning survival rates (Karr *et al.* 1990). There is a decrease in clutch size (Kulesza 1990), and an increase in incubation, nestling and post-fledging periods with a decrease in latitude (Newton 1979).

Based on these trends, I examine here the following hypotheses concerning the breeding biology of the Southern African Kestrel in South Africa and the European Kestrel:

1. Southern African Kestrels have on average smaller clutch sizes,
2. Southern African Kestrels have longer incubation, nestling, and post-fledging periods,
3. Southern African Kestrel nestlings grow more slowly, and
4. Southern African Kestrels deliver relatively less food to the incubating female and nestlings during the breeding season, thus limiting the clutch size and chick growth rates.

This chapter also provides information on basic breeding biology, as yet unavailable for the Southern African Kestrel (Steyn 1982).

#### METHODS

The breeding performance of 23 pairs of Southern African Kestrels was monitored over two breeding seasons from October 1990 to January 1992 in a hilly and a flat study area. The hilly study area was located 30 km south of Tarkastad (32°00'S, 26°15'E) in the eastern Cape Province, South Africa in the foothills of the Winterberg range (2 368 m a.s.l.). The slopes were covered in short grass or low bushes. Cliffs were a dominant feature of the landscape. The second study area was an open flat area located 15 km north of the hilly study area. The dominant vegetation was long grass or small Karoo bushes. Clumps of large exotic trees were spaced irregularly over the area. The average annual rainfall measured at Tarkastad was 426.4 mm ( $N = 29$  years; 245mm in 1990 and 539mm in 1991). Only three pairs of breeding Southern African Kestrels were found during the 1990/91 season which was possibly due to the exceptionally low rainfall. The average daily temperature measured in Queenstown (53 km north-east of the flat study area) ranged from an average minimum of 9.2°C to an average maximum of 24.5°C.

Locations of Southern African Kestrel nests were marked on a map and their activity monitored during the breeding season. Nest location (for example, a cliff or tree) and type (stick nest or scrape) were recorded and the height was estimated to the nearest 2 m from ground level. Southern African Kestrel breeding density was measured in a 21km<sup>2</sup> area, within which all the pairs were known in each of the two study areas. A further index of Southern African Kestrel breeding density was obtained by measuring the inter-nest distance between nearest neighbours on a 1 : 50 000 topographical map.

Nests were visited at least weekly and laying date, clutch size, hatching and fledging success was recorded. Where nests were found only after the laying or

hatching dates, these dates were estimated by ageing the nestlings and back-dating using incubation and nestling periods determined for the Southern African Kestrel during this study. Nestlings were aged by using regression lines of tarsus or wing measurements taken from nestlings of known age.

Five nests were observed (three in 1990/91 and two in 1991/92) for a total of 362.6 hours, covering all hours of daylight during the incubation (157.2 hr), nestling (139.3 hr) and post-fledgling (66.1 hr) periods. All prey deliveries were recorded and prey was identified where possible. Prey was categorized as vertebrate or arthropod but prey mass could not be accurately estimated. Average masses of vertebrate and invertebrate prey delivered to the nest were estimated by collecting and weighing similar-sized prey in the area. Average mass for invertebrates was  $0.6 \pm 0.6$  g ( $X \pm SD$ ,  $N = 43$ ) and  $22.8 \pm 16.3$  g ( $X \pm SD$ ,  $N = 9$ ) for vertebrates (see Chapter 4).

Differences between seasons and study areas for mean clutch size, hatching success and number of chicks fledged were tested using a Student's *t*-test (Zar 1984). Where means are given, standard deviation follows with sample sizes in brackets.

Culmen, tarsus, wing and tail lengths and mass of nine nestlings from four broods were measured every second day until they were about to fledge. Growth rates of nestlings were quantified using Ricklefs (1967) growth constant, *K*, applied to the mass of the nestlings.

## RESULTS

### Nest sites

Of 22 nest sites, 10 were on cliffs, 11 were in trees and one was on a building (Table 5.1). Most of the nest sites in the hills were on cliffs (60%), whereas most nest sites on the flats were in trees (71%). All the nests in trees were in abandoned Black Crow (*Corvus capensis*) stick nests. The Southern African Kestrels used nests in pine trees (64%) most often, followed by poplars (27%) and eucalypts (9%). Southern African Kestrels nested in sheltered scrapes (a depression in the sand) on cliffs, either in holes (36%), holes or cracks leading off from a ledge (28%) or sheltered places on open ledges (36%) such as under bushes or behind rocks. Average nest height was  $19.5 \pm 8.7$  m ( $N = 15$ ) in the hills and  $11.3 \pm 5.1$  m ( $N = 7$ ) on the flats.

### Breeding density

The average nearest-neighbour distance was  $1\ 559 \pm 494$  m ( $N = 11$ ) in the hills and  $2\ 133 \pm 1419$  m ( $N = 3$ ) on the flats. Density of breeding pairs in the hills

TABLE 5.1. Frequency of nest-site choice by Southern African Kestrels in the hilly and flat study areas.

Nest site	Hilly study area	Flat study area
Cliff	9	1
Building	0	1
Trees		
Poplar	3	0
Pine	3	4
Eucalyptus	0	1
<b>TOTAL</b>	<b>15</b>	<b>7</b>

was 28.9 pairs. $100\text{km}^{-2}$  (6 pairs in a  $21\text{ km}^2$  area) and on the flats 19.1 pairs. $100\text{km}^{-2}$  (4 pairs in a  $21\text{ km}^2$  area).

#### Breeding cycle

Incubation. - During the period just before and during egg laying, the female Southern African Kestrel spent a large proportion of her time close to the nest site where she received food from the male as in the European Kestrel (Village 1990). The male sometimes copulated with the female after a food delivery (4/17 food deliveries).

The incubation period was recorded for only one clutch. From the start of incubation (in this case, the third egg), it took 26 days before the first egg hatched. Two eggs hatched on the 26th day, one the following day and the last egg hatched five days after the first egg. Assuming that the first egg laid was the first egg that hatched, 31 days elapsed between the laying and hatching of the first egg.

Nestling period. - Nestling period was difficult to determine because chicks often left their stick nest to perch on surrounding branches several days before their first flight. At three sites where the nest was checked every second day, the chicks left by 30, 30 and 31 days.

Post-fledging period. - Parent Southern African Kestrels were observed feeding chicks near the nest site 22 and 27 days after the chicks had left the nest. By day 32 one of two chicks was present but no longer fed by the adults at one nest and all three chicks at the other nest had left the nest area after 39 days.

## Breeding success

Three reproductive parameters were measured during the study - clutch-size, hatching success and fledging success.

Clutch-size. - A total of 14 clutch-sizes was recorded over the two breeding seasons. Four were of two eggs, three were of three eggs and seven were of four eggs ( $X = 3.21 \pm 0.89$ ). Mean clutch-size for the two breeding seasons in the two study areas is given in Table 5.2.

TABLE 5.2. Mean clutch size  $\pm$  SD ( $N$ ) in the hills and on the flats during the 1990/91 and 1991/92 breeding seasons.

Breeding season	Hilly study area	Flat study area
1990/91	2.67 $\pm$ 0.58 (3)	no breeding
1991/92	3.33 $\pm$ 1.00 (9)	3.5 $\pm$ 0.71 (2)
Average for both years	3.17 $\pm$ 0.94(12)	3.5 $\pm$ 0.71 (2)

Clutch-sizes did not vary significantly between study areas ( $t = -0.22$ ,  $P = 0.83$ ,  $N = 11$ ) or between years ( $t = -1.07$ ,  $P = 0.31$ ,  $N = 12$ ).

Clutch-sizes for Common Kestrels from other latitudes are given in Table 5.3. Hatching success. - Thirty-six of 42 eggs (85.7%,  $X = 2.67 \pm 0.93$  eggs per nest) in thirteen clutches hatched successfully (Table 5.4). All clutches hatched at least one chick.

Hatching success did not vary significantly between years for Southern African Kestrels in the hills (Mann Whitney  $U$ -test,  $Z = -0.201$ ,  $P = 0.84$ ,  $N = 12$ ). The sample size was too small to test for differences between the two study areas.

TABLE 5.3. A comparison of mean clutch-sizes of the Common Kestrel.

Country	Latitude	Clutch size	$N$	Reference
South Africa	26°S	3.21	14	This study
England	52°N	4.4	233	Village 1990
Netherlands	53°N	4.5 - 5.6	66	Dijkstra <i>et al.</i> 1982
Scotland	55°N	4.6 - 5.1	120	Village 1986
Namibia	22°S	5.0	2	Mendelsohn 1990
Czechoslovakia	50°N	5.73	44	Pikula <i>et al.</i> 1984

TABLE 5.4. Mean hatching success (%) of chicks per nest  $\pm$  SD (N) in the hilly and the flat study areas for the 1990/91 and 1991/92 breeding seasons.

Breeding season	Hilly study area	Flat study area
1990/91	88.9 $\pm$ 19.2 (3)	no breeding
1991/92	83.3 $\pm$ 17.7 (9)	100.0 $\pm$ 0.00 (1)
Average for both years	84.7 $\pm$ 17.3(12)	100.0 $\pm$ 0.00 (1)

Fledging success. - On average, 2.17  $\pm$  1.27 chicks fledged per nest ( $N = 22$ ).

Mean numbers of chicks that fledged for the two breeding seasons in the two study areas are given in Table 5.5.

The number of chicks that successfully fledged did not vary significantly between study areas ( $t = -0.45$ ,  $P = 0.65$ ,  $N = 18$ ) or between years in the hills ( $t = -1.54$ ,  $P = 0.14$ ,  $N = 17$ ).

Seasonal trends. - There were insufficient data to show any trend between clutch size and laying date. There was, however, a decrease in the number of chicks that fledged successfully with an increase in laying date ( $Y = 5.04X - 0.06$ ,  $N = 10$ ,  $P = 0.004$ ) (Fig. 5.1).

TABLE 5.5. Mean number of chicks fledged per nest  $\pm$  SD (N) in the hilly and the flat study areas for the 1990/91 and 1991/92 breeding seasons.

Breeding season	Hilly study area	Flat study area
1990/91	1.25 $\pm$ 1.50 (4)	no breeding
1991/92	2.31 $\pm$ 1.11(13)	2.6 $\pm$ 1.52 (5)
Average for both years	2.06 $\pm$ 1.21(17)	2.6 $\pm$ 1.52 (5)

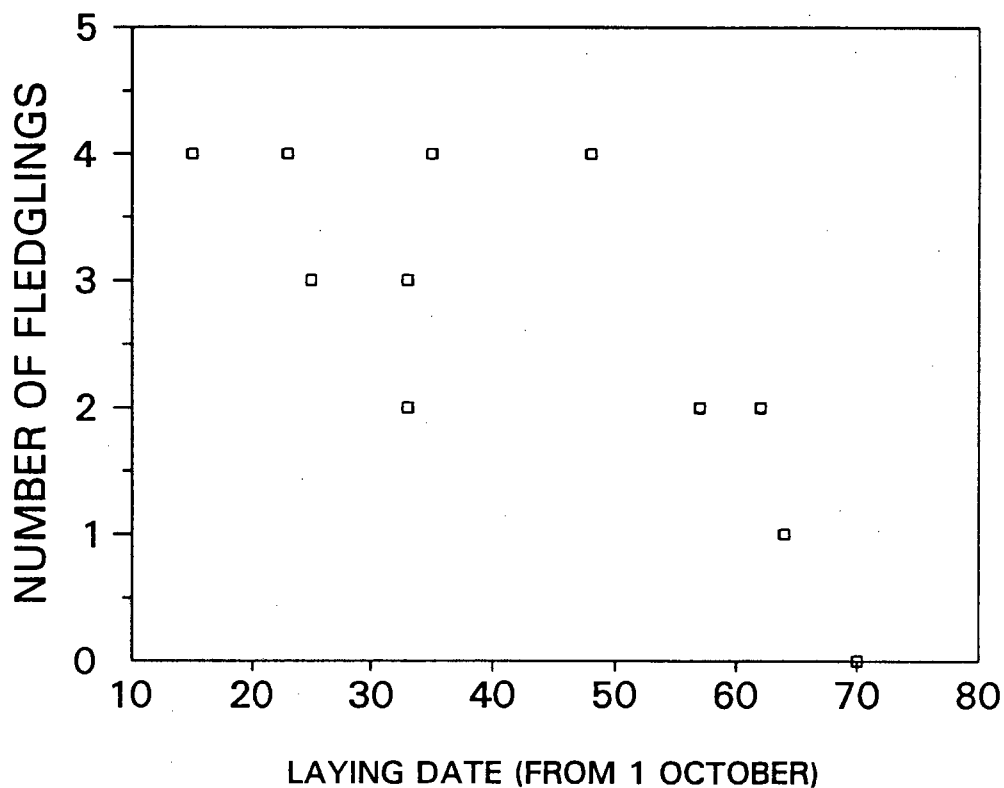


FIG. 5.1. A decline in kestrel fledging success with season in the 1991/92 breeding season ( $Y = 5.04X - 0.06$ ,  $N = 11$ ,  $P = 0.004$ ). Laying date is calculated as the number of days after 1 October that the first egg of the clutch was laid.

## Growth of nestlings

Ageing nestlings using morphometric data. - Nestling growth followed the a sigmoid shape of growth curve (Fig. 5.2a-e). Maximal tarsal growth was reached during the first two weeks after hatching and maximal wing-length growth was reached from two weeks after hatching to fledging. This allowed Southern African Kestrel nestlings to be aged by comparing tarsus or wing-lengths against the regression lines plotted during maximum growth. Regression formulae for the ageing of nestlings are given in Table 5.6.

Rate of growth of nestlings. - The average asymptotic mass of the nestlings was 206g, the growth constant was 0.257 (logistic equation) and 18.0 days elapsed between growth from 10 to 90% of the asymptotic mass. Asymptotic mass was reached 22 days after hatching.

An index of feather growth was obtained by measuring tail- and wing-lengths. Regressions for feather growth are given in Table 5.6.

TABLE 5.6. Regression formulae to calculate age of Southern African Kestrel nestlings using body measurements. Age periods during which the formulae are most applicable and correlation coefficients of the regressions are given. Measurements are for nine nestlings from four broods for which their age was known.

Measurement	Age range when most accurate (days)	Regression	<i>r</i>
Culmen (mm)	1 - 16	$A = (CL - 10.68)/0.53$	0.94
Tarsus (mm)	1 - 20	$A = (TSL - 10.22)/1.52$	0.95
Tail (mm)	14 - fledge	$A = (TLL + 79.54)/6.03$	0.96
Wing (mm)	14 - fledge	$A = (WL + 30.15)/6.62$	0.96
Mass (g)	4 - 24	$A = (M + 6.64)/9.82$	0.92

A = age in days

CL = culmen length

TSL = tarsus length

TLL = tail length

WL = wing length

M = body mass

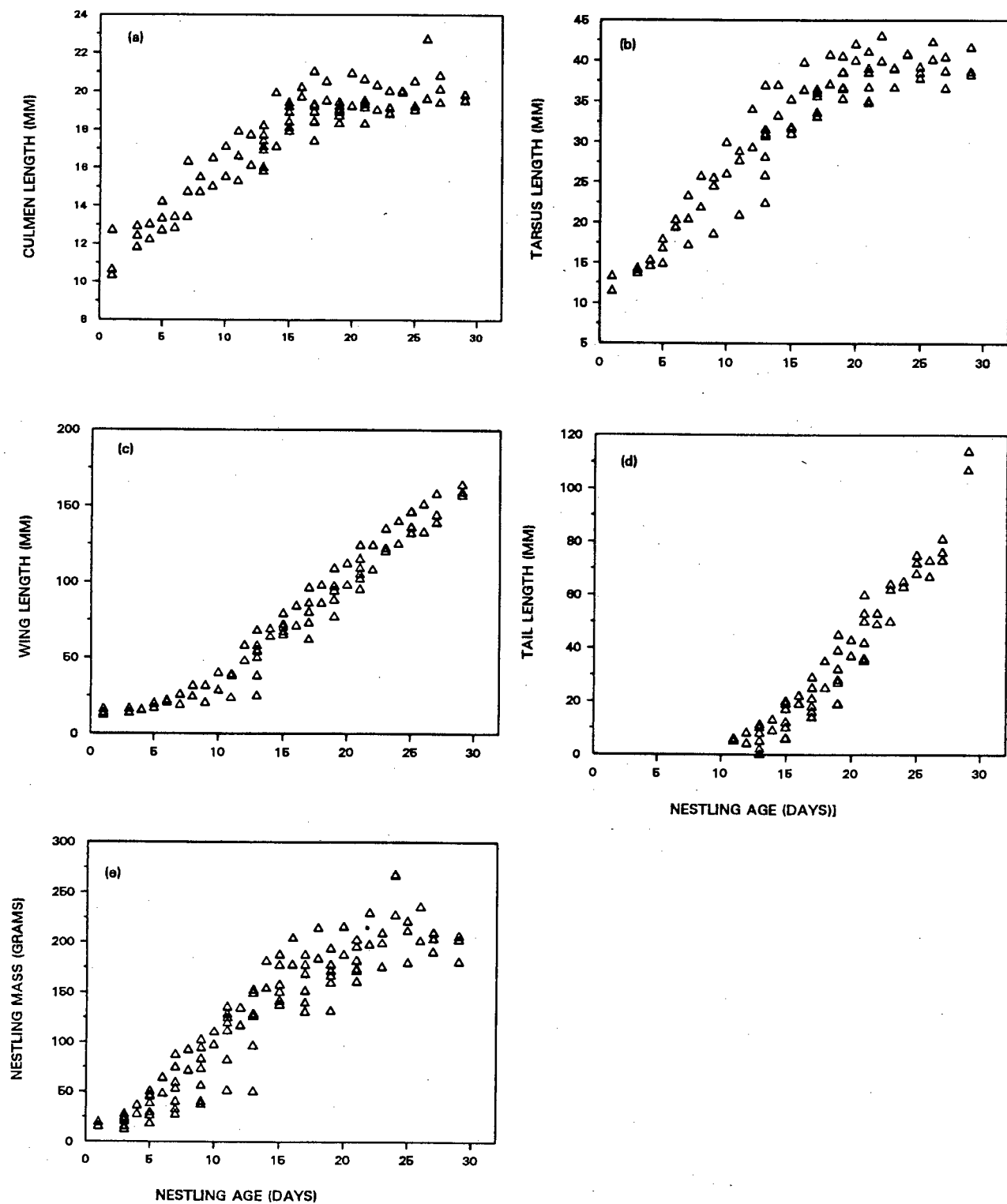


FIG. 5.2. Growth rates of nine nestlings from four broods. (a) culmen length, (b) tarsus length, (c) wing length, (d) tail length and (e) nestling mass.

### Food-provisioning rates to the nest

Rate of food provided for the female during incubation. - The average delivery rate of prey to the incubating female by the male was 6.45 deliveries per day.

Vertebrate prey was delivered more frequently than invertebrate prey (37 vertebrates vs 32 invertebrates). Of the vertebrate prey, 86.5% were reptiles.

Rate of food provided for young in the nest. - The average delivery rate to the nest was 38.1 deliveries per day averaging 15.9 deliveries per chick per day (Table 5.7).

Significantly more arthropods were fed to nestlings (208 arthropods vs 44 vertebrates) than to the female during incubation ( $\chi^2 = 37.6$ , 3 df,  $P < 0.001$ ).

Most arthropods that could be identified were grasshoppers (88.9%,  $N = 81$ ) whereas, of the vertebrates, reptiles were most frequently brought to the nest (78.6%,  $N = 42$ ). Based on estimated prey masses, each chick received on average 71 g of food per day during the nestling period (Table 5.7).

Rate of food provided for fledged young. - More deliveries were made to chicks once they fledged than to nestlings (18.4 deliveries per chick per day) but less biomass was delivered (40 g per chick per day), although this was not significant ( $t = 2.71$ ,  $P = 0.535$ ,  $N = 6$ ). There was no change in the type of prey delivered compared to that delivered to nestlings, although vertebrates formed a significantly smaller proportion (180 arthropods vs 14 vertebrates) than for prey delivered to nestlings ( $\chi^2 = 10.12$ , 3 df,  $P = 0.018$ ).

### DISCUSSION

Southern African Kestrel breeding biology as reported in this study agrees with much of the vast literature on the breeding biology of the Common Kestrel (for a review, see Village 1990). Similar nest sites were selected, the type being largely determined by availability in different areas. Breeding densities were equivalent to those in an area of intermediate density in England (Village 1982). There was a negative correlation between the number of chicks fledged and laying date, probably a consequence of the well-reported trend of a decrease in clutch size with later laying date (Klomp 1970; Dijkstra *et al.* 1982; O'Connor 1982). No obvious breeding behaviour differences were observed between Southern African and European Kestrels.

As predicted by clutch-size trends for other raptors (Newton 1979), Southern African Kestrels in this study laid on average smaller clutches than European Kestrels (see Table 5.3). Clutch sizes from Namibia were surprisingly large but the sample size is small. Mendelsohn's (1990) study was conducted in a arid city environment where the Southern African Kestrels caught large numbers of lizards. Whilst there is a general tendency for birds closer to the equator to lay smaller

TABLE 5.7. Prey delivery rate expressed as number of prey and biomass delivered to the nest per day in western Europe and South Africa.

Locality	Number of prey delivered per nest (prey.day <sup>-1</sup> )	Biomass delivered per nest (grams.day <sup>-1</sup> )	Biomass delivered per chick (grams.chick <sup>-1</sup> .day <sup>-1</sup> )	Reference
Germany	13	-	-	Tinbergen (1940)
Netherlands	19.4-22.1	-	-	Masman <i>et al.</i> (1988)
Netherlands	-	-	62.6	Masman <i>et al.</i> (1989)
Netherlands	-	325	61	Dijkstra <i>et al.</i> (1990)
Czechoslovakia	13.5	-	-	Pikula <i>et al.</i> (1984)
South Africa	38.1	170.3	71	This study

TABLE 5.8. A comparison of incubation period, nestling period and post-fledgling period of the Common Kestrel. All means and ranges are in days.

	Latitude	Mean	N	Range	Reference
Incubation period	52°N	30.8	37	26-34	Village (1990)
	51°N	30	-	28-31	Piechocki (1982)
	Europe	-	-	27-29	Cramp and Simmons (1980)
Nestling period	22°S	28	2	27-29	Mendelsohn (1990)
	32°S	26	1	-	this study
	53°N	30	-	27-32	Cavé (1968)
	51°N	-	-	30-35	Piechocki (1982)
	22°S	33	6	31-36	Mendelsohn (1990)
Post-fledgling period	32°S	-	3	30-31	this study
	Europe	-	-	14-28	Village 1990
	22°S	41.5	6	26-54	Komen and Myer (1989)
	32°S	-	2	32-39	this study

clutches, there is also a tendency for birds in tropical areas to have longer breeding seasons and hence to be multiple-brooded. Southern African and European Kestrels, however, have not been recorded having multiple broods (unpubl. data, Cramp and Simmons 1980). This life-history trait is therefore not discussed in this study as a factor influencing differences in reproductive rates in tropical and temperate environments.

Incubation period, nestling, and post-fledging periods were all within the limits determined in studies of European Kestrels (see Table 5.8; Village 1990) although both nestling and post-fledging periods were closer to the maximum periods calculated for European Kestrels. Although sample sizes in this study were low, similar incubation, nestling and post-fledging periods were found in another Namibian study (Komen and Myer 1989; Mendelsohn 1990). Overall trends in incubation, nestling and post-fledging periods were possibly not reflected in these studies because of the poor definition of starting and ending dates as well as practical difficulties in measuring these periods.

The comparison of minimum incubation, nestling and post-fledging periods may provide a more realistic representation of life-history differences. It can be assumed that minimum periods are the result of an optimum situation while any period longer than the minimum was determined by some ecological constraint. A further improvement would be to combine incubation, nestling and post-fledging periods to obtain a total development period for comparison. This would cater for any adjustments the birds might make to different environmental conditions by varying the length of the various components (incubation, nestling or post-fledging periods) of chick development. However, to compare minimum periods of development, the sample sizes must be large enough to provide a reasonable estimate of the minimum periods.

In a small sample of two broods of Southern African Kestrels in Namibia, nestling growth rates quantified by Ricklefs' (1967) growth constant, were faster than most European Kestrels (Mendelsohn 1990). These results conform to the expectation that growth rate should be faster in Southern African Kestrels as they are slightly smaller than European Kestrels (unpubl. data). However, the results were unexpected, because the longer nestling periods calculated in Mendelsohn's study, and as suggested in this study, imply that nestlings should grow more slowly, and thus fledge later. As in Namibia, Southern African Kestrel nestlings in this study grew faster than those measured in other European studies (Cavé 1968; Kostrzewa and Kostrzewa 1987; Village 1990). While mass gain was slightly faster in Southern African Kestrels, wing feathers grew more slowly than in European Kestrels. The enhanced feather growth of European Kestrels enabled

them to leave the nest earlier than Southern African Kestrels. Asymptotic mass was reached around the same time, implying a similar level of energy partitioning towards mass gain in nestlings. European Kestrels invested more energy in feather growth than Southern African Kestrels. One explanation for this is that European Kestrels need good feather insulation to endure colder temperatures (see Chapter 1) and have an early increase in feather growth. However, if this was the case, asymptotic mass would be reached at a later date because the energy available would have to be partitioned between mass gain and feather growth.

Alternatively, the reason for slower feather growth in Southern African Kestrel nestlings could be due to lower levels of food intake. This was not supported in this study because food intake rate per nestling was higher in this study than for European Kestrels. It is possible, however, that limited energy from low amounts of food delivered to the nest is channelled mostly into mass gain in nestling Southern African Kestrels with feather growth starting later as mass reaches asymptotic values. In European Kestrels there is sufficient energy available for both mass gain and earlier simultaneous feather growth.

Total amount of food brought to the nest was considerably lower in this study than in studies in the Netherlands (Table 5.7). Nestlings, however, obtained similar amounts of food in this study compared to other studies in Europe. Although there was an increase in the number of vertebrates caught by breeding Southern African Kestrels, a large proportion of food delivered to nestlings was invertebrate. Parent Southern African Kestrels presumably expended more energy flying between the hunting areas and the nest than European Kestrels in the Netherlands because of the high number of small invertebrates that are delivered. European Kestrels in the Netherlands made fewer deliveries but delivered larger prey (Table 5.7). This enabled them to spend more energy on actual hunting rather than on frequent flights to the nest with small prey. High energy expenditure transporting food to the nest could probably result in the reduction of food delivered to the nest by parent Southern African Kestrels compared to European Kestrels. The amount of food delivered to the nest could also further be reduced by low food availability in South Africa compared to Europe.

Meijer *et al.* (1990) identified adult European Kestrel hunting yield as the main proximate factor controlling clutch size and the number of chicks that successfully leave the nest. I suggest that the trend of smaller clutches, longer incubation, nestling and fledging periods and, in some cases, slower growth rates at lower latitudes can be related to the food available to the parent kestrels (Chapter 3). Low food availability at lower latitudes constrains both the clutch size, and hence the

number of chicks fledged, and the growth rates of nestlings, causing long incubation, nestling and post-fledging periods.

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#### LITERATURE CITED

- Bennett, P.M. and P.H. Harvey. 1988. How fecundity balances mortality in birds. *Nature* **333**:216-216.
- Cavé, A.J. 1968. The breeding of the Kestrel, *Falco tinnunculus* L., in the reclaimed area Oostelijk Flevoland. *Netherlands Journal of Zoology* **18**:313-407.
- Cramp, S. and K.E.L. Simmons. 1980. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 2. Hawks to bustards. Oxford University Press: London.
- Dijkstra, C., L. Vuursteen, S. Daan and D. Masman. 1982. Clutch size and laying date in the Kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis* **124**:210-213.
- Dijkstra, C., A. Bult, S. Bijlsma, S. Daan, T. Meijer and M. Zijlstra. 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *Journal of Animal Ecology* **59**:269-285.
- Drent, R.H. and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**:225-252.
- Karr, J.R., J.D. Nichols, M.K. Klimkiewicz and J.D. Brawn. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive. *The American Naturalist* **136**:277-291.
- Klomp, H. 1970. The determination of clutch size in birds: a review. *Ardea* **58**:1-125.
- Komen, J. and E. Myer. 1989. Observations on post-fledging dependence of Kestrels (*Falco tinnunculus rupicolus*) in an urban environment. *Journal of Raptor Research* **23**:94-98.
- Kostrzewa, R. and A. Kostrzewa. 1987. Biometric measurements of juvenile Kestrels (*Falco tinnunculus*) a key for ageing. *Oekologie der Vogel (Ecology of Birds)* **9**:119-125.

- Kulesza, G. 1990. An analysis of clutch-size in New World passerine birds. *Ibis* **132**:407-422.
- Masman, D., S. Daan, and C. Dijkstra. 1988. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. *Journal of Animal Ecology* **57**:411-432.
- Masman, D., C. Dijkstra, S. Aden, and A. Bult. 1989. Energetic limitation of avian parental effort: field experiments in the Kestrels (*Falco tinnunculus*). *Journal of Evolutionary Biology* **2**:435-455.
- Meijer, T., S. Daan and M. Hall. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. *Behaviour* **114**:117-136.
- Mendelsohn, J.M. 1990. Observations on the breeding of Rock Kestrels in Windhoek, Namibia. *Gabar* **5**:35-40.
- Möller, A.P. 1984. Geographical trends in breeding parameters of Swallows *Hirundo rustica* and House Martins *Delichon urbica*. *Ornis Scandinavica* **15**:43-54.
- Newton, I. 1979. Population ecology of raptors. T. & A.D. Poyser, London.
- O'Connor, R.J. 1982. Habitat occupancy and regulation of clutch size in the European Kestrel *Falco tinnunculus*. *Bird Study* **29**:17-26.
- Piechocki, R. 1982. Der Turmfalke. Lutherstadt Ziemsen Verlag: Wittenberg.
- Pikula, J., M. Beklova and V. Kubik. 1984. The nidobiology of *Falco tinnunculus*. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae Brno* **18**:1-55.
- Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology* **48**:978-983.
- . 1972. Latitudinal variation in breeding productivity of the Rough-winged Swallow. *Auk* **89**:826-836.
- Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia (Berlin)* **54**:159-169.
- Steyn, P. 1982. Birds of prey of southern Africa. Their identification and life histories. David Philip, Cape Town.
- Tinbergen, L. 1940. Beobachtungen über die Arbeitsteilung des Turmfalke (*Falco tinnunculus*) während der Fortpflanzungszeit. *Ardea* **29**:63-98.
- Village, A. 1982. The home range and density of Kestrels in relation to vole abundance. *Journal of Animal Ecology* **51**:413-428.
- . 1986. Breeding performance of Kestrels at Eskdalemuir, south Scotland. *Journal of Zoology, London* **208**:367-378.
- . 1990. The Kestrel. T. & A.D. Poyser: London.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, London.

## CHAPTER 6

## SYNTHESIS

Life-history theory predicts that particular combinations of traits should occur in specific circumstances. These life-history traits include brood size, size of young, age distribution of reproductive effort, interaction of reproductive effort with adult mortality, and variation of these traits among an individual's progeny (Stearns 1976).

Ricklefs (1991) proposed a framework for interpreting life histories as a series of structures (such as the genotype, phenotype and ethotype) linked by transformations (such as epigenesis, behaviour and ecological interactions) between the units of one structure and the next. Ricklefs' system exists within a framework of environmental factors that influence both the structures and the transformations of life histories.

Several models have been proposed to explain the variation found in life-history traits under the variation of environmental factors. Deterministic models (*r*- and *K*-selection) predict that organisms exposed to high levels of density-independent mortality, wide fluctuations in population density, or repeated episodes of colonization will evolve towards a combination of earlier maturity, larger broods, higher reproductive effort, and shorter lifespans than will organisms exposed to density-dependent mortality or constant population density (MacArthur and Wilson 1967; Pianka 1970). Stochastic models predict the same combinations of life-history traits, but for different reasons. They predict that delayed maturity, smaller reproductive effort, and greater longevity should evolve when fluctuations in the environment result in a highly variable juvenile mortality (Murphy 1968; Schaffer 1974).

Stearns (1977) evaluated the evidence for these models and concluded that the interpretation of the data was ambiguous because the theory was incomplete. There is now evidence that other factors such as scaling to body size (Calder 1983), the effect of body temperature, metabolic rate and brain size (Western and Ssemakula 1982) and certain resource limitations (Dobson and Murie 1987) explain much life-history variation.

Studies interpreting geographical variation in animals are especially useful in examining correlations between life-history traits and the environment (Berven and Gill 1983). Latitudinal gradients are useful in such studies because of the general environmental change from temperate to tropical areas. For instance, food has been shown to be a proximate factor influencing life-history traits in birds (Martin 1987;

Blondel *et al.* 1991). If food supply changes from a temperate to tropical environment, a change in life-history traits would be expected. Although correlations are unable to confirm predictions from life-history theory, they are helpful in generating hypotheses which can then be tested.

The trade-off between fecundity and mortality has been used to interpret many differences in life-history traits over a latitudinal gradient. In a study of mammal life-history variation, Promislow and Harvey (1990) showed that life-history traits varied from a high rate of living (high metabolism, large litters, etc.) and high mortality to those that lived at a slower pace but for longer. The variation of life-history traits over latitudes can be viewed in a similar manner, with animals at higher latitudes living at a higher rate but with a lower survival than those at lower latitudes.

The aim of this study was to look for correlations between life-history traits, behaviour and environmental factors in a population of Southern African Kestrels (*Falco tinnunculus rupicolus*) at a relatively low latitude (32°S) and several well-studied populations of European Kestrel (*Falco tinnunculus tinnunculus*) in Europe (50°N - 55°N). The influence of the genotype (the first structure of Ricklefs' (1991) life-history framework) was not evaluated in this study and it is possible that the two populations compared here are genetically different. However, genotype differences were minimised by studying possibly the same or closely related species in different environments. Data on life-history traits and behaviour were collected to comply with the second and third structures of Ricklefs' (1991) framework.

In this study, differences in the behaviour-time budget, hunting behaviour, diet and breeding parameters between the Southern African Kestrel and the European Kestrel were found. Southern African Kestrels in the relatively low latitude study area spent less energy hunting than the European Kestrels at relatively high latitudes (Chapter 2), but were not able to catch the same amount of food (Chapter 3). The Southern African Kestrel diet in the lower latitude study area consisted mostly of invertebrates, compared to the vertebrate-dominated diet of the European Kestrels at relatively high latitudes (Chapter 4). As predicted by current life-history theory, Southern African Kestrels at low latitudes had smaller clutches and raised fewer offspring than those at higher latitudes (Chapter 5).

In a study of the European Kestrel in the Netherlands, Meijer *et al.* (1990) demonstrated the importance of food in determining clutch size. They showed that food supply influenced laying date which in turn influenced clutch size. In brood manipulations of African Marsh Harriers (*Circus ranivorus*), Simmons (1989) showed that the parents were unable to increase the amount of food brought to the nest to comparable levels maintained by the European Marsh Harrier (*Circus*

*aeruginosus*). He concluded that breeding rates of raptors at low latitudes were constrained by the amount of food they were able to obtain. Food was probably the proximate factor controlling the reproductive rate in this study on the Southern African Kestrel. Moreover, it seems that energetic expenditure also differed between populations at high and low latitudes.

Although not demonstrated, the ecological comparison of Common Kestrels at high and low latitudes suggests that those closer to the equator have a lower but more consistent food supply. This not only constrains the number of offspring fledged each year but also increases longevity as fewer episodes of critical food supply are experienced than in the fluctuating environment of high latitudes.

To test the possible explanations for life-history differences over a latitudinal gradient, the constraints imposed on Common Kestrels will have to be examined. For instance, constraints imposed by food availability could be examined by brood manipulations and feeding experiments. Measurements of energy expenditure and gain under natural and experimental conditions of resident Common Kestrels at different latitudes should provide empirical data for comparison with other studies. The role of the genotype in life-history variation would also have to be investigated, either by translocation of Common Kestrels, or by laboratory studies of birds from different populations maintained under the same conditions.

#### LITERATURE CITED

- Berven, K.A. and D.E. Gill. 1983. Interpreting geographic variation in life-history traits. *American Zoology* **23**:85-97.
- Blondel, J., A. Dervieux, M. Maistre, and P. Perret. 1991. Feeding ecology and life history variation of the Blue Tit in Mediterranean deciduous and sclerophyllous habitats. *Oecologia* **88**:9-14.
- Calder, W.A. 1983. Ecological scaling: mammals and birds. *Annual Review of Ecology and Systematics* **14**:213-230.
- Dobson, F.S. and J.O. Murie. 1987. Interpretation of intraspecific life history patterns: evidence from Columbian ground squirrels. *American Naturalist* **129**:382-396.
- MacArthur, R.H. and E.O. Wilson. 1967. *Theory of island biogeography*. Princeton University Press, Princeton.
- Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* **18**:453-487.
- Meijer, T., S. Daan and M. Hall. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. *Behaviour* **114**:117-136.

- Murphy, G.I. 1968. Pattern in life history and the environment. *American Naturalist* **102**:391-403.
- Pianka, E.R. 1970. On "r" and "K" selection. *American Naturalist* **104**:592-597.
- Promislow, D.E.L. and P.H. Harvey. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology, London* **220**:417-437.
- Ricklefs, R.E. 1991. Structures and transformations of life histories. *Functional Ecology* **5**:174-183.
- Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. *American Naturalist* **108**:783-790.
- Simmons, R.E. 1989. Adaptation and constraint in the breeding of subtropical harriers and eagles. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.
- Stearns, S.C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3-47.
- . 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics* **8**:145-171.
- Western, D. and J. Ssemakula. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia* **54**:281-290.