Aspects of the Biology of the Greater Kestrel in SWA/Namibia

by

Christopher J. Brown*, Mark W. Paxton and Isgart Henrichsen

Directorate of Nature Conservation and Recreation Resorts
Private Bag 13306
Windhoek 9000
SWA/Namibia

* To whom correspondence should be addressed.

Received: 20th April 1986
Accepted: July 1986

ABSTRACT

Greater Kestrels *Falco rupicoloides* are widespread in SWA/Namibia, being most common in open flat terrain with low vegetation. Their numbers fluctuate in response to rainfall, but this is only reflected 1-2 years later. Greater Kestrels nested mainly in old crow nests (76%), but the collapsed nests of Lapwings Vultures *Torgos tracheliotus* (16%) as well as a Blackbreasted Snake Eagle *Circaetus gallicus* nest were also used. Laying dates of 38 clutches ranged from July to January, with most records falling in October. Clutches ranged from 1-5 eggs (mean = 3.1). In the Halali area of Etosha National Park, 12 breeding attempts resulted from 19 pairs-years, with 40 eggs being laid. Of 15 pairs-years monitored, 19 flying young were produced; i.e. 1.3 young per pair-year. 336 pellets and 57 fresh prey items were examined. Invertebrates formed 80% (by number) of food items found in pellets, mammals less than 1%, birds 5%, reptiles 9% and unidentified vertebrates 5.5%. Orthoptera (23%), Coleoptera (19%), Scorpionidae (13%), Isopods (12%) and Solifugids (10%) were the most important invertebrates. The fresh prey items yielded mainly reptiles (74%), the most important species being *Nucrurus taenioliata* (57%), *Agama* species (21%) and *Chamaeleo* species (7%).

1 INTRODUCTION

The Greater Kestrel *Falco rupicoloides* is a common resident in southern Africa, frequenting grassveld, cultivated lands, arid savannas and deserts (Brown et al. 1982; Maclean 1985). It is one of the most common resident birds of prey in the Transvaal and appears to breed successfully in intensively cultivated areas (Tarboton & Allan 1984), provided there is sufficient natural grassland in between over which it can forage (A.C. Kemp in litt.). This kestrel is not considered to be in any danger at present and its range may be increasing in some areas (Steyn 1982).

Although Brown et al. (1982) state that the general habits of the Greater Kestrel are well known in southern Africa, few published accounts exist. Kemp (1978, 1984) has investigated aspects of territoriality and population dynamics in this species in the Transvaal and Hustler (1983) studied its breeding biology at a single nest. The status of the Greater Kestrel in the Transvaal, its laying dates and clutch sizes have been determined (Tarboton & Allan 1984) and detailed information on distribution is available for Natal (Cyrus & Robson 1980) and the Cape Province (Boshoff et al. 1983.) This paper presents information on the distribution, the status, some breeding parameters and the food of the Greater Kestrel in SWA/Namibia.
2 STUDY AREAS AND METHODS

All available data from all parts of SWA/Namibia were used. The country was divided into nine bioclimatic regions based mainly on rainfall and vegetation (Figure 1). Information on the distribution of Greater Kestrels was obtained from an atlas project (Williams 1985) and a raptor road count project (Brown & Biggs 1984), both of which commenced in 1977, and records up to July 1984 are included. Relative abundances of Greater Kestrels for the nine bioclimatic regions were determined from road count data and nesting data were extracted from the national nest record card scheme.

Breeding density and some other aspects of the breeding biology were studied over three years (1982-84) in the Halali area of the Etosha National Park (19 00 S, 16 25 E; 280 000 ha). This area consists of open plains, classed by Giess (1971) as saline desert with dwarf shrub savanna (bioclimatic region 9), which borders the Etosha Pan, giving way in the south to mixed mopane woodland (bioclimatic region 8) which extends to the Park boundary. The mean annual rainfall is about 460 mm. Nests were located from horseback and vehicle, plotted on a 1:50 000 map, and checked at regular intervals (usually weekly) for breeding success.

Prey items were collected in the Etosha National Park and from the Ganab area of the Namib-Naukluft Park (23 15 S, 15 25 E). Ganab (bioclimatic region 2) is situated some 100 km due east of Walvis Bay in the central Namib Desert. The area consists of gravel plains traversed by dry river washes running predominantly from east to west. The river washes support mainly Acacia erioloba trees while between the river washes the gravel plains may be almost devoid of vegetation in years of little rainfall, or support a sparse to moderate grass growth (mainly Stipagrostis species) during years of good rainfall. The mean annual rainfall is about 86 mm.

Prey remains consisted either of pellets, found below nests, roosts or perches, or of fresh prey found in the nest. Only those parts of fresh prey needed for identification purposes were removed, the rest being returned to the nest. Prior to analysis the length and diameter of all pellets were measured using vernier calipers. Prey items were identified to genus where possible for vertebrates and to family or order for invertebrates. The following anatomical structures were used to identify and determine the abundance of different prey animals in pellets. Mammals — hair, lower jawbones and teeth; birds — feathers and bills; reptiles — scales and jawbones; gastropods — shells; arachnids — sting, pedipalps and chelicerae; Isoptera — head and jaws; orthopterans — legs; coleopterans — elytra; hymenopterans — head and jaws.

3 RESULTS

3.1 Distribution

The coverage achieved by the atlas and raptor road count projects is shown in Figure 2. Greater Kestrels were found throughout SWA/Namibia in all nine bioclimatic regions (Figure 3). Although breeding records exist for only the northern and western regions of the country this is to some extent a reflection of observer bias, i.e. a concentration of observations in Nature Conservation areas of Etosha National Park, Namib-Naukluft Park and Skeleton Coast Park, but also an indication of the areas in which the birds are most common (see status below). It is probable, however, that Greater Kestrels breed in areas of suitable habitat throughout the country.

3.2 Status and annual population changes

Greater Kestrels were found to be most common in the southern winter rainfall region of SWA/Namibia and in the saline plains region on the edge of the Etosha
TABLE 1: The relative abundance of Greater Kestrels in the nine Biodemographic regions in SWA/Namibia as obtained from raptor road count data.

<table>
<thead>
<tr>
<th>Region</th>
<th>Sample (km)</th>
<th>Birds seen</th>
<th>Birds per 1 000 km</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Northern Namib</td>
<td>11 620</td>
<td>3</td>
<td>0.3</td>
</tr>
<tr>
<td>2. Central Namib</td>
<td>35 530</td>
<td>140</td>
<td>3.9</td>
</tr>
<tr>
<td>3. Southern Namib</td>
<td>7 423</td>
<td>163</td>
<td>22.0</td>
</tr>
<tr>
<td>4. South &amp; Pro-Namib</td>
<td>140 375</td>
<td>401</td>
<td>2.9</td>
</tr>
<tr>
<td>5. Central region</td>
<td>158 122</td>
<td>206</td>
<td>1.3</td>
</tr>
<tr>
<td>6. Woodlands</td>
<td>16 295</td>
<td>24</td>
<td>1.5</td>
</tr>
<tr>
<td>7. Camelthorn savanna</td>
<td>3 820</td>
<td>4</td>
<td>1.0</td>
</tr>
<tr>
<td>8. Mopane savanna</td>
<td>10 003</td>
<td>38</td>
<td>3.8</td>
</tr>
<tr>
<td>9. Saline dwarf savanna</td>
<td>8 019</td>
<td>123</td>
<td>15.3</td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td><strong>391 207</strong></td>
<td><strong>1 102</strong></td>
<td><strong>2.8</strong></td>
</tr>
</tbody>
</table>

Pan, about eight and five times more common respectively than the overall mean for the country (Table 1). The central Namib Desert, the dry mopane savanna and the south and pro-Namib all supported above average numbers of Greater Kestrels. Open veld with low vegetation characterise these regions, all of which experience less than 450 mm of rain per annum. In the case of the mopane savanna region, the area consists mainly of low mopane scrub with interspersed grasslands. Thick mopane woodland is avoided. The central and eastern parts of SWA/Namibia contained
relatively low densities of Greater Kestrels with less than two birds per 1 000 km being recorded in the central area (region 5), the woodland habitat (region 6) and the camelthorn savanna (region 7). The surprisingly low density for the northern Namib is probably because of the very mountainous terrain.

The numbers of Greater Kestrels varied considerably from year to year (Figure 4). For those regions for which sufficient data were available (regions 2, 4 and 5) it is evident that Greater Kestrel numbers reflected rainfall patterns fairly closely. Rainfall in all three regions decreased to below their respective longterm means in the late 1970's and this is reflected in a general decline in Greater Kestrel numbers. In some cases this decline was rather dramatic, with the 1984 figure for relative abundance being 0.25 that of 1980 for region 5, and 0.1 that of the 1979 figure for region 2. Recovery of populations in these areas appears to be possible within a short period of time, however, as Greater Kestrel numbers in region 2 doubled between 1978 and 1979.
3.3 Breeding season

During the present study, laying dates of 38 clutches ranged from July to January, with a very distinct peak in October (Figure 5).

Laying of replacement clutches or second broods has been suspected by Kemp (1984 and in litt.) but not proven. During this study one instance of clutch replacement was recorded following the predation of a brood of two Greater Kestrel nestlings, about eight days of age, by a Pale Chanting Goshawk *Melierax canorus*. Relaying took place between one and two weeks later at a new nest site about 800 m away, and three nestlings were successfully raised. Although the female was not marked, it was a particularly confiding bird and we are confident that the same bird was involved in both nesting attempts. This record accounts for one of the four December laying dates.

3.4 Nest sites

Thirty-five out of 36 nests located during this study were in natural localities, the exception being on top of a lucerne bale on a disused water tank about 5 m above the ground. Natural nest sites were invariably disused nests of other birds, or collapsed portions of these nests. Crow nests were by far the most common (76%), being mainly from Black Crows *Corvus capensis*, although at least two pairs of kestrels bred in Pied Crow *Corvus albus* nests. The next most common nesting site was found to be the collapsed remains of Lappet-faced Vulture *Torgos tracheliotus* nests (16%). These tend to accumulate in a fork of the tree under the original structure. One pair was found nesting in a Lappet-faced Vulture nest in good condition and one pair in a Black-breasted Snake Eagle *Circaetus gallicus* nest.

Five of 12 crow nests in the Etosha National park whose histories were known had been used by the crow the previous year and were in good condition. Two sites had been used two years previously and were in reasonable condition and five nests had been unused for at least two years and were derelict and devoid of lining. Only one of these 12 nests was used twice in succession by Greater Kestrels, and on the second occasion all eggs were lost.

All nesting trees were indigenous, the most common being *Acacia erioloba* (26%), *Colophospermum mopane* (20%) and *A. leucomeris* (17%). Other trees used were *A. tortilis*, *A. nilotica*, *A. nebrownii*, *Eucla pseudoebenus*, *Myxurus senegalensis* and *Balanites welwitschii*. *Acacia* species constituted 74% of all nesting trees. In Etosha, *C. mopane* and *A. leucomeris* were most commonly used while in the Namib desert *A. erioloba* was the most frequently used tree.

Tree nests ranged in height above the ground from 1.5 - 11.0 m (\( \bar{x} = 3.7 \) m; S.D. = 1.7 m; N = 32). Most nests (50%) were built within the canopy (ie. surrounded by foliage), 25% were exposed above the canopy and 25% were below the canopy. No preference was found for the orientation of nests, whether in exposed or protected sites on the tree.

3.5 Clutch size

Thirty-eight completed Greater Kestrel clutches ranged from 1-5 eggs per clutch (\( \bar{x} = 3.1; \) S.D. = 0.9), with three-egg clutches being most common (42%) followed by four-egg clutches (32%) (Figure 6). Only one clutch contained five eggs, but eight two-egg clutches were recorded (21% of the sample) and one completed clutch contained only one egg.

3.6 Breeding success

Based on data from 21 breeding pair-years an average of 2.1 eggs hatched and 1.9 (range 0-5) flying young were produced per breeding pair-year. Most pairs produced two fledged young (38%), but 24% fledged no young (Figure 7). In Etosha, of 40 eggs laid during
the three seasons of this study, 21 young left the nest, giving a success rate of 53%.

Greater Kestrels did not breed every year. Nineteen pair-years monitored in Etosha produced 12 breeding attempts with no breeding being attempted in seven pair-years. Individual pairs varied from breeding in three consecutive years to breeding once in three years; most pairs bred in two of the three years. The number of breeding pairs varied from year to year: in 1982, five out of seven Greater Kestrel pairs in Halali bred, in 1983 four out of eight and in 1984 four out of six. From 15 pair-years (both breeding and non-breeding) for which the outcome was known, 19 flying young were produced, giving an overall productivity of 1.3 young per pair-year.

Mortalities at the egg stage were due to adults abandoning nests (six eggs), eggs not hatching (addled, six eggs) and predation (probably by a snake, three eggs). Mortalities during the nestling stage were due to predation (by Pale Chanting Goshawk, two nestlings) and desertion by parents (two nestlings).

3.7 Breeding biology

The breeding biology of Greater Kestrels has been described by Steyn (1982) and Hustler (1984), but there are a number of points which can be added to these accounts, particularly regarding the development of coordination by the nestlings. In the present study, eight nests produced two or more flying young. At all these nests there was a clear size difference between the nestlings which would suggest that incubation began with the laying of the first egg.

At between 14 and 18 days of age, nestlings began to stretch and move restlessly about the nest when not being shaded by an adult, and spent much time preening their back and wings. At about 21 days, they were able to stand upright while preening regularly.

At 24 days, wing-flying exercises commenced, thereafter becoming frequent, together with wing stretching and restless movements about the nest. At this stage the nestlings snatched prey aggressively from parent birds and mantled it possessively whenever an adult was nearby; they also usually swallowed prey whole in preference to tearing it into smaller pieces.

3.8 Breeding density

We found 13 breeding pairs of Greater Kestrels in the Halali area of Etosha National Park (Figure 8). Their distribution was not uniform, but concentrated on grassy plains and grassy areas of scrub mopane; no nests were found in mopane woodland. The approximate amount of suitable habitat in the study area was 30,820 hectares. The population density was therefore one pair per 2,370 hectares of open habitat, and the mean inter-nest distance was 5.5 km in suitable habitat. The home range sizes of Greater Kestrels in the Transvaal were found by Kemp (1978) and Hustler (1983) to be about 569 ha and 770 ha respectively. While home ranges in Etosha may be larger than those

in the Transvaal it is probable that not all suitable habitat is equally productive and that some areas are not utilized.

![FIGURE 8. The distribution of Greater Kestrel pairs in the Halali area of the Etosha National Park.](image)

3.9 Food

Invertebrates have been recorded as the main constituent of the diet of the Greater Kestrel (Kemp 1978; Steyn 1982; Hustler 1983; Maclean 1985), although at times during the breeding season more vertebrates may be brought to the nest, mainly by the male (Hustler 1983). During this study 57 fresh prey items were identified and 336 pellets were analysed. Pellets ranged in length from 16-38 mm and in diameter from 11-24 mm, with mean sizes of 27.4 mm (S.D. = 4.7 mm) and 15.6 mm (S.D. = 2.4 mm) respectively.

Invertebrates formed 80% (by number) of the prey items found in the pellets, whereas mammals constituted < 1%, birds 5%, reptiles 9% and unidentified vertebrates 5.5% (Table 2). Of the total sample of 3131 items found in the pellets, 21% were vegetable matter (mainly grass and small twigs) and 7.5% were small pebbles. Of 1,797 arthropod remains found, 22% comprised unidentified chitin. The most important arthropod groups identified were orthopterans (23.2%) followed by coleopterans (19.3%), scorpions (12.9%), isopterans (11.6%) and solifugids (9.8%). The only non-arthropod invertebrates in the sample were two gastropod shells.

Of the fresh prey found on nests, 74% consisted of reptiles, the most common species being *Nucras taeniolata* (57%) followed by *Agama* species (21%)
and Chamaeleo species (7%) (Table 3). Insects, predominantly dung beetles (Scarabaeidae), formed only 26% of this sample but were certainly underrepresented because they are small, difficult to see and quickly consumed by the birds.

TABLE 3: The diet of the Greater Kestrel in SWA/Namibia as determined by the identification of fresh food items found on nests and food parent birds were seen bringing to their nests.

<table>
<thead>
<tr>
<th>Prey Items</th>
<th>Number</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reptiles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nucras toeniolata</td>
<td>24</td>
<td>42.1</td>
</tr>
<tr>
<td>Agama aculeata</td>
<td>2</td>
<td>3.5</td>
</tr>
<tr>
<td>Agama etosha</td>
<td>1</td>
<td>1.8</td>
</tr>
<tr>
<td>Agama hispida</td>
<td>1</td>
<td>1.8</td>
</tr>
<tr>
<td>Agama spp.</td>
<td>5</td>
<td>8.8</td>
</tr>
<tr>
<td>Scincidae</td>
<td>1</td>
<td>1.8</td>
</tr>
<tr>
<td>Chamaeleo namibensis</td>
<td>1</td>
<td>1.8</td>
</tr>
<tr>
<td>Chamaeleo dilpis</td>
<td>2</td>
<td>3.5</td>
</tr>
<tr>
<td>Lacertida</td>
<td>5</td>
<td>8.8</td>
</tr>
<tr>
<td>Total</td>
<td>42</td>
<td>73.7</td>
</tr>
<tr>
<td>Insects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mantodea (praying mantis)</td>
<td>1</td>
<td>1.8</td>
</tr>
<tr>
<td>Orthoptera (grasshoppers)</td>
<td>3</td>
<td>5.3</td>
</tr>
<tr>
<td>Coleoptera (dung beetles)</td>
<td>8</td>
<td>14.9</td>
</tr>
<tr>
<td>Hymenoptera (wasps)</td>
<td>3</td>
<td>5.3</td>
</tr>
<tr>
<td>Total</td>
<td>15</td>
<td>26.3</td>
</tr>
<tr>
<td><strong>GRAND TOTAL</strong></td>
<td>57</td>
<td>100.3</td>
</tr>
</tbody>
</table>

4 DISCUSSION

4.1 Population trends

Population numbers seem to track rainfall patterns, with prey density probably being the ultimate causal factor involved in this relationship. Two trends emerge from Figures 4. Firstly, change in numbers of Greater Kestrels in response to rainfall is reflected only 1-2 years later. When the rainfall has shown an increase this delay may be due to the time taken for vegetation to grow and for insects and reptile populations to respond. When the rainfall has decreased the delay probably comes about because the standing crop of vegetation from the previous year still supports reasonable numbers of prey animals. The second trend indicates that increases in annual rainfall have little or no apparent effect on Greater Kestrel numbers if these increases are much below the longterm mean. This can be seen in region 5 where in both 1982 and 1983 the rainfall was about 64% higher than in 1981, yet still some 100 mm below the longterm mean. This increase in rainfall had little effect on Greater krestel numbers, probably because the amount of rain, after some years of very low rainfall combined with agricultural utilization by livestock, was insufficient to restore the veld to a condition where more prey animals could be supported. The dramatic decline in Greater Kestrel numbers in the early 1980’s in all three regions considered was not accompanied by a reciprocal increase in any other region in the country. As the whole of SWA/Namibia had below-average rainfall during this period it is unlikely that any area would have been suitable to accommodate a large influx of birds, and the Greater Kestrels must therefore have either experienced a high rate of mortality or moved out of the country.

Nomadic movement is an important adaptation to an arid environment (Serventy 1971). “The whole secret of life in arid regions is movement, a readiness and a freedom to migrate” (Debenham 1954). That nomadism in Greater Kestrels does take place is suggested by the very rapid recovery from 1978-1979 in
region 2, where the population doubled from one year to the next. This rate of increase is greater than the recruitment rate as calculated in both this study and that by Kemp (1984), in which a pair of Greater Kestrels produced on average 1.3 young per year. As mortality of the young birds after leaving the nest and adult mortality would further reduce the population growth rate, it is reasonable to assume that birds entered the area. The coincidental decline in bird numbers in the adjacent region 4 further corroborates this assumption.

4.2 Laying dates

The breeding season of the Greater Kestrel in southern Africa is given by Maclean (1985) as July to November, with a peak between August and October, while Steyn (1982) reports a nesting attempt in SWA/Namibia as "early" (late?) as March. The December and January records in this study extend the known breeding season of the species but, whereas Steyn (1982) implies that Greater Kestrels in SWA/Namibia may breed earlier than in other parts of southern Africa, we would expect the converse to be true as the rainy season commences usually only in late November or December in Etosha, and desert regions rarely receive rain before January, with March being the month of highest rainfall (Figure 5). Three of the four December breeding records and both January records were from the Namib.

During the breeding seasons of most birds, the periods of greatest food demand and availability probably coincide (Perrins 1970). Certainly, most birds of prey breed during the time of the year when food is most readily available (Newton 1979). Brown (1976) recognised two main periods of strain in the breeding cycles of raptors: (i) the pre-laying period; and (ii) the early nesting period. In the first, the female needs extra food to produce eggs and, in the second, the male has to obtain more food than at any other stage, as he has to provide for himself, his mate and his nestlings. A third important period is the time when the young become independent. Houston (1976) suggests that the breeding season of the Griffon vultures in the Serengeti is so timed that young birds become independent when food is abundant. For birds of prey to coincide their period of greatest food demand with that of greatest availability it is often necessary for them to start breeding prior to the time when food is most abundant, e.g. Blackshouldered Kites Elanus caeruleus (Mendelsohn 1981). In southern Africa, Greater Kestrels start breeding just prior to the rainy season (Brown et al. 1982; this study). In the east of the subcontinent, this may be in August and September (Kemp 1984), but in the western parts rain may not fall until January, reaching a peak in March, and in these areas Greater Kestrels start breeding mainly in October.

In the early hot dry season in SWA/Namibia (September to November) trees and shrubs, mainly Acacia species, begin to come into leaf. This results in an increase in insect activity and numbers. At the same time the grass and herbage cover is at a minimum and reptiles are most conspicuous, and, because of increasing temperatures, are becoming more active. Young Greater Kestrels fledge a little over two months after the eggs are laid, and on average this is before the peak of the rainy season. The independence of young birds, however, takes place about four to six weeks after leaving the nest (Steyn 1982), in late January and February, well after the first rains have fallen and at a time when insects are most abundant. It therefore seems likely that Greater Kestrels take advantage of an initial increase in insect numbers, while the vegetation is sparse and reptile activity is increasing, to commence breeding. During the second stage, when the male has to provide for his whole family, the vegetation is still open, reptiles are active and insects are abundant. By the time young birds are ready to become independent, they do so at a time when rains have fallen and insect life is flourishing.

4.3 Breeding success

Newton (1979) has shown that variations in breeding success are associated with variations in food supply. In times of food abundance, clutch sizes and nestling survival are greater than when the food supply is low. This has been clearly documented for many species of raptors feeding on rodents, hares and game birds, e.g. Roughlegged Buzzard Buteo lagopus (Hagen 1969), Common Buzzard Buteo buteo (Mebs 1964; Rockenbauch 1975), Redtailed Hawk Buteo jamaicensis (McInville & Keith 1974), Blackshouldered Kite (Mendelsohn 1978), Golden Eagle Aquila chrysaetus (Murphy 1974; Swartz et al. 1974). Little information exists, however, for reptile and insect feeding raptors, although a similar relationship between food supply and clutch size and breeding success would be expected.

In the Transvaal, mean clutch size (3.88 eggs) was 25% larger than in this study. In addition, the most common clutch size in the Transvaal was four eggs (Tarboton & Allan 1984) whereas in Namibia three eggs were most common. The mean annual rainfall in the range of the Greater Kestrel in the Transvaal is 400-700 mm per annum, while in SWA/Namibia all clutches in the sample came from areas with less than 450 mm per annum. As productivity and rainfall are generally accepted as being directly correlated it would be expected that in areas of high rainfall the food supply would be greater, which would account for larger clutches in the Transvaal. These figures would, however, be very general because the variation in rainfall from year to year would considerably affect productivity. Since these data were gathered over a number of years and from all parts of the Transvaal and Namibia respectively, it is nevertheless likely that they reflect the different productivity potentials of the two areas.
Comparative figures for fledgling success are available for an area on the Transvaal Highland where the rainfall is about 670 mm per annum (Kemp 1984). Of 74 Greater Kestrels pair-years monitored, 13 fledged young were produced per pair-year, the same number as produced by Greater Kestrels in the Etosha population. Why productivity should be so similar in areas of such different rainfall is not clear. It may be related to a lowering of the food supply in the Transvaal study area as a result of agricultural activities such as ploughing for crops and planting of pastures, which results in the fragmentation of the natural grassland which may also be degraded by domestic stock. Such activities reduce the biological diversity of the vegetation considerably and this presumably results in less diverse and less numerous insect and reptile communities (Liversidge 1984). Information on clutch size was not obtained during the Transvaal study but, on the basis of the above argument, it would be predicted that the mean clutch size in this area would be smaller than the overall Transvaal mean.

4.4 Food

Our study supports the findings of Hustler (1983) in which invertebrates were better represented in pellets than in observed prey brough to or found at nests, the converse being true for vertebrate prey. Invertebrate prey is usually small and easily overlooked. Also, as Hustler pointed out, it would be energetically advantageous for the male to supply the female and nestlings with large prey while presumably eating the smaller items himself. In our study most pellets were collected from below roost sites and would therefore be biased in favour of smaller food items, i.e., invertebrates rather than vertebrates.

Foraging conditions are probably also an important consideration. At the time of the incubation and nestling periods, summer rains are just starting to fall, the vegetation is still sparse and visibility is good. Reptiles are active and it would be expected that they would form a larger component of the Greater Kestrels' diet during this period than at any other time of the year. Later in the year, after the rains have fallen, vegetation would make hunting of reptiles more difficult and as winter approaches reptiles would become less active.

In general the diet of Greater Kestrels in SWA/Namibia is similar to that recorded by Hustler (1983) in the Transvaal, but differs in that the former contained higher percentages of birds, birds, cranes and beetles, but fewer solifugids, termites and grasshoppers. Our Ganab and Etosha samples were remarkably similar in most respects, the most pronounced differences being in the relative proportions of termites and ants. Both termites and ants, however, are ephemeral and very variable in numbers in any place at any time. Greater Kestrels are undoubtedly opportunistic foragers so their diet would be expected to differ temporally and spatially.

5 ACKNOWLEDGEMENTS

We are most grateful to all participants in the bird atlas project, the raptor road count project and the national nest record card scheme. Harry Biggs in particular is thanked for starting the raptor road count project in Namibia and for making his data available to us. The following are thanked for collecting Greater Kestrel prey remains: Terry Archibald, Dave Boyer, Steve Braine, Ronny Crous, Andrew Jenkins and Ben Riekert. Hartwig Berer Del'Mour, Mike Griffin and John Irish assisted with the identification of prey remains and Ben Riekert helped with the storage and retrieval of data for the raptor road count project. We thank Sue Brown, Alan Kemp, Robert Prys-Jones and David Johnson for commenting or earlier drafts of this paper.

6. REFERENCES

BOSHOFF, A.F., VERNON C.J. and BROOKE, R.K.

BROWN, C.J. and BIGGS, H.C.
1984: The raptor road count project. The Babbler 8: 4-12.

BROWN, L.H.

CYRUS, D. and ROBINSON, N.

DEBENHAM, F.

GIESS, W.

HAGEN, Y.

HOUSTON, D.C.

HUSTLER, K.

KEMP, A.C.

KEMP, A.C.

LIVERISDICE, R.

MACLEAN, G.L.
McINVAILLE, W.B. and KEITH L.B.

MEBS, T.

MENDELSONH, J.M.

MURPHY, J.R.

NEWTON, I.

PERRINS, C.M.

ROCKENBAUCH, D.

SERVENTY, D.J.

STEYN, P.

SWARTZ, L.G., WALKER, W., ROSENEAL, D.G. and SPRINGER, A.M.

TARBOTON, W.R. and ALLAN, D.G.

WILLIAMS, A.J.