

ECOLOGICAL SEGREGATION OF THE RED-BREASTED SPARROWHAWK *ACCIPITER RUFIVENTRIS* AND SIX COEXISTING ACCIPITRINE RAPTORS IN SOUTHERN AFRICA

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CONTENTS

1. Introduction	137
2. Study Area and methods	138
2.1. Data limitations	138
2.2. Methods in ecological comparisons	138
3. Ecology of the Red-breasted Sparrowhawk	140
3.1. Diet	140
3.2. Foraging method and habitat	141
3.3. Hunting rhythm	141
3.4. Sex-related difference in hunting rhythm	141
3.5. Weather and hunting rhythm	142
3.6. Mate-induced differences in hunting rhythm?	143
4. Ecological similarities among coexisting accipitrines	143
4.1. Red-breasted Sparrowhawk and 'competitors'	143
4.2. Ecological similarities between accipitrines	145
4.3. Sympatric overlap and body size	145
5. Discussion	145
5.1. Red-breasted Sparrowhawk ecology	145
5.2. Ecological similarities between species	146
5.3. Body size, sympatry and evolution	146
5.4. Comparisons with other coexisting raptors	147
6. Acknowledgements	147
7. Summary	148
8. References	148

1. INTRODUCTION

No other continent or subcontinent has such an array of potentially interacting accipitrine hawks as southern Africa (Brown & Amadon 1968). Since most of these are sympatric bird-eating raptors, one might expect some resource overlap and possibly competitive interactions between ecologically similar species. Regrettably, the only comparative work on these coexisting raptors is the morphological study of Black & Ross (1970); a picture in sharp contrast with the detailed ecological studies of sympatric accipiters in Europe (*Accipiter nisus* and *A. gentilis*: Van Beusekom 1972, Opdam 1975), and North America (*A. striatus*, *A. cooperi*, and *A. gentilis*: Storer 1966, Reynolds *et al.* 1982, Reynolds & Meslow 1984). More recently, Diamond (1985) has compared the niches of a similar set of seven coexisting accipiters on the island of New Guinea. He showed that each species could be separated using just three ecological variables – habitat, foraging method and prey

type. In this paper I undertake a similar approach and combine my own research on the little known Red-breasted Sparrowhawk *A. rufiventris* with data from other sources (Steyn 1982, Tarboton & Allan 1984) to assess the degree of ecological similarity of the seven small to medium accipitrine hawks co-occurring in southern Africa. These are: Little Sparrowhawk *A. minullus* (100 g), Little Banded Goshawk *A. badius* (145 g), Gabar Goshawk *Micronisus gabar* (170 g), Red-breasted Sparrowhawk (215 g): hereafter the RBS), Ovambo Sparrowhawk *A. ovampensis* (260 g), African Goshawk *A. tachiro* (360 g) and the Black Sparrowhawk *A. melanoleucos* (880 g) – all female weights from Biggs *et al.* (1979).

Rather than a comprehensive evaluation, this paper is a first attempt at gauging ecological similarities among African hawks. Many species have been studied in only one or two areas of their range and data on prey types may only reflect regional differences in prey abundance or availability (*e.g.* Newton & Marquiss 1982). The introduction of various pines (*Pinus* spp.) and gums (*Eucalyptus* spp.) into southern Africa in the past century has also artificially increased nesting habitat and hence the ranges of several species, including the Black Sparrowhawk (Tarboton *et al.* 1978) and the Little, Ovambo and Red-breasted Sparrowhawks (Tarboton & Allan 1984, Boshoff *et al.* 1983, Allan & Tarboton in press). Conversely, ancestral habitats of some species may have contracted under the influence of monoculture farming. Thus extant ranges or even diets may reflect recent changes to present day conditions.

Additional confounding influences in a study of ecological overlap are the determination of diet and habitat use only in the breeding season. Such periods reflect feast not famine, and resource overlap may well exist without competition necessarily occurring (Schoener 1982). This

study of resource use is therefore, not a test of competing hypotheses (e.g. Schoener 1974, Weins 1977) on the role of interspecific competition in shaping communities. Rather it is a study of the similarities and differences among seven accipitrine hawks that may compete directly or indirectly in their use of five fundamental ecological characters. The paper is presented in two parts: first, aspects of RBS ecology pertinent to the niche comparisons, second, the between species comparisons.

2. STUDY AREA AND METHODS

Two breeding pairs of RBS were studied from October 1983 (incubation) to February 1984 (independence of young) in the Giant's Castle Reserve (29°15'S, 29°30'E) in the Drakensberg mountains of South Africa. Details of this study are given in Simmons (1984, 1986). The montane study area, part of the Afro montane biome (Figs. 1, 2) supports at least 10 species of breeding raptors (Barnard & Simmons 1985) and is predominantly *Themeda triandra* grassland between 1380 and 2200 m. Forest is confined to small scattered pockets in ravines untouched by fire, while the main grassy plateau of the 360 km² reserve is maintained as fire climax montane and subalpine veld. The plateau is deeply dissected by many rivers and streams (Fig. 1).

Some prey items provided to the nests could be identified to genus or species from a hide 50 m from one nest, while prey dropped by flying young allowed further identification and biomass assessment. Rarely, I climbed to the nests to identify prey following adult departure. When prey could not be identified in the hand, tarsi of the normally headless birds were collected for later identification by Dr. J. M. Mendelsohn from Durban museum collections. Prey biomass was gauged by quantifying consumption time or estimating the size of the item relative to each adult's foot (Sim-

mons 1986). Diurnal watches (842 h) were undertaken during all hourly intervals, from first light (04.45) to dusk (19.15), and were evenly spaced throughout the day (Fig. 3). This allowed a simple assessment of diurnal rhythm in prey delivery to the nest, and is assumed to reflect the hunting periods of the birds studied. This was possible for only one intensively-studied nest.

2.1. DATA LIMITATIONS

Direct observations of prey brought to nests are assumed to reflect diet more accurately than prey remains or pellets at nests and plucking sites (Schipper 1973, Snyder & Wiley 1976, Collopy 1983). However, bias may still exist if, as predicted by central place foraging models (Schoener 1979, Orians & Pearson 1979), very small (energetically unworkable) or very large items (energetically too expensive to transport) are not delivered to nests. Although very small (4 g) items were brought to the RBS nests, very large ones were not; an upper limit to prey size of about 54 g was evident for one nest (Simmons 1986). However, this is considerably lower than the maximum weight (350 g) that the slightly larger (1.3 ×) European Sparrowhawk *A. nisus* is capable of transporting (Newton & Marquiss 1982). It is thus reasonable to assume that the RBS adults were not limited to light prey because of carrying constraints, but that the items delivered were reasonably indicative of the size ranges caught.

2.2. METHODS IN ECOLOGICAL COMPARISONS

Prey types and habitat use are fundamental ecological requirements and, therefore, probably the most valuable factors for making interspecific niche comparisons. However, for the seven species considered here, I have also included hunting mode, habitat foraged and, where possible, diurnal foraging rhythm as possible differences, and scored each factor relative to the RBS to gain a simple quantified index of niche overlap.

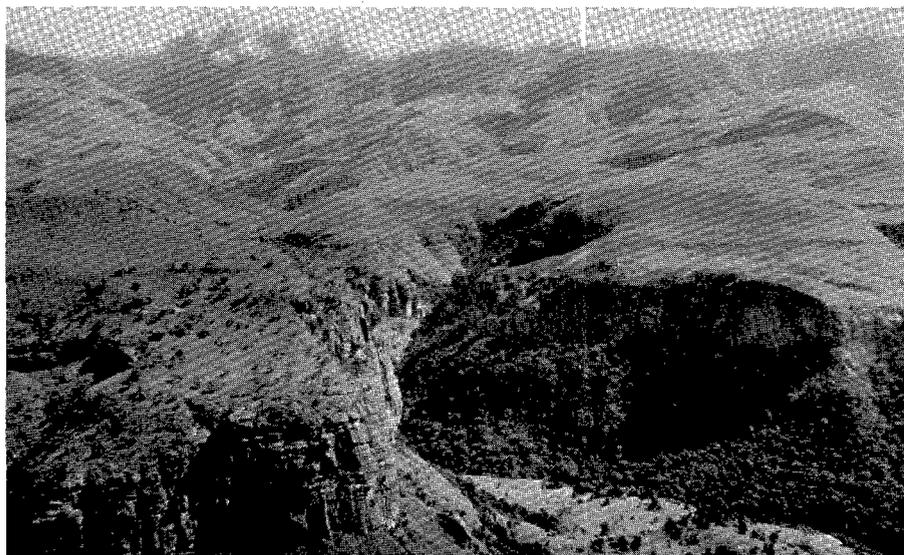


Fig. 1. Giant's Castle study area, South Africa, showing the deeply dissected valleys and predominantly *Themeda triandra* grassland foothills – foraging habitat of the RBS. The Drakensberg escarpment is cloud obscured and the woodland pictured is the largest tract in the reserve. This habitat is part of the Afro montane biome.

Scoring ecological overlap

To simplify the quantification of overlap between species, complete overlap ($> 80\%$) with the RBS in any one of the above categories (diet, biome, foraging habitat, foraging mode and rhythm) was scored 1; no overlap ($\leq 20\%$) was scored 0, and intermediate values were scored 0.5. Scores were summed for all five categories, and are expressed as a fraction (e.g. 3/5) and a percentage: a high percentage reflects high niche overlap.

Biomes

Habitats were classified according to biome type as defined in detail by Acocks (1975) and used by Boshoff *et al.* (1983) and Tarboton & Allan (1984) in mapping raptor distributions. Since these biomes are well described by Maclean (1985) and mapped simply by Newman (1971), they will not be detailed here. However, as simple predictors of these habitat types, rainfall, soils and altitude are useful. In

general, more easterly and mountainous regions of southern Africa have higher annual rainfall (750 mm or more). Western deserts and the Karoo Basin (Fig. 2) are composed of sandy soils and receive less than 250 mm of rain per annum. Raptor distributions (Fig. 2) are taken from Maclean (1985), but descriptions in Table 2 do not include the recent expansion by some accipiters into the Karoo and Fynbos (a heath-like area dominated by Ericaceae and Protaceae) because of introduced plantations (Boshoff *et al.* 1983). The Highveld (Fig. 2) is a high altitude, treeless grassland; Bushveld and Savanna are dominated by *Acacia* thorn trees and are delimited primarily on levels of rainfall, Savanna being considerably drier than Bushveld. A typical Afro montane region is depicted in Fig. 1.

Mapping geographic ranges

Although the geographic ranges of each raptor was broadly mapped according to Maclean (1985), I used the distribution maps of Boshoff *et al.* (1983) and Tarboton &

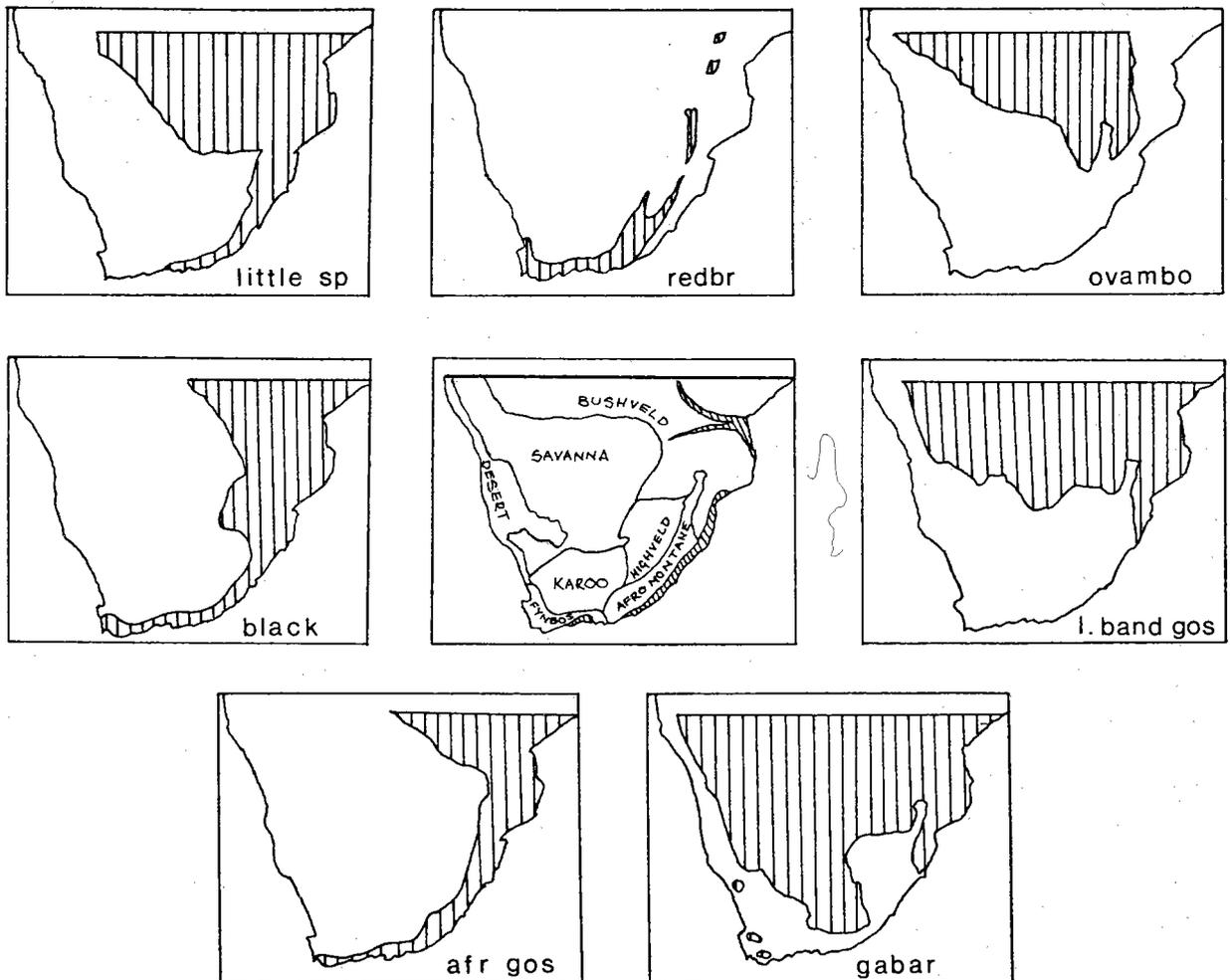


Fig. 2. Geographic ranges of seven accipitrine hawks of southern Africa and (central map) major habitat biomes of this region. The derivation of each hawk range and brief descriptions of each biome are given in section 2.2. The closely hatched portion of the central map illustrates dense coastal forest. The RBS study area is located in the A of montane.

Allan (1984) for fine-tuning. These authors indicate actual nesting locales rather than gross ranges. Sympatric overlap on a macrogeographic scale is the least accurate measure of niche similarity because gross mapping excludes basic habitat differences. For example the RBS and the African Goshawk overlap geographically about 80% according to range maps in Steyn (1982), yet habitat differences effect nearly complete allopatry on a microgeographical scale. Hence, range is replaced with biome type for greater accuracy; I have continued to use the term coexisting in its usual, macrogeographic sense.

Hunting rhythm

Jaksić (1982) and others have criticised the use of daily hunting rhythm as a measure of ecological segregation: despite temporal isolation, identical prey sources may be exploited by diurnal and nocturnal predators and indirect competition can thus occur. Because various prey species are exploited by the hawks under investigation, temporal rhythm may be due to the differential vulnerability of prey. For example a female RBS may hunt at midday because aerial prey are more vulnerable then (Table 1), or the Little Banded Goshawk may hunt in the mornings to capture exploitable reptiles and evenings to take birds (Tarboton 1978). Jaksić's (1982) caution therefore appears irrelevant

in this study because of the multiple prey species taken and their differential temporal vulnerability.

3. ECOLOGY OF THE RED-BREASTED SPARROWHAWK

3.1. DIET

Of 305 items delivered to both RBS nests, 289 were estimated for biomass, 159 were identified to class, and 31 to genus or species. Of identified prey, 98% were small (10–90 g) birds, 2% consisted of two small mammals and one skink (Table 1). Only 3 of 28 birds identified to genus were undisputably juveniles. Identified prey species brought to the nest rarely exceeded 40 g, a figure reflecting the provisioned biomass, not original biomass as is often given in nesting studies (Storer 1966, Opdam 1975, Newton & Marquiss 1982, Reynolds & Meslow 1984). In this study, the adults ate the head of the prey

Table 1. Identified prey species brought to the nests of two Red-breasted Sparrowhawk pairs in Natal, South Africa.

Prey species	No. of prey items provided by		Habitat of prey ¹	Biomass provided (g)	Maximum mass of whole animal ^{1,3} (g)
	♂	♀			
BIRDS					
Alpine Swift <i>Apus melba</i>		2	Aerial	45 ²	91
Black Swift <i>Apus barbatus</i>		2	Aerial	45 ²	50
Swift sp. adult		2	Aerial	40	—
Swift sp. juvenile	1	1	Aerial	25	—
Striped Swallow <i>Cecropius</i> sp.		1	Aerial	?	35
Orange-breasted Rockjumper <i>Chaetops aurantius</i>	3	2	Alpine/ grassland	17–35 ²	40
Orange-throated Longclaw <i>Macronyx capensis</i>	2		Grassland	25	49
Cape Bishop <i>Euplectes capensis</i>	1		Grassland/scrub	25 ²	25
Pipit sp. (<i>Anthus</i>)	1		Grassland	20	30
Rock Bunting <i>Emberiza tahapisi</i>	1		Grassland	18	22
Stonechat <i>Saxicola torquata</i>	1		Grassland/scrub	16 ²	18
Ayres' Cisticola <i>Cisticola ayresii</i>	4		Grassland	7–18 ²	18
<i>Cisticola</i> sp.	2		Grassland	14	—
Common Waxbill juvenile <i>Estrilda astrild</i>	1		Scrub	10 ²	10
Canary sp. (<i>Serinus</i>)	1		Riverine scrub	8 ²	18
Unidentified small birds	111	17	—	4–54	—
MAMMALS³					
Vlei Rat <i>Otomys irroratus</i>	1		Marsh	41 ^{2,4}	200
Fourstriped Mouse <i>Rhabdomys pumilio</i>	1		Marsh/scrub	25 ²	80
REPTILES					
Common Striped Skink <i>Mabuya striata</i>	1		Rocky grassland	4	—

¹ From Maclean (1985) and pers. obs.

² Prey item weighed, not estimated via foot size or consumption time.

³ Own data.

⁴ Half consumed, thus full weight < 90 g.

before delivery in 282 of 289 observed instances (Simmons 1984). The mean provisioned biomass was 14 g.

Sexual differences were evident in prey selection. The few identified items provided by the female were mainly swifts (*Apus* spp.) of 50–90 g (Table 1). Such agile, fast prey may be caught from a soaring position, since it is unlikely that an RBS could outfly a swift in horizontal pursuit. High aerial captures of European Starlings *Sturnus vulgaris* have been noted for *A. nisus* in Scotland (Marquiss & Newton 1982), and Kemp & Kemp (1975) recorded aerial strikes by *A. ovampensis* in southern Africa.

The male RBS selected small open-grassland birds such as the ubiquitous cisticolas (*Cisticola* spp.). All identified prey provided by both male and female RBS were species commonly found in non-wooded areas (Table 1). Doves (*Streptopelia* spp.) and Red-winged Starlings *Onychognathus morio*, relatively common in wooded ravines in the study area, were apparently not taken, suggesting either that the RBS prefers open-country foraging, or that doves are too large to take. Two attempts at capturing these species in wooded areas by juveniles (Simmons 1984), and one by an adult male, were unsuccessful. All three attempts were made from perches. Doves have been recorded only once in the diet of the RBS (Steyn 1982), and are therefore probably unusual prey.

3.2. FORAGING METHOD AND HABITAT

RBS adults were never seen to make strikes in, or from, the woods in which they bred despite my extended observations there. While in the wood, they either sat for long periods overlooking the nest, or departed into open country soon after prey delivery. The male at one nest was twice observed flying very low and fast in the manner of a Merlin *Falco columbarius* away from the wood, while a young female close to independence was also observed flying fast and low between outcrops. Two serious adult hunting sequences were observed. In the first, a male RBS hunting in mid-afternoon was seen flying fast and low over the crown of a hill, hugging the grassland contours into the adjacent valley. He encountered no prey and his momentum took him a further 0.5 km to the next hill, a

rise of about 100 m. In the second sequence, an unsexed bird flew slowly over the pine site, 30 m high, and descended sharply on reaching the periphery of the wood to snatch a small passerine from open ground.

These limited observations indicate that the RBS in this study area were open country foragers and tended to avoid hunting in woodland. This view corroborates that of Black & Ross (1970) and Tarboton & Allan (1984). Recent observations by W. R. Tarboton and D. G. Allan (*in litt.*) confirm these findings.

3.3. HUNTING RHYTHM

Significant deviations from an equal hourly rate in the timing of prey deliveries were evident over an 84 day period at one RBS nest. This was most marked in the timing of deliveries by the parents combined. A clear peak in activity was evident in late morning (09.00–12.00) which fell rapidly, becoming much lower than expected between 18.00 and 19.00. Assuming an equal hourly rate as the expected rhythm, the observed frequencies throughout the day were significantly different from expected ($\chi^2_{15} = 36.6, p < 0.01$).

3.4. SEX-RELATED DIFFERENCE IN HUNTING RHYTHM

Separating the male's ($n = 248$) from the female's ($n = 57$) observed deliveries revealed further differences in the timing of provisioning (Fig. 3). The female was never observed delivering prey before 06.00, and her contributions peaked between 13.00 and 14.00. This may have arisen from her selection of swifts, common and conspicuously active at midday in the study area. The male, selecting mainly passerines provided most items between 10.00 and 12.00 and fewest items in the last full hour of daylight (18.00–19.00). His overall rate was significantly different from expected ($\chi^2_{15} = 32.4, p < 0.01$) over the entire 16 h day, but the female's rate was not ($\chi^2_{15} = 19.1, p > 0.1$). Neither adult delivered prey in the short (± 15 min) daylight period between 19.00 and dusk. Similar midday provisioning peaks were evident at two of the three European Sparrowhawk nests studied by Newton (1978), but sexual differences were unexamined.

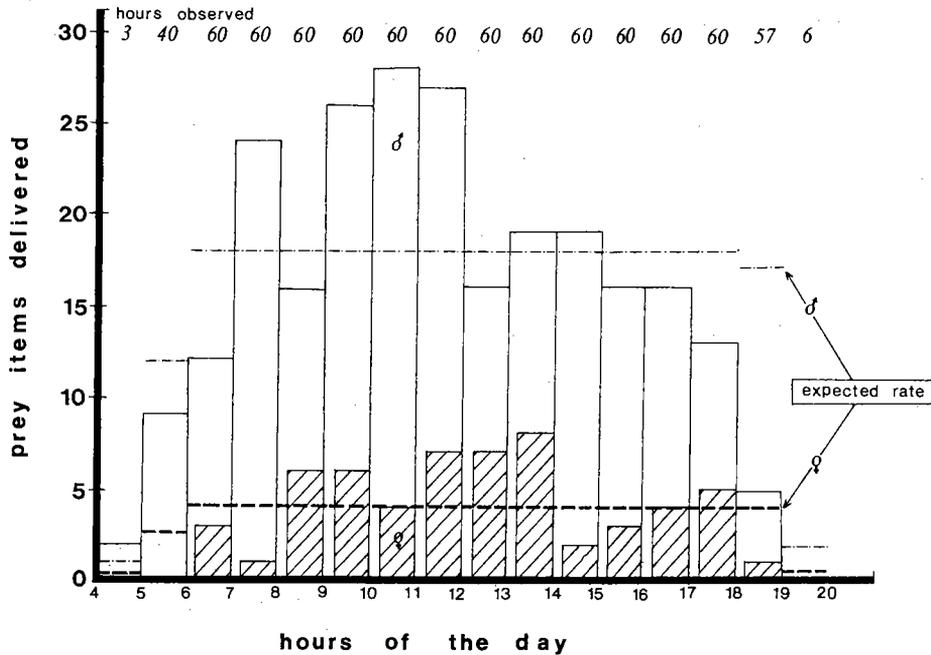


Fig. 3. Number of prey items delivered in each hourly interval by the male (highest bars) and female RBS from pre-hatch to independence. Expected numbers are based on an equal rate \times hours observed (top).

3.5. WEATHER AND HUNTING RHYTHM

The decline in provisioning rate in late afternoon could not be explained either by chick satiation, since chicks were almost constantly food stressed (Simmons 1984), or by rain-associated inhibition. Rain was evenly distributed throughout the study period (Simmons 1986) and heavy rain accounted for only 6% of 715 hours observed. Could cloud cover affect afternoon delivery rates?

Although not directly assessed in the afternoons, patterns of morning cloud cover implied that cloud could have such an effect. On overcast mornings (100% cover), the first items were delivered on average 62 min later than on completely clear mornings (Fig. 4). This difference was significant (Kruskal-Wallis $H = 4.83$; $p < 0.05$) for watches starting prior to 06.31 and lasting ≥ 3 h ($n = 52$). Partial cloud cover did not have the same effect; only a 7 min delay in the first prey delivery was observed (Fig. 4) relative to clear mornings. Because afternoon cloud build-up was a conspicuous feature of this montane region, the afternoon lull might be explained in terms of cloud cover. However, possible variation in prey activity was not examined.

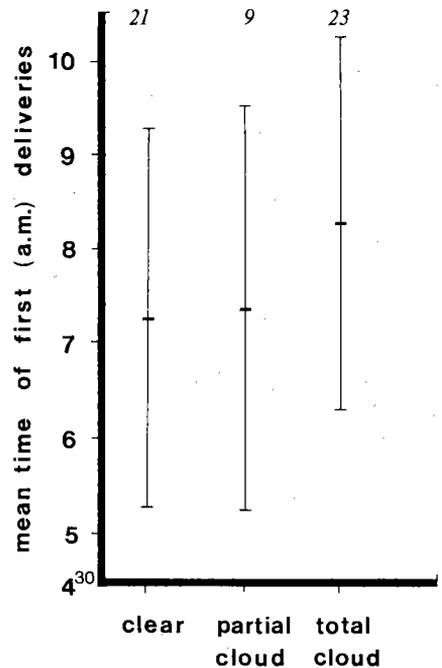


Fig. 4. Association between cloud cover and the timing of first a.m. prey deliveries. Calculated from 52 morning watches starting prior to 06.31 and lasting more than 3 h. Range limits denote \pm s.d. and associated numbers indicate the number of mornings.

3.6. MATE-INDUCED DIFFERENCES IN HUNTING RHYTHM?

The male's diurnal pattern of prey delivery appeared to be influenced by the female's provisioning activity. Fig. 5a illustrates the male's deliveries throughout the day when he alone supplied the nest (pre-hatch to day 24 and after day 56, where hatch = day 1), and when the female assisted, from day 25 to day 56 (Fig. 5b). The male provided food more evenly throughout the day while the female was dormant (Fig. 5a) than while she too provisioned (Fig. 5b). Compare especially the hours 13.00–14.00 (the female's usual peak) and 16.00–17.00, when the male without his mate, provisioned at a rate of 37 items/100 h. This rate is four times greater than in the corresponding interval when assisted by the female. These differences are not an artefact of season, because the male's rate was assessed before the female started (28 days), after

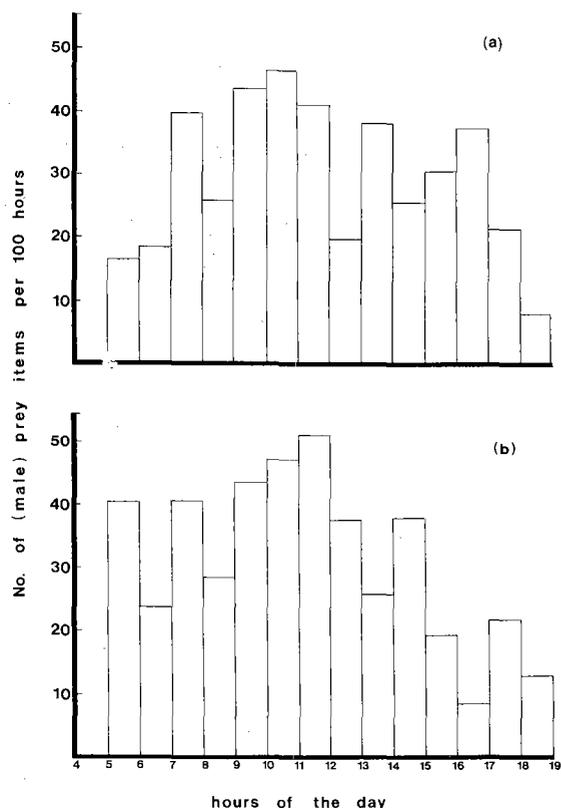


Fig. 5. Rate of male provisioning per 100 h while (a) the male was the sole provider and (b) the female also provisioned (the female's contributions are not included). Graphs are directly comparable.

she had stopped (19 days), and on 5 days when she temporarily ceased during the combined provisioning period. I interpret the male's afternoon decrease while his mate was provisioning (Fig. 5b) as a response by the male to avoid provisioning overlap with his mate in order to spread food deliveries more evenly throughout the day. This might be expected if such a tactic resulted in more even growth rates and enhanced survival for young sparrowhawks (*cf.* Newton 1978).

4. ECOLOGICAL SIMILARITIES AMONG COEXISTING ACCIPITRINES

4.1. RED-BREASTED SPARROWHAWK AND 'COMPETITORS'

Food spectra of the seven species given in Table 2 are categorised by class, percent frequency (not biomass) in the diet, and approximate size classes where available. Virtually all prey records come from breeding studies, but not all are from studies in southern Africa; no quantified prey data exist for the African Goshawk except from Kenya (Van Someren 1956).

Basic dietary differences between the RBS and the Little Banded Goshawk are evident in the mainly reptilian diet of the latter (73% of 91 items in South Africa: Tarboton 1978, 48% of 221 items in Nigeria: Smeenk & Smeenk-Enserink 1977). This species has the lowest overlap relative to the RBS of the six species considered (Table 2).

The Black Sparrowhawk has little dietary overlap with the RBS despite its bird diet (98% of 308 items in South Africa: Tarboton & Allan 1984; 83% of 145 items in Kenya: Brown & Brown 1979). This bird is almost exclusively dependent on doves and francolins (Phasianidae), which are much larger than any prey taken by the RBS in this study. Some habitat overlap may occur due to the wide spectrum of woodlands at various altitudes inhabited by *melanoleucus*, but smaller accipiters are known to avoid the woodlands in which the Black Sparrowhawk nests (Tarboton & Allan 1984). This avoidance may be due to direct predation, or to indirect competition for resources.

Small bird-eating species apparently overlapping with the RBS in diet are: a) the Gabar Goshawk whose overlap is minimal due to its

Table 2. Summary of ecological similarities in diet, biome, foraging habitat, foraging mode, and foraging period, scored relative to the Red-breasted Sparrowhawk for six coexisting raptors in southern Africa. Parentheses indicate similarity score relative to the RBS. OS=Ovambo Sparrowhawk, BS=Black Sparrowhawk, LS=Little Sparrowhawk, AG=African Goshawk, GG=Gabar Goshawk, LBG=Little Banded Goshawk. SB = small birds (< 100 g); MB = medium birds (100–300 g); LB = large birds (> 300 g); M = mammals; Rep = reptiles (< 100 g).

Species	Diet ¹	Habitat biome ²	Foraging habitat ³	Foraging mode ³	Foraging period	Score ⁴	%
RBS	SB 98% (1)	Afromontane (1)	Open grassland (1)	Open pursuit, ambush (1)	Mid-late morning (1)	5/5	100
OS	SB 68% MB 32% (0.5)	Bushveld (0)	Grassland edge (1)	Perch, open pursuit (1)	Early morning late after- noon (0.5)	3/5	60
BS	LB 98% (0)	Bushveld- Afromontane (0.5)	Open woodland (0)	Ambush, open woodland pursuit (0.5)	?	1/4	25
LS	SB 100% (1)	Bushveld- Afromontane (0.5)	Open-dense woodland (0)	Perch, woodland pursuit (0)	?	1.5/4	38
AG	SB 65% MB 27% (0.5)	Coastal Forest -Afromontane (0.5)	Dense forest (0)	Woodland pursuit, ambush, perch (0)	?	1/4	25
GG	SB 88% (1)	Savanna (0)	Open Woodland (0)	Perch, woodland pursuit, nest rob (0)	?	1/4	25
LBG	Rep 60% SB 16% (0)	Bushveld (0)	Open-dense woodland (0)	Perch, nest rob (0)	All morning late after- noon (0.5)	0.5/5	13

¹ From, this study (RBS); Tarboton & Allan 1984, Steyn 1982, Allan & Hustler pers. comm. (BS and OS); Van Someren 1956 (AG); Liversidge 1962, Tarboton & Allan 1984 (LS); Kemp & Snelling 1973 (GG); Smeenk & Smeenk-Enserink 1977, Tarboton 1978 (LBG).
² For descriptions of biomes see section 2.2. After Steyn 1982 Tarboton & Allan 1984; recently occupied biomes (Karoo and Fynbos: Boshoff *et al.* 1983) are not included.
³ Mainly after Steyn 1982, Tarboton & Allan 1984; this study (RBS); Allan & Hustler pers. comm. (OS); W. R. Tarboton pers. comm. (BS); Kemp & Snelling 1973 (GG); Tarboton 1978 (LBG).
⁴ Sum of diet, habitat biome, foraging habitat, method and period. Score represents ecological overlap relative to the RBS.

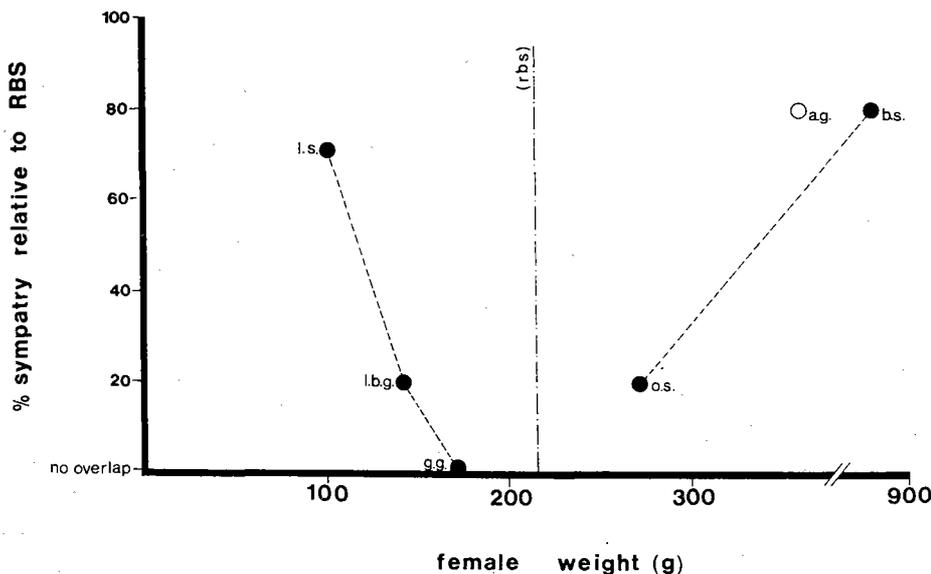


Fig. 6. Female body mass of six accipitrine hawks in relation to sympatric range overlap with the RBS. The African Goshawk is not included because of its specialised habitat.

dry savanna habitat; b) the African Goshawk which is reported by several authors to be confined to dense indigenous forest in which it hunts (Black & Ross 1970, Brown *et al.* 1982, Steyn 1982, Tarboton & Allan 1984, pers. obs.); c) the Little Sparrowhawk which is found in many habitats from dense montane woodland (Tarboton & Allan 1984) to wet *Acacia* woodland (Liversidge 1962) and hence may overlap with the RBS; and d) the Ovambo Sparrowhawk which takes both medium (100–300 g) and small birds (in a ratio of 32:68 respectively: D. G. Allan & C. W. Hustler pers. comm.). The Ovambo occurs mainly in the tall-tree Bushveld biome (Fig. 2), but hunts over similarly structured habitats and in a similar fashion to the RBS (Kemp & Kemp 1975).

Therefore, based on diet, biome and foraging habitat, the RBS overlaps most with the Little and Ovambo Sparrowhawks. Further analysis of other ecological parameters reveals strong altitudinal differences in habitat use by the Ovambo, but not the Little Sparrowhawk (Tarboton & Allan 1984). Hunting method separates the perch-hunting Little Sparrowhawk from the open-country pursuit habits of the RBS and the Ovambo Sparrowhawk (Black & Ross 1970, Kemp & Kemp 1975, Steyn 1982, this study). The three could not be compared for hunting rhythm, since this aspect is unknown for the Little Sparrowhawk.

Summing and ordering all ecological parameters reveals the Ovambo Sparrowhawk (60% similarity) as the closest in resource use to the RBS, while the niche of the Little Sparrowhawk overlaps about 40% (Table 2).

4.2. ECOLOGICAL SIMILARITIES BETWEEN ACCIPITRINES

Factors listed in Table 2 allow a comparison not only between the RBS and its ecological neighbours, but between all other southern African hawks; 21 comparisons are possible, six of which have been investigated above. Treating the remaining 15 species-species combinations in a similar fashion shows that the Little Sparrowhawk and the Gabar Goshawk, both inhabiting dry savanna to a greater (*gabar*) or lesser (*minullus*) degree, taking small birds, and hunting in similarly structured habitat, overlap 63%

– slightly higher than the RBS/Ovambo relationship. They differ primarily by the more arid, lowland preferences of the Gabar. Curiously, the Gabar Goshawk is not known to breed in introduced plantations (Tarboton & Allan 1984), despite the opportunity to do so.

At the opposite end of the spectrum, the lowest overlap is consistently found between the African Goshawk and its congeners. The least overlap (13%) occurs between *tachiro* and both *badius* and *ovampensis*. This consistently low scoring is due primarily to the partly mammalian diet of *tachiro* and its dense forest habitat. This conclusion is tentative, since the African Goshawk is the poorest studied of all the species considered here.

4.3. SYMPATRIC OVERLAP AND BODY SIZE

In Fig. 6, the body mass of each species is plotted against the percentage overlap in range (Fig. 2) with respect to the RBS. Body weights were taken from Biggs *et al.* (1979) and Schmitt *et al.* (1982), and sympatry was expressed as a percentage of the RBS range. The African Goshawk was not included on the plotted line because of its specialised, dense forest habitat, but its inclusion would be consistent with the pattern. For all species, as body size approaches that of the RBS, sympatry decreases to zero: the more divergent in size, the greater the sympatric overlap. This phenomenon may be fortuitous with the choice of the RBS as a comparison, but it may also be interpreted in the light of competition theory (section 5.3).

5. DISCUSSION

5.1. RED-BREASTED SPARROWHAWK ECOLOGY

Principle findings of the RBS study were: a) the RBS diet consisted almost entirely of birds between 10 and 90 g, but included a few mammals (*cf.* Grobler 1980); b) the hunting style of the RBS was a fast, low direct flight over open grassland with a marked propensity to avoid woodlands; c) the pair monitored most intensively delivered prey mainly in late morning (*cf.* Newton 1978) to their nest, although sexual differences were evident; and d) cloud cover and female provisioning activity both appeared to influence the timing and spread of prey deliv-

eries to nests. Other factors considered by Simmons (1986), but found to have no influence on the rate of prey delivery, were brood size and temperature, while both chick age (Simmons 1984) and rainfall did affect the number of deliveries. However, rainfall was of insufficient duration to decrease potential provisioning rates by more than 4 g/chick/day, and could not have affected overall rates significantly (Simmons 1986). Similarly, although cloud build-up in the afternoons was a common phenomenon, rain was not always associated with it. Hence cloud was the most likely cause of the decline in afternoon provisioning rates (Fig. 3).

Point b) above contrasts with previous opinions on the hunting mode of the RBS. Brown & Amadon (1968 : 482), Brown *et al.* (1982), McLachlan & Liversidge (1982), and Steyn (1982) contended that the RBS is partly or completely a woodland hunter. This misinformation probably arose through comparison with its congener *A. nisus* (Marquiss & Newton 1982), with which it may form a superspecies (Wattel 1970). The view is in error because of 1) observed hunting methods reported in this study and by W. R. Tarboton and D. G. Allan; 2) habitat of the prey taken (Table 1); 3) the long manus relative to the small inner wing area, indicating a fast-pursuit (rather than dextrous and manoeuvrable) flight mode (Black & Ross 1970), 4) the open grassland habitat surrounding nests throughout South Africa (Black & Ross 1970, Grobler 1980, pers. obs.), and 5) the invasion by the RBS into otherwise treeless areas (Fig. 2) on the introduction of small pine and eucalypt plantations (Boshoff *et al.* 1983).

5.2. ECOLOGICAL SIMILARITIES BETWEEN SPECIES

Based on morphology alone, Black & Ross (1970) assumed that the Ovambo and Red-breasted Sparrowhawks were alike in hunting techniques, and Tarboton & Allan (1984) suggested that the Ovambo is the lowland ecological equivalent of the RBS. Using additional information on diet, hunting method and rhythm of the RBS, this study supports the notion that the Ovambo is the closest ecological neighbour of the RBS. Young of the two species are almost identical in colouration in some areas, di-

verging only at the post-juvenile moult; they may have a very close phylogenetic origin (Irwin *et al.* 1982).

A diet of small birds was found to be common to five of the seven species, yet potential niche overlap does not occur because of differences in habitat biome and hunting method. None of the five species share all three characters (Table 2). Unfortunately, few studies in Africa have taken account of sexual differences in prey selection as noted by Storer (1966) for six inter-/intraspecific combinations of three coexisting North American accipiters. A higher frequency of doves found at late-season plucking sites in a study of the Ovambo Sparrowhawk has led D. G. Allan and C. W. Hustler to postulate that females were selecting these species. If so, dietary overlap with the female RBS may be less marked than presently suggested.

That further observations are clearly needed before comparative studies can accurately reflect species traits has already been shown by erroneous reports of RBS hunting behaviour. Morphological studies may also lead to misinterpretations about hunting mode. In a first attempt at distinguishing ecological traits of the accipiters considered here, Black & Ross (1970) grouped the Little Banded Goshawk alongside the RBS and Ovambo Sparrowhawk as a long-winged, swift flying species. Subsequent observations, however, have shown that *badius* hunts mainly from a perch and does not generally 'fly down' its prey in active pursuit (Smeenk & Smeenk-Enserink 1977, Tarboton 1978). Despite its long middle toe, normally a trait of bird-catching raptors, *badius* takes primarily lizards (Tarboton 1978). This paradox may be explained as a case of 'the ghost of predation past': *badius* originally hunted birds but has in recent times altered its behaviour (but not morphology) to perch-hunt for reptiles.

5.3. BODY SIZE, SYMPATRY AND EVOLUTION

A currently held view among students of speciation, and one compatible with Gould & Eldredge's (1977) model of the tempo and mode of evolution, is that species arise from small, spatially isolated subpopulations and acquire species-specific traits in allopatry. These traits (*e.g.* hunting mode, habitat, and behavioural

repertoires) are thought to remain unaltered until the next speciation event (Paterson 1978, 1982, see Vrba 1980 for review). According to Walter *et al.* (1983), this view infers that interspecific competition is not an important evolutionary force and cannot shape the niche characteristics of an incipient species. A prediction arising from Walter *et al.*'s (1983) view is that one species is as likely to arise in a niche already occupied by another species as it is in a vacant niche. The alternative prediction, arising from the idea that interspecific competition has played a role, is that two species are most unlikely to occur in very close ecological proximity because of competitive interactions.

The results of this study lend no support to the view of Walter *et al.* First, little niche overlap was evident among the five accipiters eating small birds (Table 2). Second, an inverse correlation was apparent between an indicator of prey size (accipitrine body mass), and the degree of range overlap relative to the RBS (Fig. 6). I suggest that the latter inverse relationship reflects past or present competition between species, allowing only those accipitrine hawks taking dissimilar prey to the RBS to occupy the same range. Those taking prey of a similar size are thought to have either shifted their range (a post speciation event) or arisen only where the RBS was not present. Although allopatric models of speciation dictate that the most closely allied species (*e.g.* the RBS and Ovambo Sparrowhawk) cannot arise in the same habitat, this model cannot explain why the other accipiters considered in Fig. 6 exhibit predominantly non overlapping ranges when close in body size to the RBS. Interspecific competition remains the most plausible explanation for these trends.

5.4. COMPARISONS WITH OTHER COEXISTING RAPTORS

All but one other study of resource overlap among congeneric diurnal raptors have suggested that species do not compete for critical, limiting resources. For example, Schmutz *et al.* (1980) found that coexisting *Buteos* exploited the same prey, but the source was not limiting. Reynolds & Meslow (1984) found a difference in habitat use and only minimal overlap in prey resources of two co-occurring accipiters. Storer

(1966) noted specialisations in certain prey genera with some overlap in prey size, while Van Beusekom (1972) and Opdam (1975) found almost no overlap in the mean prey biomass of co-existing hawks, particularly in winter when prey sources may have been numerically limited. Only Steenhof & Kochert (1985) provided an unexpected result. In a study of the same *Buteo* species as Schmutz *et al.* (1980) they noted that during a prey decline the sympatric hawks converged towards a similar-sized prey resource, even though dietary composition diverged as expected. They interpreted this result as optimisation of foraging efficiency by the *Buteos* with little apparent effect from present-day interspecific competition. Diamond (1985) analysing a similar array of seven New Guinea accipiters with considerable body size overlap, showed the most closely related species could not be ecologically separated on prey type and foraging technique alone (this was also true of the six accipiters in this study: Table 2). They were however, completely separable by habitat or altitude. In this study, as in Diamond's, two niche variables (biome and approximate prey size) could not ecologically distinguish the seven species examined. In conjunction with foraging habitat however, clear cut ecological differences became apparent. It was perhaps surprising that the African species could be separated at all in this way, given that dietary overlap is more likely during times of feast (the period when most of the studies cited here were carried out) than famine. Further studies during winter or dry seasons would help elucidate the possible role of interspecific competition in separating the ecological niches of these southern African accipitrine hawks.

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7. SUMMARY

Of seven small to medium (100–900 g) accipitrine hawks in southern Africa, the Red-breasted Sparrowhawk (RBS) is among the poorest known. Two pairs studied intensively in the Drakensberg mountains of South Africa, fed almost exclusively (98%) on small (10–90 g) birds. A diurnal rhythm in prey delivery was evident for one nest, peaking between 09.00 and 12.00. Also evident were a fast low pursuit mode of hunting (in contrast to previous opinions), over the species' grassland habitat, and a difference in prey selection between the sexes. In a comparison of diet, biome, hunting rhythm, hunting mode and foraged habitat of the RBS with six coexisting species, the Ovambo Sparrowhawk showed 60% similarity, and the Little Sparrowhawk 38% ecological similarity with the RBS. None of the five species with a predominantly small bird diet shared both hunting habitat and biome in common. Ecological overlap between species was thus clearcut and minimal. Of the raptors studied, those closest in body mass to the RBS overlapped least in geographic range, while those much heavier or lighter were the most sympatric. I hypothesize that this may have resulted from interspecific interactions during the speciation of some species or as a post-speciation phenomenon. Although the majority of studies of coexisting congeneric raptors reflect the results outlined here, it is recommended that future studies cover periods when food resources may be limiting.

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