Resource partitioning in coexisting Namib Desert owls, *Bubo africanus* and *Tyto alba*

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ABSTRACT

Resource partitioning in two coexisting owls, spotted eagle (*Bubo africanus*) and barn (*Tyto alba*), was studied in the Kuiseb, a long, seasonally dry river that crosses the central Namib Desert of SWA/Namibia. Significant differences in the proportions of different captured prey were found to exist between owls ($p < 0.005$), habitats ($p < 0.01$), seasons ($p < 0.005$) and prey size classes ($p < 0.005$), even though extensive overlap in many categories was evident. The *Gerbillurus* spp. group accounted for over half of the prey for both species of owl. Large rodents (*Petromus typicus, Thallomys paedulcus* and *Desmodillus auricularis*) accounted for an additional one-third of the spotted eagle owl prey. In comparison, smaller mammals, (*Rhabdomys pumilio* and *Eremitalpa granti*) and birds (*Eremopterix* spp.) comprised one-third of the barn owl prey. Both species of owl captured and consumed high numbers of arthropods. The results suggest that 1) for this population of owls interspecific competition is no more apparent than intraspecific competition for the same resources, and 2) selection of different mean prey size may be the most important characteristic facilitating their coexistence.

CONTENTS

1 INTRODUCTION

Two species of owls, spotted eagle (*Bubo africanus*) and barn (*Tyto alba*), occur together in the Kuiseb River where it crosses the central Namib Desert in the Namib-Naukluft Park, SWA/Namibia. Previous studies on the prey of these owls have been made at various localities in the Namib, but none have been long-term or comparative. These sites include Koichab Pan [Skinner, *et al.*, 1980], Sossus Vlei [Bauer and Niethammer, 1959; Nel. 1969], Mirabib [Vernon, 1972, Brain, 1974; Brain and Brain, 1977], Sandwich Harbour [Stuart, 1975a], and the Kuiseb River at Natab [Meester, 1962] and Homeb [Brain, 1974]. This study was made to assess resource utilisation and niche differentiation of the owls at two sites representing different riparian forest habitats in the Kuiseb River during a one-year period. Primary objectives were (1) to analyse and compare prey composition of each owl species, considering both the number and biomass contributed by each prey species, and (2) to compare the results of prey capture between different habitats in the river. The interpretation of these data is to enhance our understanding of the Kuiseb River's intrinsic contribution to the ecology of the central Namib ecosystem in general and to the trophic structure of these two owls in particular.

2 MATERIALS AND METHODS

Field work was conducted at two sites in the Kuiseb River between January and December 1978. The canyon site, called **Nareb,** is 35 – 40 km from the down-river site, called **Gobabeb**, where the Namib Research Institute (23°34′S, 15°03′E) is located. The Kuiseb is a seasonally dry river, with its source in the central highlands of SWA/Namibia. Where the river crosses the Namib it forms an alluvial flood-plain at bends in the river-bed that supports a thin riparian forest, characterised by isolated stands of *Acacia albida*

and a few, irregularly spaced fig trees, *Ficus sycomorus* and *F. cordata*. Down-river the flood-plain widens to over 750 m and supports a near continuous canopy of *A. albida* broken occasionally by stands of *Tamarix usneoides, Ricinus communis,* and *Euclea pseudebenus*. On flood-plains between the river channel and canyon walls *A. erioloba* trees are interspersed with sprawling clumps of *Salvadora persica* and sparse cover of shrubs and grasses [Giess, 1962; Theron *et al.,* 1980]. The Kuiseb flows most years following seasonal rains in the highlands (mean annual ppt is 367 mm versus 17 mm at Gobabeb). After floods, the river-bed dries for most of its length, but subterranean water 2 – 5 m below the surface nourishes the forest throughout the year. Thus, the two sites, Nareb and Gobabeb, support differing vegetation communities [see subsections B-5 and C-5 in Theron *et al.,* 1980] which presumably are occupied by different avian and mammalian prey of the two coexisting owls. Both species of owl had access to the extensive Namib dune field immediately adjacent to the south and the gravel plains to the north, both of which harbour a different but relatively sparse fauna and flora.

The weather of the central Namib is characterised by high average temperatures, low rainfall, low humidity and the presence of fog [Seely, 1978]. To assess the effects of seasonality on prey capture by owls we divided the year into three periods: January – April, the weather is hot and some rain occurs; May – August, it is cold and dry; September – December, it is hot again but much dryer. These arbitrary divisions do not necessarily reflect the predictable seasons of the central Namib, as rain may fall during any month of the year and vary more than 100-fold between years. Temperatures are equally variable. These divisions, however, suggest an impression of the general climatic conditions that prevailed during the year of our study.

We located nests and roosts of the two owl species at Nareb (N = 2 *Bubo* and 3 *Tyto*) and Gobabeb (N = 2 *Bubo* and 3 *Tyto*), then cleared the accumulated, regurgitated pellets and parts of disintegrated pellets. Subsequently, at four-month intervals, all pellets were collected and broken apart using conventional methods [e.g., Marti, 1974]. The remains were identified to species if possible. For most small mammalian prey this was straightforward, except for the *Gerbillurus* group, for which complete dentaries and bullae are needed to identify species. Skulls and feathers were used in identification of birds. Insect remains useful for identification were heads, legs, and jaws, especially for sun spiders. Uncommon prey, such as lizards and scorpions, were identified by jaws and other remaining chitinous parts.

Average weights of prey species were estimated from locally collected specimens (Tables 1 and 2). Using these and prey numbers determined from skulls in the owl's diet, the proportion of biomass each prey group represented in each owl's food at the two different sites was estimated. Dice-Leraas diagrams of prey weight were constructed from complete prey lists to compare prey weight among the owls. Prey were also grouped in weight classes for comparisons.

Chi-square contingency tables were used to compare diet compositions between owls, among seasons for each owl, and between habitats for each owl.

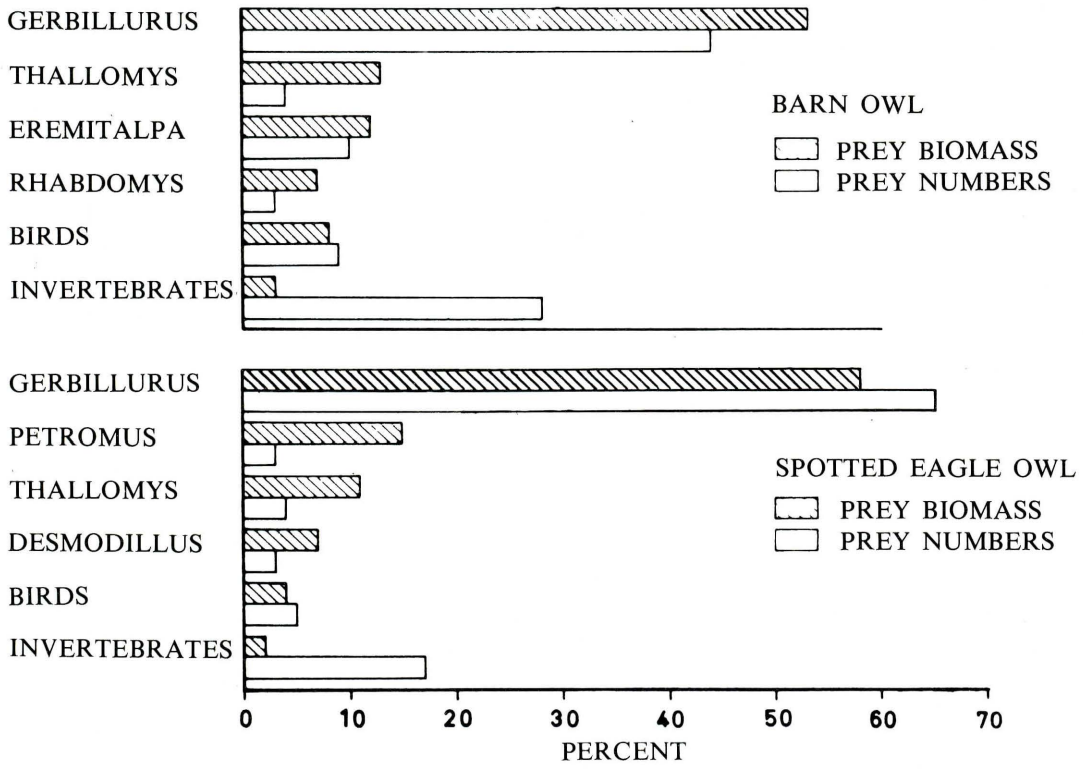

FIGURE 1: Comparison of major prey of barn and spotted eagle owls in the Kuiseb River.

3 RESULTS

3.1 Comparison of prey species between owls

A significant difference was found in prey composition between spotted eagle owls and barn owls ($X^2 = 89.59$, $p < 0.005$, 9 d.f.), indicating prey were selected in different proportions. For both owl species the *Gerbillurus* species group comprised the most important prey, both numerically and in terms of biomass contributed (Figure 1). The next important prey species for spotted eagle owls were strictly diurnal rock rats (*Petromus typicus*), black-tailed tree rats (*Thallomys paedulcus*) and Namaqua gerbils (*Desmodillus auricularis*). Together these three species accounted for over one-third of the owl's annual diet (Table 1).

In contrast, the most important prey species after *Gerbillurus* for barn owls were *Thallomys*, golden moles (*Eremitalpa granti*) and small birds, probably grey-backed finch-larks (*Eremopterix verticalis*). These three species accounted for over one-third of the diet (Table 2). Both species of owls consumed numerous sun spiders, represented by a single nocturnal species (*Solfugid lawrence*) and numerous insects (mostly unidentified scarabid and carabid beetles), but because of their small size, they were considered insignificant prey relative to the larger species described above (Figure 1). The only prey species of spotted eagle owl not found in the barn owl assemblage was the large bodied *Petromus typicus*. Conversely, only barn owls preyed on short-eared elephant shrews (*Macroscelides proboscideus*) (Table 1). Both of these last two species share the same rocky habitat.

Only for barn owls were a sufficient number of complete skulls of the *Gerbillurus* group recovered to identify species. Of 66 individuals, the bush-tailed gerbil (*G. setzeri*) accounted for 68,2%, the lesser gerbil (*G. paeba*) for 25,8% and *G. tytonis* for 6,1% of the total. All twelve complete skulls from the spotted eagle owl collection were *G. setzeri* (Coetzee, per. comm.).

TABLE 1: Comparison of spotted eagle owl prey (biomass) from two habitats.

		GOBABEB		NAREB		TOTAL		
Prey species	Weight (g)	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass	Total No.
Mammals		(71,3)	(92,3)	(85,7)	(96,8)	(78,4)	(94,7)	(307)
Gerbillurus spp.	*25 – 36	59,2	62,2	70,1	53,9	64,6	58,1	253
Desmodillus auricularis	55	5,3	12,3	1,1	1,8	3,2	7,1	13
Rhabdomys pumilio	42	1,9	3,4	1,1	1,4	1,5	2,4	6
Thallomus paedulcus	75	3,4	10,7	4,8	11,1	4,1	10,9	16
Petromus typicus	150	0,5	3,0	5,9	27,2	3,2	15,1	12
Erimitalpa granti	25	0,5	0,5	1,1	0,8	0,8	0,7	3
Crocidura cyanea	12	0,5	0,2	1,6	0,6	1,0	0,4	4
Birds								
Eremopterix spp.	18	6,8	5,1	3,7	2,1	5,2	3,6	21
Reptiles	5	1,0	0,2	2,7	0,4	1,8	0,3	7
Insects	2	10,2	0,8	3,7	0,2	7,0	0,7	28
Solifuges	3	10,2	1,3	3,7	0,3	7,0	0,8	28
Scorpions	5	0,5	0,1	0,5	0,1	0,5	0,1	2
Totals		100,0	99,8	100,0	99,9	99,9	100,2	393

*Mean masses range from 25 g for *G. paeba* to 36 g for *G. setzeri*.

TABLE 2: Comparison of barn owl prey (biomass) from two habitats.

		GOBABEB		NAREB		TOTAL		
Prey species	Weight (g)	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass	Total No.
Mammals		(63,5)	(88,0)	(62,9)	(88,0)	(63,1)	(88,0)	(547)
Gerbillurus spp.	*25 – 36	45,6	58,7	41,8	46,8	43,7	52,8	379
Desmodillus auricularis	55	1,5	4,2	0,8	1,9	1,1	3,1	10
Rhabdomys pumilio	42	2,1	4,6	4,5	8,5	3,3	6,6	28
Thallomus paedulcus	75	1,5	5,8	6,0	20,3	3,7	13,0	31
Eremitalpa granti	25	10,9	14,1	8,3	9,3	9,6	11,7	84
Macroscelides proboscideus	42	0,2	0,5	0,2	0,5	0,2	0,5	2
Crocidura cyanea	12	1,7	1,0	1,3	0,7	1,5	0,9	13
Birds								
Eremopterix spp.	18	7,3	6,7	11,1	8,9	9,2	7,8	78
Reptiles	5	1,9	0,5	1,5	0,3	1,7	0,4	15
Insects	2	8,8	0,9	9,6	0,9	9,2	0,9	79
Solifuges	3	18,4	2,8	14,9	2,0	16,6	2,4	145
Totals		99,9	99,8	100,0	100,1	99,8	100,1	864

*Mean masses range from 25 g for *G. paeba* to 36 for *G. setzeri*.

Other species of small prey known to occur in or near the Kuiseb River [Stuart, 1975b; Griffin, per. comm.] but not represented in either owl's diet were the pygmy rock mouse (*Petromyscus collinus*), two species of *Elephantulus, Mus musculus* and *M. minutoides*, two species of *Graphiurus* and *Tatera leucogaster*. There are also several species of bats which at times are commonly found in barn owl pellets. The rock dassie (*Procavia capensis*), Cape hare (*Lepus capensis*), red rock hare (*Pronolagus randensis*) and several species of mustellids and viverrids are also present but are presumably too large as their remains were not found in either of the owl's regurgitated pellets at the collection sites.

3.2 Comparison of prey species between habitats

Collection sites for spotted eagle and barn owls were classified as either (1) lower riverine, called *Gobabeb,* where a wide, alluvial flood-plain supports a dense *Acacia* woodland, and (2) upper canyon, called *Nareb,* where the forest is reduced to patches of *Acacia* and a few fig trees. A significant difference in prey composition was found for spotted eagle owls ($X^2 = 32.62$, $p < 0.005$, 8 d.f.) and for barn owls ($X^2 = 25.21$, $p < 0.01$, 10 d.f.) between the habitat types described. A separate analysis of mammals only shows similar differences in significance in prey capture between habitats for both spotted eagle owls ($X^2 = 15.42$, $p < 0.01$, 5 d.f.) and barn owls ($X^2 = 19.60$, $p < 0.005$, d.f.). In both habitat types, *Gerbillurus* spp. were the most important prey for both species of owls (Tables 1 and 2). However, the data are significant only in that the relative proportions differed between habitats. Thus, differences in habitat structure were not reflected in the species of prey that the owls captured, nor was any indicator species identified for a particular habitat. Rather, both species of owls preyed upon nearly identical prey assemblages in both the down-river (Gobabeb) and canyon (Nareb) habitats, but in different proportions. Further, an analysis of habitat partitioning by the major prey species suggests that both barn and spotted eagle owls hunt and capture their prey in all three representative habitats (dunes, riverine and gravel plains) and that no clear distinction can be drawn as to which habitat either species of owl prefers to hunt in.

3.3 Seasonal assessment of prey species

Seasonal variation of prey species was found to be significantly different for both spotted eagle owls ($X^2 = 54.79$, $p < 0.005$, 6 d.f.; Table 3) and barn owls ($X^2 = 115.70$, $p < 0.005$, 16 d.f., Table 4). After brief rains (January – April) the *Gerbillurus* group totally dominates the spotted eagle owl's diet at both the down-river (Gobabeb = 81.2%) and canyon (Nareb = 83.3%) sites. For the next four months (May – August) it is dry and mostly cold in the Namib. In this period gerbils still dominate the spotted eagle owl's diet, with birds becoming the second most important prey species at Gobabeb (no data are available for Nareb). For the last four months (September – December), a period of extreme aridity and high temperatures, *Gerbillurus* contribute less than half of the spotted eagle owl's diet at both sites. *Thallomys* and *Petromus* are important prey for spotted eagle owls at Nareb during this period, but not at Gobabeb (Table 3).

With two exceptions, the same kinds of seasonal trends were found with barn owls; the proportion of gerbils in the diet remains constant at both sites regardless of season, while the proportion of golden moles (*Eremitalpa*) in the diet shows a marked increase during the May – August period at both the down-river and canyon sites (Table 4).

TABLE 3: Seasonal variation in spotted eagle owl prey in the Kuiseb River.

	GOBABEB								NAREB							
	Jan – Apr		May – Aug		Sept – Dec		Totals		Jan – Apr		May – Aug		Sept – Dec		Totals	
Prey species	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Mammals																
Gerbillurus spp.	56	81,2	37	57,8	29	39,7	122	59,2	95	83,3	No Data		36	49,3	131	70,1
Desmodillus auricularis	4	5,8	3	4,7	4	5,5	11	5,3	0	0,0			2	2,7	2	1,1
Rhabdomys pumilio	2	2,9	1	1,6	1	1,4	4	1,9	0	0,0			2	2,7	2	1,1
Thallomys paedulcus	0	0,0	3	4,7	4	5,5	7	3,4	0	0,0			9	12,3	9	4,8
Petromus typicus	1	1,4	0	0,0	0	0.0	1	0,5	2	1,7			9	12,3	11	5,9
Eremitalpa granti	1	1,4	0	0,0	0	0,0	1	0,5	2	1,7			0	0,0	2	1,1
Crocidura cyanea	0	0,0	0	0,0	1	1,4	1	0,5	0	0,0			3	4,1	3	1,6
Birds																
Eremopterix spp.	0	0,0	12	18,7	2	2,7	14	6,8	3	2,6			4	5,5	7	3,7
Reptiles	1	1,4	0	0,0	1	1,4	2	1,0	3	2,6			2	2,7	5	2,7
Insects	1	1,4	8	12,5	12	16,4	21	10,2	1	1,7			6	8,2	7	3,7
Solifuges	3	4,3	0	0,0	18	24,7	21	10,2	7	6,1			0	0,0	7	3,7
Scorpions	0	0,0	0	0,0	1	1,4	1	0,5	1	1,7			0	0,0	1	0,5
Totals	69		64		73		206		114				73		187	

TABLE 4: Seasonal variation in barn owl prey in the Kuiseb River.

	GOBABEB								NAREB							
	Jan – Apr		May – Aug		Sept – Dec		Totals		Jan – Apr		May – Aug		Sept – Dec		Totals	
Prey species	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Mammals																
Gerbillurus spp.	47	42,3	102	49,0	64	43,2	213	45,6	24	35,8	107	49,1	35	31,3	166	41,8
Desmodillus aricularis	2	1,8	2	1,0	3	2,0	7	1,5	3	4,5	0	0,0	0	0,0	3	0,8
Rhabdomys pumilio	1	0,9	2	1,0	7	4,7	10	2,1	2	3,0	5	2,3	11	9,8	18	4,5
Thallomys paedulcus	2	1,8	2	1,0	3	2,0	7	1,5	3	4,5	14	6,4	7	6,3	24	6,0
Eremitalpa granti	15	13,5	35	16,8	1	0,7	51	10,9	19	28,3	13	5,9	1	0,9	33	8,3
Macroscelides proboscideus	0	0,0	1	0,5	0	0,0	1	0,2	1	1,5	0	0,0	0	0,0	1	0,2
Crocidura cyanea	3	2,7	1	0,5	4	2,7	8	1,7	0	0,0	2	0,9	3	2,7	5	1,3
Birds																
Eremopterix spp.	10	9,0	16	7,7	8	5,4	34	7,3	2	3,0	33	15,1	9	8,0	44	11,1
Reptiles	3	2,7	3	1,4	3	2,0	9	1,9	1	1,5	2	0,9	3	2,7	6	1,5
Insects	2	1,8	16	7,7	23	15,5	41	8,8	1	1,5	12	5,5	25	22,3	38	9,6
Solifuges	26	23,4	28	13,5	32	21,6	86	18,4	11	16,4	30	13,8	18	16,1	59	14,9
Totals	111		208		148		467		67		218		112		397	

Thus, members of the genus *Gerbillurus* are the most important prey for spotted eagle owls throughout the year. As the dry season progresses, they become less important, and are replaced by *Thallomys* and *Petromus* at the canyon site. In comparison, members of the genus *Gerbillurus* are also the most important prey for barn owls throughout the year, but *Eremitalpa* is a close second from January through August. Like the comparison of prey species between habitats, comparisons among seasons show significant differences that reflect relative proportions of prey composition rather than absolute differences.

3.4 Comparison of prey size between owls

An average prey size was calculated for each owl species using total prey numbers and mean prey weights. Dice-Leraas diagrams indicated significant differences in mean prey size selected by the two owls ($X^2 = 25.43$, $p < 0.005$, 4 d.f.; Table 5) (Figure 1). The mean prey size for spotted eagle owls was 28 g; for barn owls it was 20 g. The largest prey species, *Petromus typicus,* was captured by spotted eagle owls but not barn owls. The larger mean prey size for spotted eagle owls can probably be attributed to their greater body size (length: 43 – 47 cm) compared to the smaller barn owl (length: 30 – 33 cm).

TABLE 5: Estimated weight distribution of the prey of spotted eagle and barn owls in the Kuiseb River.

	Per cent in each class	
Prey weight (g)	Spotted Eagle Owl	Barn Owl
0 – 10	16,5	27,7
10 – 20	6,4	10,5
20 – 40	65,1	53,6
40 – 60	4,8	4,6
60 – 80	4,1	3,6
80 – 150	3,1	–

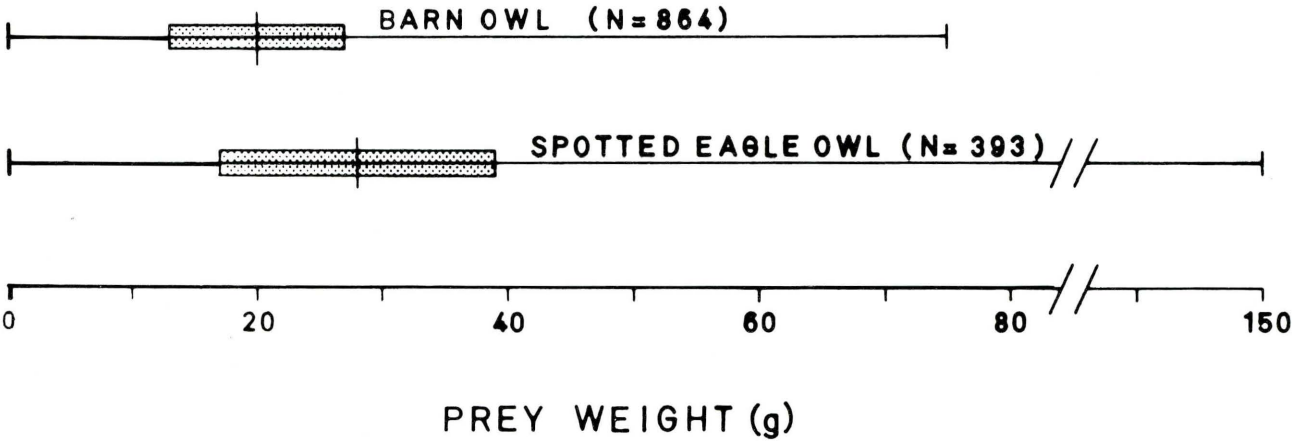

FIGURE 2: Mean prey weight of barn and spotted eagle owls in the Kuiseb River. Horizontal line indicates the range of prey weights; the vertical line is the mean, the black rectangle represents the 95% confidence limits of the mean.

4 DISCUSSION

Consideration of competition, resource utilisation, niche differentiation, and coexistence among or between ecologically similar species have been a central focus in ecology for several decades now [reviewed by Schoener, 1974; Brown, 1975; Pianka, 1976]. Most studies of resource utilisation and partitioning have been aimed at documenting the adaptations that facilitate stable coexistence or at analysing the limits that competition may place on community development, seeking answers to questions such as how do coexisting species differ in their utilisation of resources and thus avoid competitive exclusion [Brown, 1975]. Although not explicitly stated, earlier studies of owl resource utilisation in various localities of the Namib [Bauer and Niethammer, 1959; Meester, 1962; Nel, 1969; Vernon, 1972; Brain, 1974; Stuart, 1975a; Brain and Brain, 1977; Skinner *et al.*, 1980] suggest that only one species of owl was in occupancy. In contrast, both the spotted eagle owl and barn owl occur together in the Kuiseb, and although there were significant differences in the proportions of different prey captured by the two owl species, there was extensive overlap in all but a few categories.

Two trends are evident. The first is that even though significant differences in the proportions of prey were found to exist between the two species of owls, nearly similar differences were found to exist between the same species living in different habitats of the Kuiseb. Thus, interspecific competition is no more apparent than intraspecific competition for the same resources, regardless of where the owl is living. Secondly, the larger mean prey size for spotted eagle owls compared to that of barn owls may be the most important characteristic that facilitates the coexistence of these two owls within the central Namib.

The results of this study can be compared to the results of other studies made in the Namib Desert. Skinner's (1980) analysis of spotted eagle owl prey in the southern Namib at Koichab Pan had members of the genus *Gerbillurus* (50,2%) as the most common prey, followed in importance by *Eremitalpa granti* (30,6%) and species of *Gekkonidae* (16,6%). Several hundred kilometres to the north at Sossus Vlei, Nel (1969) also found *Gerbillurus* spp. (74,1%) to be the most important prey of spotted eagle owls, followed by *Eremitalpa* (22,7%) and unidentified geckos (6,8%), while birds and insects were negligible. At Homeb, approximately 120 kilometres to the north-north-west, which is near to where this study was made, Brain (1974) found that the *Gerbillurus* group (73,3%) was again the most common prey, with *Eremitalpa* (15,2%) a distant second. Along the coast of Sandwich Harbour, which is another 80 kilometres to the west-north-west, Stuart (1975) recorded the prey of barn owls; *Gerbillurus* (45,8%), *Crocidura cyanea* (14,9%), *Rhabdomys pumilio* (13,1%) and unidentified small wading birds (15,9%) were the major prey selected.

All of these studies within the Namib clearly show that the *Gerbillurus* species group is the single most important prey of both species of owls, accounting for about half or more of the total prey assemblage. Unfortunately, this group can be difficult to separate into species. Any assessment of resource partitioning by the owls is thus obscured. Differences between the dietary preferences of owl species become more apparent when secondary prey items are considered, but it is not clear if the differences reflect different hunting strategies, prey preferences, or simply prey availability at the various localities when the studies were made.

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