

HABITAT ASSOCIATION OF THE TORTOISES *GEOCHELONE PARDALIS* AND *KINIXYS SPEKII* IN THE SENGWA WILDLIFE RESEARCH AREA, ZIMBABWE

ADRIAN HAILEY¹ AND IAN M. COULSON^{2,3}

¹*Department of Biological Sciences, University of Zimbabwe,
P.O.Box MP 167, Mount Pleasant, Harare, Zimbabwe*

²*Sengwa Wildlife Research Institute, Department of National
Parks and Wild Life Management, Private Bag 6002, Gokwe, Zimbabwe*

³*Deceased*

There have been few studies of the mechanism of niche separation in sympatric tortoises. This paper examines the habitat association of *Geochelone pardalis* and *Kinixys spekii* at the Sengwa Wildlife Research Area, using data on 460 tortoises marked from 1982 to 1992. Tortoises were found in most of the vegetation types present. Habitat niche breadth was slightly greater in *G. pardalis* ($B=0.48$) than in *K. spekii* ($B=0.36$). There was considerable niche overlap between the two species ($O=0.76$), the only major difference being the greater use of riverine grassland by *G. pardalis*. Home range areas of individuals recaptured in several years were significantly larger in *G. pardalis* (mean 26 ha) than in *K. spekii* (mean 3.1 ha). The pattern of refuge use differed between the two species; *K. spekii* used burrows, and *G. pardalis* used thickets and felled trees.

INTRODUCTION

Much of the species diversity of tortoises (Testudinidae) reflects geographical replacement of one species by another. For example, the four species in North America are allopatric (Lamb, Avise & Gibbons, 1989). In areas where sympatric tortoises occur, the means of coexistence have not been investigated in detail. Wright, Steer & Hailey (1988) found that *Testudo hermanni* and *T. graeca* were separated by habitat utilization in north-eastern Greece, and the same may apply to *T. hermanni* and *T. marginata* in western and southern Greece (Willemsen, 1991).

Southern Africa has the most diverse tortoise fauna of any region of the world (Swingland & Klemens, 1989); the mechanisms of niche separation in this region are clearly of interest. Three species occur in Zimbabwe; the leopard tortoise *Geochelone pardalis*, found over most of the country, and the hingeback tortoises *Kinixys belliana* and *K. spekii*. The latter has only recently been confirmed as a full species (Broadley, 1993). *Kinixys spekii* occurs over most of Zimbabwe, while *K. belliana* is restricted to the Eastern Highlands, where populations of the two species may be found close together (Broadley, personal communication).

Geochelone pardalis and *Kinixys spekii* are thus broadly sympatric. These two tortoises have been studied in the Sengwa Wildlife Research Area, Gokwe District, the largest area in Africa devoted solely to ecological research (Cumming, 1983). The present paper describes the habitat association of the two species, using data collected over a ten year period. Additional information is presented on their long-term movements and use of refuges.

METHODS

Tortoise sightings were incidentally recorded during routine work in the Sengwa Wildlife Research Area (18° 6' S, 28° 12' E) from 1982 to 1992, mostly by game scouts. Tortoises were brought into the Sengwa Wildlife Research Institute office, marked with numbered metal tags glued on to the centre of the 3rd vertebral scute (Gaymer, 1973) with epoxy adhesive, and immediately returned to the exact capture location. Only the first capture of each individual was used in the analysis of habitat utilization. Locations were recorded to the nearest 100 m using a grid reference system. The vegetation type at each capture location was found from the 1:50 000 scale vegetation map of the Sengwa area (Cumming, 1970), a simplified version of which is given by Cumming (1975). Tortoise capture locations were plotted by computer to the same scale, together with a 1 km grid to facilitate comparison with the vegetation map.

The scale over which vegetation types varied was measured to compare with the 100 m resolution of tortoise locations. Four rectangles, totalling 108 square km, were selected (on the basis of excluding the Sengwa and Lutope rivers). The number of areas of different vegetation identified within these rectangles totalled 66 (including all patches more than half inside the rectangle boundaries). The mean size of an area of vegetation was therefore about 1.6 square km, which would correspond to 160 tortoise grid locations. It was concluded that the grid system had sufficient resolution to identify the vegetation types used by tortoises. The scale over which vegetation types varied was smaller around the Sengwa and Lutope rivers, but this was felt to be unimportant for two reasons. First, several

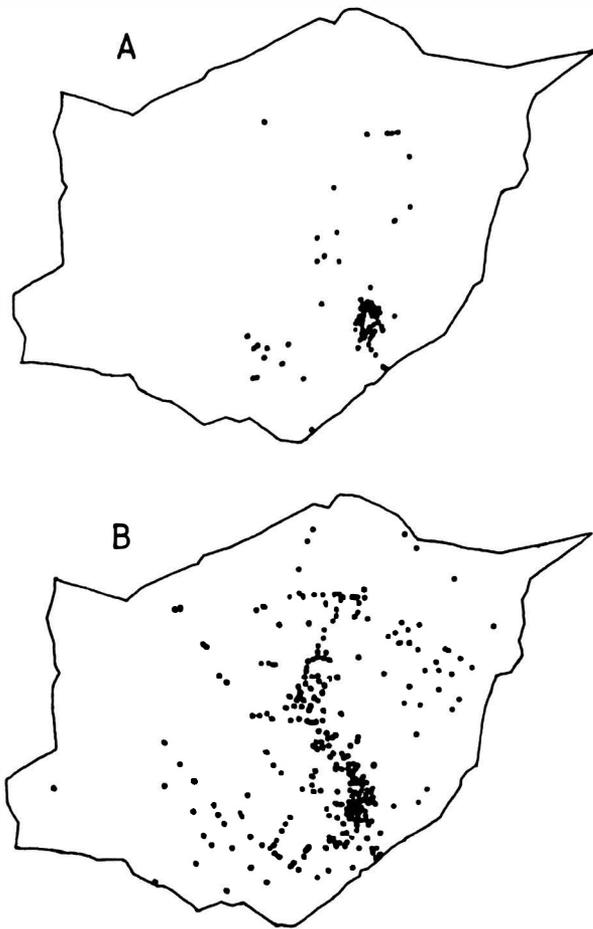


FIG. 1. Maps of the capture locations of *Kinixys spekii* (A) and *Geochelone pardalis* (B) in the Sengwa Wildlife Research Area, 1982-1992.

of the riverine types were combined in analysis. Second, recording of tortoise locations was probably more accurate around the rivers, which formed obvious landmarks.

Niche breadth (*B*) was calculated as:

$$B = \frac{1/\sum p_i^2}{n}$$

where p_i is the proportion of the i^{th} category used from n possible categories (Pianka, 1973). Niche overlap was calculated using Pianka's (1973) symmetric measure:

$$O = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of the i^{th} category for species j and k .

Home ranges were calculated for tortoises captured five or more times in three or more different years. Capture locations were plotted and the home range area was measured as a minimum convex polygon. Information on the refuges used by thread-trailed tortoises is also presented here. Eight *K. spekii* and nine *G. pardalis* were trailed for up to ten days in January and February 1992. They were relocated each

morning. When the tortoise was clearly in a refuge, the characteristics of the refuge were noted.

RESULTS

Records of both species were clustered in the area around the Institute office and staff compound (Fig. 1). The extent of this clustering differed significantly between the two species. The two 1 km squares of the office area included 59.8% of the 107 records of *K. spekii*, but only 19.3% of the 353 records of *G. pardalis* ($\chi^2 = 66.0$, 1 df, $P < 0.001$). Possibly game scouts were less likely to see the small *K. spekii* when away from

TABLE 1. Vegetation types used by *G. pardalis* and *K. spekii*.

Type	All observations		Except office area	
	<i>G. p.</i>	<i>K. s.</i>	<i>G. p.</i>	<i>K. s.</i>
a	25.2	32.7	15.8	11.6
b	18.7	17.8	21.4	32.6
c	2.8	6.5	3.5	16.3
d	2.3	0.9	2.8	2.3
e	2.0	0	2.5	0
f	2.5	0.9	3.2	2.3
g	15.9	1.9	19.6	4.6
h	2.8	0	3.5	0
i	3.4	6.5	3.2	13.9
j	0.3	1.9	0.4	4.6
k	5.9	3.7	6.7	4.6
l	3.1	0	3.9	0
m	7.4	0.9	9.1	2.3
n	3.1	1.9	3.5	2.3
o	2.0	15.0	0.3	0
p	2.5	9.3	0.7	2.3
<i>N</i>	353	107	285	43
<i>B</i>	0.447	0.345	0.478	0.358
<i>O</i>	0.841		0.761	

Data are percentages of *N* observations for each species, with niche breadth (*B*) and overlap (*O*). Vegetation types are: a, *Brachystegia-Julbernardia* mixed woodland (Miombo); b, *Colophospermum mopane* woodland (Mopane); c, *C. mopane-Combretum-Erythroxylum* woodland and bushland; d, *C. mopane-Acacia nigrescens-Ximenia* woodland and bushland; e, *Baikiaea-Baphia-Combretum* wooded bushland thicket; f, *Commiphora-Combretum* wooded bushland thicket; g, *Acacia tortilis-Grewia* riparian communities; h, *Combretum-Terminalia* low woodland and bushed grassland; i, *Julbernardia-Vellozia* wooded and bushed grassland; j, *Brachystegia boehmii-Combretum* wooded and bushed grassland; k, *C. mopane-Combretum-Tristachya* wooded and bushed grassland; l, *Acacia albida-Hyparrhenia* wooded grassland; m, River terrace (flood plain) grassland; n, Grassland on alluvial or saline soil, and drainage line grassland (vlei); o, Grassland with *C. mopane* scrub; p, Dense riverine woodland. Types a to o correspond to those in Fig. 2 of Cumming (1975); n includes two of Cumming's types. Type p is an addition; it occurs mostly along the Kove river. (See Appendix 1 for full vegetation map coder).

TABLE 2. Tests of association between the two tortoise species and vegetation type. Values are the percentage of the total records of each species which occur in that vegetation type. Also shown is a χ^2 test of association between species and vegetation (against all other vegetation types pooled): NS = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Vegetation type	All observations				Except office area			
	<i>G. p.</i>	<i>K. s.</i>	χ^2	<i>P</i>	<i>G. p.</i>	<i>K. s.</i>	χ^2	<i>P</i>
Miombo woodland (a)	25.2	32.7	2.34	NS	18.7	11.6	0.50	NS
Miombo total (a,i,j)	28.9	41.1	5.66	*	19.3	30.2	2.72	NS
Mopane woodland (b)	18.7	17.8	0.05	NS	14.4	32.6	2.64	NS
Mopane total (b,c,d,o)	31.7	43.9	5.40	*	34.7	55.8	7.08	**
Open riverine (g,m)	23.2	2.8	22.74	***	28.8	7.0	9.24	**

the office, because they were then concentrating on large game and/or poachers. The occurrence of the tortoises in the different vegetation types has therefore been analysed both including and excluding the two 1 km squares around the office.

The two analyses are broadly similar (Table 1). The major effect of excluding the data from around the office was to decrease the proportion of records from miombo woodland, which was the major vegetation type in that area. Niche breadth increased slightly for both species, and the overlap was slightly lower, when the office area was excluded. Niche breadth was slightly higher in *G. pardalis* than in *K. spekii*: about 0.45 and 0.35, respectively, in both analyses. There was considerable overlap between the two species: $O = 0.76$ for the restricted data set and $O = 0.84$ for the full data.

The number of sightings was low in several vegetation types. A test of the significance of the differences in habitat association thus depends on the appropriate grouping of vegetation types. The basis of the grouping used is three *a priori* hypotheses suggested by observations of tortoises in 1992 and 1993 (rather than derived from the data being analysed):

(1). *Kinixys spekii* occurs more frequently in miombo woodland than does *G. pardalis*. In fact there was no significant association between tortoise species and miombo woodland (Table 2). There was an association, in the expected direction, when mixed miombo/grassland vegetation types (i, j) were included, but this was significant only for the total data.

(2). *Geochelone pardalis* occurs more frequently in mopane woodland than does *K. spekii*. There was no significant association between tortoise species and mopane woodland (Table 2). There was an association when mopane scrub and mixed mopane/grassland vegetation types (c,d,o) were included. This association was significant for both the total data and the data excluding the office area, but was in the opposite direction to that predicted.

(3). *Geochelone pardalis* occurs more frequently in open riverine vegetation than does *K. spekii*. There

was a significant association between tortoise species and open riverine habitats (*Acacia tortilis* open woodland and riparian grassland), for both the full data and the data excluding the office area. The association was in the expected direction.

Four individuals of both species were captured on five or more occasions in three or more years. *Geochelone pardalis* were captured more frequently, but over shorter periods (Table 3); both species were captured on average in four different years. Home ranges of *G. pardalis* (mean: 26 ha) were about ten times larger than those of *K. spekii* (mean: 3.1 ha). The difference between the two species was significant: analysis of variance of log-transformed data, $F_{1,6} = 16.7$, $P < 0.01$.

Two thirds of the refuges of *K. spekii* were the burrows of mammals (Table 4), principally those of the springhare (*Pedetes capensis*) and the antbear (*Orycteropus afer*). The pangolin (*Manis temmincki*) burrows were constructed by springhares or antbears, but had been occupied by a radiotracked pangolin. *Geochelone pardalis* was not found in burrows, though on two occasions the thread trail entered and left antbear holes. This species used mostly shrubs, thickets and felled trees. The association between species and use of burrows vs other refuges was highly significant ($\chi^2 = 46.3$, $P < 0.001$).

TABLE 3. Movements of recaptured tortoises. Values are means (with range), or \pm SD. Duration is the number of years from the first to the last capture, inclusive.

	<i>G. pardalis</i>	<i>K. spekii</i>
Number of tortoises	4	4
Number of captures	11.2 (6-21)	6.2 (5-8)
Number of years	4.0 (3-6)	4.0 (3-6)
Duration (years)	4.2 (3-6)	6.0 (4-7)
Home range (ha)	26 \pm 14	3.1 \pm 1.1

TABLE 4. Refuge use by traileed tortoises. Data are the percentages of *N* refuges. * Shrubs were: *Brachystegia boehmii*, *Colophospermum mopane*, *Combretum* spp., *Diplorhynchus condylocarpon*, *Erythroxyllum zambesiacum*, *Friesoldielsia obovata*, *Grewia monticola*, *Julbernardia globiflora*, *Lannea stuhlmanni*, *Pseudolachnostylis maprouneifolia*, *Catunaregum spinosa*.

	<i>G. pardalis</i>	<i>K. spekii</i>
Springhare burrow	0	30
Antbear burrow	0	20
Pangolin burrow	0	16
Shrub/thicket*	46	12
Felled tree (dead)	37	18
Felled tree (live)	15	4
Grass	2	0
<i>N</i>	46	50

Apart from one *G. pardalis* in a grass pallet, all the refuges occupied by the tortoises provided both shelter and protection. Nevertheless, there was no indication that the tortoises selected thorny shrubs. Only one (*Catunaregum spinosa*) of the eleven taxa identified had thorns, in an environment where thorny shrubs were rather common.

DISCUSSION

Sightings of tortoises were made incidental to other work, due to their low population density; the sighting frequency of tortoises at Sengwa was under one per observer per day (both species combined), even for an experienced observer searching specifically for them. As a result, there was no attempt to sample all habitats equally, or to avoid bias from greater ease of sighting in open habitat types. It is therefore not possible to calculate habitat preferences: that is, the number of sightings in relation to the area of each vegetation type. Nevertheless, these problems will not affect a comparison of the habitat associations of the two species of tortoise. Tortoises were found in most vegetation types, which therefore appear to have been sampled adequately.

Both species of tortoise used almost all of the vegetation types present at Sengwa. *Geochelone pardalis* has previously been noted as a habitat generalist (Greig & Burdett, 1976; Rall, 1985; Scoones, 1986). There was considerable habitat overlap between *G. pardalis* and *K. spekii*, which suggests that either (1) separation is along some other dimension, such as food, or (2) there is no competition because populations are limited by some other factor, such as predation. The diets of the two species do in fact differ widely. *Geochelone pardalis* is completely herbivorous, taking grasses as well as herbs (Milton, 1992, Rall & Fairall, 1993, and personal observations at Sengwa). *Kinixys spekii* is omnivorous, taking herbs, invertebrates and fungi (Hailey, Coulson & Loveridge, in preparation), as do other species of *Kinixys* (Blackwell, 1968).

The pattern of habitat association did not confirm two of the three hypotheses tested. The expectation that *K. spekii* was associated with miombo woodland was perhaps due to the concentration of observations around the Institute office, where this vegetation predominated. The second hypothesis, association of *G. pardalis* with mopane, was also rejected; indeed, *K. spekii* was more associated with mopane when mixed vegetation types were included. This is perhaps due to the wide variety of habitats which include mopane trees. While in our experience only *G. pardalis* are found in large areas of pure mopane woodland, both species use small patches of mopane, and mixed mopane habitats. The third pattern was confirmed; an association between *G. pardalis* and open riverine habitats, which occur along the Sengwa and Lutope rivers. This does not seem to be an association with water as such, as *K. spekii* was associated with the dense riverine woodland along the Kove river (vegetation type p).

Home range areas determined by recaptures were similar to those found by thread-trailing over a ten day period: 1.9 and 26 ha in *K. spekii* and *G. pardalis*, respectively. Bertram (1979a) also found a home range of 1.9 ha in a female *K. spekii* radiotracked for two years. (That paper refers to the animal as *K. belliana*, but this would now be *K. spekii*; Broadley, personal communication). This female spent most time in a core area of only 0.24 ha, and it seems likely that the true home range area of *K. spekii* is indeed only a few hectares. The true home range area of *G. pardalis*, however, is likely to be greater than that measured by short-term studies or those based on few capture locations. Rall (1985) found an average home range area of 12 ha in three *G. pardalis* radiotracked over two weeks, but other studies have found substantially larger home ranges. Four home ranges estimated from Figure 3 of Van Zyl (1966) average 107 ha, and Bertram (1979b) gives a home range area of 160 ha for a radiotracked adult female.

Geochelone pardalis and *K. spekii* used significantly different refuges, probably related to the inability of the larger species to enter mammal burrows. Both African tortoises used refuges providing both protection and shelter, in contrast to the Mediterranean *Testudo hermanni* which often utilizes flimsy pallets (Hailey, 1989). The burrows of springhare in particular are deep and long (Butynski & Mattingly, 1979) and provide excellent protection for the small *K. spekii*, which is vulnerable to predation by several animals at Sengwa, including the ground hornbill and spotted hyaena.

ACKNOWLEDGEMENTS

We thank Elias Gubunja, Charles Gava and Kirisimasi Mbulawa for assistance in the field, Don Kennedy for correcting plant names, and Don Broadley for information on tortoise distributions. Supported by the Research Board of the University of

Zimbabwe. This paper is published with the approval of the Director of the Department of National Parks and Wildlife Management.

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APPENDIX 1

The lettered vegetation types used here correspond to the following numerical codes for the full Sengwa vegetation map (Cumming, 1970).

a-2; b-4; c-7; d-6; e-3, 18; f-17; g-5, 10, 14, 19; h-8, 9; i-12; j-11; k-13; l-15, 16; m-22; n-23, 24, 25, 26; o-20, 21; p-1.

Accepted: 17.3.95