

CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

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Kinixys spekii Gray 1863 –
Speke's Hinge-back Tortoise, Speke's Hinged Tortoise

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SUMMARY. — Speke's Hinge-back Tortoise, *Kinixys spekii* (Family Testudinidae), is a medium-sized terrestrial species with an average straight carapace length (SCL) of ca. 130–180 mm, with a maximum SCL of 181 mm for males and 210 mm for the slightly larger females. The species is widespread in the savannahs of the central plateau areas of Africa south of the Equator; it inhabits grassland, bushed and wooded grassland, and woodland such as Miombo and Mopane. A morphological distinction of *Kinixys* from other tortoise genera is the carapacial hinge; *K. spekii* has a depressed carapace, with the ratio of shell length to height usually more than 2.3. Carapace scutes usually have a concentric or zonary color pattern, but adult males are often uniform. Clutch size is 2–6 eggs, mean 3.8; egg size is large, mean 31 x 41 mm and 23 g. Annual survival of adults is relatively low (0.74), with high mortality from mammalian and avian predators, especially the Ground Hornbill. Population density is low (0.16/ha) in undisturbed areas. The diet is omnivorous, with 47% vascular plants, 41% fungi, and 12% invertebrates. Fungi are the preferred food, and give the greatest energy intake, but *K. spekii* shows true diet mixing, taking other food types for other nutrients. Mean body temperature is a relatively low 27.0°C, giving a wide safety margin before overheating. Seasonal activity is limited by rainfall and food supply, and daily activity is limited by high temperature. The species has entered local and international trade, but remains relatively common even in densely human-populated areas; disturbed areas may have higher population densities due to a lack of predators. *Kinixys spekii* is protected in many National Parks and Game Reserves throughout its wide range. Captive husbandry is recorded, and improved conservation legislation, such as inclusion in nationally protected faunas, is suggested, in addition to ongoing monitoring of native populations and national and international trade.

DISTRIBUTION. — Angola, Botswana, Burundi, Congo (DRC), Eswatini, Kenya, Malawi, Mozambique, Namibia, Rwanda, South Africa, Tanzania, Zambia, Zimbabwe. The species ranges from the savannahs of Rwanda, Tanzania and southern Kenya south to Eswatini and KwaZulu-Natal in South Africa, west to southeastern Democratic Republic of Congo, northern Angola, northeastern Namibia, Zambia, northern Botswana, and Zimbabwe.

SYNONYMY. — *Kinixys spekii* Gray 1863, *Cinixys spekii*, *Kinixys belliana spekii*, *Homopus darlingi* Boulenger 1902, *Kinixys darlingi*, *Kinixys belliana darlingi*, *Testudo procterae* Loveridge 1923, *Malacochersus procterae*, *Kinixys australis* Hewitt 1931, *Kinixys australis australis*, *Kinixys belliana australis*, *Kinixys jordani* Hewitt 1931, *Kinixys youngi* Hewitt 1931, *Kinixys australis mababiensis* FitzSimons 1932, *Kinixys belliana mababiensis*.

STATUS. — IUCN Red List: Not Evaluated (NE); TFTSG Provisional Red List: Vulnerable (VU, assessed 2013); CITES: Appendix II, as Testudinidae spp.

Taxonomy. — Although this species was described by Gray (1863) and recognized by Hewitt (1931) and Loveridge (1936), it was subsequently synonymised with *Kinixys belliana belliana* by Loveridge (1942) and Loveridge and Williams (1957). It was reinstated as a distinct subspecies by Broadley (1981) and recognized as a full species by Broadley (1992, 1993). No subspecies are recognized, but

there is regional genetic variation: Kindler et al. (2012) found that DNA sequences of *K. spekii* from Namibia, South Africa, Zambia, and Zimbabwe were only weakly differentiated, but a sequence from the Democratic Republic of Congo was clearly distinct. In molecular phylogenetic analyses Guillon et al. (2012) and Thomson et al. (2021) found *K. spekii* to be sister to *K. belliana*, but Thomson and



Figure 1. Adult female Speke's Hinged Tortoise (*Kinixys spekii*) from Dinedor Farm, Eswatini, with bright semi-radial carapacial pattern. Photo by R.C. Boycott.

Shaffer (2010) found *K. spekii* to diverge before the sister species *K. belliana* and *K. natalensis*. Such studies have, however, so far included only limited species of *Kinixys* (*spekii*, *belliana*, *homeana*, *erosa*, and either *natalensis* or *zombensis*) within large turtle phylogenies. A molecular phylogeny of all *Kinixys* species is desirable.

Description. — Carapace depressed (shell length to height ratio 2.24 to 2.93), highest point frequently on vertebral one or two; scarcely or not notched in the nuchal region (rarely deeply notched when the nuchal is absent); anterior margin not or only feebly expanded, not reverted, not spinose in young; posterior marginals not expanded, weakly reverted, not serrated, not spinose in young; rear carapace in young sloping more or less steeply, in adults even more so; carapace scutes relatively flat, with well-defined growth annuli (except in old males, which usually have very worn shells). Nuchal scute moderate to elongate in adults (rarely divided or absent); vertebrals five (rarely

four, six, seven or eight), not or only slightly convex, first broader than long in young, variable in adults, second to fifth as broad as or broader than long, second narrower than fifth in adults (or subequal in young), fifth flat in young, more or less convex in adults; costals four, rarely five or six; marginals 10–13, usually 11, and occasionally 14 (Boycott and Bourquin 2000); supracaudal undivided, with the underside narrowed or proximally excavated in both sexes.

Coulson (1988) noted a relatively high proportion of abnormal shield counts (17.9% of 112 specimens) in this species. McMahon (1990) reported on a specimen from Hoedspruit with 7 vertebrals, 6 costals, and 10 marginals on the right hand side. In adults a carapacial hinge develops between marginals 7 and 8, eventually extending between costals 2 and 3; this hinge is not visible in hatchlings and juveniles. Boycott and Bourquin (2000) observed that supernumerary shields occur infrequently in the southern



Figure 2. Adult male Speke's Hinged Tortoise (*Kinixys spekii*) from Mlawula Game Reserve, Eswatini, with zonary concentric carapacial pattern. Photo by R.C. Boycott.



Figure 3. Adult male Speke's Hinged Tortoise (*Kinixys spekii*) from Nyonyane Ranch, Eswatini, with no carapacial pattern, only dark areolae. Photo by R.C. Boycott.



Figure 4. Old adult Speke's Hinged Tortoise (*Kinixys spekii*) from Sarara, Kenya, with faded zonary concentric carapacial pattern. Photo by J. Haureljuk.



Figure 5. Adult Speke's Hinged Tortoise (*Kinixys spekii*), from Lephalale area, Limpopo Prov., South Africa, with zonary concentric carapacial pattern. Photo by V. Loehr.

African population and mostly involve the costals and marginals. In such cases the position of the carapacial hinge can vary.

Front lobe of the plastron is truncate anteriorly, thick, projecting well beyond the anterior border of the carapace in both sexes, not or only moderately notched; gulars paired, usually less than twice as broad as long; pectorals with a moderate median sulcus; two axillaries, of moderate size; inguinal large, usually in contact with sixth marginal, in broad contact with the femoral; hind lobe of the plastron short and truncate, with a very shallow posterior notch. Plastron usually concave in adult males.

Carapace with a concentric or zonary color pattern in juveniles and subadults. This may persist in adult males, but older males often become uniform olive-brown or yellow-brown. In females, the dark brown to black zones tend to break up into short ragged radiations. In adult males the plastron is uniform yellow, or may show traces of a zonary pattern. The head, limbs and tail are usually uniform yellow to light brown, but may be speckled with black.

The largest known male recorded (TM 41761; Maputo Elephant Reserve, Mozambique) had a straight carapace length (SCL) of 181 mm, width 124 mm, and depth of 79 mm; a large female (TM 39412; 10 km S of Kongola Ferry,

Caprivi, Namibia) had a SCL of 198 mm, width 126 mm, and depth of 79 mm. Boycott (2001) recorded a larger female of exceptional size from Dinedor Farm, Eswatini; this specimen (TM 83681), a complete shell, had a SCL of 210 mm, a width of 134 mm, and a depth of 89 mm. Adult females weigh up to 1.5 kg and males usually around 820 g, but in larger specimens may exceed 1.0 kg (Boycott and Bourquin 2000).

The maxillary beak is either weakly to moderately hooked and unicuspid or not hooked; the edge of the jaws are not serrated; the prefrontal scale is large, semi-divided or divided longitudinally; the frontal scale is large and entire; and upper head scales are small and irregular. The forelimb is anteriorly covered with large, unequal, juxtaposed, more or less imbricate, more or less pointed scales, which on the anterior edge form a longitudinal series of 7–10 scales from the elbow to the lateral fifth claw. The thigh is without enlarged tubercles; the heel may or may not have well defined spur-like tubercles and there are four hindfoot claws. The tail terminates in a more or less distinct horny tubercle, often much larger in males.

Distribution. — Ihlow et al. (2019) reviewed the distribution of *K. spekii*, including genetic confirmation and new records. They noted that morphological overlap

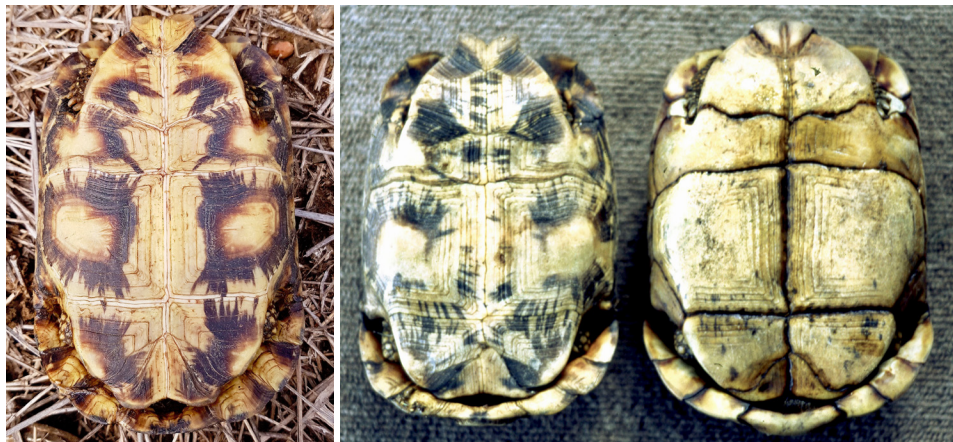


Figure 6. Plastron pattern variation in Speke's Hinged Tortoises (*Kinixys spekii*). Left: Big Bend region, Eswatini. Photo by F. Ihlow. Right: Malindi, Kenya. Photo by S. Spawls.



Figure 7. Juvenile Speke's Hinged Tortoise (*Kinixys spekii*) from Mpumalanga Prov., South Africa. Photo by R.C. Boycott.

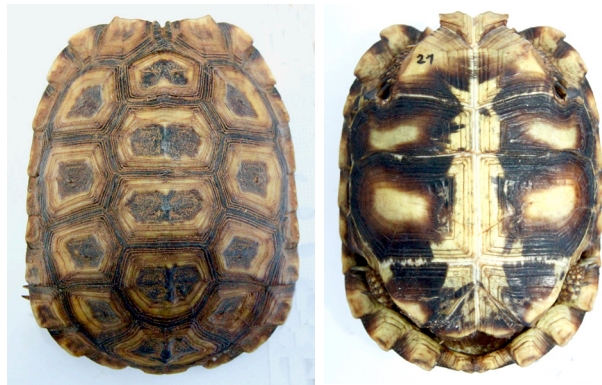


Figure 8. Juvenile Speke's Hinged Tortoise (*Kinixys spekii*) from Alldays, Limpopo Prov., South Africa. Photos by F. Ihlow.

of *K. spekii* occurs with *K. zombensis*, *K. lobatsiana*, and *K. natalensis*, ranging from 2% to 66% misidentification of specimens, respectively, and concluded that genetic confirmation will be needed in future studies of the species.

Kinixys spekii ranges west from the Kenya coast through Tsavo and Ukambani, almost to Nairobi (Kapiti Plains), across northern Tanzania to Ujiji, Kigoma, and southern Burundi, with isolated records from the southern Kerio Valley, Akagera in Rwanda, and the Ruzizi Plain (Spawls et al. 2002, 2018). The species occurs in eastern Democratic Republic of Congo, northern Angola (Ceríaco et al. 2014), Zambia, and Malawi to northern Botswana and northeastern Namibia, Zimbabwe, and western and coastal Mozambique (Ihlow et al. 2019) to northeastern South Africa and Eswatini.

The southernmost limit of the species appears to be Abercorn Drift in the extreme northern KwaZulu-Natal province of South Africa (Bourquin 2004). This is based on a shell (TM78154) that could have been transported by a non-chelonian agency (Bourquin 2004) or possibly washed down the Great Usuthu River. It has been suggested that the river could represent a geographical barrier to the species (Boycott 2014). Two genetically confirmed records of *K. spekii* from the St. Lucia area and Mfolozi mouth have been documented by Ihlow et al. (2019). As these localities

are far removed from the recognized distribution of the species in South Africa and Eswatini (see Boycott and Jacobsen 1988; Broadley 1993; Bourquin 2004; Boycott 2014), it is possible that they could be translocations or escaped pets. Consequently, further verification through the acquisition of additional material is required. Many of the field observations reviewed below were made at the Sengwa Wildlife Research Area (SWRA) in Gokwe district, northwest Zimbabwe, roughly in the center of the species' range.

Habitat and Ecology. — In East Africa, *K. spekii* is found in savannah and coastal thicket from sea level to 1600 m a.s.l., often in rocky areas (Spawls et al. 2002). In southern Africa, it is found in moist savannah woodlands, especially Miombo and Mopane, but extending into drier *Acacia* and *Commiphora* deciduous woodland and thicket in the northeastern part of its range. Hailey and Coulson (1995) recorded *K. spekii* in 13 of the 16 vegetation types present in the SWRA, Zimbabwe, with the greatest numbers in *Brachystegia-Julbernardia* mixed woodland (Miombo), *Colophospermum mopane* woodland (Mopane), grassland with *C. mopane* scrub, *C. mopane* – *Combretum* – *Erythroxylum* mixed woodland and bushland, and *Julbernardia* – *Vellozia* wooded and bushed grassland. There was high habitat niche overlap (O) with the sympatric Leopard Tortoise, *Stigmochelys pardalis* ($O = 0.76$), the main difference being that *K. spekii* used open riverine vegetation (grassland) less.

Growth, Maturity, and Reproduction. — Midline plastron length (MPL) was used as the standard measure in field studies because the carapace is jointed and straight carapace length (SCL) is therefore variable. For comparison, SCL can be calculated from MPL using the factor 1.165, which was determined from 15 dried shells (Hailey and Coulson, unpubl. data); the range was 1.13 to 1.20, both extremes being for adult females. Coulson and Hailey (2001) estimated (from the sizes of the smallest reproductively active individuals) that *K. spekii* at the SWRA became mature at a MPL of 14 cm (estimated SCL 163 mm) or 9 years old in females and 12 cm MPL (SCL 140 mm) or 7 years old in males. Sex could be distinguished in individuals with a MPL of 10 cm or more. There was sexual size dimorphism with females on average 1.4 cm longer (by MPL) and 1.43 times heavier than males. The mean sizes (MPL) of mature *K. spekii* at SWRA were 152 mm in females and 138 mm in males; maximum sizes were 172 mm in females and 159 mm in males. These values represent sexual size dimorphism of 10% and 8%, respectively, similar to the 9% for SCL (Coulson and Hailey 2001). The mean mass of mature tortoises was 752 g in females and 524 g in males. The growth rate of juveniles was 15 mm MPL/yr, equivalent to about 19 mm SCL/yr (Coulson and Hailey 2001).

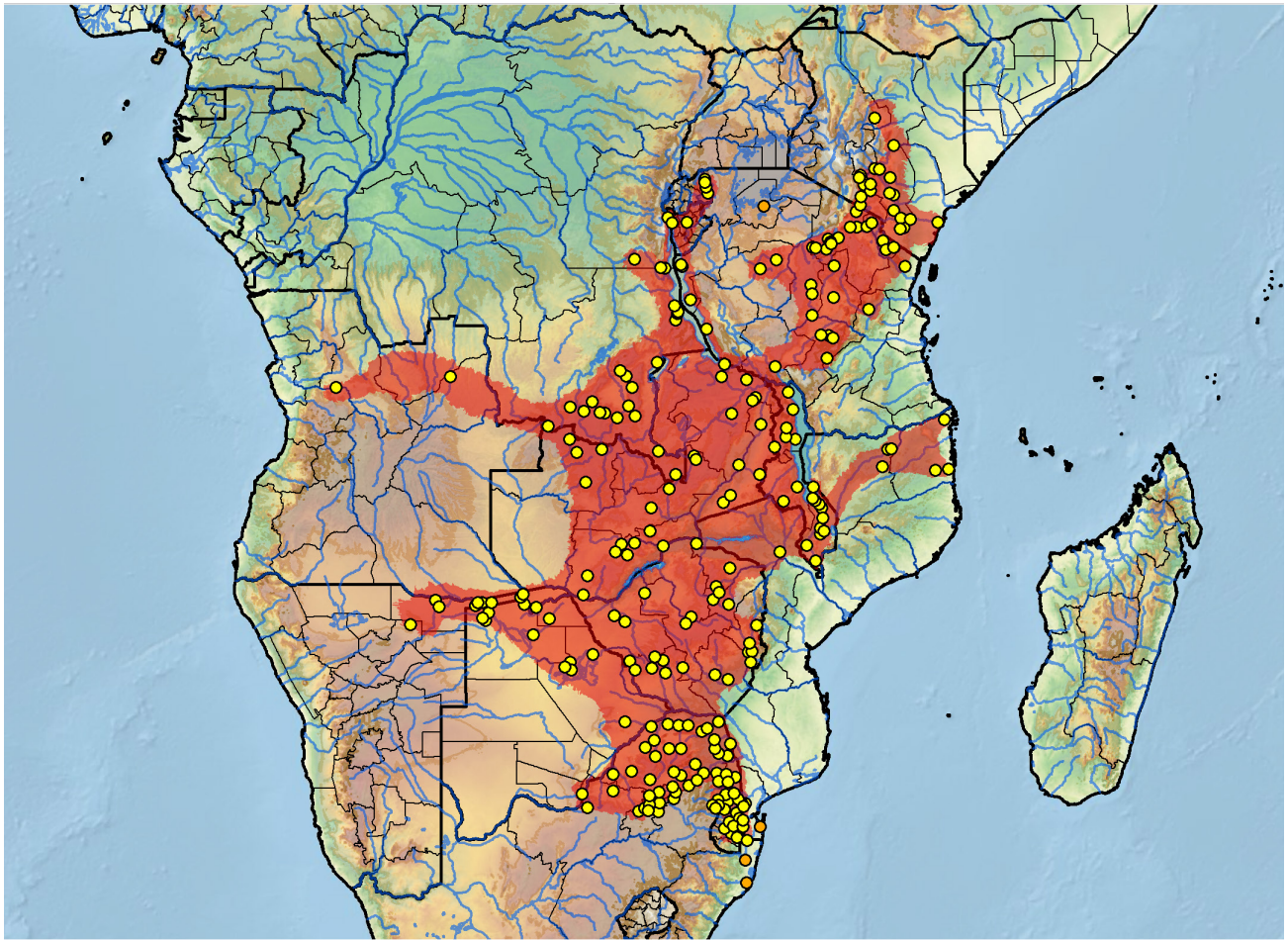


Figure 9. Distribution of *Kinixys spekii* in Africa in Angola, Botswana, Burundi, Congo (DRC), Eswatini, Kenya, Malawi, Mozambique, Namibia, Rwanda, South Africa, Tanzania, Zambia, and Zimbabwe. Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992), Broadley (1993), Boycott (2014), TTWG (2017, 2021), Ihlow et al. (2019), and authors' more recent data; orange dots = possible trade, introduced, or misidentified specimens; red shading = presumed native historic indigenous range. Distribution based on GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al. 2009; TTWG 2017, 2021) and adjusted based on authors' data.

Nesting occurs from November to April in the southern part of the species' range. More than one clutch may be laid per year (Boycott and Bourquin 2000). Normally two or three eggs (but up to a maximum of six) are laid; the mean for eight clutches was 3.75 eggs, with a tendency for larger females to lay larger clutches ($r^2 = 43\%$) (Hailey and Coulson 1997). Eggs are oval, measuring 33–47 x 28–34 mm, and hatch after about a year. The mean egg size for 10 clutches was 40.8 x 30.7 mm and 23.0 g (range 20–28 g), relatively large for a tortoise of this body size (egg mass relative to spent body mass 2.44%; Hailey and Coulson 1997), as in other tropical chelonians (Ewert 1979). The relative clutch mass calculated from clutch size and relative egg mass was 9.15%. Hatchlings measure 30–50 mm CL, and have been found from November to April. Nolan (2006) described captive breeding in Europe and documented a modal clutch size of 3 eggs, with an average egg size of 41 x 34 mm, and one egg hatching after 220 days at 29°C.

Hailey and Coulson (1997) described nesting by a female *K. spekii* thread-trailed over a six-week period. The female moved 100 m outside of her 5.5 ha home range to nest, with longer than typical daily movement distances (DMD) from and back to the home range at the start (5 February) and end (8 February) of the nesting sortie. She dug two abandoned nests on 6 February, and one abandoned and the completed nest on 7 February. Nest locations were within a 30 m² area of bushes and small trees, all under tree canopies. Nesting was in the late afternoon and evening, the successful nest being 10 cm deep and 4.5 cm diameter, with 3 eggs (average 41 x 32 mm, 25 g) in an 8 cm wide sock-shaped chamber. Nest temperatures monitored on one day ranged from 23.5–27°C, while the same depth in soil exposed to the sun reached 36°C. Scoones (1986) noted nesting at dusk and during the night in captivity.

Home Range and Movements. — The long-term home range, based on the minimum convex polygon method for



Figure 10. Habitats of Speke's Hinged Tortoise, *Kinixys spekii*, in Limpopo Province, South Africa. *Left:* Central Sandy Bushveld near Vaalwater, with *in-situ* tortoise. *Middle:* Musina Mopane Bushveld near Alldays. *Right:* Soutpansberg Mountain Bushveld at Medike Mountain Reserve, with *in-situ* tortoise. Photos by F. Ihlow.

mapped mark-recapture records, was 3.1 ha at the SWRA, Zimbabwe (Hailey and Coulson 1995). The short-term home range, based on movements of thread-trailed tortoises over week-long periods, was 1.9 ha, with a mean DMD of 172 m (Hailey and Coulson 1996a). That study was conducted during a period of high temperatures; in cooler more typical conditions the modal DMD was 200–400 m, with daily movements up to 1171 m (Hailey and Coulson 1996b). Movements were longer than those of the similarly-sized *Testudo hermanni*, but followed a similar geometric pattern; there was no sign of the wider-scale movements to sodic soils of the sympatric *S. pardalis* (Hailey and Coulson 1996a). Bertram (1979) recorded a similar sized home range of 1.9 ha in a female (that would now be assigned to *K. spekii*) radiotracked for two years, with most movements within a 0.24 ha core area. Lambiris et al. (1989) recorded displacements between captures of 80–820 m, suggesting a larger home range in this area of lower predation pressure (see below).

Kinixys spekii utilizes substantial refuges that provide both shelter from the environment and protection from predators. Hailey and Coulson (1995) found that 66% of the 50 refuges identified in thread-trailed *K. spekii* were mammal burrows, mostly of the springhare *Pedetes capensis* and the antbear *Orycteropus afer*. The former especially are deep and long (Butynsky and Mattingly 1979) and provide excellent protection for a small tortoise. Other refuges were under felled trees (22%) or in scrub thickets (12%). Bertram (1979) also noted the use by his radiotracked female of four holes under overhanging rocks in a kopje on the edge of the home range.

Population Density, Survival, and Predation. — Two mark-recapture studies have been conducted on *K. spekii*, in areas of Zimbabwe differing notably in the abundance of predators, which provide an instructive contrast.

Lambiris et al. (1989; preliminary analysis also reported by Scoones 1986) marked 83 *K. spekii* in the 58 ha Boulton Atlantica Research Station over 18 months from 1979–1981. This site is an ecological research station on the Zimbabwe highveld (1420 m a.s.l.) among large commercial farms 23 km from Harare. Thirteen tortoises were recaptured, giving a population estimate of 130 individuals, at a density of 2.25/ha. This was assumed by the authors to be a low density, and tortoises were infrequently seen during previous general field work at the site from 1965–78 and by Scoones in 1985–86 (Lambiris et al. 1989). The density is, however, comparable to many recorded for Mediterranean tortoises (e.g., Bertolero et al. 2011), and probably reflects a similar situation with a low level of predation, concentrated on juveniles. Scoones (1986) noted that a fire had apparently not affected this population of *K. spekii*, and Lambiris et al. (1989) recorded few natural predators in the reserve, with only the Secretary Bird (*Sagittarius serpentarius*) and Monitor lizards (*Varanus niloticus* and *V. albigularis*) present, both observed as predators only of hatchlings and juveniles. There were no records of mammal predators in the area. This situation is thus equivalent to that of a Mediterranean tortoise population, with significant predators having been removed during decades of commercial farming.

There was a 2.6:1 female-biased sex ratio, which was attributed to differences in habitat utilization and sampling



Figure 11. Habitats of Speke's Hinged Tortoise, *Kinixys spekii*, in Kenya. *Left:* Low-altitude dry savanna along Galana R., 300 m a.s.l., Tsavo East National Park. *Right:* Medium to high-altitude grassland on the Kapiti Plains, 1600 m a.s.l. Photos by S. Spawls.

between males and females, with seasonal movements between woodland, wooded grassland, and grassland. Females were more associated with grassland, where they were apparently easier to find, perhaps due to nesting in open areas; all juveniles were also found in grassland or woodland/grassland (Scoones 1986, Lambiris et al. 1989).

Coulson (1988) and subsequent papers, unfortunately published posthumously following his untimely death in a plane crash while counting elephants in 1994, studied *K. spekii* at the SWRA in central Zimbabwe from 1982 to 1988. This is an area of lowveld (800–950 m a.s.l.), the largest area in Africa devoted solely to ecological research (described by Cumming 1975, 1983), and with the intact indigenous African fauna including many potential predators of tortoises. A total of 109 *K. spekii* were marked and 51 dead tortoises collected, of which two had been marked alive. A further 50 *K. spekii* were marked from 1991–94, of which only two were recaptures from the earlier period. There was an even sex ratio. Most *K. spekii* were from two 1 km² grid squares close to the office area, in which 66 individuals were marked, 21 of which were recaptured. The analysis for this 2 km² area gave an estimate of 38 individuals, i.e., a density of 0.16/ha (Coulson and Hailey 2001). This is more than an order of magnitude lower than the density estimated in the highveld, a difference which may be readily explained by the number of potential predators in the SWRA. These are too numerous to list but include 8 species of Viverridae, 6 Felidae, 18 Ciconiiformes, 35 Falconiformes, and many other species of reptiles, birds and mammals that are possible predators of juvenile or adult tortoises. The species most likely to attack adult *K. spekii* include Chacma Baboon *Papio ursinus*, the Jackal *Canis adustus*, Ratel *Mellivora capensis*, Spotted Hyena *Crocuta crocuta*, Leopard *Panthera pardus*, three eagles, the Ground Hornbill; the Secretary Bird was also present and was the only species actually observed to attack tortoises at the SWRA (Coulson and Hailey 2001), although other

raptors are known to prey on tortoises in Zimbabwe (Gargett 1990). Lion *Panthera leo* is also a known predator of *K. spekii* (Spawls et al. 2018).

The identification of the SWRA as a low-density, high-predation population of *K. spekii* was supported by evidence of survival and mortality. Survival rates of larger individuals (excluding juveniles) were estimated in three ways, from mark-recapture, age at death of dead tortoises, and mean age of live individuals. These gave a mean annual survival rate of $S = 0.74$, much lower than for a Mediterranean tortoise of similar size, for example, which would have $S = 0.90$ (Bertolero et al. 2011). The annual mortality rate of *K. spekii* was thus at least twice that of other tortoises of similar size, and readily accounts for the low population density; no *K. spekii* at the SWRA reached advanced age sufficient for the growth rings to be worn away. A similar conclusion is reached from the dead *K. spekii*. Most of these showed some evidence of predation; 77% had physical damage, increasing to 89% including indirect evidence from location (bodies grouped near mammal burrows). Damage took two characteristic forms (figured by Coulson and Hailey 2001): damage to the front or rear of the plastron associated with chew marks or location in groups near mammal burrows attributed to mammalian predators. Damage as holes punched through the carapace and/or plastron was attributed to the Ground Hornbill (*Bucorvus leadbeateri*), which can penetrate the carapace with its powerful bill. The bones of the shell are much more fragile than those of *K. belliana*. The hinged carapace had obviously been ineffective in the dead damaged *K. spekii*, although possibly useful against smaller predators such as viverrids that would attack the limbs.

Behavior and Thermoregulation. — *Kinixys spekii* individuals generally feed in the early morning and evening, when it is cool, seeking cover during the hottest part of the day. During the dry season they are dormant in rock crevices, inside hollow logs, holes in termitaria, or in

burrows excavated under tree roots or rocks. They tend to spend the dry season in woodland, which provides more cover, but move into the woodland/grassland ecotone, which provides more food, during the rainy season (Scoones 1986). When alarmed, this species withdraws its head with a hiss and closes the forelimbs over it, simultaneously curling the tail tightly under the shell and withdrawing the hind legs, so that when the rear portion of the carapace is pulled down, only the soles of the hind feet are exposed. If picked up, it will react by defecating copiously and odoriferously. It may also snap its jaws and flail its limbs. Combat between males occurs at the beginning of the rainy season. They fight by ramming each other until the weaker individual is overturned or driven off. When mating, the male climbs onto the back of the female, bracing himself with his forelimbs while thrusting his tail beneath the rear edge of her carapace. Observations in captivity show that males regularly follow females prior to mating (Scoones 1986). Copulation is accompanied by continuous wheezing gasps from the male, while the female seems quite disinterested.

Hailey and Coulson (1999) and several game scouts followed five thread-trailed *K. spekii* continuously for four days during a six-week period (January to mid-February), recording their behavior at 5-min intervals from 0600 to 1900 hrs. Tortoises were active in all hours during this period (and sometimes after 1900 hrs), so that the population daily activity period exceeded 13 hrs. Individuals averaged 8.2 hrs per day of surface activity, between emergence from and retreat into overnight refugia. This activity comprised, on average, 2.0 hrs moving, 0.9 hrs feeding, 0.1 hrs courtship, and 5.2 hrs stationary above ground, including in surface refugia. This thread-trailing method is a useful technique for measuring time budgets of tortoises; those based on sighting data alone were shown to be highly biased by the difficulty of finding inactive tortoises. There was a strongly significant correlation ($r^2 = 76\%$) between the number of records of behavioral activity (moving, feeding, and courting) and the DMD. The total of 2.1 hrs moving (including courting) per day is, surprisingly, more than most lizards, including some species of the notably active genus *Varanus* (Hailey and Coulson 1999).

Additionally, Hailey and Coulson (1996b) analyzed the movements of the five individual *K. spekii* thread-trailed over six weeks, in relation to weather and thermal environment. The mean DMD of 200–400 m was much greater than for a herbivorous tortoise of similar size (80 m/day in *Testudo hermanni*; Bertolero et al. 2011). The DMD was negatively correlated with maximum daily shade air temperature (T_a), indicating a thermal constraint on activity in *K. spekii*. The DMD was not, however, significantly related to minimum T_a or current or past daily rainfall levels, the presence of rain, or humidity. The latter result contrasts with previous reports that activity or emergence

in *K. spekii* was associated with rainfall or humidity (Bertram 1979; Scoones 1986; Broadley 1989; Lambiris et al. 1989), although those do not separate seasonal from daily differences in activity (see below). It is also possible that tortoises emerge in response to rainfall but this does not lead to increased activity in terms of DMD, or that *K. spekii* use more open areas in the cool conditions during or after rainfall and are thus more noticeable.

There was a midday inactivity period of increasing length as maximum T_a exceeded 29°C. Physical models suggested that there was a risk of overheating within about one hour in this small tropical species, which has a relatively low mean field body temperature (T_b) of 27.0°C. Salivation occurred at high temperatures and was an effective mechanism to stabilize T_b by evaporative heat loss, preventing the tortoise from reaching critical levels. The mean T_b at which salivation occurred was 38.4°C, comparable to other tortoise species; there was thus a wide safety margin between mean field T_b and overheating (Hailey and Coulson 1996b). Burrow refuges had temperatures of 23–26°C throughout the day, and were always available as thermal sinks. Models showed that individuals were in no danger of overheating on cloudy (cool) days, but exposed models rapidly exceeded salivation temperatures on hot days, reaching 50°C or more within an hour.

The annual activity season of *K. spekii* was short, with 95% of sightings (by game scouts over the period 1982–91) in the four wettest months of December to March. Monthly activity levels were correlated with rainfall but not with temperature or humidity. Inactivity in the winter and the following hot dry season was due to low food availability, not to low temperatures. The overall pattern is that seasonal activity is related to precipitation, constrained by low rainfall, but within the activity season the level and pattern of daily activity is related to thermal conditions, constrained by high temperatures (Hailey and Coulson 1996b). There was little individual variation of DMD in *K. spekii*, in contrast to the tropical forest tortoises (*Chelonoidis denticulatus* and *C. carbonarius*) followed by Moskovits and Kiester (1987). This is a reflection of the more severe environmental conditions for a small tortoise in seasonal savannah habitats compared to the benign conditions of the rainforest.

Within the active season, the pattern of body temperatures differed between cool and hot days (Hailey and Coulson 1996c). Tortoises had a lower T_b when starting daily activity (mean $22.8 \pm 1.4^\circ\text{C}$; \pm S.D.), but there was no significant variation in T_b for other types of activity, with a mean of $27.1 \pm 3.1^\circ\text{C}$. There was no difference between males and females. On hot days, with maximum $T_a > 29^\circ\text{C}$, tortoises heated rapidly in the morning, were in shaded retreats at midday, and emerged in the late afternoon and then had stable body temperatures. On cool days the overall

mean T_b was the same as on hot days, but achieved by a slower increase during the morning and a decrease after midday, with no inactivity period (Hailey and Coulson 1996c). Tortoises began to move rapidly and seek shade when T_b exceeded 32°C. Detailed comparison of T_b with temperatures of null models showed that tortoises were thermoregulating by choice of cooler microenvironments on hot days, not merely by stopping activity when they got too warm. *Kinixys spekii* did not bask in the lowveld environment of the SWRA, but was able to maintain similar body temperatures in the highveld (Harare, 1500 m a.s.l.; mean T_b 27.6 ± 3.0°C) compared to the lowveld (SWRA, 27.0 ± 3.1°C), although the environment of the highveld is about 5°C cooler throughout the year. This pattern contrasts with *S. pardalis*, which is not found naturally in the highveld and which has lower body temperatures when held in captivity there (Hailey and Loveridge 1998). Lambiris et al. (1989) found diurnal activity in *K. spekii* from 0700–1730 hrs in the highveld, with a peak from 1100–1400 hrs, so that activity was unimodal in the middle of the day.

The geographic range of *K. spekii* overlaps that of six other species of *Kinixys*, indeed with all species in the genus except *K. nogueyi* (*sensu* Kindler et al. 2012). Behavioral and ecological interactions with congeners are unstudied but would be of considerable interest, as *K. spekii* is apparently sympatric with more similar species than any other tortoise, including *K. belliana* in Rwanda (Hinkel 1992).

Diet. — These tortoises are truly omnivorous, with vascular plants making up less than half of the food intake, and part of that is fruit rather than foliage. In this they (and other species of *Kinixys*) differ from other tortoises, which are predominantly herbivorous, though sometimes taking a small proportion of other types of food. Hailey et al. (1997) quantitatively analysed 77 fecal samples from *K. spekii* in the SWRA, correcting intake for differences of digestibility and recognizability among food types. The diet composition by wet mass was 47% vascular plants, 41% fungi, and 12% invertebrates. The most frequently observed items were monocotyledon leaves and stems (grasses), found in 92% of samples, followed by dicotyledon leaves and stems (69%). The high prevalence of grass material is probably due to its indigestibility and ease of recognition rather than high intake. Lambiris et al. (1989) also noted high incidence of fragments of grass (*Hyparrhenia*) in feces of *K. spekii*, and unrecognizable (finely chewed) dicotyledon leaves. Plants identified in the diet at the SWRA included Graminae, Convolvulaceae, Acanthaceae, Vitaceae, Leguminosae, Liliaceae, and the fern *Ophioglossum* in fecal samples (Hailey et al. 1997), and *Brachiaria nigropedata* (Graminae), *Ipomoea senensis* (Convolvulaceae), *Rhinacanthus gracilis* and *Duosperma crenatum* (Acanthaceae), *Cyphostemma*

lovemorei (Vitaceae), *Zornia glochidiata* (Leguminosae), and *Chlorophytum colubrinum* (Liliaceae) from direct field observations of feeding (Hailey et al. 2001). Seeds and fruits were identified in 19% of the fecal samples, excluding grass seeds which were probably ingested accidentally (and always associated with grass leaves or stems). Other seeds and fruits were often (7 of 15 cases) not associated with foliage in the feces, and presumably consumed deliberately; they included the tree *Erythroxylum*, Convolvulaceae (*Ipomoea*), and Cucurbitaceae (Hailey et al. 1997, 2001).

Lambiris et al. (1989) noted identifiable fragments of the mahobohobo fruit from the tree *Uapaca kirkiana* in the feces. In an unreported experiment similar to the food selection trials on millipedes described by Hailey et al. (2001), seven individually-housed *K. spekii* were given the choice of three fruits each of both *U. kirkiana* (also known as mujanje, mazhanje, or sugar plum) and *Parinari curatellifolia* (muchakata or mobola plum). The proportion of the edible parts of the fruits eaten was recorded after one day. Both types were eaten but *Parinari* was significantly preferred, with an average 1.6 ± 1.2 (± S.D.) fruits consumed compared to 0.2 ± 0.3 for *Uapaca* (ANOVA of log-transformed values to equalize variances, $F_{1,12} = 5.7$, $P = 0.035$). The low consumption of *Uapaca* may be explained by their fruits having a hard shell. *Uapaca* and *Parinari* fruits have large seeds that are not likely to be ingested, so their contribution to the diet may be underestimated. Other fruits consumed by *K. spekii* have small seeds, which may be found in large numbers in the feces. In the case of Cucurbitaceae such as the bitter melon *Cucurbita pepo* at SWRA, each fruit has many small seeds so the presence of multiple seeds in feces (two samples had 19 and 42 seeds, respectively) may represent extended feeding on a single fruit (Hailey et al. 2001). The other species represented by multiple seeds was the tree *Erythroxylum zambeziacum*, which has small fruits (ca. 10 x 4 mm) with a single seed. In this case multiple seeds represent an extended period of foraging for fallen fruits (Hailey et al. 2001), as was observed in a thread-trailed individual (Hailey and Coulson 1997).

The second largest component of the diet at SWRA was fungi, making up 41% of consumption by wet mass, and identified in 49% of fecal samples (Hailey et al. 1997). Field observations of feeding included the genera *Agaricus* and *Volvariella* (Agaricaceae), *Pluteus* (Amanitaceae), *Laccaria* (Tricholomataceae) and *Clavaria* (Clavariaceae) (Hailey et al. 2001). Captive *K. spekii* given a three-way choice in cafeteria trials consumed mostly fungi (mushrooms), making up 83% by wet mass, with 13% foliage (kale leaves) and 4% invertebrates (millipedes) (Hailey et al. 1997). Males notably ate a higher proportion of fungi than females in these trials (97% vs. 75%), and were more likely than females to have fungi in field fecal samples (68% vs.

36%), both sexual differences being significant (Hailey et al. 1997). Fungi provide energy but are deficient in other nutrients (see below), and the lower intake of fungi by females may be due to their greater needs for protein and/or calcium for egg production. It is possible that the importance of fungi in the diet limits the activity season of *K. spekii*, which was much shorter than that of sympatric *S. pardalis* in the SWRA, with 75% of sightings being in two months, December and January. This is also the peak season for fungi, as indicated by the timing of mushroom poisoning in humans in Zimbabwe, with 66% of cases in December and January (Nhachi 1996). Scoones (1986) also noted that *K. spekii* was traditionally associated with the appearance of mushrooms, its preferred food. Elliott et al. (2019) made the interesting suggestion that eating fungi may enhance the value of a fruit-eating, seed-dispersing symbiosis between *K. spekii* and trees in Miombo woodland. Many of the common trees, including *Brachystegia*, *Julbernardia*, and *Uapaca*, are ectomycorrhizal, these making up 70% of the basal area of Miombo woodland (Högberg and Pearce 1986, Mwamba 1995). Elliott et al. (2019) noted that the ectomycorrhizal symbionts probably include many of the fungi eaten by *K. spekii*, so that tree seeds passed in the feces would benefit from fungal inoculants, as well as dispersal and fertilizer.

These tortoises also feed on a variety of invertebrates, especially millipedes, which are chased, pinned to the ground, and manipulated with the forelegs, and torn to pieces by ingestion. Similar behavior occurs in other carnivorous chelonians such as *Chelydra serpentina* and *Macrochelys temminckii*, but also in herbivorous tortoises feeding on plants, and cannot be regarded as a specialized behavior pattern (Hailey et al. 2001). Snails (small *Achatina* and the introduced *Helix*) are eaten after the shells have been broken. *Kinixys spekii* also scavenges, devouring dried corpses of amphibians and other small animals, as well as small bone fragments. Invertebrates were estimated to make up 12% of the diet by wet mass, mostly millipedes (67% by volume) and beetles (33%), with other taxa representing only 0.1% (Hailey et al. 2001). Millipedes were found in 61% of fecal samples, and beetles in 49% (Hailey et al. 1997). Millipedes represented in the feces had an average volume of 0.9 ml, and beetles (excluding small specimens likely taken secondarily in fungi, for example) an average volume of 1.4 ml. Beetles identified were mostly Tenebrionidae (37 specimens of nine species, including the genera *Alphitobius*, *Dichtha*, *Micranterius*, *Psammodes*, and *Vutismus*), with three specimens of two species of Meloidae (*Mylabris*) and Scarabidae (Hailey et al. 2001).

Mean prey volume was 1.0 ml, equivalent to a mean relative prey mass (RPM) of 0.19% of tortoise mass, which seems small but is similar to the value for many

insectivorous lizards (Hailey et al. 2001). In captive trials, *K. spekii* preferentially attacked moving millipedes at or just behind the head, but feeding was otherwise unspecialized. In three cases, however, millipedes were ingested spaghetti-like while being crushed along their length, similar to the behavior of a box turtle ingesting a snake (Hutchison and Vinegar 1962). Most (34/37) individual *K. spekii* tested in captivity consumed millipedes, especially females which were more likely to consume the whole millipede than males, whereas none of 10 *S. pardalis* did so (Hailey et al. 2001). The noxious secretions of millipedes (including *Alloporus* and *Bicoxidens* consumed in captivity) did not prevent ingestion by *K. spekii* (Lambiris et al. 1989; Hailey et al. 2001). Handling time was strongly correlated with RPM ($r^2 = 67\%$), and depended on behavior of both tortoise and millipede. Ingestion was faster when the millipede was consumed head-first; not (as in snakes consuming vertebrates) because of reduced obstruction from limbs, but because the millipede was then unable to form a tight coil (Hailey et al. 2001). Ingestion was also faster when the millipede formed a flat coil, leaving the back exposed, compared to a spiral coil which was hard for the tortoise to consume. The maximum size of millipede that could be ingested had a RPM of 2.3%. The profitability (food intake / handling time) was maximum at a RPM of 0.2%, similar to the mean value estimated to be consumed in the field (0.19%). This similarity is, however, probably fortuitous. Theory suggests that *K. spekii* should consume all suitable invertebrate prey within the usable range (RPM 0.01–2%), and not select any on the basis of profitability, as handling time is a small proportion of total foraging time (Hailey et al. 2001).

Energetics. — The omnivorous genus *Kinixys* has presumably evolved from an herbivorous ancestor in the otherwise predominantly herbivorous Testudinidae; adaptation to an omnivorous diet has had the consequence of decreased ability to digest vascular plants (Hailey 1997). *Kinixys spekii* has a relatively short colon, giving fast digestive throughput to feces and low digestibility of plant material as compared to *S. pardalis*. In particular, *K. spekii* has a low ability to process coarse vegetation such as grass, and it does not routinely ingest grass in large amounts even when no other food is available (Hailey 1997). The importance of both invertebrates and fungi in the diet suggests that *K. spekii* may be able to digest chitin, which is present in fungal cell walls as well as arthropod exoskeletons. Chitinase is not present in herbivorous tortoises (Jeuniaux 1961), which rarely consume fungi (Hailey et al. 1997).

Kinixys spekii displays true diet mixing, rather than merely making up the balance when the preferred food is limited, as demonstrated in choice and digestion experiments using fungi (mushrooms), foliage (kale

leaves), and invertebrates (*Alloporus* millipedes) (Hailey et al. 1998). Tortoises feeding *ad libitum* on three pure diets had a digestible energy intake greatest on fungi, lower on leaves, and least on millipedes (69, 42, and 31 kJ/g/d, respectively). In paired cafeteria tests, tortoises took mostly the food giving highest digestible energy intake, but in each case took a proportion (9–27% by wet mass) of food giving a lower energy intake. Diet mixing was not due to interactions between food types during digestion, as the mixture of leaves and invertebrates gave a significant negative associative effect, i.e., lower digestibility than predicted from arithmetic combination of the pure diets. This negative effect was likely due to the mixed diet passing through the gut at the same rate as a pure leaf diet, more rapidly than the pure millipede diet, so that the millipede component was digested less completely when in the mixture (Hailey et al. 1998). The gut passage time (for recovery of 50% of markers in feces) was 5 days for fungi and leaves, and 9 days for millipedes.

The pure diets varied widely in terms of intake by wet mass, ranging from 10 g/kg/d for millipedes to 54 g/kg/d for fungi. In contrast, the intake of dry mass was very constant, at 3–4 g/kg/d, for all pure diets and for the mixed diet, suggesting that the digestive system is limited by processing of dry mass, irrespective of diet composition (Hailey et al. 1998). *Kinixys spekii* has a relatively low body temperature in the field; keeping tortoises at constant 30°C increased their intake from a mean of 3.6 to 5.0 g/kg/d of dry mass. The main limitation of food intake was therefore the ability to digest food, especially dry mass, rather than ingestion and handling time. Intake of leaves or millipedes reduces the intake of fungi by an equivalent amount when expressed as dry mass. The mixed diet observed in the field is therefore not just opportunism, nor selection for a single nutrient, but for the need to balance energy intake (optimally provided by fungi) with foods providing other nutrients (Hailey et al. 1998). Fungi are an inadequate diet, lacking micronutrients; they do not provide a complete protein source, and have a low sodium:potassium ratio, and very low calcium content. Invertebrates are therefore added to give high quality animal protein, calcium, and a high sodium:potassium ratio (Hailey et al. 2001).

Metabolic rate (oxygen consumption) may be elevated for 3–4 days after a single meal, peaking when most food is in the stomach rather than the intestines. The elevated metabolism represents a substantial proportion of the energy absorbed from the food; 16%, 21% and 30% for diets of fungi, vascular plant leaves, and millipedes, respectively, but equal to 0.8 L O₂/g protein in each case (Hailey 1998). This specific dynamic action doubled when continuously feeding on leaves (to 42% of the absorbed energy), and was therefore due to the cost of assimilation of protein, not to a cost of gut up-regulation (as that would cause a fall in

subsequent meals). The inclusion of invertebrates in the diet may thus have metabolic costs, although beneficial in terms of protein intake.

Kinixys spekii may be dormant for 7–8 months per year in Zimbabwe, in winter (April to August) and the following hot dry season (September to October or November). Dormant *K. spekii* had reduced metabolic rate (oxygen consumption) at a broad range of temperatures from 10–25°C, compared to individuals measured in the active season or controls kept active (by providing food) in winter (Hailey and Loveridge 1997). Metabolic rate was reduced on average to 59% of active season levels, and at its lowest to just under half, similar to other hibernating reptiles, showing this to be a true physiological adaptation rather than merely inactivity. The thermal environment of *K. spekii* in winter and the hot dry season is benign in terms of lethal temperatures, rarely going below 20°C at the SWRA, but presents a challenge in terms of high energy costs due to the protracted length and high temperatures involved (Hailey and Loveridge 1997). Lambiris et al. (1989) found *K. spekii* in a very torpid state when removed from old antbear burrows in winter.

Parasites and Epibionts. — Lambiris et al. (1989) recorded *Amblyomma* ticks on *K. spekii* and small nematodes in their feces, both of which have also been observed at the SWRA.

Population Status. — Due to its small size, cryptic coloration and preference for a moist savannah habitat, *K. spekii* often escapes observation and remains relatively common even in densely populated areas. A 12-year study at SWRA, Zimbabwe, showed a population density of 0.16 tortoises per hectare and a high mortality rate due to predation by mammalian and avian predators (Coulson and Hailey 2001). Lambiris et al. (1989) recorded a population density of 2.2 *Kinixys spekii* per hectare in Zimbabwe in habitat without major predators.

Threats to Survival. — *Kinixys spekii* is collected and consumed by humans throughout most of its range, and has been since the Stone Age (Broadley 2007). There is some local trade in East Africa; Wambugu et al. (2010) bought 37 adults from a professional licensed provider for a laboratory study. There is also a low level of international trade; Cheung and Dudgeon (2006) listed *K. spekii* from turtle markets in Hong Kong, where it featured in the pet trade only (other species of *Kinixys* also entered the food trade, which was ten times greater than the pet trade). More than 1500 *K. spekii* were exported from Africa from 2007–12, almost 80% of them from Mozambique (CITES Trade Database 2012, in Mifsud and Stapleton 2014). Tortoises, possibly including *K. spekii*, have limited use in traditional medicine in South Africa (Simelane and Kerley 1997), and *K. spekii* has been used as a laboratory model in veterinary studies (Wambugu et al. 2010, Dahlin et al. 2012).

Erasmus et al. (2002) identified *K. spekii* as susceptible to climate change in South Africa, being one of the species with a predicted > 50% range change (shift and contraction) after global warming (mean 2°C temperature increase and increasing aridity). The South African distribution is, however, at the edge of the species' geographic range, and the extensive change in this peripheral area is not likely to be matched over the whole range. Mortality in electric game fences is a possible problem, especially if *K. spekii* becomes restricted to National Parks and Game Reserves. A literature survey by Beck (2010) noted mortality of *K. belliana* (which may have included *K. spekii*) in electric game fences, although less frequently than *K. lobatsiana*. This mortality is readily soluble by raising the height of the lower fence wire to 25 cm (Beck 2010).

Conservation Measures Taken. — The species is protected in many National Parks and Game Reserves throughout its wide range (e.g., Caro et al. 2011), including Amboseli and Tsavo in East Africa (see Spawls et al. 2002) and Kruger and Hwange in southern Africa. Branch et al. (1995) list *K. spekii* as present in 16 major reserves in southern Africa; ten in South Africa and Eswatini and six in Zimbabwe.

Although the species has not yet been formally assessed for inclusion on the IUCN Red List, the IUCN SSC Tortoise and Freshwater Turtle Specialist Group provisionally assessed the species as globally Vulnerable based on a workshop of experts convened in Togo in 2013 (TTWG 2017, 2021; Rhodin et al. 2018). Its regional status in its small South Africa range was assessed as Least Concern (Boycott 2014). The species is included on CITES Appendix II as part of the listing of all Testudinidae.

Conservation Measures Proposed. — Further legislation should be developed to protect *K. spekii* on both national and international levels, and the species should be included among protected fauna of each country of occurrence (Mifsud and Stapleton 2014). Ongoing surveys of native populations should be pursued in order to identify potential declines in abundance and density and the impacts of developing or worsening threats. In addition, continued monitoring of national and international trade of the species is important to identify potential emerging and changing patterns of unsustainable use.

Captive Husbandry. — In captivity in southern Africa, combat between males has been noted from September to November, and mating behavior has been observed in January and February (Boycott and Bourquin 2000). Nesting has been recorded from November to April, two to six eggs are laid, and more than one clutch may be laid during a season. On one occasion six eggs were laid over a period of 15 days, initially one egg was laid, then three eggs a few days later, and finally two more eggs. Hatching has been recorded in September, October and April, with

incubation periods of 313–365 days (Boycott and Bourquin 2000). Nolan (2006) recorded details of husbandry care and breeding of *K. spekii* in captivity in Europe with an incubation period of 220 days.

Current Research. — None known.

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