Seasonal Shelter Selection by Leopard Tortoises (*Geochelone pardalis*) in the Franklin Nature Reserve, Free State, South Africa

Author(s) :Rod M. Douglas and Magda Rall
Source: Chelonian Conservation and Biology, 5(1):121-129. 2006.
Published By: Chelonian Research Foundation
DOI:
URL: http://www.bioone.org/doi/full/10.2744/1071-8443%282006%295%5B121%3ASSSBLT%5D2.0.CO%3B2

Chelonian Conservation and Biology, 2006, 5(1): 121–129

Seasonal Shelter Selection by Leopard Tortoises (*Geochelone pardalis)* in the Franklin Nature Reserve, Free State, South Africa

Rod M. Douglas[1] **and Magda Rall**[2]

[1]*Department of Herpetology, National Museum, PO Box 266, 9300 Bloemfontein, South Africa [reptile@nasmus.co.za];*
[2]*PO Box 3034, 1200 Nelspruit, South Africa [bbcnelspruit@bostonbc.co.za]*

Abstract. – **Seasonal habitat utilization, refugia selection, and sheltering behavior by the leopard tortoise (*Geochelone pardalis)* was investigated over a 24-month period (September 1990–September 1992) in the Franklin Nature Reserve, South Africa. The study area was located on Naval Hill, a dolerite and shale mesa which provided diverse topographical and vegetation aspects from which the tortoises could select habitats and refugia. Results showed that considerable shifts occurred in habitat and shelter selection between summer days, summer nights, and winter, with tortoises predominantly utilizing the plateau area. This was ascribed to the availability of shelter, exposure to solar radiation, accessibility, food resources, and the presence of water. Shelters were selected to meet specific needs governed by environmental conditions at the time, with 64.6% of shelters being exclusively utilized within one of the three periods monitored. Thirty-three plant species were utilized as shelters. Tortoises selected dense shelter cover during summer days, light shelter cover or none at all for summer nights, and light shelter cover for winter. Of the latter category, 67.4% of tortoises selected $<$ 50% cover. Day and night shelter orientation was completely random in summer. The orientation of winter shelters was predominantly westerly with light cover shelters, and within which 67.4% of tortoises remained throughout winter. Under the cold conditions encountered on Naval Hill this appeared to be the best-suited survival strategy and provided the best conditions for tortoises to build up and retain sufficient heat during the day in order for them to maintain a temperature above that of ambient through most of the night.**

Key Words. – **Reptilia; Testudines; Testudinidae; *Geochelone pardalis*; tortoise; habitat utilization; refugia selection; sheltering behavior; orientation; thermoregulation; nest predation; South Africa**

Geochelone pardalis, also known as the leopard, or mountain tortoise, is the most widely distributed tortoise species in Africa. Its range extends over almost the entire southern African region, southern Angola, through to central and east Africa, and as far north as Sudan and Ethiopia (Iverson 1992; Boycott and Bourquin 2000). Due to its wide distribution, *G. pardalis* also occupies a wide variety of habitats ranging from desert to tropical bushveld (Boycott and Bourquin 2000). Although Boycott and Bourquin (1988) stated that *G. pardalis* is generally absent from mountainous terrain, other authors (Archer 1968, 1971; Grobler 1982; McMaster 2001) confirmed that these tortoises do in fact inhabit mountainous terrain. Archer (1968, 1971) mentioned an exceptionally large specimen of 47.6 kg from mountains in the Graaff Reinet district, South Africa. Despite its wide distribution range, relatively little detailed ecological research has been carried out on *G. pardalis*.

Further research on *G. pardalis* is important in creating a greater pool of knowledge that can be used to benefit the species in the areas of conservation, public awareness, and husbandry. Kabigumila (1998a; 2001) recommended the raising of public awareness for tortoise conservation due to a low per capita income and a decline in cultural norms in many districts of Tanzania, where people placed more emphasis on the cash value of wildlife trade and tourism, than conservation. With the ever-increasing destruction of natural habitats for agricultural purposes, Kabigumila (1998a) noted that 89.6% of the human population in one of his tortoise survey areas in northern Tanzania claimed to have suffered significant crop damage by tortoises. This along with other factors mentioned by Kabigumila (1998a), such as the tortoise's medicinal value and totem beliefs, are important factors from a conservation point of view. In the far east of Zambia, Wilson (1968) recorded no tortoises $>$5400 g, with most being in the region of 3600 g, while tortoises from less populated areas attained masses of up to 11,200 g. This was directly ascribed to the use of tortoise meat by the local population (Wilson 1968).

Detailed studies on the utilization of plant species by *G. pardalis* as seasonal refugia appear to have only recently been carried out by Mason (1997) in Valley Bushveld of the Addo district, and by McMaster (2001) in the Nama-Karoo biome of the De Aar district. The aim of our study was to determine the seasonal selection and utilization of habitats, vegetation types, and refugia by *G. pardalis*, in the Franklin Nature Reserve, and to determine whether there were any patterns in shelter orientation and the degree of cover density used for shelters.

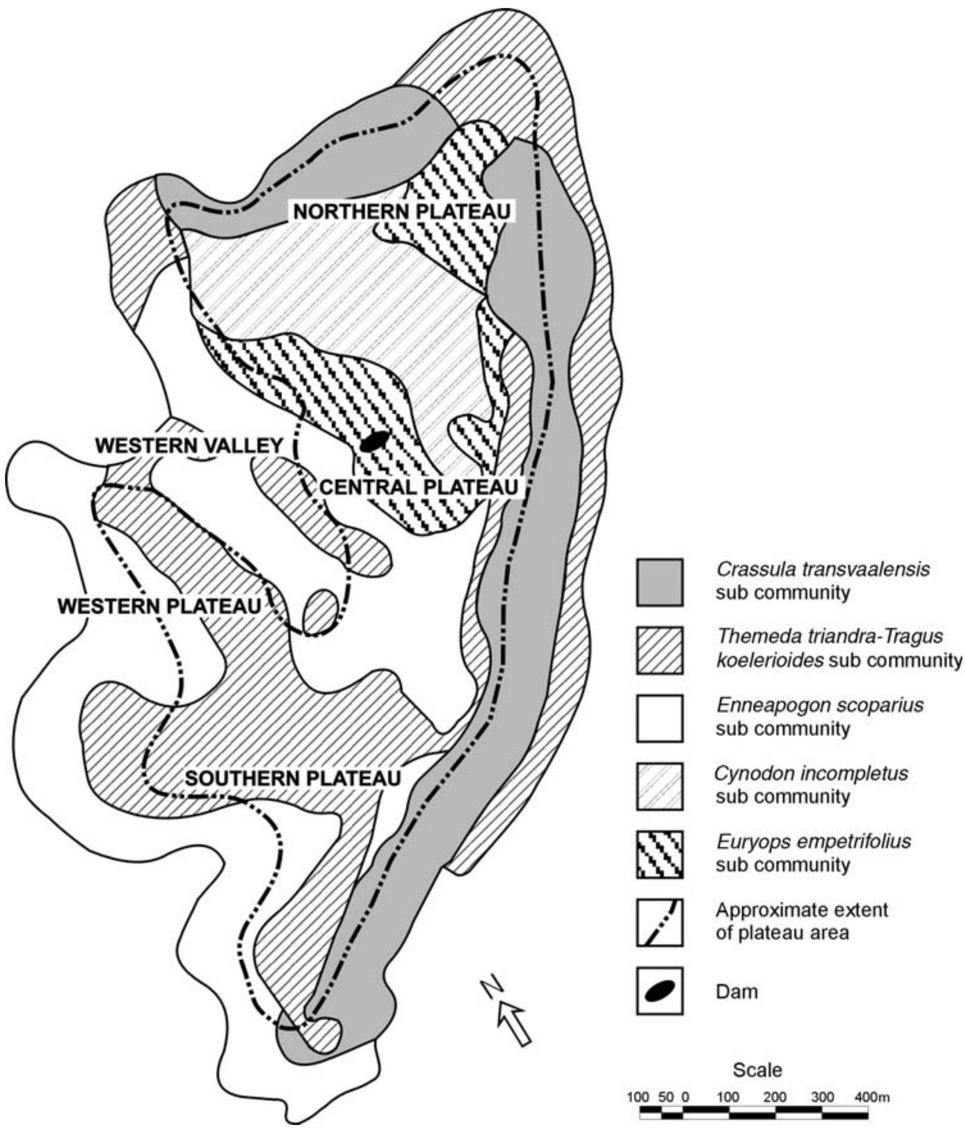

Figure 1. Map showing the plant subcommunities occurring on Naval Hill (simplified after Du Preez 1979) and main topographic features.

METHODS

Study Area. — The study area comprised the 251-ha Franklin Nature Reserve (26°14′E; 29°06′S), which lies within the Bloemfontein city limits, Free State, South Africa. As the entire Nature Reserve was searched on numerous occasions in order to determine tortoise distribution, the study area is delineated by the boundaries of the Reserve as given in Fig. 1. It was calculated from distribution patterns that, during the study period, the tortoises were not utilizing approximately 40% of the Reserve, resulting in 150.6 ha being utilized. The Reserve encompasses Naval Hill, a typical mesa rising from the surrounding plains, with an elevation of between 1407 and 1499 m above sea level (Du Preez 1979). Valleys and dry watercourses drain the plateau area, which accounts for a significant part of the Reserve. Naval Hill comprises a hard dolerite sheet overlying softer Beaufort system shale, which in turn have been intruded by younger vertical dolerite dykes (Du Preez 1979). Soils are variable, but primarily shallow, sandy, and acidic, with a pH of below 7.0 (min pH 4.6) (Du Preez 1979). Bloemfontein lies in the summer rainfall region with an average annual rainfall of 560 mm. During the survey period mean maximum and minimum temperatures during summer (January) were 30.5° and 15.3°C, respectively, and during winter (July) 16.7° and −1.5°C, respectively. However, a maximum of 37.8°C was record in December 1992 and a minimum of −11.7°C in June 1992.

Bloemfontein is also located within the south central variation of the dry *Cymbopogon/Themeda* veld, with the effects of Karoo encroachment being evident (Du Preez 1979). Two main plant communities occur within the Reserve, namely, the *Buddleja saligne/Olea europea* community and the *Hermannia coccocarpa/Tragus koeleroides* community (Du Preez 1979). Fire has never been used as a management tool and the area shows signs of overgrazing by the animals kept in the Reserve (Du Preez

1979). Five plant subcommunities are also evident, namely, *Crassula transvaalensis*, *Themeda triandra*/*Tragus koelerioides*, *Enneapogon scoparius*, *Cynodon incompletus*, and *Europys empetriflius* (Du Preez 1979) (Fig. 1). A marshy area has formed on the plateau below a small dam, where leakage from the weir has resulted in a steady supply of water. Despite the shallow soils, Du Preez (1979) recorded 71 plant families representing 279 species.

Methodology. — The study was carried out over a 24-month period from September 1990 through to September 1992, with the area being systematically searched in sections twice weekly on foot, in both summer and winter. Searches for quiescent tortoises in summer commenced at 1100 hours and continued to 1500 hours. From arguments put forward by Douglas (2002), the term quiescent is used here as the preferred term for resting states in South African reptiles. To establish the localities of nocturnal shelters, searches over the same area commenced again at 1700 hours and continued until the tortoises had settled for the night. Checks were made on known nocturnal shelters again at 0600 hours the following morning to record any nocturnal movement. Using these methods, the entire area was covered more than twice a month. Specimens 1 to 26 were marked between September 1990 and December 1990, specimens 27 to 60 were marked between January 1991 and December 1991, and specimens 61 to 68 between January 1992 and September 1992.

To locate quiescent tortoises through the colder winter months, from mid-May to the end of August 1991 and 1992, systematic searching of the study area took place from 1100 hrs to darkness at ca. 1700–1730 hours. Due to an extremely low tortoise dropping count on the slopes of Naval Hill in May 1991, a more intensified search was concentrated on other topographical aspects such as the plateau, pre-slopes, and valley. The extent to which a tortoise was covered by vegetation in its shelter was categorized as percentages ranging from 0%–25%, 26%–50%, 51%–75%, or 76%–100% cover.

Information such as location, topography, habitat, vegetation type at each shelter, as well as the percentage cover of the shelter and its orientation, were recorded. In addition to these data, all tortoises were weighed (g) and measured (mm, plastron length—gular notch to anal notch) in the field.

The marking method was implemented with the least possible disturbance of the specimens in mind. Using weatherproof roof paint, tortoises were marked with 5-cm high numerals on the posterior end of the carapace. Orange was used to mark females, and yellow for males. The position of the number allowed for identification of the specimens in their shelters without being handled, and colors allowed for individual identification and determination of sex at a distance. Winter shelters were marked by hammering a steel dropper into the ground next to the shelter with the number of the quiescent specimen written in waterproof ink on a piece of unbleached calico, which was firmly tied to the dropper. White calico was used for 1991 and blue for 1992.

RESULTS

Sixty-eight tortoises were marked over the 24-month period from September 1990 to September 1992. This comprised 37 (54.4%) females and 31 (45.6%) males, with a male to female ratio of 1:1.19. During the winter period, May to August 1991, 22 tortoises were located, and for the winter period June to August 1992, 32 tortoises were located. Fifty-four tortoises were classed as adults with a plastron length > 200 mm ($n = 24$ males, $n = 30$ females), 14 as subadults ($n = 7$ males, $n = 7$ females), with no hatchlings being recorded. Eleven specimens were lost from the study area over the period. Seven of these were found dead, a motorcar killed 1, and 3 were never recorded again subsequent to being marked. The remaining 57 specimens were all encountered more than once during the study period.

Morphometric data for 1 tortoise was missing, resulting in further analysis being based on 67 specimens. Masses ranged from 850 to 14,800 g ($n = 67$, mean $= 6358.2$ g, SE $= \pm 3788.2$), with both the smallest and largest specimen being females (female mean $= 7775$ g, SE $= \pm 4089.3$). Male mass ranged from 1000 to 12,200 g (mean $= 4712.9$ g, SE $= \pm 2618.2$), with females being on average 65% heavier than males. Plastron lengths ranged from 131 to 338 mm (mean $= 250.2$ mm, SE $= \pm 54.7$) with both the smallest and largest specimens being females (female mean $= 266$ mm, SE $= \pm 58.4$), and male plastron lengths ranged from 140 to 314 mm (mean $= 231.9$ mm, SE $= \pm 44.9$).

The central plateau (Fig. 1) was the most populous area where 42.3% of tortoises were encountered. This was followed by the southern plateau with 19.2%; the eastern pre-slope with 11.5%; the northern plateau with 9.6%; the northwest plateau and northwest pre-slope, both with 7.6%; the northwest slope with 1.9%; and the western valley with 0.0%. The density of tortoises for the Reserve as a whole was 0.27 tortoises/ha with a biomass of 1.70 kg/ha while the utilized area (150.6 ha) had a tortoise density of 0.444 tortoises/ha and a biomass of 2.82 kg/ha.

Table 1 reflects the percentage use of vegetation types as shelters through summer (day vs. night) and winter. Tortoises utilized 33 plant species resulting in 62 shelter categories comprising 99 component plant species and combinations thereof. Component species were defined as being the two most prominent plant species occurring at a shelter site. Grasses were the most-utilized vegetation type comprising 41.4% of component species, while *Rhus* spp. were the next most-utilized vegetation type at 16.2%. Of the latter, *R. ciliata* accounted for 11.1%. The table indicates that tortoises selected 19.4% of vegetation shelter categories specifically for summer day shelters, 25.8% specifically for summer night shelters, and 19.4% specifically for winter shelters. This resulted in 64.6% of vegetation shelter categories being utilized exclusively for one specific period only, with 24.2% of vegetation shelter categories being utilized during any two given periods (summer days and nights 12.9%, summer days and winter 6.5%, summer nights and winter 4.8%), and 11.3% over all three periods. Of the vegetation shelter categories utilized as shelters, 34% were utilized during summer days, 37% during summer nights, and 28% over winter.

The utilization of the various plant subcommunities as habitats is also provided in Table 1, and shows an often noteworthy habitat shift between both summer days and nights, as well as between summer and winter. During summer, the *Cynodon incompletus* grass subcommunity was the most-utilized habitat (mean = 35.8%), with 40.8% night utilization and 30.8% day utilization. Contrary to this, the *Cynodon incompletus* subcommunity was the least-utilized habitat during winter at 7.6%. The *Euryops empetrifolius* shrub subcommunity was the second most-utilized summer habitat (mean = 33.9%) with day utilization (41.4%) being far greater then night utilization (26.4%). Day utilization of the *Euryops empetrifolius* subcommunity was influenced by the small marsh area below the dam which, alone, was utilized 23.2% during summer days. However, the marsh area was vacated by the tortoises in the late afternoon to seek night shelter in the *Cynodon incompletus* and *Enneapogon scoparius* grass subcommunities, reducing night utilization of the marsh area to 4.0%.

The *Themeda triandra* grass subcommunity was the second most underutilized summer subcommunity (mean = 10.4%), being neither a preferred day (12.7%) nor night (8.1%) habitat, but became the most-utilized winter subcommunity at 36.5%. The *Enneapogon scoparius* grass subcommunity was the second most-utilized winter subcommunity (25.0%) and the third most-utilized summer subcommunity (17.6%). Despite being predominantly located along the eastern side of Naval Hill, which would ensure the best location for early morning solar radiation, the *Crassula transvaalensis* succulent subcommunity was the least-utilized summer subcommunity, as well as being the second least-utilized winter subcommunity. This could have been due to the extreme slope of the eastern side of the hill as well as an unsuitable type of shelter for the tortoises.

The utilization of cover provided by shelters is summarised in Fig. 2. Tortoises predominantly utilized denser summer day shelters with a cover of 51%–75% (40.4%) and 76%–100% (37.1%), while 0%–25% cover was utilized 9.5% of the time and 26%–50%, 12.7%. Contrary to this, summer night shelter selection concentrated on lighter cover of 26%–50% (34.6%) and 0%–25% (31.6%), while 51%–75% cover was utilized 20.4% of the time and 76%–100%, 12.3%. During summer nights, some specimens simply elected to sleep out in the open with no cover. The selection of winter shelters was similar to that of summer night shelters, with predominant use being made of 26%–50% (55.7%) cover and 0%–25% (23.0%) cover. Use was also made of 51%–75% (21.1%) cover, while > 75% cover was totally avoided.

The relationship between a plant species and cover density is a question of whether or not it loses or retains its foliage through winter. This also applies to the plant subcommunities that are inhabited by the tortoises. For example, all the grasses are deciduous, and yet they retain their foliage throughout winter and provide shelter. Table 1 reflects whether a plant species maintained or lost its foliage over winter. Only 2 plant species utilized by the tortoises lost their foliage during winter, with neither being utilized during this period. Therefore, cover presented by plant species does not vary much between summer and winter. This shows the importance of selected plants being able to provide at least some shelter at all times of the year, even though specific plants appear to be selected for specific periods.

In the context of this paper orientation refers to shelter orientation, or the direction in which the opening of the shelter was directed, and not the direction in which the tortoise faced. The combined winter orientations for 1991 and 1992 are shown in Fig. 3, demonstrating the preference of *G. pardalis* to select winter shelters with predominantly westerly openings (66.7%). West openings were selected 3.5 times more often than northwest openings and more than twice as often as north openings. Easterly openings were seldom selected while southerly openings were completely avoided. The orientation of both diurnal and nocturnal summer shelters was random, with the same shelter rarely being used more than once, and many tortoises simply electing to spend summer nights in the open.

The movement of tortoises in and out of winter shelters revealed there was no obvious movement in 15.4% of tortoises, limited shifting in 36.5%, and partial body rotation in 13.5%, indicating that 65.4% of tortoises remained in their shelters throughout the entire winter with little or no movement. Movement in and out of a particular shelter was recorded in 21.1% of tortoises, with a further 7.7% making use of more than one shelter under the same bush. This resulted in 94.2% of tortoises remaining within the original shelter or immediate vicinity thereof. Only 5.8% of tortoises moved away from their original winter shelters to seek other shelter.

DISCUSSION

In nearly all aspects the Naval Hill *G. pardalis* specimens were not as large as those from similar studies. With a mean total mass of 6359 g (male mean = 4713 g, females mean = 7775 g) this was considerably lower than populations studied by Mason (1997) with a mean total mass of 7100 g (male mean = 4770 g, female mean = 8640 g), Rall (1985) 8320 g (male mean = 6900 g, female mean = 10,400 g), Grobler (1982) 8859 g (male mean = 10,460 g, female mean = 12,170 g), and McMaster (2001) 11,100 g (male mean = 7600 g, female

Table 1. The seasonal utilization of vegetation types as shelters and plant subcommunity preferences by *Geochelone pardalis* in the Franklin Nature Reserve, South Africa.[a]

Vegetation cover	% Summer utilization		Mean	% Winter utilization
	Day	Night		
Asparagus spp. (F)	1.2		0.60	
Buddleja salviifolia (F) and *Eragrostis lehmanniana** (F)	1.2		0.60	
B. salviifolia (F) and *Solanum spp*. (?)	1.2		0.60	
Euryops empetrifolius (F) and *Aristida congesta** (F)	1.2		0.60	
Grewia occidentalis (D)	1.2		0.60	
Melolobium canescens (F)	2.3		1.15	
Olea europaea (F)	3.5		1.75	
Pentzia viridis (F) and *E. lehmanniana** (F)	2.3		1.15	
Rhus ciliata (F) and *Digitaria smutsii** (F)	1.2		0.60	
Rhus lancea (F) and *Panicum stapfianum** (F)	1.2		0.60	
*Schinus molle*** (F) and a variety of grasses (F)	7.0		3.50	
Ziziphus mucronata (D)	1.2		0.60	
*Aristida diffusa** (F)		1.1	0.55	
*A. diffusa** (F) and *Eragrostis obtusa** (F)		1.1	0.55	
B. salviifolia (F) and *S. molle*** (F)		1.1	0.55	
*Cynodon incompletes** (F)		2.2	1.10	
*E. lehmanniana** (F) and *A. congesta** (F)		1.1	0.55	
E. empetrifolius (F) and *E. lehmanniana** (F)		1.1	0.55	
Nierembergia spp.** (F) and *A. congesta** (F)		1.1	0.55	
Nierembergia spp.** (F) and *E. lehmanniana** (F)		1.1	0.55	
O. europaea (F) and *E. lehmanniana** (F)		1.1	0.55	
*Panicum coloratum** (F)		1.1	0.55	
R. ciliata (F) and *B. salviifolia* (F)		1.1	0.55	
R. ciliata (F) and *P. viridis* (F)		1.1	0.55	
Rhus dentata (D)		1.1	0.55	
R. dentata (D) and *Asparagus* spp.(F)		1.1	0.55	
*Themeda triandra** (F) and *A. congesta** (F)		3.3	1.65	
*T. triandra** (F) and *E. lehmanniana** (F)		1.1	0.55	
*A. congesta** (F) and *Chloris virgata** (F)	1.2	2.2	1.70	
*A. diffusa** (F) and *E. lehmanniana** (F)	1.2	1.1	1.15	
B. salviifolia (F) and *T. triandra** (F)	2.3	1.1	1.70	
Cyperus esculentus (F) and *Mariscus* spp. (F) (Vlei area)	23.3	4.4	13.9	
Nierembergia spp.** (F)	2.3	7.8	5.05	
P. viridis (F)	4.7	2.2	3.45	
R. ciliata (F) and *Nierembergia* spp.** (F)	1.2	1.1	1.15	
R. lancea (F)	2.3	1.1	1.70	
B. salviifolia (F) and *A. congesta** (F)				1.8
*Cymbopogon plurinodis** (F)				3.6
E. empetrifolius (F) and *T. triandra** (F)				1.8
Euclea crispa (F)				3.6
E. crispa (F) and *A. congesta** (F)				1.8
E. crispa (F) and *T. triandra** (F)				1.8
Felicia muricata (F)				1.8
Melolobium burchelli (F)				1.8
Rhus burchellii (F) and *A. congesta** (F)				1.8
R ciliata (F) and *B. saligna* (F)				1.8
R ciliata (F) and *Digitaria eriantha** (F)				1.8
*Sporobolus frimbriatus** (F)				1.8
B. salviifolia (F)	1.2		0.60	1.8
Buddleja saligna (F)	1.2		0.60	10.7
F. muricata (F) and *E. scoparius* (F)	1.2		0.60	1.8
R. ciliata (F) and *A. congesta** (F)	5.8		2.90	3.6
P. viridis (F) and *A.congesta** (F)		1.1	0.55	1.8
R. ciliata (F) and *C. plurinodus** (F)		1.1	0.55	1.8
R. ciliata (F) and *E. lehmanniana** (F)		5.6	2.80	3.6
*A. congesta** (F)	4.7	16.7	10.70	3.6
*E. lehmanniana** (F)	3.5	3.3	3.40	3.6
E. empetrifolius (F)	5.8	4.4	5.10	8.9
R. ciliata (F)	3.5	15.6	9.50	16.1
R. ciliata (F) and *T. triandra** (F)	4.7	1.1	2.90	7.1
*S. molle*** (F)	2.3	4.4	3.35	1.8
*T. triandra** (F)	3.5	4.4	3.95	8.9
Plant subcommunities (see Fig. 1)				
*Themeda triandra** (F) *Tragus koelerioides* (F)	12.7	8.1	10.4	36.5
Euryops empetrifolius (F) (including vlei area)	41.4	26.4	33.9	21.1
Enneapogon scoparius (F)	11.7	23.4	17.6	25.0
*Cynodon incompletus** (F)	30.8	40.8	35.8	7.6
Crassula transvaalensis (F)	3.1	1.0	2.1	9.6

[a] * Grasses; ** exotic species; (F) foliage throughout the year; (D) plant defoliates during winter.

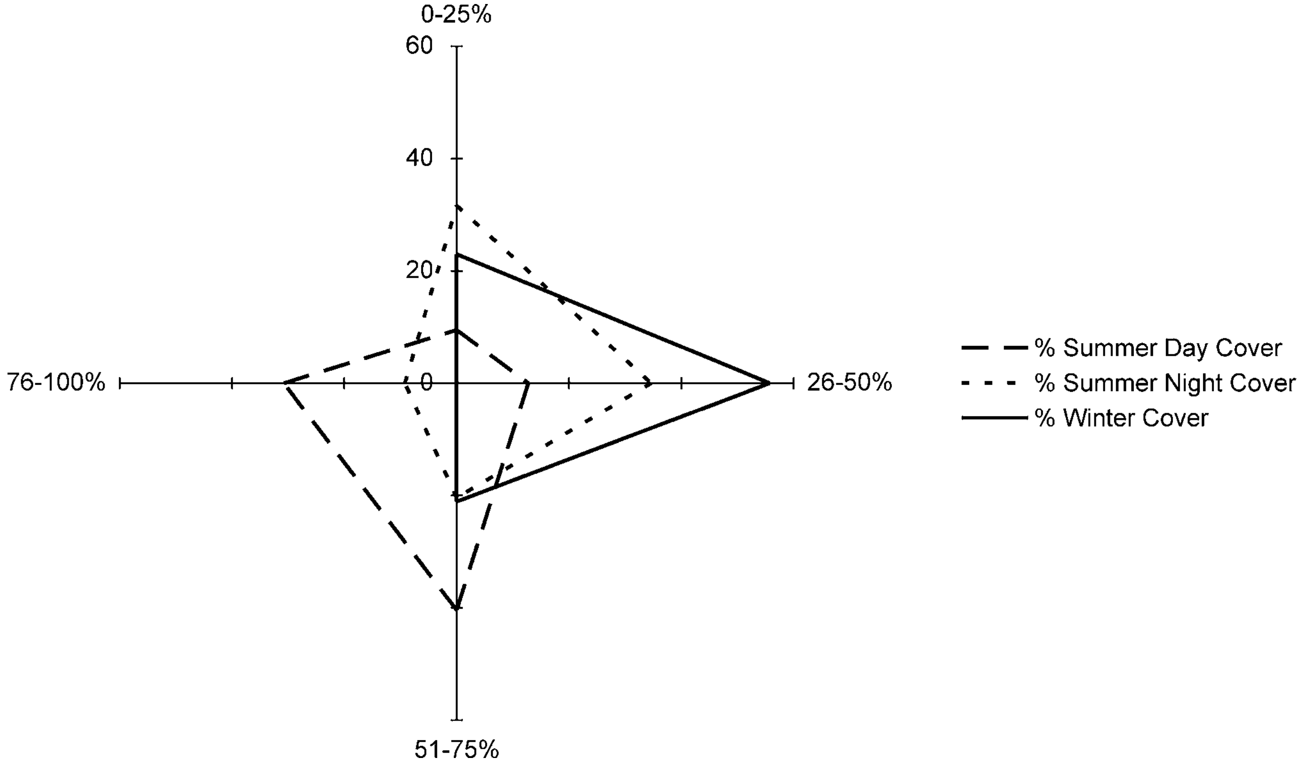

Figure 2. The percentage vegetation cover utilized by *Geochelone pardalis* during summer and winter quiescence periods on Naval Hill.

mean = 15,200 g). The mean mass difference between male and female *G. pardalis* varies considerably between populations, with Grobler's (1982) females being 16% heavier than the males, Rall's (1985) being 51% heavier, this study being 65% heavier, Mason's (1997) being 81% heavier, and McMaster's (2001) being 100% heavier. The Free State male to female sex ratio also appears to be lower than that of other areas, with Rall (1985) recording a ratio of 1:1.10 for the central Free State and this study recording 1:1.19. In similar studies Mason (1997) recorded a ratio of 1:1.44 in Valley Bushveld, McMaster (2001) 1:1.60 in the Nama-Karoo, and Grobler (1982) 1:1.75 for the Mountain Zebra Park.

The density (0.27 tortoises/ha for the Reserve and 0.44 tortoises/ha for the utilized area) and biomass (1.70 kg/ha for the Reserve and 2.82 kg/ha for the utilized area) of tortoise for the Reserve was lower than the 0.48 tortoises/ha and 3.94 kg/ha recorded by Rall (1985), and the 0.85 tortoises/ha and 6.02 kg/ha recorded by Mason (1979). However, the biomass of the Naval Hill population was higher than the 0.017 tortoises/ha and biomass of 0.002 kg/ha recorded by McMaster (2001). No agreement could be reached with a recalculation of McMaster's (2001) biomass, and further calculations indicated that, based on the number of tortoises marked, biomass was 0.127 kg/ha, and on estimated population size, 0.080 kg/ha, with the latter giving a tortoise density of 0.010 tortoise/ha.

The lack of tortoises inhabiting the western valley can be ascribed to it being one of the most densely vegetated areas on Naval Hill, and that it is located on the western side of the hill. This did not allow for a suitable morning thermoregulatory regime, while later in the day the valley was shaded by dense vegetation. Due to the steep and rocky nature of the slopes encountered on Naval Hill, 78.7% of tortoises were encountered on the flatter plateau area (Fig. 1). This can also be ascribed to early morning exposure to solar radiation, accessibility, food resources, and the presence of water. The utilization of the marsh area during summer days, but not summer nights (Table 1) could be due to a number of factors. First, the dampness would have ensured fresh vegetation throughout the summer months, even during relatively dry periods; second, the presence of semipermanent water would have made it a preferred drinking site; and third, the dense stands of *Cyperus* spp. would have provided shelter during the heat of the day. Yet another reason may have been that the damp surface provided a cool environment on which to rest and assist in thermoregulation during the heat of the day. Why the marsh area was evacuated in the evenings can, at this stage, only be explained by the possibility that, being the only standing water in the area, it provided an ideal breeding ground for biting insects such as mosquitoes. The avoidance of the *Crassula transvaalensis* succulent subcommunity was possibly due to the lack of shelter it provided.

It would appear that the selection of denser summer diurnal shelter largely reflects the need for protection from the sun, in close proximity to a suitable and sustainable food source. The selection of lighter summer night shelter,

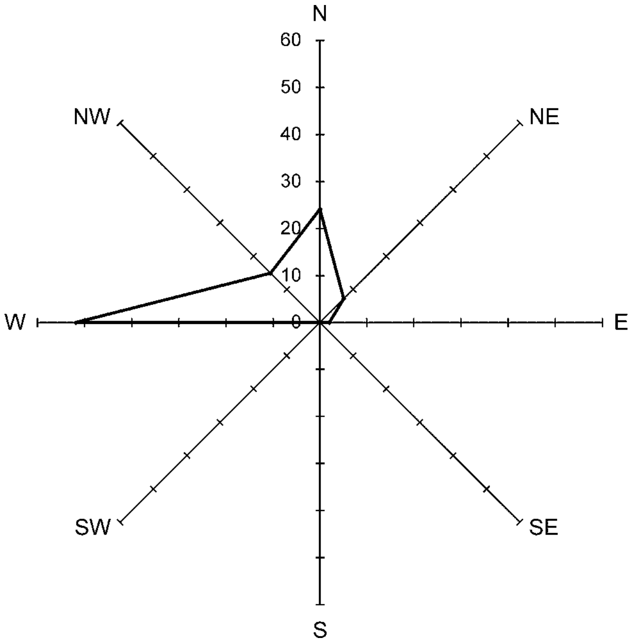

Figure 3. The orientation of *G. pardalis* shelters during winter quiescence on Naval Hill.

after late afternoon activity, and the avoidance of denser vegetation cover was possibly necessitated by the need for tortoises to receive direct early morning sun for thermoregulation and the resumption of activity well before the onset of higher temperatures later in the day. This could explain why many tortoises did not bother to seek out summer night shelters, but simply slept in the open. However, due to relatively high dawn temperatures in summer, tortoises are capable of moving from dense shelters into direct sunlight for thermoregulatory purposes, suggesting that the former strategy may have had other advantages for the tortoises. On the other hand, winter shelters reflected a similar pattern to that of summer night shelters, but with the total avoidance of dense vegetation with > 75% cover in combination with selective orientation. This latter strategy satisfied the long-term requirements for winter quiescence based on building up body temperature during the day by receiving maximum solar radiation in order to survive the often extremely cold nights. Since 64.6% of vegetation categories were used exclusively for the three specific periods examined, it suggests that shelter selection was not random, but that vegetation types and shelters were selected to meet specific needs governed by environmental conditions during those periods.

A similar conclusion was reached by Mason (1997), who recorded the use of 39 plant species as shelters, noting that tortoises were not selecting shelter plants in relation to their frequency in the habitat, indicating that they were selectively selecting specific plants as shelters. On the other hand, McMaster (2001) recorded the use of only 10 plant species as shelters, noting that, with the exception of one period, all plants were utilized over all four seasons, with none being used for a specific period. However, this may have been due to a lesser diversity of plant species in McMaster's (2001) study area.

The 67.4% of tortoises that remained in their shelters throughout winter was similar to the 71% recorded by McMaster (2001). However, winter shelter selection in our study was different from the findings of Grobler (1982) who noted that Mountain Zebra National Park specimens took winter refuge under dense undergrowth. This may have been due to the more sheltered nature of the Mountain Zebra National Park's valleys, as opposed to the extremely exposed Naval Hill plateau with its lower temperatures and the possible need for less cover and greater exposure to solar radiation. The suggestion by McMaster (2001) that it was advantageous for tortoises to orientate themselves in order to obtain exposure to the sun, while still remaining protected from the cold and wind, would appear to be somewhat contradictory. This is because greater exposure to the sun would imply less cover, and therefore greater exposure to the cold and wind. It is therefore suggested that cover density, and the degree of shelter it provides may play little role in protection from the cold. This is supported by the fact that 78.7% of our study population selected < 50% cover during winter.

Not only will light winter cover, and completely exposed and light summer night cover, be of benefit to the tortoises from a thermoregulatory aspect, but it may also improve tortoise survival in the event of veld-fires. Fires occur almost annually on Naval Hill, but usually these are kept under control and only relatively small areas are burnt at a time. On the Highveld, veld-fires most often occur through human factors during winter, when the grasses and bushes are very dry, while during frequently occurring, and often extended dry periods in summer, lightning is often responsible for fires. Dense shelter cover would produce extremely intense (hot) burns, from which the tortoises may have little chance of escape, while lighter cover would produce much milder burns from which the tortoises might well escape. Variables such as the composition and density of vegetation in the immediate area of the shelter would also be important factors in determining the intensity of any such burn. It is therefore evident that in the long term, regular veld-fires, which keep the density of the vegetation low, are beneficial to the survival of the tortoises in that only mild burns would result.

The impact of fire on tortoise populations is highlighted in a report by Baard et al. (2001) following a runaway fire which swept through approximately 18,000 ha, both inside and outside, the West Coast National Park. Baard et al. (2001) surveyed a 95.04 ha area and recorded 1360 dead *Chersina angulata* ($n = 1459$), indicating a 93.2% mortality and 6.8% survival rate; this equated to an estimate of between 98,000 and 275,000 tortoises having burnt to death over the total area of the fire. The vegetation at the site of that fire was approximately 30 years old, with an ambient temperature of > 40°C and a strong south-easterly wind (E.W.H. Baard, *pers. comm.,* May 2002).

While summer orientation showed no particular directional preference, the predominantly westerly orientation of winter shelters on Naval Hill was of interest because it has generally been speculated that tortoises select easterly orientated shelters to capture the first rays of the morning sun after cold nights. It is postulated here that, in climates where very cold conditions prevail at night, it is more advantageous for tortoises to become exposed to solar radiation later in the day when the ambient temperature has already begun to rise. Westerly exposure would also allow for exposure throughout the greater part of the day, right through to sunset when the ambient temperature is still relatively high, as opposed to an easterly exposure when early morning sun is received in a very low ambient temperature, with direct solar radiation being lost much earlier in the day, possibly well before the maximum ambient is reached.

In order for tortoises to best benefit from a strategy of maintaining maximum exposure to solar radiation in the highest ambient temperature, the selection of a westerly orientation would be ideal. This would allow for an optimal build up of body temperature, allowing residual heat to become more effective in preventing the night body temperature from falling too rapidly, or from reaching the low early morning ambient temperature, which may be well below freezing.

Latitude could be an important factor in winter shelter orientation because the further south tortoises are located in the southern hemisphere, the more likely they would be to orientate in a northerly direction to obtain maximum exposure to the sun in winter. Therefore, factors such as latitude, location of the site, topography, and environmental factors—such as temperature and wind direction—will all play important roles in determining the shelter orientation of tortoises during winter. For example, it could be expected that the most frequently used direction for orientation would vary between Mason's (1997) site, McMaster's (2001) site, and this study. At Mason's (1997) site, where the mean monthly minimum temperature for June, July, and August was 4.5°C (minimum 3°C), the valley and mountains provided a certain degree of shelter from a number of environmental factors, as opposed to the extremely exposed nature on the Naval Hill plateau where the temperature fell to −11.7°C.

The lack of hatchlings and low subadult count of *G. pardalis* on Naval Hill appears to be a common factor in most similar studies, and was not interpreted as unusual. Mason (1997) recorded only 7 specimens with carapace lengths of < 200 mm ($n = 53$) and no hatchlings, while Grobler (1982) recorded no specimens < 4800 g. When considering that, based on this study, sexual maturity occurs at around 3000 g, an extremely large proportion of Grobler's (1982) adult population was also absent. Contrary to these low subadult counts, McMaster (2001) recorded 26 subadults and 4 hatchlings ($n = 92$), using < 5000 g for subadult males and < 10,000 g for subadult females.

Based on the size (220-mm carapace length) and mass (3000 g) at sexual maturity used in this study, McMaster's (2001) males were well above this mass with a carapace length of approximately 250 mm. There was even a greater difference between the sizes of sexually mature females between the two studies, with McMaster's (2001) females equating to a carapace length of approximately 300 mm. The high number of subadults in McMaster's (2001) study could possibly have been due to having chosen too high a mass for determining, particularly, subadult females, while a number of males < 5000 g were later noted to be sexually active. This difference in the size selected for sexual maturity is reflected in that, if McMaster's (2001) criteria were applied to the Naval Hill population, the population dynamics would change from 7 subadult females to 22, and 7 subadult males to 21, or 64% of the population would have been subadult instead of the 21%.

A number of reasons have been given for low counts of hatchlings and juveniles in field studies. Some of these are: the vulnerability of young tortoises to predation, which is compensated for by the longevity of adults; that sighting, mark–recapture, and random transect methods may give a relative rather than absolute measure of abundance; that only a portion of the population may be prone to detection even at peak activity periods; and that smaller tortoises are less active and also more difficult to detect (Stubbs et al. 1984; Judd and Rose 1983; Hailey 1988; Mason 1997).

Although the above factors contribute to the apparent low numbers of hatchlings recorded, we hypothesize that the reproductive success of the species is affected primarily by the mortality of the eggs through predation, environmental factors such as precipitation and temperature, and possibly infertility. This is supported by the disturbance of nest sites reported in most surveys. In this study, 14 nests were found excavated and 2 clutches were found laid on the surface, although none of the actual predators were identified. Grobler (1982) noted 10 excavated nests in the Mountain Zebra Park survey and expressed concern about the predation of eggs, while nests destroyed by predators were common in Mason's (1997) survey area. The most important factor contributing to the predation of eggs is most probably that they may remain buried for periods of up to 485 days (Boycott and Bourquin 2000) and still remain viable. This exposes them to an extremely long period where predation can occur. Although there is ample evidence in the literature of predation on hatchling and juvenile size classes (Boycott and Bourquin 2000), we believe this is relatively low in comparison to the mortality of eggs.

LITERATURE CITED

ARCHER, W.H. 1968. A classification problem. African Wildlife 22(3):249–254.

ARCHER, W.H. 1971. Turtles, terrapins and tortoises of the Eastern Cape Province, Part III. Eastern Cape Naturalist 43:18–22.

Baard, E.W.H., Hofmeyr, M.D., Moore, K., de Villiers, A.L., and Sutton, T. 2001. Impact of fire on the angulate tortoise *Chersina angulata* population of the West Coast National Park, South Africa. Herpetological Association of Afruica, 6th Symposium on African Herpetology, Stellenbosch, 10 pp.

Boycott, R.C. and Bourquin, O. 1988. The South African Tortoise Book. A Guide to South AfricanTortoises, Terrapins and Turtles. Johannesburg: Southern Book Publ., 148 pp.

Boycott, R.C. and Bourquin, O. 2000. The Southern African Tortoise Book. A Guide to Southern African Tortoises, Terrapins and Turtles. Revised expanded edition. Pietermaritzburg: Interpak, 228 pp.

Douglas, R.M. 2002. The semantics of resting states in reptiles and amphibians. African Herp News 34:4–8.

Du Preez, P.C. (1979). ’n Plantekologiese ondersoek van Naval Hill. M.Sc. Thesis, University of the Orange Free State, Bloemfontein.

Grobler, J.H. 1982. The leopard tortoise in the Mountain Zebra National Park. Koedoe 25:49–53.

Hailey, A. 1988. Population ecology and conservation of tortoises: the estimation of density, and dynamicsof a small population. Herpetological Journal 1(7):263–271.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Judd, F.W. and Rose, F.L. 1983. Population structure, density and movements of the Texas tortoise *Gopherus berlandieri*. Southwestern Naturalist 28(4):387–398.

Kabigumila, J. 1998. Community attitudes to tortoises (*Geochelone pardalis babcocki*) and their conservation in northern Tanzania. African Study Monographs 19(4):201–216.

Kabigumila, J. 2001. Sighting frequency and food habits of the leopard tortoise, *Geochelone pardalis*, in northern Tanzania. African Journal of Ecology 39:276–285.

Mason, m.c. 1997. Leopard and angulate tortoises in Valley Bushveld: habitat, populations and diet. M.Sc. Thesis, University of Port Elizabeth.

McMaster, m.k. 2001. The status and ecology of the leopard tortoise (*Geochelone pardalis*) on farmland in the Nama-Karoo. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Rall, M. 1985. Ekologiese waarnemings van ‘n bergskilpadpopulasie, *Geochelone pardalis* Bell, 1828, soos aangeteken in die Soetdoring-Natuurreservaat in die Oranje-Vrystaat. Koedoe 28:47–60.

Stubbs, D., Hailey, A., Pulford, E., and Tyler, W. 1984. Population ecology of European tortoises: review of field techniques. Amphibia-Reptilia 5(1):57–68.

Wilson, V.J. 1968. The leopard tortoise, *Testudo pardalis babcocki*, in eastern Zambia. Arnoldia 3(40):1–11.

Received: 20 March 2003
Revised and Accepted: 12 March 2004