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SLEEP-LIKE BEHAVIOUR IN THE GALAPAGOS TORTOISE (*GEOCHELONE ELEPHANTOPUS*)

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ABSTRACT

Sleep-like behaviour of Galápagos tortoises (*Geochelone elephantopus*) was studied at Volcán Alcedo, Isabela Island, Galápagos Islands, Ecuador. At midday, most tortoises found asleep were in the open with head and limbs extended; during cooler evening hours, sleeping tortoises usually occupied forms with head and limbs withdrawn. Variability in sleep-like postures during different periods of inactivity probably reflects alternative thermoregulatory strategies. Forms occupied by inactive tortoises ($n = 53$) comprised vegetation (51%), soil (30%) and other tortoises (19%). The absence of native predators on Galápagos implies a thermoregulatory rather than antipredator function for form use.

INTRODUCTION

The electrophysiological and behavioural presence of sleep has been documented in several species of terrestrial chelonians (e.g., Vasilescu, 1970; Flanigan, 1974; Flanigan *et al.*, 1974; Ayala-Guerrero, 1988). However, Susic (1972) and Walker and Berger (1973) failed to detect evidence of sleep in *Caretta caretta* and *Geochelone denticulata*, respectively. Consistent with most studies of sleep in reptiles, the electrophysiological characteristics of sleep in chelonians have received more attention than behavioural or ecological aspects. Such an emphasis has emerged because of the interest of researchers in the evolution of sleep phenomena, in particular the electroencephalographic correlates of specific sleep states (see reviews by Karmanova, 1982; Meddis, 1983; Vasilescu, 1983). Consequently, all investigation of sleep in chelonians has taken place in the laboratory without corroborative field studies.

The studies above confirm that sleep in chelonians may be recognized in the field by simple behavioural criteria. Behavioural sleep is defined as behavioural quiescence associated with a stereotypic posture, an elevated arousal threshold, and rapid-state reversibility with relatively intense stimulation (Flanigan, 1974; Flanigan *et al.*, 1974). Several investigators reported that the limbs of sleeping tortoises are extended, usually posteriorly and parallel to the body axis; the head likewise is extended, and rests upon the plastron edge or substrate with the eyes closed (Flanigan, 1974; Flanigan *et al.*, 1974; Douglass and Layne, 1978).

Under natural conditions, chelonians might exhibit much greater variability in sleep behaviour than that observed under laboratory conditions. In this paper we report and analyse our observations of sleep postures and sleep sites selected by Galápagos tortoises (*Geochelone elephantopus*) in their natural ecological setting. We further discuss how the patterns that we observed may reflect alternative thermoregulatory strategies.

METHODS

During 22-24 June 1984, we studied free-ranging tortoises (*G. e. vandenburghi*) from a large resident population (3,000-5,000 individuals; MacFarland *et al.*, 1974) on Volcán Alcedo, Isabela Island, Galápagos Islands, Ecuador. Tortoises were considered to be asleep when completely immobile with the head resting on the plastron or substrate and the eyes closed. However, without electrophysiological data we prefer to call this behaviour "sleep-like". For tortoises found in sleep-like repose, we recorded (1) whether the subject occupied a "form" (facing into a soil bank, vegetation or another tortoise; c.f. Auffenberg and Weaver, 1969; Judd and Rose, 1977; Strass *et al.*, 1982); (2) whether the head and neck were extended, partially extended or withdrawn; (3) the number of legs extended; (4) the composition of forms (soil, vegetation or another tortoise) when used; and (5) the substrate (soil or grass) upon which non-form users rested.

Observations were made at midday (1200-1400 hr) and near dusk (1650-1730 hr). Maximum and minimum daily temperatures during the study were 18.5°C and 15.6°C, respectively. Humidity ranged from 93.0% to 97.0%; all three days were mostly overcast. In several cases (<10%) we could not record all data for an individual without the risk of disturbing other nearby tortoises. Conventional two-sample chi-square tests (χ^2 statistic; Siegel, 1956) were used to test for associations between variables associated with sleep-like behaviour.

RESULTS

Depending on the time of day, inactive tortoises assumed two distinctive postures: (1) at midday, most tortoises found asleep were in the open with head and limbs extended, whereas (2) during cooler evening hours, sleeping tortoises usually occupied forms with head and limbs retracted (Table 1). The substrate (soil or grass) selected by inactive tortoises in the open did not vary during these periods, nor did the composition of forms (Table 1).

Variable	Number of Tortoises		df	χ^2	P
	Midday	Dusk			
Exposure					
Open	59	20	1	47.52	<0.001
Form	6	46			
Substrate					
Soil	22	14	1	3.20	0.07
Grass	26	5			
Form Composition					
Soil	3	13	2	2.16	0.34
Vegetation	3	24			
Other tortoise	0	10			
Head					
Extended	48	3	2	71.76	<0.001
Partially Extended	11	17			
Withdrawn	6	46			
Number of Legs Extended					
Zero	14	58	4	64.84	<0.001
One	12	7			
Two	23	2			
Three	15	0			
Four	4	0			

TABLE 1. Conditional cell totals for variables associated with tortoises in sleep-like repose at midday and dusk. Substrate comparisons are for tortoises in the open (non-form users).

Regardless of the time of day, the head and limbs of sleeping tortoises were more likely to be extended when in the open than when in forms, and there was a positive association between leg and head extension (Table 2). Forms occupied by tortoises during both periods combined ($n = 53$) comprised vegetation (51%), dirt (30%) and other tortoises (19%).

Variables	Number of Tortoises		df	χ^2	P
	Open	Form			
Exposure X Head	<i>Exposure</i>				
Head Extended	50	1	2	81.90	<0.001
Head Partially Extended	22	6			
Head Withdrawn	7	45			
Exposure X Legs					
Legs Extended	54	5	1	41.37	<0.001
Legs Withdrawn	25	47			
Head X Legs	<i>Legs</i>				
Head Extended	49	2	2	94.60	<0.001
Head Partially Extended	9	19			
Head Withdrawn	1	51			

TABLE 2. Conditional cell totals for variables associated with tortoises in sleep-like repose, independent of time of day.

DISCUSSION

Voigt (1975) described thermoregulatory postures in the desert tortoise (*Gopherus agassizii*) that were similar to our observations of *G. elephantopus*. At midday, when shade was often sought, heat was offloaded by extension of limbs and head; this posture was also maintained during periods of basking, when body temperatures rapidly increased. At night, heat was retained by a

decrease in surface to volume ratio when the head and limbs were withdrawn. Our observations (see also Douglass and Layne, 1978; Auffenberg and Iverson, 1979) suggest that tortoises sleep much of the time when in these various postures. Hence, variation in sleep-like postures during inactivity likely reflects alternative thermoregulatory strategies.

In the absence of body temperature measurements, it cannot be determined whether the midday postures of *G. elephantopus* represented basking or shading behaviour. Considering the cool, overcast conditions at the time of our study, the tortoises were more likely trying to absorb rather than offload heat. In apparent contrast, the Aldabran tortoise (*Geochelone gigantea*), which must seek shade at midday during warm weather, remains active throughout cool, cloudy days (Swingland and Frazier, 1980).

The use of forms may reduce overnight heat loss from convection, conduction and radiation, and may reduce water loss as well (Auffenburg and Weaver, 1969; Judd and Rose, 1977). Forms may also provide concealment from predators during periods of inactivity (Strass *et al.*, 1982). Because native predators are absent from Galápagos (MacFarland *et al.* 1974), a thermoregulatory function for form use seems most plausible for Galápagos tortoises; however, antipredator strategies are still retained by *G. elephantopus* (Hayes *et al.*, 1988). Our observation that tortoises frequently aggregate at night suggests a possible thermoregulatory function similar to form use. Boersma (1982) found that aggregates of marine iguanas (*Amblyrhynchus cristatus*), also endemic to Galápagos, maintained higher overnight temperatures than solitary iguanas, as observed likewise in other reptile groups.

Maximization of heat retention during nocturnal inactivity may facilitate increased morning foraging time. Marlow (in Huey, 1982) found that burrow use by *G. agassizii* at night appeared to decrease morning basking time and increase foraging time relative to more exposed form users (see also McGinnis and Voigt, 1971). Heat conservation at night may also facilitate digestion and reduce vulnerability to predation (Boersma, 1982).

With the exception of studies by Susic (1972) and Walker and Berger (1973), there is ample evidence for behavioural sleep in chelonians. Walker and Berger (1973, 1980) argue that sleep in reptiles is merely an ectothermic manifestation of thermoregulatory behaviour, and not actual sleep. However, sleep and thermoregulation certainly are not exclusive activities in birds (Amlaner and Ball, 1983) or mammals (Walker and Berger, 1980), and recent electrophysiological evidence also refutes the position of Walker and Berger (Hartse and Rechtshaffen, 1982). Accordingly, we suspect that thermoregulation is a dynamic and integral aspect of reptilian sleep, both processes serving unique but complementary functions. The relationship between reptilian sleep and thermoregulation merits further investigation.

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