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Orientation of giant tortoises, *Geochelone gigantea* (Schweigger) while grazing on Aldabra Atoll

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Abstract. The Aldabran giant tortoise is one of the few testudines that feeds in dense herds, and in so doing the animals frequently exhibit a conspicuous orientation away from the sun. This orientation is most marked when ambient temperature is high, and it breaks down when the tortoises are shielded from direct sunlight. It was previously hypothesized that negative heliotaxis is related to thermoregulation—to reduce heat inflow to the exposed anterior appendages and instead expose the protected posterior of the shell. There has been no test of the thermoregulatory function, and pilot experiments indicate that orientation away form the sun occurs to reduce direct glare into the tortoise's eyes. The glare of the sun seems to interfere with accurately oriented biting movements and reduce feeding efficiency. Speed and intensity of reaction to solar glare is inversely related to the animal's body size. The possibility of a thermoregulatory component to the away-from-the-sun orientation cannot be discounted, but it must be investigated directly.

Introduction

An immense population of giant tortoises, *Geochelone gigantea* (Schweigger) occurs on Aldabra Atoll, and during austral spring and summer dense congregations of tortoises feed on the coastal plains of *Sporobulus virginicus* along the eastern and southern coasts of the Atoll. There are bimodal peaks in the diel activity cycle, with a major part of the population grazing between sunrise and about 0900 h, and after a midday period of rest a slightly smaller number of tortoises actively grazes from about 1600 h to sunset (Frazier, 1971).

While grazing, the majority of animals face directly away from the sun ("negative heliotaxis")—that is, approximately west during the morning and approximately east during the afternoon. An individual tortoise that is in a shadow frequently lacks this orientation, and when clouds shade the sun over the grass plain, the general orientation of the grazing herd often breaks down (Frazier, 1971).

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As the amount of time a tortoise spends active (feeding, searching for food, etc.) is inversely related to its rate of heating, any mechanism that would reduce the rate of heat influx would enable an animal to spend more time feeding and carrying on other activities and also reduce the chances of heat prostration in the event that the animal "overstays" its time exposed to the sun. When a tortoise faces away from the sun it exposes the horny posterior of the carapace directly to the solar radiation and keeps the anterior appendages (head, neck and front limbs) in the shade. The proportion of the herd that orients away from the sun is strongly related to air temperature. Hence, it was hypothesized that in orienting away from the sun, and reducing the amount of solar energy falling directly on the anterior appendages, a tortoise reduces the rate of heat influx. Facing away from the sun was thought to be a thermoregulatory response (Frazier, 1971).

There has as yet been no study of the relationship between orientation to the sun and thermal characteristics of the giant tortoise, and a recent endorsement of Frazier's (1971) hypothesis (Coe and Swingland, 1984) has discussed the orientation phenomenon in simpler terms than it was originally described, thus omitting various alternate interpretations in explaining the behaviour. The present study reports on the results of simple, "Tinbergenesque", experiments on the effect of reflected sunlight on tortoise orientation.

Material and Methods

Wild giant tortoises were studied between 14 and 21 March 1985 on Aldabra Atoll, Seychelles. Animals grazing on the east plain of Dune Jean Louis, Grand Terre, were observed for several minutes; this enabled the selection of a tortoise that was grazing intently while oriented away from the sun, and if possible within several m of at least one other grazing tortoise, also orienting away from the sun. An experimental subject was selected and approached from its anterior end to about 10 to 15 m: "the aiming station". After the investigator had sat several minutes directly in front of the tortoise, a plane mirror 30 × 30 cm was supported on top of a red plastic soft-drink carton 30 cm high. By changing the angle of the mirror relative to the sun, the glare could be directed at the subject's head, hind foot or other target. Behavioural observations were timed with a stop watch and recorded into a portable tape recorder or note book. If during the course of the experiment the subject moved so far as to impede the accurate aiming of the mirror, the aiming station was moved again to about 10 m directly in front of the tortoise.

A total of 15 tortoises were tested in 19 experiments that lasted from 5 to 60 min. each. Most experiments were run in the morning because clouds often interferred with experimental conditions during the afternoon. Because the tortoises were in completely natural conditions, and they were subjected to no interference other than the mirror's glare and the presence of the aiming station, experiments were run opportunistically: when experimental animals were available and when weather conditions allowed an uninterrupted interval of direct sunlight. From the second day of experimentation onwards, the procedure was changed from one continuous bout of glare aimed at the face to several bouts interrupted by glare to hind foot or no glare exposure. This enabled the observation of additional responses, notably recovery from glare.

Results

All but 3 of the 19 experiments resulted in an avoidance response which involved turning away from the mirror—and toward the sun. When the glare on the head was

stopped, the tortoise reoriented away from the sun, and toward the aiming station. This occurred in at least 63% of the experiments, but the response was more common than recorded because the earlier experiments were not designed to check for re-orientation. The behaviour of several tortoises was quite mechanical and immediate, and their orientation was simply determined by shining a mirror at the head or by stopping the glare.

Standing and walking followed the beginning of the mirror's glare in all but 4 of the 19 experiments. This resulted in an end, or disruption, to intense grazing (the selection of each experimental animal was based on its orientation away from sun *and* exhibiting intense grazing). Nearly half of the tortoises settled and resumed intense grazing once the mirror's glare stopped.

In about half of the experiments the tortoises stopped biting grass and looked up; this was often followed directly by 2 or 3 mandibulations and a swallow. The "look up" is evidence that the animal had been distracted, and the "chew-swallow" sequence is often a displacement behaviour which indicates that the animal is in a situation of conflict. The "look up" was often the first response to the mirror's glare and often occurred within 20 seconds of the beginning of the test. The response was not recorded systematically in the first experiments, and it was probably more common than indicated.

Other notable behaviours that were observed less regularly were hissing, retracting the head, rejecting a bite of grass and walking in a zigzag rather than a straight line. The indirect path indicates that the tortoise was ambivalent about how to orient, evidently trying to avoide the glare of the sun on one side and the glare of the mirror on the other; under normal conditions tortoises walk in straight lines, not in zigzags. The hiss-retract-eject indicates that the animal was disturbed and disoriented while grazing; normally a grazing tortoise appears to focus its attention on the short-cropped grass several cm in front of its nose. A precise biting movement is required to nip off blades about 1 cm long just above the sandy substrate: too high and little is bitten off, too low and tough stems or even pebbles will be taken into the mouth. In the latter case, the tortoise invariably looks up and makes conspicuous gagging movements to reject the unwanted object. It is likely that a bright glare directly in the face not only disturbs, but partially blinds the tortoise, interferring with the orientation of feeding movements.

Several tortoises not only reoriented the body, but the head was held in an unusual position. It was positioned immediately behind and close to a front leg, which served as a shield from the mirror's glare. Also, the neck was extended away from the mirror so that the head was in the sun, not in the body's shadow.

These results are comparable with those from the two experiments run on tortoises that were completely shaded from direct sunlight: whether or not the body was shaded, the tortoise avoided glare in its face. There was no apparent difference in the behaviour of tortoises in the morning and in the afternoon. In various experiments where glare to the face was interrupted by glare directed at a tortoise's back leg—well away from its

head—the response was the same as if there were no glare; the animal reoriented and resumed grazing. There was a tendency for smaller animals to react faster to the mirror's glare (reaction time to body size, discounting the incomplete observations from the first day, $r = 0.82$; d.f. $= 6$; $p < 0.05$). They also reacted more intensely to the glare, showing more conspicuous avoidance and greater perturbation to their grazing activities.

Where control animals were present alongside the experimentals, invariably the controls grazed intently and oriented away from the sun, while the experimentals reacted to the mirror's glare. In no instance was there any indication that the presence of a person and paraphernalia (other than the aimed mirror) at the aiming station disturbed or repulsed a tortoise. Indeed, it was common for both control and experimental tortoises to approach the aiming station to within about 1 m.

Discussion

In a previous study involving detailed regression analysis (Frazier, 1971), it was found that the proportion of grazing tortoises that face away from the sun increases as the morning wears on. There was no such relationship for afternoons, but in general a greater portion of the herd faced away from the sun during the afternoon. The degree of cloud cover, for mornings or afternoons, did not show a strong relationship with the percent of the herd facing away from the sun.

If glare were a factor in the orientation response, it was argued, the strongest avoidance should occur when the sun is at a low angle (i.e. shining into the tortoise's eyes), and in addition cloud cover should have a marked effect. That neither of these premises was true led to the postulation that glare is not a primary factor in the orientation away from the sun. Instead, it was hypothesized that the Aldabra tortoise behaves as a 'heliotherm'' and modifies its body posture relative to the sun for thermoregulation, facing away from the sun in the late morning when an excess of heat is a problem. It also faces away from the sun at the beginning of the afternoon, when the ambient temperature is near its maximum, and because there is no marked positive heliotaxis the tortoises stay oriented away from the sun throughout the afternoon (Frazier, 1971).

However, results of the present study clearly show that grazing tortoises are repulsed by glare from a mirror when the face is exposed. The animals are also likely to make imprecise biting movements and stop, or greatly reduce, their grazing activities. Glare directed at the body, but not the head, does not produce this response and when the glare is removed from the head the animals reorient away from the sun (toward the mirror). The function of orienting away from the mirror seems to be to avoid glare to the face, which interferes with accurate visual orientation needed in making precise biting movements for efficient grazing.

This does not negate the possibility of a thermoregulatory function in the orientation behaviour—especially in the light of the earlier findings with regression analysis (Frazier, 1971). The tendency for smaller animals to react more quickly and strongly

also suggests that sensitivity to glare is related to thermoliability. However, the results show that negative heliotaxis in giant tortoises on Aldabra is not simply related to a single stimulus, as has been suggested (Frazier, 1971; Coe and Swingland, 1984). A direct investigation of the thermal effect of heliotaxis is required to understand the thermoregulatory function of this behaviour. Other factors which cannot be ignored in future experiments include the effect of an unnatural source of strongly polarized light, which may cause stimulus overloading and confusion in the tortoise.

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