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Heat Balance in the Black Rhinoceros
(Diceros bicornis)

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Grant 2428: To study factors determining the survival of black rhinoceros calves.

Size-related evolutionary convergence in small mammals has been described at length; however, size-related behavioral and physiological adaptations of the largest terrestrial mammals and their young have not been described until recently. The first general studies of the behavior and physiology of an animal weighing over 1000 kg, a giraffe, described a new type of endotherm, the committed heterotherm, an animal with daily fluctuations in body temperature of up to 10°C. The large body mass creates a thermal inertia that functions to buffer heat gain and loss.

If size-related evolutionary convergence exists in large animals, then other animals with adult body weights of more than 1000 kg should also exhibit thermally related adaptations like those found in the giraffe. This project set out to determine how the black rhinoceros regulates its body temperature.

Methods

Three captive black rhinoceros were trained to enter and stand in blind-ended crushes during instrumentation and metabolic measurements. Body weights were calculated using the relationship between body girth, body length, and body mass reported by Freeman and King (1969). The weights for the three specimens were 740 kg, 1000 kg, and 1300 kg. The methods used to measure and calculate energy budget or heat balance have been described by Finch (1976) and Porter and Gates (1969). Metabolic rates were measured using an open system oxygen collection technique (Fedak et al., 1981). Rectal temperature measurements were made hourly using biotelemetry and hand-held rectal thermometers. All experimental runs lasted from 72 to 96 hours. A total of 1100 hours of measurements are summarized below.

RESULTS

The black rhinoceros is primarily nocturnal and thermally labile. The reduction in diurnal activity coincides with the hottest times of the day. The captive animals in this study closely followed previously reported patterns with high levels of activity at night, gradually decreasing in the morning, and not increasing again until late afternoon.

The maximum daily fluctuation in rectal temperature measured in these experiments was 7.1°C. Temperature change was directly related to the behavior of the animal and variations in the ambient temperature. Measured heterothermia in the black rhinoceros was independent of the state of hydration. Although shivering was recorded at a rectal temperature of 31.8°C and post-exercise sweating was noted at a rectal temperature of 41.9°C, generally the black rhinoceros was a committed heterotherm.

Periods of depressed rectal temperature occurred between the hours of 0600 to 0800, reaching an average low of 35.8°C at 0630 hours. Maximum rectal temperatures were recorded between 1400 and 1700 hours, peaking at 1500 hours, with an average of 37.7°C. The average ambient air temperature for all of the runs was 21.5°C. Measured standing metabolic rates were very close to the values predicted for animals within this body size range (Kleiber, 1975). The measured average was 0.176 ml $O_2 g^{-1} h^{-1}$ as compared with a predicted 0.12 ml $O_2 g^{-1} h^{-1}$.

On external examination a black rhinoceros would seem to have few anatomical similarities with a giraffe. However, both have unusually thick skin; it averages 2.2 cm thick (range 1.0 to 3.2 cm) on the back, sides, and neck. Two theories put forward to explain this do not hold up. That the dermal thickening is structural and necessary to hold a larger animal together can be disputed because skin thickness is not uniform. The skin is thinnest on the abdomen where the mechanical strain is the greatest. Nor can the skin be necessary, protective dermal armor. Thickening is found in all terrestrial animals with body weights exceeding 1000 kg, and it would be very unusual for unrelated species to have the same dermal armor requirements.

The variation in skin thickness most closely resembles variation in coat thickness found on sheep (Macfarlane, 1968), and may serve a similar function. To test the hypothesis of dermal thickening in the black rhinoceros as an adaptation for thermal insulation, a series of temperature measurements was made at the skin surface, under the skin, and from

the rectum. Although air temperatures were unseasonally cool, nyctohemeral differences of 3°C to 10°C between core and surface temperatures were measured. Using these values and the metabolic rates reported above, an average thermal conductivity of 0.47 W m^{-1}°C^{-1} was calculated for the rhinoceros skin. This value is within Mount's (1979) range of thermal conductivities for fur coats.

The thick dermis is an effective insulator against heat gain during the daytime. By allowing the skin-surface temperature to exceed ambient temperature, some long-wave radiation is reradiated to the environment. High surface temperatures recorded during the night may be due to vasodilation of the epidermis, a mechanism that hypothetically could regulate heat loss via long-wave radiation to the night sky. Thick skin may surpass a fur coat as insulation against heat because the surface temperature of skin can be selectively controlled.

A study of heat gain and heat loss pathways for a single black rhinoceros (Finch, 1976) indicated that perhaps the most important component of the heat balance is long-wave radiation, which is entirely passive. Long-wave radiation contributes over 50% of the diurnal heat gain and nearly 70% of the heat loss.

The large body mass of an adult black rhinoceros acts as a thermal buffer against body-temperature fluctuations. The thick skin is an effective thermal insulator that results in most of the incoming heat's being reradiated to the environment. Little heat is lost by evaporation, a conservative measure that leads to range extension in semiarid conditions.

The black rhinoceros uses behavioral thermoregulation extensively to avoid heat accumulation. By browsing and moving at night and seeking shady cover during the day, most of the heat that would be gained from long- and short-wave radiation can be avoided. Black rhinoceros become inactive in the mid-morning and sleep until late afternoon. This greatly reduces the amount of heat they must store each day.

A paradox remains, however. How do the very young rhinoceros survive? With a body weight of less than 300 kg and a much higher surface-to-volume ratio, the infant has relatively little thermal inertia and cannot avoid as much heat gain as the adult. Assuming the adult and infant are physiologically the same, the infant must use behavioral thermoregulation to a much greater extent during the first year postpartum. How this is accomplished still remains unknown.

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V. A. Langman

Early Farming Societies in the Negev Desert

Grant Recipient: Thomas Evan Levy, Negev Museum, Be'er Sheva, Israel.[1]

Grants 2470, 2678, 2829: To investigate social, economic, and paleoenvironmental aspects of Chalcolithic village sites in the northern Negev desert, Israel.

This long-term multidisciplinary study is concerned with change in protohistoric social organization and subsistence strategies in the northern Negev desert of Israel. Fieldwork and research focuses on sites dating to the formative Chalcolithic period (ca. 4500 to 3200 B.C.). In Palestine the Chalcolithic period precedes the Early Bronze Age, when the first urban centers emerged in the region. In the northern Negev one of the largest Early Bronze urban centers emerged at the site of Tel Arad (Amiran, 1978). Sites dating to the preceding Chalcolithic period should reveal some of the processes responsible for the evolution of urbanism in the southern Levant.

National Geographic Society funding made excavations possible at Shiqmim, one of the largest (about 9.5 ha) and best preserved Chalcolithic sites in the northern Negev desert. The site is located along the Nahal (Arabic, *Wadi*—a seasonal drainage) Be'er Sheva, approximately 18 km west of the city of Be'er Sheva. The site is along the interface between semiarid and arid zones. Shiqmim is important in that large Chalcolithic village sites with abundant architectural remains are rare in western Palestine.

Geology[2]

To place the site in its regional geomorphic setting, geological reconnaissance was made in 1982 along a 4-km section of the Nahal Be'er Sheva from the Shiqmim well to MeZad Aluf. A distinct gravel deposit,

[1] Co-investigator was David Alon, Israel Department of Antiquities, Jerusalem.

[2] This section is by staff geologist Paul Goldberg, Institute of Archaeology, Hebrew University, Jerusalem.