Elephants shuttle to thermoregulate

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Abstract

Overheating is a major concern for large mammals, and many species make landscape-scale movements to avoid thermal stress. The movements of savanna elephants *Loxodonta africana* have received much attention in the context of water dependence, yet temperature has seldom been invoked to explain them. We tracked 14 herds of elephants in Kruger National Park, South Africa using GPS collars over a period of 02 years. We quantified the extent to which elephants used the landscape in terms of total residence time, first passage time, and number of revisits. Using conservative criteria, we identified habitual water-points and studied elephant movement between successive visits to water. We found that elephants in Kruger are dependent on water sources, with more short trips away from water in the hot-wet season, and more long-distance forays in the cool-dry season. 80% of elephant movements between water-points are loops, ie, individuals returning to the water-point of origin. In a 24-hour period, elephants arrive at water-points when temperatures are highest (afternoon), and are farthest away when they are lowest (midnight). Elephant speed is highest when approaching and leaving water, ie, when ambient temperatures are high, which has implications for management decisions that alter water dependence to control their space use in a rapidly warming world.

# Introduction

Animals faced with heat stress thermoregulate by altering their physiology and behaviour (Angilletta 2012). Most physiological responses to high temperatures, such as sweating in mammals, rely on water evaporation to transfer heat away from the core-body. Many animals must complement physiological thermoregulation with behavioural mechanisms of losing heat. In general, behavioural responses to overheating involve utilising heat-sinks to which excess body-heat may be transferred. For example, the large ears of savanna elephants *Loxodonta africana* aid in rapid cooling by offering a large surface area that readily loses heat to the environment (Wright 1984). Thermal stress may also be avoided by temporal changes in activity. Most desert dwelling mammals are nocturnal, yet even in milder climates, ibex *Capra ibex* and elephants shift their activity peaks to earlier in the day in the hot season (Aublet *et al.* 2009; Leggett 2010). Occupying landscapes that promote heat loss, such as water sources or shade under dense vegetation constitutes another important class of behavioural responses to heat stress. For example, moose *Alces alces* seek refuge from high temperatures in shady coniferous forests in summer (Beest et al. 2012), while Arabian oryx *Oryx leucoryx* select for covered sites during the hottest part of the day (Hetem *et al.* 2012). Some landscapes, such as water sources, may promote both behavioural and physiological thermoregulation, as water is both a direct heat sink as well as a critical resource for evaporative water loss. This allows large tropical herbivores such as Cape buffalo *Syncerus caffer* and elephants to wallow and drink at water sources to cool down (Bennitt *et al.* 2014; Purdon 2016).

Animals must balance the energetic benefits of using water as a thermoregulatory aid against the costs of negative interactions such as predation and competition at crowded waterholes (Cain *et al.* 2012; Owen-Smith and Goodall 2014). Individuals may attempt to avoid such costs by periodically shuttling between water and more optimal foraging and resting sites, but this increases movement costs and decreases time that could have been spent feeding (Johnson *et al.* 2002; Cain *et al.* 2012; Owen-Smith and Goodall 2014; Giotto *et al.* 2015). Body size may mediate how a species reckons with the costs and benefits of visiting water. Large species such as buffalo and eland *Taurotragus oryx* that overheat more quickly are likely to be more water-dependent than smaller ones such as sable antelope *Hippotragus niger,* and zebra *Equus quagga* (Cain *et al.* 2012; Shrestha *et al.* 2012; Bennitt *et al.* 2014; Owen-Smith and Goodall 2014). Water-dependence can introduce periodicity to an animal’s movement, such as that corresponding to the diel or seasonal cycle (Giotto *et al.* 2015). However, it is in turn affected by seasonal changes. For example, buffalo in the Okavango delta are found farther from permanent water sources in the hot-wet season when they can use ephemeral pools, and closer to water in the cool-dry season (Bennitt *et al.* 2014). Further, seasonal changes in temperature and resource availability can affect the activity and movement of ungulates, changing their distribution in relation to water (Leggett 2010; van Beest *et al.* 2012; Shrestha *et al.* 2012; Owen-Smith and Goodall 2014). This sets up an interaction between environmental conditions such as ambient temperature, an individual’s physiological state, and its position in relation to water sources.

Savanna elephants in southern Africa are an excellent study system to investigate the effect of temperature on movement strategies in relation to water. Elephants lack a substantial evaporative heat-loss mechanism, relying instead on behavioural strategies to avoid heat stress (Hiley 1975; Wright 1984; Wright and Luck 1984). Additionally, elephants select for thermally stable landscapes (Johnson *et al.* 2002; Kinahan *et al.* 2007), regularly returning to water sources to drink (Valls Fox 2015). Desert living suggesting a direct effect of temperature on movement speed. Kruger experiences a contrasting and atypical combination of hot-wet and cool-dry seasons, allowing the effect of decreased water provisioning to be decoupled from that of increased temperature. Here, we first test whether in-built temperature sensors (hereafter thermochrons) accurately report the thermal landscape of elephants, and then proceed to characterise elephant movement in relation to water sources and ambient temperature.

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