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SHORT COMMUNICATION

Spatial relationship between elephant and sodium concentration of water disappears as density increases in Hwange National Park, Zimbabwe

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African elephants *Loxodonta africana* (Blumenbach) may profoundly affect vegetation and associated animal biodiversity in savannas (Conybeare 2004, Skarpe *et al.* 2004). Understanding the patterns of habitat use by elephants is crucial to predict their impacts on ecosystems (Ben-Shahar 1993, Nelleman *et al.* 2002), particularly now that many populations are recovering from past culling events or poaching outbreaks (Blanc *et al.* 2007). Surface water is one of the major constraints on elephant distribution (Chamaillé-Jammes *et al.* 2007, Stokke & du Toit 2002), and accordingly, elephant impacts are higher in the vicinity of water (Ben-Shahar 1993, de Beer *et al.* 2006). However, waterhole selection by elephant remains poorly understood. Weir (1972) showed in Hwange National Park (hereafter Hwange NP), Zimbabwe, that elephant numbers at waterholes over 24 h increased with the sodium concentration of water on nutrient-poor Kalahari sands. His work has become widely cited in elephant studies as it remains the only one, to the best of our knowledge, to have studied elephant use of waterholes in relation to the mineral concentration of water. Weir's work, however, took place when elephant densities in Hwange NP were low, likely below 0.5 elephants km^{-2} as estimated by aerial censuses (Williamson 1975). Since then, the elephant population has increased dramatically, particularly since the halt to culling operations in 1986 (Chamaillé-Jammes 2006, Cumming 1981). The present elephant density is much higher, estimated to be over 2 elephants km^{-2} (Chamaillé-Jammes *et al.* 2007, in press), and is one of the highest in the world (Blanc *et al.* 2007). Increased density may modify ecological constraints and affect the hierarchy of habitat selection processes (Morris 2003), and the extent to which water-nutrient selection still constrains elephant distribution at high population density – when their impact on savanna vegetation is the highest – remains unknown.

We revisited the relationship between elephant number at waterholes and sodium water concentration. Weir (1972) originally surveyed elephant numbers at eight waterholes over 24-h periods during four consecutive dry seasons (1959–1962). Monitoring of these waterholes continued between 1967 and 2005 using a similar protocol conducted by Wildlife Environment Zimbabwe, although not all waterholes were surveyed in all years due to logistical constraints. We used these data to study the relationship between elephant number and water sodium concentration during four time periods with contrasting elephant population numbers and dynamics. (1) The period of Weir's study, using Weir's original data. We use this as a baseline and provide a statistical test of the relationship (missing in the original publication). The elephant population was estimated to be around 4000 elephants (Cumming 1981, Williamson 1975). (2) The 1967–1986 period, when the elephant population was controlled through culling, ranging between 6500 and 21 853 individuals (Chamaillé-Jammes *et al.* 2006, Williamson 1975). (3) The 1987–1992 interval, when culling was discontinued and the elephant population increased steadily from 17 559 to 35 793 (Chamaillé-Jammes *et al.* in press). Elephant abundance at waterholes however remained low due to high surface-water availability throughout the park caused by good rainfall. (4) The 1993–2005 period, when the population fluctuated widely at a high level, census estimates being between 22 548 and 44 492 elephants (Blanc *et al.* 2007, Chamaillé-Jammes *et al.* in press).

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Sodium concentration of water was re-evaluated in 1997 at four out of the eight waterholes studied by Weir. We compared the sodium concentration of these waterholes between October 1962 (flame emission photometry, Weir 1972) and October 1997 (atomic absorption spectrophotometry, Holdo *et al.* 2002), i.e. during the dry season when elephant numbers were monitored. Although the very low sample size prevented us from reaching definitive conclusions, the strength of the relationship ($r^2 = 0.999$, $P = 0.0006$) suggested that the relative dry-season sodium concentrations in water among waterholes did not vary much since Weir's study. Sodium concentration of rainfall is very low (Jonnalagadda & Nyika 1996) therefore sodium in waterholes must predominantly derive from pumped water with sodium concentration reflecting the local geology of the water table. It is therefore not surprising that relative sodium concentration did not vary much over 30 y, and we used the more complete data set of Weir's sodium concentration in all analyses. Additionally, this suggests that sodium attraction must be particularly expressed during the dry season when water at most waterholes is provided through artificial pumping of groundwater.

The relationship between water sodium and elephant number in the early 1960s was highly significant on a logarithmic scale (Figure 1a; $r^2 = 0.895$, $F_{1,6} = 51.3$, $P = 0.0004$). This relationship, however, was not significant in any of the three subsequent periods when mean elephant numbers at waterholes were higher (Figure 1b–d; 1967–1986: $r^2 = 0.245$, $F_{1,6} = 1.95$, $P = 0.212$; 1987–1992: $r^2 = 0.013$, $F_{1,6} = 0.08$, $P = 0.786$; 1993–2005: $r^2 = 0.290$, $F_{1,6} = 2.45$, $P = 0.168$). Overall, the relationship was significant ($P < 0.05$) for only one out of the 17 y for which the eight studied waterholes were simultaneously surveyed. Our study supports observations from aerial censuses (Williamson 1975) that large elephant concentrations were already evident in the early 1970s around waterholes with low sodium concentrations.

Why has the strong relationship demonstrated by Weir (1972) disappeared? Many factors affect herbivore foraging (Bailey *et al.* 1996), and the extent to which sodium will affect elephant distribution is likely to depend not only on sodium concentration of water, but also on factors such as sodium requirements, distance between sodium-rich waterholes, forage availability around waterholes as well as daily ranging behaviour and social interactions. Using data collected in 1997, Holdo *et al.* (2002) showed that elephants were unable to meet sodium requirements by forage consumption only in this region of Hwange NP. It has to be noted that geophagy at salt licks allows elephants to maintain a positive sodium balance even when drinking at sodium-poor pans (Holdo *et al.* 2002). This did not however prevent the observation

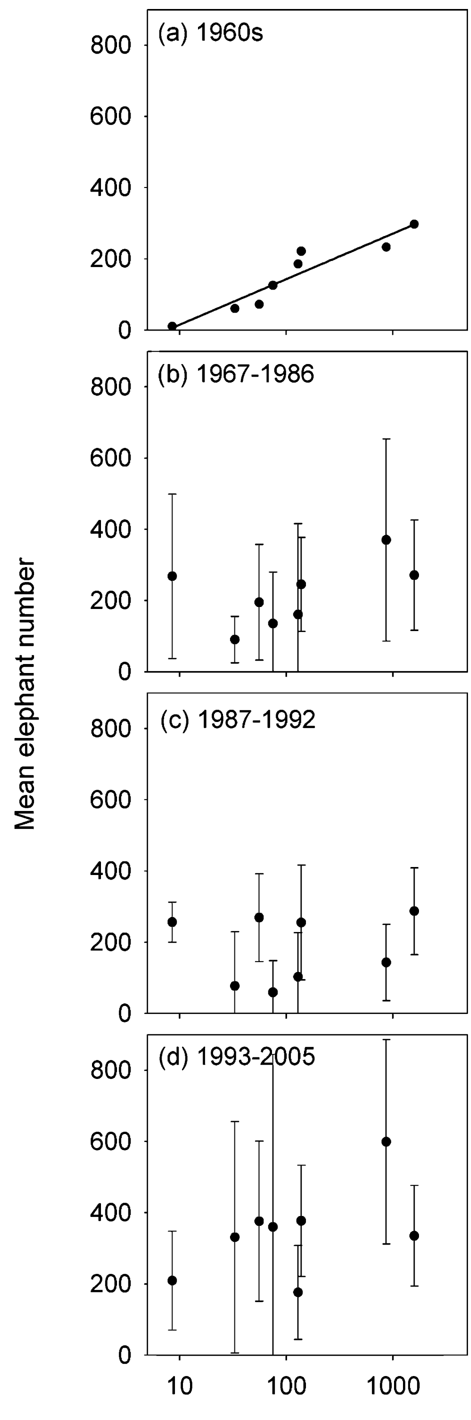

Figure 1. Relationships between sodium concentration of water and 24-h elephant number (± SD) at waterhole during the dry season in the 1960s (from Weir's original data, Weir 1972) (a), prior to 1986 under a culling management policy (b), during the fast population increase after culling stopped in 1986 (c), and from 1993 onwards when the population fluctuated at high density levels (d).

of a positive association between elephant numbers and sodium concentration at waterholes during Weir's study. Thus, elephants should still have favoured sodium-rich waterholes to drink, particularly as foraging itself was not directed towards sodium-rich vegetation (Holdo 2003).

Increase in the elephant population represents the major change over the periods studied here, consequently influencing elephant number at waterholes. For instance, daily activity patterns are modified when crowding at waterholes increases (Valeix *et al.* 2007). Elephants also tend to distribute themselves more evenly across waterholes when elephant numbers at waterholes increase, numbers increasing mostly at the less-crowded waterholes (Chamaillé-Jammes *et al.* 2007). Spill-over effects from crowded waterholes to neighbouring, less-attractive waterholes, could lead to spatial autocorrelation in distributions that would mask actual selection towards sodium-rich waterholes. With the limited dataset of eight waterholes used for the analyses, however, no spatial autocorrelation was found underlying the elephant–sodium relationship in any of the four periods studied (Moran test on residuals, all $P > 0.1$). Elephant numbers (but not sodium concentrations) were also surveyed at additional waterholes, revealing that positive spatial autocorrelation was significant only during 3 y (1991, 1998, 2003; Moran's I, $P < 0.05$, $n = 29$ waterholes).

Elephant numbers at waterholes are also strongly affected by surface-water availability associated with annual rainfall (Chamaillé-Jammes *et al.* 2007), and elephant numbers at waterholes could remain low even at high population size during rainy years (see the large standard deviations in Figure 1). The relationship between elephant number and sodium concentration was significant in only one of the years studied after Weir's work, however, suggesting that factors other than short-term crowding and associated water depletion and interference between individuals were responsible for the lack of a relationship. High elephant densities around waterholes probably have long-term cumulative effects on vegetation structure and forage production. Most boreholes were drilled between 1935 and 1968 (Williamson 1975) and at the time of Weir's work vegetation and forage availability changes due to elephant numbers may have remained low even at the most crowded waterholes. Over time, impacts may have accumulated and reduced the potential benefits of drinking at sodium-rich, crowded, waterholes. This idea is however countered by the observation that elephant numbers at the most crowded waterholes did not decrease since the time of Weir's study (Figure 1), indicating that ecological conditions did not deteriorate significantly, and still sustained high elephant numbers.

The causes underlying the simultaneous disappearance of the elephant–sodium relationship with increased density remain obscure. In Hwange NP the elephant population has now levelled-off at a high density (Chamaillé-Jammes *et al.* in press), and it will be difficult to accurately assess why sodium does not play the same important role as before. In order to confirm and understand the disruption of the association between elephant numbers and sodium concentration at waterholes when density increases, we call for regular monitoring of these variables, as well as of additional data on factors that may affect elephant selection of waterholes, in presently increasing populations (Blanc *et al.* 2005, 2007). This may help in predicting the extent and distribution of elephant effects on vegetation in the vicinity of water. Our study not only cautions against the uncritical use of the widely cited work of Weir (1972), but also shows how a once-strong relationship (shown elsewhere for other herbivores: Grant & Scholes 2006, McNaughton 1988) can vanish with population changes, suggesting that it may be important to bring a dynamic perspective in our understanding of herbivore mineral nutrition.

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