IN FOCUS

Having your water and drinking it too: resource limitation modifies density regulation

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S. Chamaillé-Jammes, H. Fritz, M. Valeix, F. Murindagomo & J. Clobert (2007) Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology*, **77**, 135–144.

Determining the interaction between extrinsic and intrinsic drivers of variation in population abundance through time continues to challenge ecologists. Chamaillé-Jammes and colleagues (this issue) examined African elephant time series to explore how water availability alters the density feedback mechanisms restricting population growth. The relationship between population growth rate and density shifted from an upward convex to a more linear form after controlling for rainfall. Spatial variation in water availability also attenuated density dependence as elephants adjusted their distribution relative to current environmental conditions. This work has important climate change implications for the conservation management of African herbivores.

We have come a long way since the early days of population ecology, when the foundational mathematical developments of self-limitation and population cycling were emerging (e.g. Lotka 1925; Fisher 1930; Nicholson 1933; Andrewartha & Birch 1954; Caughley 1977). This period was followed by the fixation on collecting empirical support and designing analytical tools for the detection of density dependence (reviewed in Turchin 1995). With increasing mechanistic (reviewed in Sibly & Hone 2002) and phenomenological evidence (Woiwod & Hanski 1992; Brook & Bradshaw 2006) for density feedback as a major determinant of population structure, cycling, sustainable yield and persistence (Sibly &

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Hone 2002), recent work has focused less on the existence and detection of the phenomenon itself, and more on its strength and form (Turchin 2003; Sibly *et al.* 2005; Owen-Smith 2006).

Even more recently, population ecologists have sharpened their focus to investigate the complex interactions between intrinsic (density-dependent) and extrinsic (environmental stochasticity) forces that shape long-term population dynamics. This has been a particular challenge in population ecology because so many different factors can simultaneously affect a population's rate of change (Dennis & Otten 2000; Sibly & Hone 2002). An elegant new study on African elephant population dynamics by Simon Chamaillé-Jammes *et al.* (2007) represents another simple, yet clever leap forward in this regard. Examining elephant census data from a recovering population in Hwange National Park (Zimbabwe) in relation to rainfall and density patterns, Chamaillé-Jammes *et al.* used information-theoretic methods of multimodel inference to contrast a series of density-independent and density-dependent models relating population rate of change (r) to abundance (N) (Fig. 1). As predicted for large, long-generation species (Fowler 1981; Sibly & Hone 2002; Owen-Smith 2006), they found an upward convex relationship between r and N – the onset of density dependence was relatively abrupt at high population densities (Fig. 1A). They were also careful to test for any potential bias resulting from measurement error that can seriously compromise conclusions about density dependence based on phenomenological evidence (Freckleton *et al.* 2006).

The phenomenon of density dependence, as measured by abundance time series, is an emergent property of the changing interactions between organisms and their food resources, predators and environmental conditions that modify survival and reproductive rates (Owen-Smith 2006). Environmental variability can modify apparent patterns of density feedback. Factors such as weather that alter food availability may result in demographic rates and corresponding values of r that fluctuate independently of population density, or the relationship between r and N may itself be substantially modified by weather effects (a well-established phenomenon in ungulates, e.g.: Owen-Smith 1990; Milner, Elston & Albon 1999; Owen-Smith 2006; Wang *et al.* 2006). Chamaillé-Jammes *et al.* addressed this problem well for the world's largest herbivore by introducing rainfall variability (the main driver of herbivore food availability in African savannas) as a modifier of carrying capacity (K), expressed using variants of the θ-logistic population model (see also Hone & Clutton-Brock 2007). This is particularly important because θ-logistic density feedback models that do not take environmental variability into account assume a constant (average) K over the interval of investigation (Fig. 1A). As predicted, the rainfall-modified K-ratio model produced quite a different result – a linear relationship between r and rainfall-scaled abundance (expressed
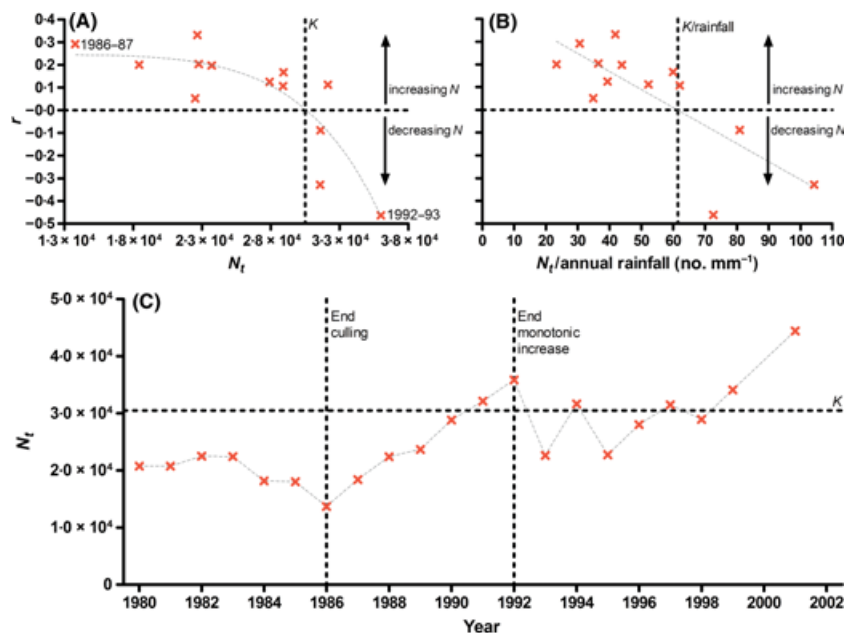

Fig. 1. Phenomenological expressions of density dependence in a population of African elephants in Hwange National Park, Zimbabwe monitored from 1980 to 2002 (data from Chamaillé-Jammes *et al.* 2007). (A) Population growth rate ($r = \log_e(N_{t+1}/N_t)$) vs. annual (t) abundance (N_t). When $r > 0$, the population is increasing and when $r < 0$, it is decreasing – thus, carrying capacity (K) is calculated as the N_t where $r = 0$. The upward convex shape of the relationship is typical of large mammalian herbivores where negative density feedback is evident only when population size is large (i.e. near K) (Fowler 1981; Sibly & Hone 2002; Owen-Smith 2006). (B) However, when N_t is scaled by annual rainfall (mm), the upward convex pattern disappears and the relationship between r and environmentally scaled N_t becomes linear (the 'K-ratio' model – Hone & Clutton-Brock 2007). (C) The abundance time series on which the r vs. N_t relationship is based (1986 onwards) shows how the population increased rapidly after culling ceased in 1986 and then began to fluctuate around carrying capacity after 1992 in response to variable annual rainfall. Generally, long (i.e. relative to the generation length of the study organism – Brook & Bradshaw 2006) and precise (Freckleton *et al.* 2006) time series are required to pick out the subtleties of the r vs. N_t relationship, although when monitoring spans a wide range of densities (e.g. such as after culling has ceased) and environmental conditions, revealing patterns can emerge quickly.

graphically in Fig. 1B). Furthermore, the predicted abundance patterns based on this linear ratio-dependent model mimicked the observed patterns in elephant abundance better than strictly density-dependent models.

Landscape-scale patterns in resource availability can also reveal much about the processes governing population-level density feedback patterns (Wang *et al.* 2006). For example, local 'crowding' effects brought on by extreme weather conditions can increase intraspecific competition and strengthen negative density feedback. Taking their analysis one step further along these lines, Chamaillé-Jammes *et al.* demonstrate over a broad range of individual waterholes that elephant numbers increased more rapidly at waterholes where elephant densities were initially low, but there was no predicted increase at waterholes already densely populated. This observation provides indirect evidence in support of the findings of Wang *et al.* (2006) that spatial heterogeneity in resource availability can attenuate the effects of negative density feedback in wide-ranging herbivores that can move in response to landscape variation, even though the entire population on average responds to lower rainfall by increasing the strength of density dependence. Thus, the spatial configuration of water resources and the corresponding response of elephant density across the study area show clearly just how the broader-scale abundance trends are a reflection of the fine-scale dynamics of water-limited sub-populations exploiting limited resources patches.

Population ecologists are placing increasing emphasis on teasing apart the complex interactions between environmental and intrinsic regulatory mechanisms; however, these analyses generally demand particularly detailed and long-term data to provide useful insight (e.g. Sæther 1997; Sæther *et al.* 2002; Kéry, Madsen & Lebreton 2006; de Little *et al.* 2007). Chamaillé-Jammes *et al.* have provided us with a simple yet insightful way of using population abundance data to infer intrinsic regulatory processes and how these are modified by environmental context. The study's empirically supported take-home message is that failing to incorporate environmental stochasticity may result in a reduced capacity of models to describe systems where resource limitation alters the population-level expression of density dependence. Further, the spatial heterogeneity of resource availability can modify the strength and form of density regulation, even over short time scales (i.e. < 1 generation).

The form of the density-dependent relationship is an essential determinant of the type of long-term dynamics manifested by a population. For example, a rapid decline in *r* around the region of carrying capacity (zero net population growth) or time lags can lead to oscillations in abundance rather than equilibrium (Owen-Smith 2006). This curvilinearity in the phenomenon is an emergent property of the different ways in which demographic rates begin to respond to increases in density (Owen-Smith 2006). For example, upward convex relationships between *r* and density in African ungulates tends to result mainly from density-independent juvenile mortality at lower densities, reduced fertility at intermediate densities followed by declining adult survival at high densities (Eberhardt 2002; Owen-Smith 2006). A natural progression

from Chamaillé-Jammes *et al.*'s detailed temporal and landscape-scale analyses now would be to investigate such mechanisms more closely. In other words, which demographic rates (survival, fertility) and behavioural processes (immigration, emigration) operating on which age classes drive the strength and form of broad density regulation features? This paper provides an effective empirical starting point to address strategically just such mechanistic questions in the elephant system, and it builds generally on the many classic and recent advances in population regulation theory published in *Journal of Animal Ecology* and elsewhere.

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