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On Predicting Elephant Population Dynamics

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The Stable Age Distribution (SAD)

A long-discussed concept in management planning is the 'stable age distribution.' A population achieves a Stable Age Distribution (SAD) when the proportion of individuals in a particular age class does not change from one time interval to the next. In elephant management, SAD has two potential uses. First, it may serve as an aid in predicting growth and anticipating ecological impacts (Fowler & Smith 1973; Calef 1988; Woodd 1999; Mackey *et al*. 2006, 2009). Second, it could signal a healthy, undisturbed population whereas deviations indicate the impact of disturbance (Sukumar 1993; Wittemyer 2001). Here I examine the former application, discussing what can be learned from case studies of African elephant (*Loxodonta africana*) populations, and their relevance for managing Asian elephants (*Elephas maximus*).

Mathematically, SAD requires constant survival and fecundity over time in each age class, which results in an unchanging growth rate, often referred to as the 'intrinsic' growth rate (Birch 1948 and references therein). This is not to say that the survival (or its complement, mortality) and fecundity are the same across age classes – they may well be age-specific. The SAD is also not to be confused with 0% growth; on the contrary, a population can exhibit a SAD during the exponential growth phase. If it attains a logistic or 'S' shaped growth curve, a population may be said to have reached its equilibrium density (and may be called 'density dependent' or 'density regulated'), as dictated by the ecological carrying capacity (Owen-Smith *et al*. 2006). A population may reach equilibrium density only under very limited conditions, and if it occurs at all that *particular* SAD is referred to as the "equilibrium age structure" (c.f. Fowler & Smith 1973; further discussion of interpretations and misinterpretations of the age distributions may be found in Caughly & Gunn 1996).

The notion that calculating the equilibrium age structure can be a useful tool for managing elephant populations goes back to at least Fowler & Smith (1973), who try to define these limited conditions for specific populations. Several authors have used or referenced the (non-equilibrium) SAD as aids in management planning (Fowler & Smith 1973; Calef 1988; Dominy *et al*. 1998; Woodd 1999; Mackey *et al*. 2006). But, species such as elephants can change their habitats without the population stabilizing (Gough & Kerley 2006; van Aarde & Jackson 2007; Woolley *et al*. 2008). The alteration of habitats by elephants, primarily through damage to trees, has other ecological consequences (Mackey *et al*. 2006; Owen-Smith *et al*. 2006; Woolley *et al*. 2008). Could elephant populations ever reach SAD, and would it be reasonable for managers to plan around an anticipated equilibrium age structure?

Case studies of African elephant populations

Large, well-established elephant populations may have relatively stable age distributions with low growth rates of 4%-7% (Whyte *et al*. 1998). Calef (1988) states: "Actually it makes little difference what age structure exists initially, since any population increasing at a constant exponential rate reaches a stable age distribution." The premise is that in comparable environments, achieving such an age distribution should settle the population into equilibrium density.

This is not necessarily true for small populations. Crucial considerations are *how long* it would take an elephant population to reach any kind of stable state if at all, whether it can be maintained naturally, and how much area it would then require. The Addo Elephant National Park (AENP) population started from near-extinction with 11 individuals in 1931, grew steadily, undisturbed by poaching, and remained closed to migrants (Woodd 1999). It had a nearly unbiased 1:1 sex ratio and nearly every individual was known. Wood (1999) compares models of population growth to the actual for the period 1976-1998 and projects it ahead 120 years. A stable age distribution (defined as no further fluctuations to the nearest 0.1% in all age/sex classes) was possible by 2045 with an annual growth rate of 5.2%. But the projected time to attaining SAD was at least 114 years.

Whitehouse & Hall-Martin (2000) conducted a massive reconstruction of individual histories for this same population, from 1931-2000 using park records and photographs. It did in fact show a mean annual growth rate of 5.53 % for the period 1976-1998, close to Woodd's prediction (Whitehouse & Hall-Martin 2000). Age distributions were not discussed. Woodd (1999) states that a proposed expansion of the park has a pre-determined carrying capacity of 2700 elephants, reached by 2043. He argues that because the current population is far from reaching a SAD, an age-structured model is a better predictor of future growth than simple exponential growth projections. It is conceivable that this population would never in reality be allowed to reach a SAD, even if it could, due to space limitations (Whitehouse & Kerley 2002).

Dominy *et al*. (1998) tried to determine when the population of elephants in Hluhluwe-Umfolozi park (HUP) would reach a pre-determined limit of 320 animals. HUP is similar to AENP, starting from a small founder population of 18 animals, but there were waves of juveniles as a result of new introductions. Such re-introductions are now becoming quite common, especially in South Africa (Mackey *et al*. 2006, 2009). They ran a simulation for 30 years starting at 1990 (the birth of the first calf to a re-introduced female), yielding an annual growth rate of 6.6 percent and SAD within 20-25 years. But in similar parks, where newly introduced or poached populations have very young age structures and female biased sex ratios, population growth rates can be higher, anywhere from 7% (Foley & Faust 2010), 10% (Mackey *et al*. 2006) or even >16% (Van Jaarsveld *et al*. 1999; Slotow *et al*. 2005). SAD would not be realistic to expect before parks reach their limits. Mackey *et al*. (2009) argue that: "It would not be practical to wait to model and develop management plans for such populations until their age structures stabilized. Instead, focus should be placed on the fact that because of their younger population structures and higher growth rates…small, closed, recently introduced elephant populations may have management requirements different from those for large, well-established populations."

The reintroduction waves at HUP are analogous to natural birth pulses, as occurred in Amboseli during recovery from drought or hunting (Moss 2001), with similar demographic consequences. By the end of 1978 Amboseli contained only 480 animals, not much larger than HUP's limit, but the population has since more than doubled. Even this large, well-established has shown no signs of a SAD (Moss 2001). These two populations had similar beginnings; though the model projects a SAD between 20-25 years, this may not occur in reality.

Reality violates model assumptions

Models that project population growth based on SAD may rely on a few simplifications. Woodd (1999) assumes "all demographic parameters are constants" and justifies it on the basis that his model was primarily developed to predict population growth as the area allotted for the park increases, and thus he assumes there will be no effect of crowding (density dependence). In addition, he assumes a) equal fecundity of all breeding females b) stable environments. Condition a) is justified on the basis that although younger individuals are more productive, mortality is not appreciably different among age classes and thus on average fecundity can be treated as constant. Condition b) this is an implicit rather than explicit assumption. Clearly, in this case the SAD is built into the model itself. A sensitivity analysis shows the population to be responsive to initial conditions (the number and age structure of the starting population) as well as to changes in fecundity and survivability (Dominy *et al*. 1998). Even a 10%

decrease in survivability in age classes >5 yrs leads to extinction of the population. The latter assumptions are also not very realistic for many populations. Fecundity is generally not constant with age (Moss 2001), the reproductive success of an individual can depend on other individuals in her social group (including those that are much older), and not all social groups may be equally successful (McComb *et al*. 2001). Environmental fluctuations do occur. Not only does survivorship decrease during droughts, younger age classes are more vulnerable (Moss 2001). Therefore while mathematical simplifications can be useful, if the goal is to manage real populations, models will have to be tailored to the specific conditions of areas in question.

A population model showing steady logistic growth becomes chaotic if environmental stochasticity is incorporated (Armbruster & Lande 1993). This may be in part because the long gestation period results in a birthrate that lags far behind ecological conditions (Armbruster *et al*. 1999). For species with long generation times, trends in growth or decline may take on the order of 200 years or more to become established (Armbruster *et al*. 1999). By considering genetic viability and land yield, Armbruster & Lande (1993) find that an area of 1000 miles^2 as minimum habitat size in semi-arid areas. This technique can be modified to fit the conditions of any particular area under consideration, such as rainfall schedules. Projections based on stochastic simulations, paired with sensitivity analyses of age and gender-specific effects, would be more instructive than models relying on SAD and intrinsic growth rates. The challenge to applying such models, of course, is in acquiring enough baseline data to determine what parameter values are appropriate.

Similarities and dissimilarities with Asian elephant populations

Why is this discussion relevant to managers of Asian elephants? For Asian elephants there may be no distinction between large, well-established populations and small "irrupting" populations (Mackey *et al*. 2009) because most populations are likely to be much smaller than those of African elephants (Choudhury *et al*. 2008). With increasing pressure to relegate elephant populations to small, fenced reserves, managers of Asian elephants will find themselves in situations similar to those just described. Moreover, the translocation and release of cohorts of young animals, as in Sri Lanka, may have demographic effects analogous to those reported here. The population dynamics of small African elephant populations should well inform our expectations. Many populations of Asian elephants, occupying highly fragmented environments, are unlikely to be at a SAD.

Data on fecundity, age at first reproduction, inter-birth intervals, the number of individuals by age and sex class, age- and sex-specific survival, and age at senescence are essential for understanding population trends. But whereas the visibility of savannah elephants allows individual-based studies, comparable studies are difficult for forest species. Censuses have often relied on indirect methods such as dung transects, which can have sizeable errors associated with them, especially for small populations (Barnes 2002), and since they are not individual-based, do not permit estimates of these critical variables. Current census data on Asian elephants are sparse (Blake & Hedges 2004; Choudhury *et al*. 2008).

We have little idea of population trends and their actual needs. As a consequence, protected areas are hardly designated on the basis of ecology. In Asian elephant management, in contrast to African elephant management, there is a greater focus on males than females, as the former are perceived to contribute more to human-elephant conflict (pers. obs.). Elephant movements may be restricted and habitats fragmented such that areas that may have formerly been able to recover from elephant activity will no longer be able to do so, resulting in edge effects and habitat degradation (Kinnaird *et al*. 2003; Leimgruber *et al*. 2003; Rood *et al*. 2010). Finally, the creation of artificial sources of water may heighten the impact (including the promotion of HEC) on areas that otherwise would not have had heavy elephant pressure, all of which has been observed in African elephants (Owen-Smith *et al*. 2006; de Beer & van Aarde, 2008; Loarie *et al*. 2009).

Elephant conservation, paradoxically, should not be elephant-centric from the standpoint of protecting biodiversity and ecosystem integrity. A pertinent question: is there any such thing as a 'natural' Asian elephant population today? Are there *any* that demonstrate what the equilibrium state would be? We simply do not know.

Longitudinal studies of individually-identified Asian elephant populations are needed. Recently Goswami *et al*. (2007) have conducted a capture-recapture based census on males. Capture-recapture is one promising means obtaining the requisite demographic variables and should be more widely used on females (de Silva 2010). Together with the demographic modelling approaches described above, it would also enable presence-only modelling of habitat use (Rood *et al*. 2010). Models that consider time scales on the order of 200 years or more would be needed to predict the fates of elephant populations and their environments, which ultimately affect the human populations surrounding them. This leaves us with a very important question that cannot yet be answered – given the rapid pace of habitat loss and ecological change today, on what time scale and to what end do we wish to carry out our conservation efforts? Surely if our aim is to preserve biota intact for future generations, and indeed for our own survival - particularly those with long-lived species, whether they are elephants or trees - we must learn to think and plan on longer timescales than we currently do.

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