

Note and record

Black rhinoceros demography should be stage, not age, based

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Sauer and Slade (1987) emphasized that age-based demography is a peculiarity of human demography, not a general feature of vertebrate demography. Caswell (2001:39) noted, 'For many organisms, however, the age of an individual tells little or nothing about its demographic properties'.

Life stages are well-defined biological states, not necessarily or solely determined by age. Transitions between life stages are also biologically meaningful and interesting (Caswell, 2001). In this note, we argue that stages of calf, subadult and adult are the appropriate basis for demographic study of rhinoceros and that these stages are not purely age based. For specificity, we focus on the black rhinoceros *Diceros bicornis* (Linnaeus, 1758).

The terms 'calf', 'subadult' and 'adult' are typically defined as age classes rather than as biological states (Walpole *et al.*, 2001; Hrabar & du Toit, 2005; Brodie *et al.*, 2011; Ferreira, Greaver & Knight, 2011), which obscures the biological meaning of such demographic studies. Adults are reproductively mature. Subadults must provide their own food and security, direct maternal investment having ceased, but have not yet achieved reproductive maturity. The calf stage is the state upon which maternal investment in offspring is focused, providing food and security. But age correlates poorly with life stage. Consequently, age-based demography conflates distinct agents of mortality; age of death,

without also knowing the state during which death occurred, is demographically ambiguous. Moreover, a purely age-based designation of female adulthood may misrepresent female fecundity by including individuals that are still biologically subadults or excluding individuals that have already reproduced.

It is vital to adopt standardized notions of life stages for black rhinoceros demography so that future demographic studies are biologically meaningful and comparable, so that confusions regarding risks and rates of mortality and rates of fecundity do not arise. We propose the definitions given in Table 1, from Law, Fike and Lent (2013). We underscore that these definitions are not age classes and that transitions between these states are biologically meaningful. Emslie, Adcock and Hansen's (1995) age classes are useful for ageing black rhinoceros, but their biological significance is ambiguous (Owen-Smith, 1988:133).

The biological meaning of 'calf' is dependency upon the mother. As definitions must be practical as well as biologically meaningful, dependency is judged by association of the offspring with its mother. If disassociation is not directly observed, it may be judged by birth of the mother's next offspring. In some cases, a calf may maintain continuous association with its mother beyond actual dependency, for example, in the absence of another birth, a failed birth or early mortality of the younger offspring. Such behaviour is best viewed as idiosyncratic and of social significance rather than demographically informative. Mortality of the individual during such an association but at an age beyond which direct maternal investment has ended is more appropriately viewed as the death of a subadult rather than a calf. It is necessary therefore to set an age by which the calf-subadult transition occurs despite ongoing association with the mother. After reviewing the literature (Owen-Smith, 1988; Emslie, Adcock & Hansen, 1995; Walpole *et al.*, 2001; Hrabar & du Toit, 2005; Skinner & Chimimba, 2005; Brodie *et al.*, 2011; Ferreira, Greaver & Knight, 2011), we adopted the fourth birthday as the upper limit of the 'calf' stage.

Although an offspring may re-associate with its mother and younger sibling (Owen-Smith, 1988:136–137; Lent

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Table 1 Proposed definitions of biological life stages for demography of the black rhinoceros. No postreproductive adult stages are defined, but future research may require them, particularly for males

Life stage	Proposed definition
Calf	From birth to: observed separation from the mother; at the birth of the mother's next calf; or the calf's fourth birthday; whichever comes first
Subadult	From ceasing to be a calf until becoming an adult
Female adult	The subadult–adult transition occurs for females at first calving or at the seventh birthday, whichever comes first
Male adult	The subadult–adult transition occurs at the eighth birthday

& Fike, 2003), we do not regard such behaviour as undermining the definition of subadult as independent of its mother. Such associations are thought to be more temporary and although they may reduce the chance of mortality, that possibility is an individual characteristic, not a stage- or age-based trait.

Subadult means effective independence from the mother but prior to reproductive maturity, which refers to the behavioural, not just physiological, capability of reproduction. Following Owen-Smith (1988:139), we propose that the female subadult–adult transition occurs at first calving. As with the calf–subadult transition, it is necessary to impose an age limit; females that suffer delayed reproduction or fail to reproduce altogether must still be construed as adult at some point independently of reproductive history. Based on the literature cited previously, we adopted the seventh birthday as this limit.

Without further knowledge of male reproductive behaviour, for example, through genetic studies (Garnier, Bruford & Goossens, 2001), it is not practical at this time to define other than an age-based criterion for the male subadult–adult transition. We follow Emslie, Adcock and Hansen (1995), based on Hitchins and Anderson (1983), that males become adults upon their eighth birthday. While sparse evidence suggests female rhinoceros do not experience an extended period of senescence, too little is known, especially concerning male fecundity, to advocate postreproductive states.

In Law, Fike and Lent (2013), the mean age (in months) that female calves became subadults was 28.0 (± 5.9 ; $n = 45$), that male calves became subadults was 29.5

(± 6.9 ; $n = 33$) and that female subadults became adults was 76.9 (± 8.3 ; $n = 19$). Only three calves transitioned to subadulthood by reaching their fourth birthday prior to separation from their mother, one female and two males. Nine female subadults transitioned to adulthood upon reaching their seventh birthday without having calved; three of these females had still not calved at the end of the study, when they were 116, 88 and 87 months of age, respectively. Mortality was concentrated in the subadult stage; all subadults that died did so after separation from their mother. Only one calf died. The population was young, and few animals died from old age during the study.

Demography requires meaningful biological states, which must be standardized for comparisons amongst studies. Demographic studies are vital for understanding and managing the critically endangered black rhinoceros. We have offered robust definitions of life stages for their demography. We encourage the community of rhino researchers to reach a consensus on definitions to be adopted and advocated by the African Rhino Specialist Group and to extend this approach to demography to other species of rhinoceros.

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