



## REPLY TO RIGGIO ET AL.:

## Ongoing lion declines across most of Africa warrant urgent action

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In dismissing the conclusions of our paper, "Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas," Riggio et al. (1) misrepresent our treatment of specific survey sites and raise erroneous objections to our overall statistical approach.

They question our data from two sites in East Africa: Masai Mara and Katavi. However, our Masai Mara analysis was based on the best available data for the reserve as a whole: A 12-mo study in 1991–1992 and Dloniak's 2005 survey, cited by Packer et al. (2), that replicated the earlier methods and indicated a 40% decline in 14 years. Kiffner et al.'s 2005 survey in Katavi (3) responded to conservation concerns over declining ecosystem health (4) and reported a lion density of only 15% of estimated carrying capacity (168 lions compared with an expected 1,100) (2). Our paper acknowledges the imprecision inherent in the Katavi time series of ground surveys, which were recently used to report a significant decline in lion numbers from 1995 to 2010 (5). Our Bayesian analysis fully considers uncertainty resulting from observation and process errors, and our conclusions do not depend on the Katavi time series: Excluding Katavi only reduces the probability of a one-half decline in three lion generations in East Africa from 37% to 32%.

They query our classifying of two areas as fenced where fencing encompassed only part of the perimeter. Our title emphasizes the conservation success of

"intensively managed areas," and Kruger is one of the most heavily managed reserves in Africa, whereas Kgalagadi is fenced near areas of human habitation in the otherwise unoccupied Kalahari. Besides their greater investments in wildlife management, low human densities give countries in southern Africa a unique advantage in conserving their wildlife (2), and herbivore populations are also declining at a far greater rate in West, Central, and East Africa than in southern Africa (6).

Our regional population analyses include all reported time series data for both increasing and declining populations; we calculated the projected growth rate  $\lambda^T$  of T years (7), but these metrics were not intended to provide a Bayesian forecast of population sizes (8). Weighting these metrics by population size would introduce a serious bias because sites that had previously suffered the largest declines would contribute relatively little to aggregated projected growth rates.

Our assessment is based on the widely accepted criteria of the Red List and is entirely consistent with similar trends described for specific sites and for Africa as a whole (e.g., references 1, 4, 5, 23, 31, 32, and 38 of ref. 9). Many of these references were coauthored by the authors of Riggio et al. (1), and their arguments do not undermine our conclusions. Our conclusions call for urgent action; lion conservation will require unstinting efforts by stakeholders at local, national, and international levels (9).

- 1 Riggio J, et al. (2016) Lion populations may be declining in Africa but not as Bauer et al. suggest. Proc Natl Acad Sci USA, 10.1073/pnas.1521506113.
- 2 Packer C, et al. (2013) Conserving large carnivores: Dollars and fence. Ecol Lett 16(5):635-641.
- 3 Kiffner C, Meyer B, Mühlenberg M, Waltert M (2009) Plenty of prey, few predators: What limits lions Panthera leo in Katavi National Park, western Tanzania? Oryx 43(1):52–59.
- 4 Caro T, Kerley GIH (2008) Decline of large mammals in the Katavi-Rukwa ecosystem of western Tanzania. Afr Zool 43(1):99–116.
- **5** Caro T (2011) On the merits and feasibility of wildlife monitoring for conservation: A case study from Katavi National Park, Tanzania. *Afr J Ecol* 49:320–331.
- 6 Craigie ID, et al. (2010) Large mammal population declines in Africa's protected areas. Biol Conserv 143(9):2221-2228.
- 7 Caswell H (2011) Matrix Population Models (Sinauer, Sunderland, MA).
- 8 Hobbs NT, Hooten MB (2015) Bayesian Models: A Statistical Primer for Ecologists (Princeton Univ Press, Princeton).
- **9** Bauer H, et al. (2015) Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc Natl Acad Sci USA* 112(48):14894–14899.

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The authors declare no conflict of interest.

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