

TECHNICAL COMMENT

Conserving large populations of lions – the argument for fences has holes

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Abstract

Packer *et al.* reported that fenced lion populations attain densities closer to carrying capacity than unfenced populations. However, fenced populations are often maintained above carrying capacity, and most are small. Many more lions are conserved per dollar invested in unfenced ecosystems, which avoid the ecological and economic costs of fencing.

Keywords

Carnivores, conservation, cost-effectiveness, fence, lions, population density, population size.

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The highest priority of large carnivore conservation is to maintain large populations in the face of habitat loss, environmental degradation, overharvest and direct persecution (Brashares *et al.* 2001; Wittemyer *et al.* 2008; Riggio *et al.* 2012). Packer *et al.* (2013) recently argued that building fences around protected areas is the best method to conserve African lions. Their deterministic population projections suggested that all fenced populations would maintain densities near carrying capacity for 100 years, 'whereas less than half of unfenced reserves are likely to persist above 10% of their carrying capacity for the next 20–40 years' (although this statement contradicts their Fig. 3, which shows > 50% of unfenced populations remaining above the criterion for 75 years).

Packer *et al.*'s argument for perimeter fencing depends heavily on the criterion used to evaluate conservation success. Although they stated 'we explicitly test the effectiveness of fencing and management budgets on lion population size and growth rates,' they actually examined population density rather than population size – a critical distinction because many fenced, high-density lion populations hold few individuals. Clearly, a low-density population of 2000 individuals has more conservation value than a high-density population of 20. Consideration of this issue of scale alone weakens the argument for fencing, but other concerns exist.

MANY FENCED POPULATIONS WERE MAINTAINED ABOVE CARRYING CAPACITY

Packer *et al.* emphasized that lions were closer to estimated carrying capacity in fenced populations than in unfenced populations. However, mean lion density was 153.9% of estimated carrying capacity for fenced reserves smaller than 1000 km², and 67% of these populations were maintained above carrying capacity (Fig. 1). At the extreme, lion density was > 290% of estimated carrying capacity in Madikwe and Tembwe GRs. In large areas such as the 93 000 km² Selous ecosystem, super-saturation with lions would not be possible or desirable (Creel & Creel 1996; Durant 2000). Enclosed, super-saturated populations have conservation value, but are not a good model for conservation in naturally-regulated ecosystems. Restricting the analysis to populations at or below their carrying capacity and controlling for management expenditure per km² (see below), lion density relative to carrying capacity was not detectably related to fencing (effect size = 2.4%, $t_{27} = 1.04$, $P = 0.31$, OLS regression with continuous variables logged, centered and scaled, data from Packer *et al.* Table S1).

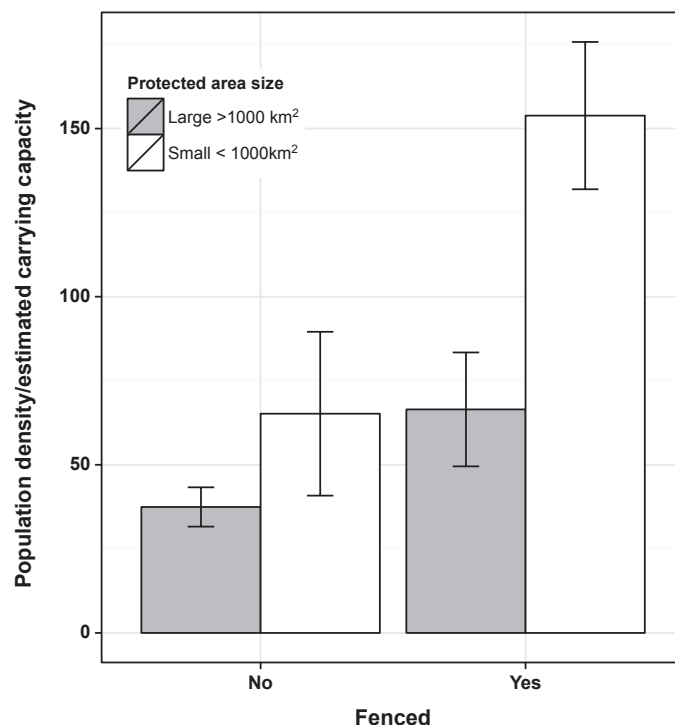


Figure 1 The relationship of lion population density to the use of perimeter fences in large and small protected areas. Density is expressed as a percentage of estimated carrying capacity, as in Packer *et al.* Error bars show ± 1 SEM. In fenced reserves smaller than 1000 km² (the majority of fenced populations) lion densities were significantly above the predicted carrying capacities reported by Packer *et al.* Some of the estimates of density were approximate, but we retained all estimates so that differences in our inferences and those of Packer *et al.* are not due to differences in the data set. However, estimation error is generally large for measures of population growth derived from such data. Packer *et al.* did not report variances for population density, and thus they could not propagate this variance into estimates of population growth or simulations to estimate population persistence. Incorporating such variance reduces the likelihood of persistence (Case 2001), with a stronger effect on smaller populations (most of which were fenced, see Fig. 2b).

MANY FENCED POPULATIONS WERE SMALL

In their Fig. 3, Packer *et al.* compared the proportions of fenced and unfenced populations that remained above 10% of estimated

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carrying capacity in deterministic projections over 100 years. To evaluate this result, one must recognize that for 10 of 17 fenced reserves, 10% of carrying capacity is ≤ 5 lions. Because Packer *et al.*'s criterion does not directly consider population size, as few as 29 lions across 10 fenced reserves would be considered 10 successes, while the conservation of 640 lions in the Selous Game Reserve would be considered a failure. A population of 640 lions that is below its carrying capacity has more conservation value and potential than a smaller number of lions already at higher density. Clearly, population sizes must be explicitly considered for meaningful conservation priorities.

FENCED AND UNFENCED RESERVES DIFFER IN WAYS OTHER THAN FENCING

Fenced protected areas were operated with median expenditure per km² 7.6 times larger than unfenced areas (Fig. 2a, $t_{38} = 3.72$, $P = 0.00064$, medians: 1900 USD km⁻², 251 USD km⁻²). Fenced

reserves were $1/11$ th the size of unfenced reserves (Fig. 2b, medians: 399 km², 4471 km²). This difference in area is important because it affects total population size, and because the effect of fencing on density was much stronger in small reserves (Fig. 1). Finally, lions in most fenced areas were managed more intensively [e.g. translocations into 56% of fenced populations during the period of study (often repeatedly) vs. 0% of unfenced reserves; anthropogenic removals were common in both types].

CONSERVATION OF UNFENCED LION POPULATIONS WAS MORE COST EFFECTIVE

Packer *et al.* presented data on lions/km² and management expenditure/km², from which we calculated lions conserved per dollar of management expenditure. For each management dollar, unfenced reserves conserved many more lions than fenced reserves. (Fig. 2c, $t_{37} = 2.11$, $P = 0.042$).

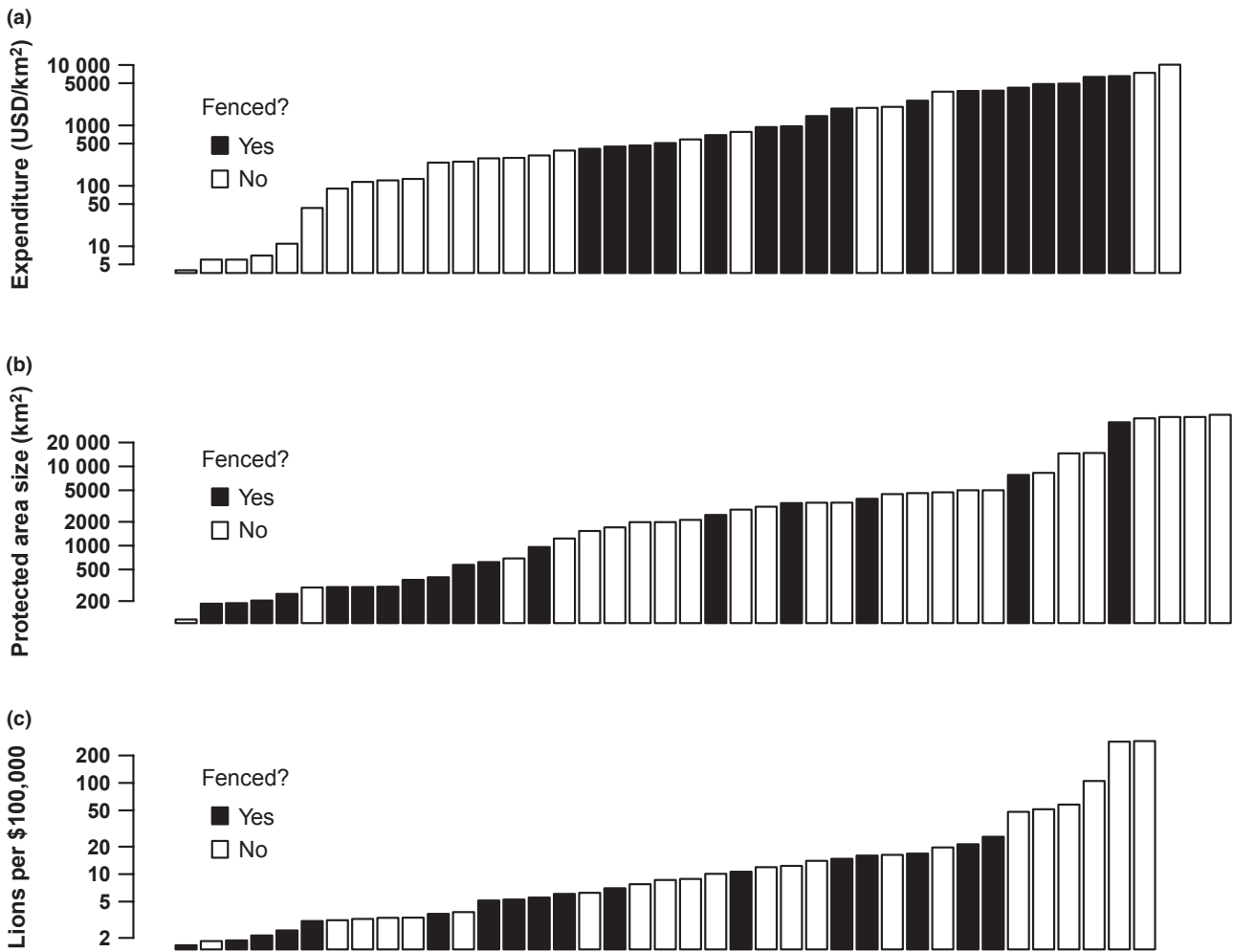


Figure 2 Lion populations with and without perimeter fences, ranked by (a) management expenditure per km², (b) protected area size and (c) lions conserved per \$100 000 of management expenditure. Unfenced populations were larger, were managed with smaller budgets (per unit area), and were more cost-effective. The ordinate is logarithmically scaled in all panels. In panel C, we assume that lion density (like other ecological attributes) responds directly or indirectly to the level of management expenditure used to conserve an area. If lion density was estimated for a subset of a protected area, we assume similar effects of expenditure on lion density (but not equal density) inside and outside the study site. The significantly larger number of lions conserved per dollar of management expenditure in unfenced populations runs opposite to the primary inference of Packer *et al.*, although they did not present any statistical test of cost-effectiveness.

FENCES CAUSE A BROAD RANGE OF ECOLOGICAL, ECONOMIC AND SOCIAL EFFECTS

Fences can prevent edge effects from penetrating into protected areas and reduce conflicts outside protected areas (Ogada *et al.* 2003; Hayward & Kerley 2009), but also carry important costs, including ecosystem fragmentation, loss of dispersal and migration routes, genetic isolation, reduced conservation value of buffer zones (and consequent loss of wildlife-based economic benefits in buffer zones), and utilization of fencing materials for wire snare poaching (Newmark 1996, 2008; Hayward & Kerley 2009; Lindsey *et al.* 2011; Gadd 2012; Becker *et al.* 2013). Lions can maintain good densities with little conflict in areas that maintain connectivity for wildlife while allowing avoidance of people and livestock (Schuette *et al.* 2013). We concur with Packer *et al.* that effective lion conservation will require better funding, but rather than fencing, we recommend better-funded law enforcement inside reserves, reduced and better-regulated hunting, landscape-level strategies that reduce human-wildlife conflict outside reserves, and a high priority for conservation in large and intact ecosystems.

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AUTHORSHIP

All authors contributed to the development of hypotheses and points of discussion. Scott Creel conducted the statistical and graphical analysis. Scott Creel, Sarah Durant and Matt Becker wrote the first draft.

REFERENCES

- Becker, M.S., McRobb, R., Watson, F., Dröge, E., Kanyembo, B. & Kakumbi, C. (2013). Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biol. Conserv.*, 158, 26–36.
- Brashares, J., Arces, P. & Sam, M.K. (2001). Human demography and reserve size predict wildlife extinction in West Africa. *Proc. Roy. Soc. Lond. Ser. B*, 268, 2473–2478.
- Case, T.J. (2001). *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, New York.
- Creel, S. & Creel, N.M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Cons. Biol.*, 10, 526–538.
- Durant, S. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behav. Ecol.*, 11, 624–632.
- Gadd, M. (2012). Barriers, the beef industry and unnatural selection: a review of the impact of veterinary fencing on mammals in Southern Africa. In: *Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes?* (eds Sommers, M.J. & Hayward, M.). Springer Science, New York, 153–186.
- Hayward, M.W. & Kerley, G.I.H. (2009). Fencing for conservation: restriction of ecological potential or a riposte to threatening processes? *Biol. Cons.*, 142, 1–13.
- Lindsey, P.A., Romañach, S.S., Tambling, C.J., Chartier, K. & Groom, R. (2011). Ecological and financial impacts of illegal bushmeat trade in Zimbabwe. *Oryx*, 45, 96.
- Newmark, W.D. (1996). Insularization of Tanzanian parks and the local extinction of large mammals. *Conserv. Biol.*, 10, 1549–1556.
- Newmark, W.D. (2008). Isolation of African protected areas. *Front. Ecol. Environ.*, 6, 321–328.
- Ogada, M.O., Woodroffe, R., Oguge, N. & Frank, L.G. (2003). Limiting depredation by African carnivores: the role of livestock husbandry. *Cons. Biol.*, 17, 1521–153.
- Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M. *et al.* (2013). Large carnivore conservation: dollars and fence. *Ecol. Lett.*, 16, 635–641.
- Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A. *et al.* (2012). The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiv. & Cons.*, 22, 17–35.
- Schuette, P., Creel, S. & Christianson, D. (2013). Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. *Biol. Cons.*, 157, 148–154.
- Wittemyer, G., Elsen, P., Bean, W.T., Coleman, A., Burton, O. & Brashares, J.S. (2008). Accelerated human population growth at protected area edges. *Science*, 321, 123–126.

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