Response to Comment on "On the Regulation of Populations of Mammals, Birds, Fish, and Insects"

Richard M. Sibly,[1]* Daniel Barker,[2] Michael C. Denham,[3] Jim Hone,[4] Mark Pagel[1]

Our conclusions are unaffected by removal of the time series identified by Peacock and Garshelis as harvest data. The relationship between a population's growth rate and its size is generally concave in mammals, irrespective of their body sizes. However, our data set includes quality data for only five mammals larger than 20 kilograms, so strong conclusions cannot be made about these animals.

Our analysis of the relationship between the abundance of a population and its rate of growth (*pgr*) used data from 4926 different populations in the Global Population Dynamics Database, GPDD (*1*). After filtering for data quality, there remained 1780 time series of mammals, birds, fish, and insects. We reported that the relationship between *pgr* and abundance is concave in 78% of species and that there is little variation between the major taxonomic groups. In their comment, Peacock and Garshelis (*2*) suggest that many of the mammal data sets in the GPDD are harvest data and are therefore uninformative about population size; that when unreliable large mammal data are removed, only one case remains; and that the general conclusions do not, therefore, apply to large mammals. We do not accept that all harvest data should be removed from the GPDD, because several analyses have reported that, where checks could be made, harvest sizes were proportional to population sizes (*3*–*6*). Nevertheless we here rerun the mammal analyses removing the data sets that Peacock and Garshelis identify as harvest data and show that our original conclusions are unaffected by this reanalysis.

[1]School of Biological Sciences, University of Reading, Whiteknights, Reading RG6 6AJ, UK. [2]Sir Harold Mitchell Building, School of Biology, University of St. Andrews, St. Andrews, Fife, KY16 9TH, UK. [3]Statistical Sciences Europe, GlaxoSmithKline Research and Development Limited, New Frontiers Science Park, Third Avenue, Harlow, Essex CM19 5AW, UK. [4]Institute for Applied Ecology, University of Canberra ACT 2601, Australia.

*To whom correspondence should be addressed. E-mail: r.m.sibly@reading.ac.uk

The GPDD was set up and is used as a collection of time series of population abundance (*7*–*12*). These measures of population abundance come from a wide range of sources and do vary considerably in data quality, as discussed on the GPDD Web site (*13*). In the absence of accurate, objective measures of data quality, the constructors of the GPDD used subjective judgment to assign a rank for apparent data quality on a scale from 1 (low) to 5 (high), using criteria such as the type of environment sampled, the species in question, the area of the sampling site, and the method of sampling. The GPDD does not classify the data as being harvest or otherwise. The two time series highlighted in the figures in (*2*) are graded 1. We accept that they should not have been included in our original analysis.

Our approach to the issue of variation in data quality was to run the analyses both on the whole data set and on a data set restricted to the top two GPDD gradings (i.e., grades 4 and 5). As we reported, we found no difference in conclusions between these two analyses, and this gave us confidence in the general validity of our results (*1*). In the case of the mammals, there are 19 time series, corresponding to 14 species, in the top two GPDD gradings.

We repeated our analysis without the harvest data identified by Peacock and Garshelis but now including the top four GPDD gradings. Peacock and Garshelis identified 52 mammal time series in this category, and these correspond to 29 separate species [see table S1 in (*2*)]. Of these species, 23 have a concave relationship between *pgr* and abundance, and 6 are convex (Fig. 1A, chi-square test of equal proportions: $\chi_1^2 = 10.0$, $P < 0.005$). The proportion that are concave is 0.79, similar to the overall figure of 0.78 that we reported for birds, fish, mammals, and insects (*1*). There is no evidence of an increase in θ with body size; indeed, the reverse is the case (Fig. 1A, Spearman's $\rho_{22} = -0.37$, $P = 0.07$). If harvest species are included in the above analysis, the proportion of curves that are concave is 0.80, and again θ decreases rather than increases with body size (Fig. 1B, Spearman's $\rho_{32} = -0.40$, $P = 0.02$).

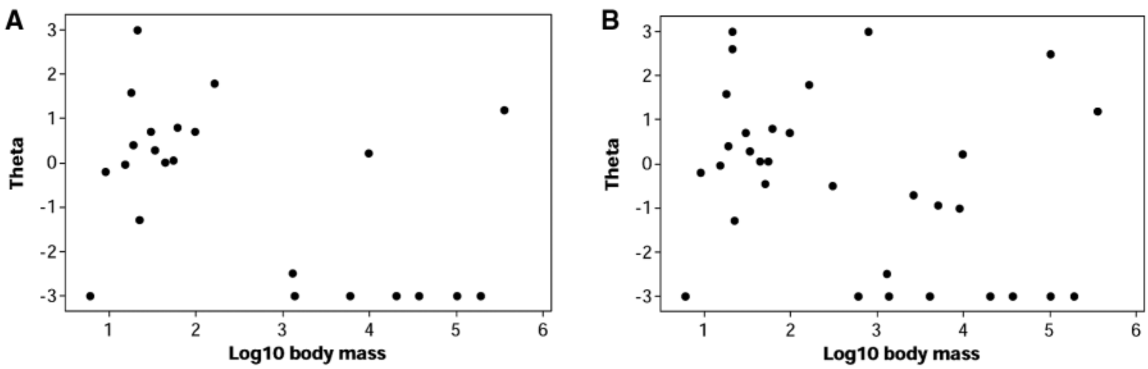

Fig. 1. Plots of θ against body mass *g* for mammals, one point per species. θ is the parameter fitted by (*1*) that specifies the curvature of the relationship between *pgr* and abundance. θ < 1 indicates a concave relationship, θ > 1 convex. θ values above 3 have been plotted as 3 (and similarly for θ < –3) to avoid giving undue prominence to large values of θ. Body mass data are not available for all species, but in some cases it has been possible to supplement GPDD data from (*16*). (**A**) The GPDD higher quality data (grades 2 to 5) classified by Peacock and Garshelis as nonharvest data. (**B**) As (A), but including harvest data. The GPDD data ID reference numbers of the time series from which these data were calculated are (A) 63, 64, 3605, 3606, 3607, 1318, 10532, 10543, 65, 66, 1301, 3512, 3514, 3581, 1308, 3969, 3970, 2723, 2724, 3888, 3515, 1295, 1296, 10545, 3580, 3256, 1328, 1330, 1331, 1332, 1333, 3404, 3198, 1273, 1274, 1275, 1276, 10533, 3466, 1327, 3736, 3582, 10541, 1292, 10535, 10540, 3603, 3268, 3877, 3879, 3880, and 3881. (B) also includes 1343, 1345, 1540, 1541, 3569, 3655, 3702, 3705, 3706, 3708, 3709, 3721, 3724, 3731, 4006, 4007, 10538, 10539, 11012, and 11015.

Restricting attention to the top two GPDD gradings, four of the five mammal species with body mass >20 kg have concave relationships (θ < 1). These are *Canis lupus*, *Panthera leo*, *Phoca vitulina*, and *Tragelaphus strepsiceros*. Only *Mirounga leonina* has θ > 1. Peacock and Garshelis discarded all four species with concave relationships. They discarded two on the grounds that the estimates of θ and its lower confidence limit appeared the same, i.e., equal to –31.6 in the GPDD. In reality, however, $-31.6 = -10^{-1.5}$ is the lowest value we could reliably estimate, so our estimates of θ are never below –31.6, and where we report that a lower confidence limit is –31.6, this means ≤ –31.6, as specified in our supporting online material for (*1*). Peacock and Garshelis argue that the other two species should be discounted because an extrinsic factor (rainfall) affected *pgr* independent of abundance. Extrinsic variation is, however, universal, and it would be difficult to estimate the *pgr*-abundance relationship without it.

Finally, Peacock and Garshelis imply the existence of a number of careful long-term studies showing the existence of convex *pgr*-abundance relationships, but of the four references they cite, two do not estimate *pgr* and one is based on unpublished data (*14*). We agree that the fourth, just published, is an exemplary study (*15*).

In summary, our original conclusions are unaffected by removal of the data sets identified by Peacock and Garshelis as harvest data. In particular, our conclusion is correct that, for the data in the GPDD, the relationship between a population's growth rate and its size is generally concave in mammals. Four of the five mammal species with body mass >20 kg have concave relationships, but strong conclusions cannot be drawn from just five cases, and more studies of large mammals are needed.

References

1. R. M. Sibly, D. Barker, M. C. Denham, J. Hone, M. Pagel, *Science* **309**, 607 (2005).
2. E. Peacock, D. L. Garshelis, *Science* **313**, 45 (2006); www.sciencemag.org/cgi/content/full/313/5783/45a.
3. N. C. Stenseth *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 15430 (1998).
4. I. M. Cattadori, D. T. Haydon, P. J. Hudson, *Nature* **433**, 737 (2005).
5. M. C. Forchhammer, T. Asferg, *Proc. R. Soc. London B. Biol. Sci.* **267**, 779 (2000).
6. I. M. Cattadori, D. T. Haydon, S. J. Thirgood, P. J. Hudson, *Oikos* **100**, 439 (2003).
7. J. M. Halley, K. I. Stergiou, *Fish Fish.* **6**, 266 (2005).
8. D. H. Reed, G. R. Hobbs, *Anim. Conserv.* **7**, 1 (2004).
9. D. H. Reed, J. J. O'Grady, J. D. Ballou, R. Frankham, *Anim. Conserv.* **6**, 109 (2003).
10. P. Inchausti, J. Halley, *Science* **293**, 655 (2001).
11. W. F. Fagan, E. Meir, J. Prendergast, A. Folarin, P. Karieva, *Ecol. Lett.* **4**, 132 (2001).
12. B. E. Kendall, J. Prendergast, O. N. Bjornstad, *Ecol. Lett.* **1**, 160 (1998).
13. Global Population Dynamics Database, http://cpbnts1.bio.ic.ac.uk/gpdd/quality.htm.
14. A. R. E. Sinclair, *Philos. Trans. R. Soc. London Ser. B* **358**, 1729 (2003).
15. N. Owen-Smith, *Ecol. Monogr.* **76**, 93 (2006).
16. S. K. M. Ernest, *Ecology* **84**, 3402 (2003).

21 February 2006; accepted 6 June 2006
10.1126/science.1124973

Science

Response to Comment on "On the Regulation of Populations of Mammals, Birds, Fish, and Insects"

Richard M. Sibly, Daniel Barker, Michael C. Denham, Jim Hone and Mark Pagel

Science **313** (5783), 45.
DOI: 10.1126/science.1124493