BERTRAM *ET AL.* REPLY—Koenig is spelling out as space prevented us[1] originally from doing that there are a variety of possible ways in which male lions (*Panthera leo*) may benefit from cooperating in large long-term breeding coalitions. We concentrated on large (≥3) as opposed to small (=2) coalitions and showed an absolute and *per capita* increase in reproductive success with increasing coalition size; this increase was obtained partly through an increase in the coalition's chances of gaining tenure of a pride and partly through an increase in the time for which they could retain it. Both gaining and retaining tenure are presumably assisted by a combination of Koenig's 'direct' and 'indirect' advantages, which are difficult to distinguish. For example, it is likely that the enhanced hunting success of larger groups[2], and their advantage in competitions with rival scavengers[3] such as hyaenas (*Crocuta crocuta*) and other lions, will improve the general condition of the coalition members and therefore help them to fight rival coalitions before and during pride tenure. 'Intrinsic' as opposed to ecologically imposed advantages are surely inseparable.

Singletons are an interesting case. We[1] presented data on only two singleton males (compared with 70 males in coalitions) because single males rarely hold prides. Those two who did manage to had reproductive success not significantly different from that of the far more numerous males in coalitions. Thus the data do not justify considering the formation of coalitions in lions to be 'making the best of a bad job'. It seems more reasonable to consider them, as with many other adaptations, as a way of making a good job better.

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Senegal River runoff

FAURE AND GAC[1] have used an unweighted 7-yr running mean of annual Senegal River runoff to predict future rainfall trends in the Sahel. They forecast a return to wetter conditions by 1985. Several questions arise from their analysis.

The first is whether the Senegal River runoff reflects Sahelian rainfall. The river rises in the more humid mountainous region to the south of the Sahel. We have correlated the published runoff figures in the paper with normalized annual rainfall departures for the Sahel (available up to 1975) (ref. 2 and S. E. Nicholson, personal communication). The correlation coefficient is 0.76 which is significant at the 0.1% level. Therefore, the runoff data are a reasonable proxy for Sahelian rainfall.

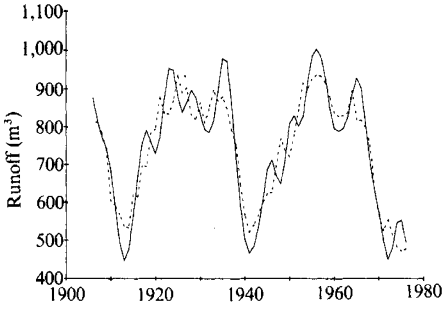

Fig. 1 Filtered Senegal River runoff flow. ——, 7-yr binomial filter; – – –, 7-yr moving average.

The second problem concerns the use of unweighted running means. These are notorious for introducing spurious cyclicity into the data, and for shifting the position of peaks and troughs[3]. We performed a spectral analysis on the runoff data (which are approximately normally distributed) and found strong cycles at around 30 and 2.29 yr. This shows reasonable agreement with Faure and Gac. We then introduced a 7-yr binomial filter to the raw runoff data, which produced the curve shown in Fig. 1. It can be seen that the 1975 trough has now moved back to 1972, and the smooth upward trend of Faure and Gac has been lost. On this basis, the return to wetter conditions by 1985 can no longer be assumed. It is by no means certain that the 30-yr cycle will be repeated for a third time. This points clearly to the dangers of a prediction based on a record length only double that of the wavelength of the cycle. The statistical problem is further reinforced by Nicholson's evidence that synoptic conditions in the two recent drought phases were quite different (ref. 2 and S. E. Nicholson, personal communication).

One final problem is the use by Faure and Gac of gradient lines *a* and *b* (in their Fig. 4) as estimation limits of the slope of return to wetter conditions. Because they are based on a sample of two, they give an unjustified air of accuracy to the results.

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FAURE AND GAC REPLY—We are grateful for the statistical demonstration of Palutikof *et al.* that the Senegal River discharge data are a good proxy for Sahelian rainfall, although this has long been known by inhabitants, nomads and those who have studied the Sahel. The spectral analysis and binomial filtering of the discharge data by Palutikof *et al.* are in good agreement with our Fig. 4[1] and illustrate well the general tempo of Sahelian drought in this century.

However, the conclusion of a return to wetter conditions after a drought, and the approximately 30-yr cycle, are not based solely on this century's discharge data for the Senegal River. Our conclusion is rather the result of a convergent series of arguments from various disciplines and data at several time scales, which yield evidence of a dramatic fluctuation in rainfall over recent centuries with period of several decades between wet and dry peaks (Fig. A). It is these data which we primarily use to establish the existence of the rough time scale of fluctuation, and which would be enough to inform us that severe Sahelian drought can be expected at time intervals of several decades. The river discharge data merely provide more accurate time series data. We use this to argue that if the inferred fluctuations of the past few centuries were similar to those observed during this century, then the next severe droughts could be expected in about 2005, with an intervening wet period around 1992.

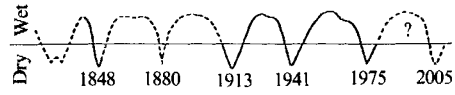

Fig. A General trend of annual rainfall in Sahel from historical information (modified from ref. 3).

Geological, prehistoric and historical data in this region[2] show a variability of climate in which the inferred rates of change are a function of the time scale of study.

Drought is not a simple mathematical, statistical or philosophical phenomenon. It is a natural phenomenon, and must be studied as such by a multidisciplinary approach.

We thank G. S. Boulton for clarifying and rewriting our reply.

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