For the former Soviet Union, analysis of station history documentation[3] yielded a network of 190 homogeneous evaporation-pan reporting stations, with data starting in 1951. The digital US pan-evaporation network was determined to be homogeneous by the good agreement in trends between all 746 stations and a small subset whose station history indicated no possible inhomogeneity-inducing changes.

The data used are seasonal averages of mean daily pan evaporation from May to

Area-average pan evaporation (solid lines) and diurnal temperature range (DTR, dotted line, updated from Karl et al.[1]) for three regions in the former Soviet Union and two regions in the United States. All time series are presented as standard deviation anomalies from the long-term mean values. The smooth curves result from 11-point binomial smoothing (for DTR only smoothed lines are presented). Linear trend estimates for these regions (in standardized anomalies per 100 yr) are shown in parentheses. They are significant at the 99% level except for the former Soviet Union Middle Asian region. The largest actual change in pan evaporation is in the western United States, where the area-averaged linear regression slope corresponds to a decrease in pan evaporation of 97 mm per warm season (May–September) during the past 45 years in a region with a mean pan evaporation of 1,130 mm per warm season.

September for the United States, and months when there was no ice in the pans for the former Soviet Union. Pan evaporation for four of five geographical regions show significant downward trends over the past 50 years (see figure). Area-averaged time series of pan evaporation for each of these regions were compared with similar area-averaged time series for various climatic parameters, including mean minimum temperature, mean maximum temperature, diurnal temperature range (DTR), total cloud cover, and precipitation. Of these, pan evaporation was most highly correlated with DTR, with a mean r^2 of 0.48. Widespread decreases in DTR over the past several decades are also among the primary findings of analyses of asymmetrical trends in daily maximum and minimum temperature[1]. Pan evaporation and DTR have varied similarly in recent decades.

The downward trend in pan evaporation over most of the United States and former Soviet Union implies that, for large regions of the globe, the terrestrial evaporation component of the hydrological cycle has been decreasing. This partially explains increases in runoff over the past two decades in the European part of the former Soviet Union[4] and the northern United States[5], and corresponds well with both decreases in maximum summer temperatures over these regions[1] and a decrease in growing-season degree-days (annual sum of daily temperatures above

5 °C) over the Siberian and European former Soviet Union[6].

Karl et al.[1] speculated that increases in cloud cover, especially low cloud cover, may explain the decreases in DTR. Our results support this speculation, as pan evaporation has been decreasing and is correlated negatively with cloud cover with a mean r^2 of 0.34 for the five regions. Aspects of the temperature and hydrological cycles have changed in tandem over the past 50 years, and the features of this recent climate change include decreases in potential evaporation.

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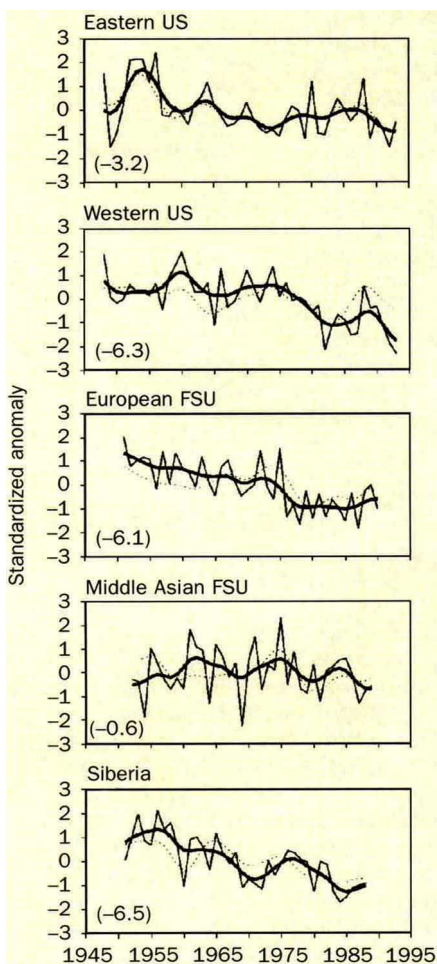*Asheville, North Carolina 28801, USA*
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Baboon fertility and social status

SIR — Packer and colleagues[1] reported that for the baboon population of Gombe, as for many other primate populations[2-5], high dominance status had salutary effects on several components of female reproductive success. They also reported that high status entailed certain reproductive costs, and proposed behavioural and endocrine mechanisms for their production. Here we address the generality of the costs reported, a potential methodological problem in the results, and the validity of the behavioural and endocrine assumptions of the proposed model of reproductive costs.

The conclusion that high rank is associated with increased risk of lifetime infertility[1] derived from the finding that, of Gombe females that had no successful pregnancies or matured extremely late, one was high-ranking, three had high-ranking mothers and the fifth was a 'social climber' who rose above her family to achieve high rank. The significance of the positive relationship between dominance and lifetime reproductive success was $P = 0.0675$ when all low-fertility females were included, and $P = 0.0354$ when the 2 of 37 females that never gave birth to live young were excluded from the data

set[1]. Analyses for other sites[3-6] have not reported cases of lifetime infertility.

Our 25-year longitudinal studies in Amboseli, Kenya, include 133 adult females in two wild-foraging groups (stable in size, 50% survival through two years) and a third that is partially food-enhanced (expanding in size, 90% survival). We have had only one case of lifetime infertility; this individual was not high-ranking. Similarly, neither of our two 'social climbers' was infertile. If individuals with non-lethal pathologies are more likely to survive when infant mortality is low, higher incidences of reproductive pathologies might be expected when infant survival is high. However, none of the 31 females in the expanding group has been infertile. Present evidence is, therefore, inadequate to determine either whether incidences of lifetime infertility or its relationship to social status differ significantly among groups or populations.

The most surprising observation made by Packer et al. was an association of high rank with high rates of spontaneous abortion[1], in contrast to a large literature that has implicitly or explicitly linked reproductive impairment and spontaneous abortion to the physical and

social stressors of social subordinance[7]. Pregnancy was judged by the female's perineum turning pink[1], which is variable in timing and does not usually occur until 4–6 weeks into the 25-week gestation, precluding detection of early pregnancies and abortions. Therefore, while high status was clearly associated with mid- and late-pregnancy losses, the picture for early losses, and so total losses, cannot be discerned. Yet the bulk of pregnancy losses occur during this initial period and are those that seem to be most sensitive to stressors[8,9].

If the overall rate of stress-induced pregnancy loss was higher in subordinate females (as expected from the existing literature), the authors' apparently opposite finding might have resulted from their detection method, which is nonrandom with respect to pregnancy stage. Nor does the absence of a rank-related statistical difference in cycling time[1] remove this possibility, as the interval difference resulting from these early losses would be small. Wasser[6] reported the same association between high status and high rate of spontaneous abortion at Mikumi; however, this same pregnancy detection method was used (personal communication).

For 474 conceptions in Amboseli in which we identified pregnancies just over two weeks from conception (less than a week after expected implantation), no relationship was found between dominance rank and rate of spontaneous abortion ($P>0.40$); in each group, higher-ranking females tended to have lower rates of fetal loss, not higher, as reported for Gombe and Mikumi.

Packer and colleagues speculated that high rank is associated with higher rates of agonistic encounters and, as a result, with high levels of circulating androgens which would produce the reported reproductive dysfunction of dominant adults[1]. Although high rates of aggression might play a role in the initial establishment of dominance[10], they are not normally associated with the maintenance of the stable dominance relationships[10–12] characteristic of adult female baboons. Nor does high rank seem to be associated with high rates of agonistic inter-
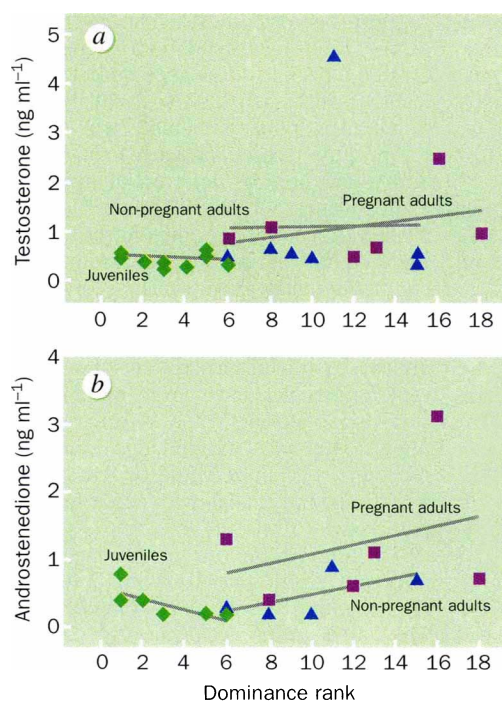
The relationship between social dominance rank and serum androgen levels in female baboons (a, testosterone; b, androstenedione; diamonds, juveniles; triangles, non-pregnant adults; squares, pregnant adults). Dominance status is presented solely as status within age–sex class; an integrated female ranking would place juveniles scattered throughout the adult female ranking and reduce any slope and significance of status. Serum was collected and analysed as reported[15,16], with control for season, time of day and time from darting to blood drawing. Juveniles weighing less than 5 kg, females beyond the first half of pregnancy, and lactating females with young infants were not immobilized; the data, therefore, do not include individuals in these categories.

actions[11,12]. Moreover, the literature does not support the notion that, among primates, increased levels of aggression within the normative range of social behaviour can raise androgen levels into a pathophysiological range[13]. Should such pathologically elevated androgen levels occur, all aspects of reproduction would be impaired[14], whereas Packer and colleagues noted salutary effects of dominance on most measures of reproduction.

Packer and colleagues predicted that, over the entire rank range, higher

rank should be associated with higher androgen levels. No information exists regarding wild female primates. The closest approximations are our own limited data (see figure), in which no relationship of testosterone with rank is observed, while for androstenedione the pattern for juveniles supports this prediction ($P=0.047$), but that for adults runs counter to it ($P=0.17$). Thus, overall, the data give little support for the notion of dominant females being exposed to even slightly higher androgen levels than subordinates.

In conclusion, without dismissing the Packer *et al.* data or suggesting that high status is always advantageous, we note that dominance rank has almost always been found either to confer advantage or to be neutral with respect to a variety of fitness components, and the Packer *et al.* report provides some of the strongest evidence thus far for those advantages. Whether the higher miscarriage rates[1,6] result from a methodological artefact or represent a difference among sites is unknown. In either case, neither the behavioural nor the endocrine hypotheses proposed to explain the apparent Gombe result are supported by available evidence, nor are the endocrine hypotheses proposed for Mikumi[6] applicable to Gombe. Nevertheless, Packer and colleagues rightly insist that any fitness relationship to dominance requires adequate physiological and behavioural mechanisms to arise and be maintained, a point often ignored in the evolutionary literature and a subject of much needed research.

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PACKER REPLIES — Altmann *et al.* imply that reproductive performance is always positively correlated with dominance rank, when neither of their principal references[2,4] provide compelling evidence of an overall relationship between rank and lifetime reproductive success. Indeed, Silk[2] concludes her review with the statement, "The lack of consistency among these results has created consider-

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able controversy about the significance between dominance rank, reproductive success, and genetic fitness among females."

We emphasized that the presence or absence of just one or two high-ranking females with reproductive pathology would influence perception of the significance of rank. We reported on five such females at Gombe and cited examples in other populations and species. While it is interesting that such rank-related pathologies have not yet been observed at Amboseli, there is no reason to dismiss them from our data set. A more productive approach would be to ask why such females might be more common at one site rather than another. Perhaps the historically high rate of infant mortality at Amboseli[4] has removed infertile animals from this population.

Altmann et al. suggest that, since field data cannot detect pregnancy for the first few days after conception, we may have missed many spontaneous abortions in the initial stages of pregnancy, and they predict that early abortions would be highest in low-ranking females. This prediction, however, is not confirmed by the Gombe data. If low-ranking females suffered a higher rate of undetected abortions immediately after implantation, they should take significantly more cycles to become obviously pregnant. However, once Gombe females resume cycling, there is no significant effect of rank on their interval to the next detectable pregnancy. Thus, early abortion is independent of rank at Gombe, and our miscarriage data are unbiased.

Further, we did not solely detect miscarriage on the basis of perineal coloration. Our analysis also included six miscarriages detected on the basis of delayed menstruation, and these all occurred in the first four weeks after conception (out of 50 miscarriages where the day of conception was known). There was no relationship between a female's rank and the gestation length of her failed pregnancy ($t=0.52$, $P=0.6081$, $n=48$ females of known rank). Our conclusion therefore remains unaltered: high-ranking Gombe females suffer more miscarriages, and this demographic pattern has been confirmed by Wasser[6] in a third baboon population.

We suggested that high-ranking females might show higher levels of androgens, as these have been implicated in the reproductive pathologies of several other mammalian females. The data presented by Altmann et al. are too limited to provide a rigorous test of this hypothesis. Most miscarriages at Gombe were suffered by females ranking fourth or higher, and Altmann et al. provide no data for any adult female ranked higher than sixth. Further, their data on androstenedione levels in juvenile females actually

support our hypothesis. The regression of the log-transformed androstenedione levels on juvenile dominance rank is significantly positive ($P=0.0470$, $n=6$). Female dominance rank is established during the juvenile period and early exposure to androstenedione is believed to influence aggressiveness of adult females[17]. However, androgens are not the only hormones involved in aggressive behaviour, and competition may also be balanced by other physiological costs (see ref. 6). Further, reproductive pathologies at Gombe appear to be hit or miss — some high-ranking females have large numbers of surviving offspring whereas others have none. The most compelling data on reproductive failure would be from those specific adult females with some form of pathology.

The pattern in our miscarriage data does not result from our methodology. High-ranking females at Gombe and Mikumi[6] suffer significantly higher rates of miscarriage during detectable pregnancies. At Gombe, the greater incidence of reproductive pathology and

the high miscarriage rate in high-ranking females essentially cancel the striking advantages of high rank from shorter post-partum amenorrhoea, higher infant survival and an earlier age of sexual maturation. These trends may or may not hold at all field sites, and contrasting results may prove useful in clarifying the costs and benefits of aggressive competition in different ecological settings. Although limited, the Altmann et al. data support our suggestion that female rank is correlated with androgen levels, androstenedione being highest in juvenile females of highest dominance rank. Wasser's[6] study of yellow baboons and findings by Frank et al.[18] on spotted hyaenas further emphasize the value of investigating the reproductive costs of aggressive competition in female mammals.

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Predicting the Vostok CO2 curve

SIR — To provide more than an *ad hoc* explanation of observed phenomena, a theoretical model must predict some as yet unobserved variability that places the model 'at risk' in some verifiable respect. In our phenomenological dynamical-system model governing changes in global ice volume, atmospheric CO_2 and the deep ocean state over the late Cenozoic[1,2], as influenced by Earth-orbital and slow tectonic CO_2 forcing, free parameters were assigned to account for the complex variations in global ice volume revealed by $\delta^{18}O$ proxy evidence. This includes internal bifurcations to the 'ice age' around 2.5 Myr ago and to the main near-100-kyr-period variations around 0.7 Myr ago. As a side consequence, the main features of the variations in CO_2 over the past 218 kyr were deduced and these compare favourably with those determined by the Vostok core trapped-air measurements[1-4].

As the drilling of the Vostok core is now projected to approach a depth corresponding to roughly 500 kyr ago[3], we now offer, as a further prediction of our model, the expected variation in CO_2 for
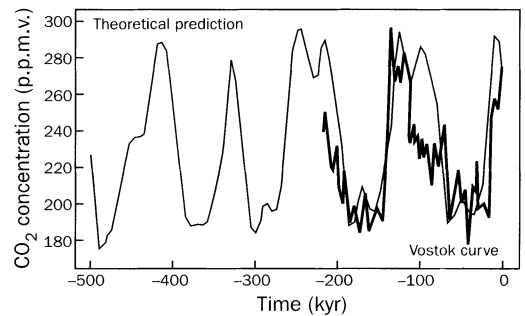
Variations over the Late Pleistocene of atmospheric CO_2 as inferred from the Vostok ice core[3] (heavy line) and from the dynamical theory[1,2,4] (thin line).

the additional 300 kyr (see figure). According to the theory, the character of the variations should change somewhat, showing a shorter-period fluctuation, with new minima near 300 and 370 kyr ago. At present, this model is the only one from which such a prediction can be made as a response to purely external forcing, dealing with CO_2 as a free, internal, dynamic variable[5,6] rather than as a prescribed function (as in refs 7–9).

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