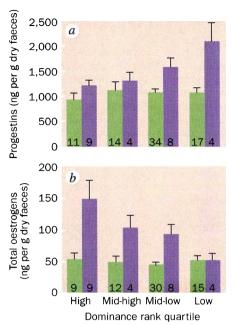
Mean luteal-phase (post-ovulation days 4-11) progestin (a) and total oestrogen (b) concentrations in faeces of conceptive (purple) and nonconceptive (green) cycles as a function of female dominance rank. Post-ovulation day 4 corresponds to the day in which progestin and oestrogen concentrations in conceptive cycles became significantly different from those in nonconceptive cycles. Post-ovulation day 11 corresponds to the time of implantation<sup>15</sup>, given the 36-h time lag between steroid secretion in blood and excretion in faeces<sup>5</sup>. Mean luteal-phase progestin and oestrogen concentrations were significantly higher in conceptive than nonconceptive cycles (P < 0.0001 in both cases), as well as significantly associated with dominance rank (P < 0.04 and < 0.02, respectively). The interaction between pregnancy and dominance rank was also significant for oestrogens (P < 0.03; ANOVA). Rank was quantified based on the outcome of bouts of aggression systematically recorded<sup>16</sup>. Sample sizes are shown in bars. Subjects were fully habituated to human observers, having been studied almost daily since 1974. Faecal samples were obtained from each female approximately 1-3 times



per week, depending on reproductive condition. Samples were stored, extracted and assayed for progestins and oestradiol using the methods in refs 4-7. Total oestrogens were measured using the RSL <sup>125</sup>I total oestrogen kit (ICN Biomedicals, Costa Mesa, CA). Every attempt was made to include only ovulatory cycles in this study, based on a transient rise in luteal-phase progestin concentrations. Ovulation was presumed to have occurred 2 days before onset of sex-skin detumescence<sup>15</sup>. All conceptive cycles in this study ended with a birth. Some cycles classified as nonconceptive undoubtedly represented early abortions. The 17 miscarriages described in the text occurred before the hormone study.

during nonconceptive cycles (a in the figure). The dominance-related faecal oestrogen pattern was opposite to that of faecal progestins (b in the figure). Oestrogen concentrations during conceptive cycles were greatest in females of high- versus lowdominance rank, while showing no rank effect during nonconceptive cycles.

The rank-related progestin patterns in conceptive cycles appear to be tied to oestrogen-mediated changes in progesterone receptor densities. Oestrogen increases progesterone receptor densities in the epithelial layer of the endometrium (where implantation occurs), but has little effect in the deeper layers (stroma and myometrium) that maintain pregnancy in Old World primates $^{12-15}$ . Progesterone has the opposite effect, decreasing progesterone receptor densities in the epithelial layer.

These findings suggest that the higher oestrogen concentrations observed in the early luteal phase of dominant females (b in the figure) may be dampening the progesterone-induced decline in progesteronereceptor densities over the early luteal phase. The resultant higher receptor density should make implantation easier to achieve in dominant females with less progesterone present. However, the lack of similar receptor-density changes in the stroma and myometrium seems to compromise the ability of this lower progesterone in dominant females to sustain the pregnancy. Subordinate females would experience the opposite: based on

oestrogen concentrations (b in the figure), their progesterone receptor densities would be lower, requiring more progesterone for implantation, which also should improve their ability to sustain pregnancy (a in the figure).

In conclusion, high-ranking females can afford to conceive more readily because their offspring are more buffered from the social conditions in which they are born. However, the physiological mechanisms that facilitate these conceptions seem to bear a cost of increased susceptibility to miscarriage.

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## Hot PUMPing plants ?

SIR — In their Scientific Correspondence, Vercesi and colleagues<sup>1</sup> suggest that the presence of PUMP, an uncoupler-like protein in potato tuber mitochondria, may correspond with the absence of the alternative oxidase in this tissue. But is the alternative oxidase thermogenic; does the location of PUMP correspond with the absence of the alternative oxidase; and does PUMP fulfil an analogous role?

The alternative oxidase is responsible for heat production in thermogenic lilies<sup>2</sup>, but in this system heat production is linked to a massive increase in enzyme activity concurrent with a complete decrease in cytochrome oxidase activity<sup>2,3</sup> There are no reports linking alternative oxidase activity to thermogenesis in other plants. Why should a plant need this heat production mechanism? At the levels of activity reported for the alternative oxidase (about 100 nmol O<sub>2</sub> per mg mitochondrial protein per min) in plant tissues, the heat change would be very small compared with the rate that can be achieved in thermogenic lilies (2 µmol  $O_2$  per mg mitochondrial protein per min)<sup>4</sup>. The alternative oxidase is implicated in various processes, such as wounding, pathogen attack, elevated carbohydrate status and addition of salicylic acid<sup>5</sup>, but none of these requires thermogenesis.

Is the presence of PUMP correlated with the absence of the alternative oxidase? Although potato tuber mitochondria do not naturally exhibit alternative oxidase activity, it can be easily induced in these tissues<sup>6</sup>, showing that they can express this enzyme.

Do PUMP and the alternative oxidase function in an analogous role? The alternative oxidase has been implicated in various processes. Although its exact role is unclear, it does function to oxidize reduced compounds without the production of ATP. Rather than this function being related to the generation of heat, it is more easily envisaged as being related to the diversion of metabolites in the Krebs cycle to other biosynthetic functions<sup>5</sup>. The uncoupled oxidation of reduced compounds allows the cycling of cofactors necessary for glycolysis and the Krebs cycle and so keeps catabolism at a high rate<sup>7</sup>. Under such conditions plants will be synthesizing a number of compounds for growth and development. The control of alternative oxidase activity by two separate biochemical parameters<sup>8</sup> ensures that this activity is highly regulated in reference to the metabolism of the cell/plant. In my view, there is no evidence to suggest that the PUMP protein has this role.

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