GIEDRIUS STAKAUSKAS/ALAMY

Are old hinds **better mothers?**

F.J. Pérez-Barbería considers the evidence

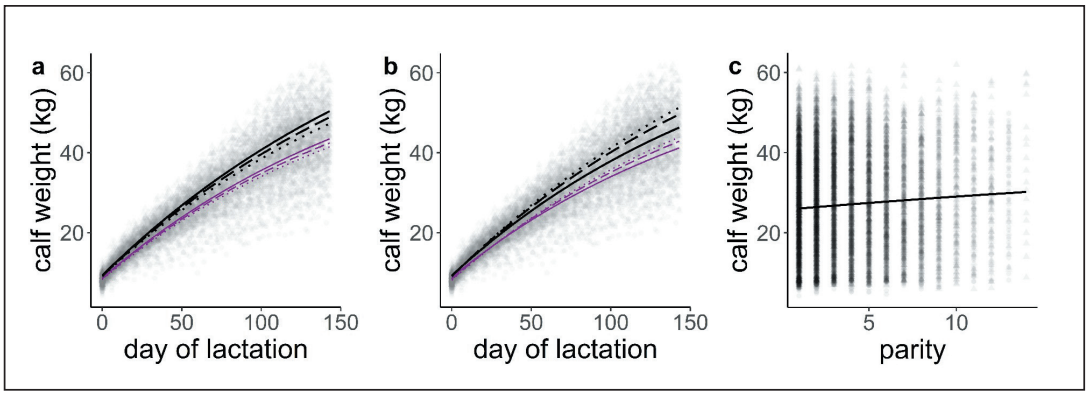
Evolutionary theory attempts to unravel the consequences of ageing on animal performance and how individuals adapt their reproductive effort to balance their own physiological and environmental constraints throughout their reproductive life. It has been shown that, in many cases, parental input (the care or resources they provide to offspring) evolves towards improving the fitness of the offspring at the expense of the parents.[1,2]

Senescence is the process of deterioration of physiological function in old age[3] and, in general, negatively affects the survival and reproductive performance of individuals.[3,4] On the other hand, with old age comes experience, which can provide elderly individuals with skills that help them to improve their survival and reproductive success.[5]

In species with sexual dimorphism in body size, where males are larger than females (such as red deer), the outcome of the reproductive input per unit weight of offspring may depend on the sex of the offspring. This is because, depending on the social and environmental conditions, the number of offspring that a male and a female can produce is different.[6] This has been formalised under the differential maternal allocation theory,[7,8] which states that mothers in better body condition will invest in offspring of the most costly and higher reproductive output sex (male), while mothers with poor condition will invest in offspring of the sex for which body condition is less dependent on mating success (female). This is because in males, mating success depends largely on their competitive fighting skills and body size to capitalise on large harems,[9] whereas a hind, which can only produce one calf per season, depends entirely on the length of her reproductive life to produce many offspring.[5,10]

In order to shed light on these evolutionary ideas, the Spanish and Scottish group led by Landete-Castillejos of the University of Castilla-La Mancha, conducted a 22-year-long sectional study using data of an Iberian captive population of 156 red deer hinds and 635 calves.[11] The authors monitored three key reproductive traits: calf growth, milk production and milk composition from the birth of the calf until day 134 of

Figure 1



Prediction of male and female red deer calf weight against day of lactation contingent upon hind weight (a), hind age (b) and parity (c). (a) thin-magenta line: female calf; thick-black line: male calf; dotted, dashed and solid lines are 90 kg, 98 kg and 107 kg hind body weight, respectively. (b) thin-magenta line: female calf; thick-black line: male calf; dotted, dashed and solid lines are hinds at age 3 years, 5 years and 8 years old. Triangle: male; circle: female. Figure from Pérez-Barbería *et al*.[11]

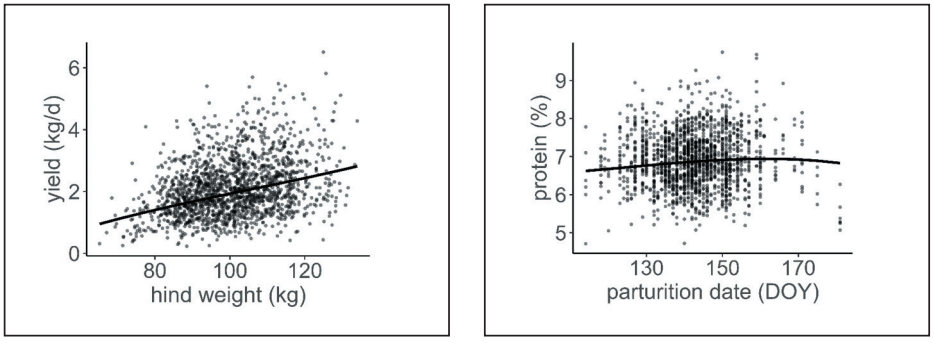
lactation, when forced weaning occurred. Lactation is the major reproductive energy expenditure for female mammals, and milk provides the neonate with water, minerals, nutrients and antibodies that enable the neonate to reach a self-sufficient nutritional state.[12] The study was carried out at the deer farm of the UCLM (Albacete, Spain). Deer were fed a mixture of chopped alfalfa hay and orange pulp supplemented with a commercial pelleted feed and minerals. Hinds were milked six times during the lactation season; the body weight of calves and hinds were recorded at birth and then weekly throughout their lifetime. Milking was carried out after hinds were separated from their calves for 6 hours. Total milk yield was measured, with milk kept refrigerated at 4°C until chemical analysis. Estimation of daily milk yield assumed that milk collected at one milking event was representative of the milk produced in 6 hours over a 24 hour period. Milk composition traits were fat, protein and lactose percentages, and milk energy (kg/d).

The authors hypothesised that milk yield, milk composition and calf growth should be negatively affected by maternal age, but would improve with increasing mother´s reproductive experience (i.e., parity, the number of calves produced by the mother over her lifetime), and also improve with the mother's weight, and contingent upon offspring sex and reproductive phenology (specific dates at which reproductive outcome is favoured).

This study found that (i) calf growth, milk yield, milk energy and milk fat content were negatively affected by the age of the hind in old mothers, and these milk traits (except milk yield) improved with increasing parity; (ii) for hinds of the same age, the heavier the hind the higher its milk yield; (iii) there were specific parturition dates at which milk yield and milk protein content peak; (iv) sons grew faster than daughters and the growth of sons was more hampered by maternal age than that of daughters. These results on offspring growth are consistent with the differential allocation theory.

It has been suggested that mammary gland development may be affected during pregnancy by exposure to foetal testosterone, which in the presence of estrogen synthase produces estradiol that may promote milk fat content. The dependence of milk yield energy on maternal age has been associated with differences in sensitivity to foetal hormones of endocrine systems of immature and adult mothers.[13,14] However, this study and the literature reviewed by the authors revealed that there was little evidence for the differential allocation theory in milk traits, as there was no strong evidence that milk composition was related to the sex of the offspring. The authors concluded that maternal allocation responds to offspring energy requirements, which are mainly driven by offspring body weight, and contingent upon mother age and weight and previous maternal reproductive effort.

Figure 2



Predictions of milk yield and milk protein content against red deer hind body weight and parturition date. DOY: day of year. Figure from Pérez-Barbería *et al*.[11]

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