

The results of this magnetostratigraphic study, according to radiometric ages and biostratigraphic levels, are shown in Fig. 3. The Viallette fauna is thus attributed to the beginning of the Gauss Epoch (3.40–3.15 Myr) which agrees with previous estimates. The Sainzelles fauna with hominid evidence is younger than the end of the Olduvai Event (1.67 Myr) but older than about 1.30 Myr. In Soleihac, the fauna and the prehistoric levels correspond to the Jaramillo Event (0.97–0.90 Myr). This agrees well with the age of the deposits of Le Vallonet and Isernia. This period corresponds to a well known critical moment for the Pleistocene environment but also for hominid technology as evidenced by the oldest 'architectural' work in Europe.

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Maternal dominance, breeding success and birth sex ratios in red deer

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That female vertebrates who are able to invest more than average in their offspring should produce male-biased sex ratios was first suggested by Trivers and Willard¹ who reasoned that the breeding success of males is more variable than that of females and so may be more strongly influenced by parental investment. Their evidence for a positive association between maternal condition and birth sex ratios was unconvincing^{2,3} and no subsequent studies have produced conclusive evidence supporting their hypothesis^{4,8}. We show here that, in polygynous red deer (*Cervus elaphus*), dominant mothers produce significantly more sons than subordinates and that maternal rank has a greater effect on the breeding success of males than females.

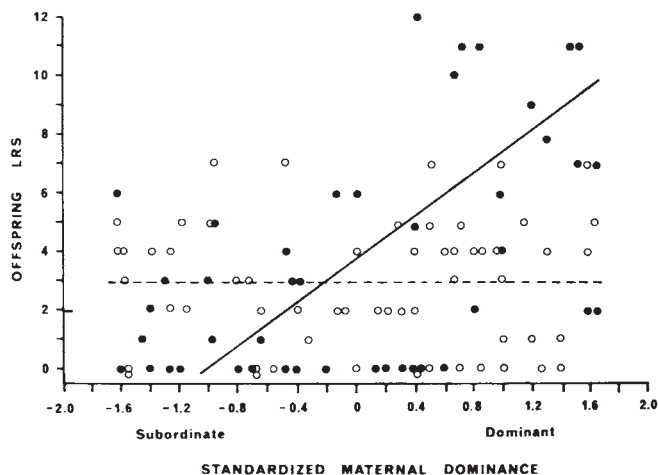


Fig. 1 Lifetime reproductive success (LRS) of sons and daughters of red deer hinds in relation to their mother's social rank. See text for details (●, males; ○, females). The slope shown is the reduced major axis³².

Records for around 120 red deer hinds and 100 stags on the Isle of Rhum (Scotland) collected between 1971 and 1983 show the breeding success of each individual and the proportion of male and female calves born to each mother⁹. The social dominance of each hind is measured by calculating the total number of other hinds more than 1 yr old that she has been seen to threaten or displace, weighted by their ranks, and divided by the total number of hinds that threaten or displace her, again weighted by their ranks^{9,10}. Previous analyses have shown that this index is closely related to other measures of dominance including the ratio of the number of older animals a hind dominates to the number of younger ones that dominate her¹⁰. Since the hind population was divided into four segments by preferred habitat, and hinds rarely interact with members of segments other than their own¹¹, ranks are calculated within each segment of the population, and then combined on a standardized scale. Estimates of rank calculated in this way are stable from year to year and are not affected by whether or not the hind has a calf at foot⁹.

Among hinds, most components of breeding success are related to dominance rank, except for fecundity (the proportion of years in which a hind produces a calf; Table 1). Dominant hinds also conceive and change coat earlier than subordinates. As the timing of both coat change and conception is known to be influenced by body condition in red deer^{12,13}, this indicates that, as in primates¹⁴, dominant animals are of a superior body condition compared with subordinates. Dominance rank is also correlated with the hind's body size ($r=0.397$, $t_{24}=2.116$, $P<0.05$) as well as with the social rank of her mother ($r=0.201$, $t_{102}=2.069$, $P<0.05$).

Previous analysis of sex ratio data from Rhum failed to show that birth sex ratios varied significantly with the mother's age, parity or home-range area^{9,15}. However, comparison of the sex ratios produced by hinds allocated to three equal groups on the basis of rank, revealed a significant relationship between a hind's dominance and the sex ratio of her offspring (Table 2a: $G_2=6.586$, $P<0.05$). The sex ratio of offspring born to high-ranking females is significantly male-biased (60.6% male, $n=149$; binomial test; $z=3.25$, $P<0.01$) while the sex ratio of offspring born to medium- and low-ranking hinds does not deviate significantly from parity (medium-ranking mothers: 53.9% male, $z=0.929$, not significant; low-ranking mothers: 46.9% male, $z=0.868$, not significant). This difference is consistent within all four segments in the study population and also within all seven cohorts of hinds born between 1966 and 1972 (Wilcoxon matched-pairs signed ranks test: $T=0$, $P<0.02$), showing that the relationship between rank and the sex ratio is not a consequence of any association between a hind's dominance and her age or the location of her home range.

Finally, we examined the correlation between the rank of hinds and the birth sex ratio of their progeny, using a sample of 50 mothers (see below). Since the number of calves per hind was small (3–12), we weighted each point by the number of calves on which it was based. This analysis, too, showed a significant association between a hind's rank and the sex ratio of her progeny ($r=0.291$, $t_{48}=2.106$, $P<0.05$).

If the relationship between maternal rank and the sex ratio is an adaptive one, a mother's rank should affect the breeding success of her sons more than that of her daughters. Our records indicate that this is the case. Measures of breeding success spanning at least half the average reproductive life are available for 58 female and 44 male offspring born between 1971 and 1974 to 50 different mothers of known dominance rank. Analysis of 16 males and 29 females born between 1967 and 1970

shows that individual differences in breeding success are consistent across the lifespan¹⁶ and that lifetime reproductive success (LRS) can be accurately predicted from a knowledge of breeding success over the first half of the average breeding lifespan (correlation and least-squares regression for LRS on breeding success up to 8 yr old for 16 stags: $r=0.937$, $t_{14}=9.994$, $P<0.001$; $y=1.07+0.17x$; correlation and least-squares regression for LRS on breeding success up to 8 yr old for 29 hinds: $r=0.873$, $t_{27}=9.301$, $P<0.001$; $y=0.46+1.65x$). Using these equations, we estimated the residual reproductive success of the animals in our sample that were still alive in 1983 (11 of the 44 stags and 37 of the 58 hinds) and added this to their observed breeding success during the 9 or more years for which we have followed them. (In practice, this involved only a small error, since the average remaining life expectancy was only 1.1 yr for the 11 stags and 2.3 yr for the 37 hinds.)

Figure 1 shows that breeding success of males was positively correlated with their mothers' ranks ($r=0.519$). Slopes were calculated using least-squares regression and reduced major axis since error was to be expected on both axes (least-squares regression: $t_{42}=3.936$, $P<0.001$; reduced major axis: $t=7.583$, $P<0.001$). In contrast, there is no consistent relationship between maternal rank and the breeding success of females ($r=0.027$, $n=58$; not significant). When the two relationships were compared, the slope for sons was significantly steeper than that for daughters (least-squares regression: $F_{1,98}=12.22$, $P<0.001$; reduced major axis, $z=6.450$, $P<0.001$). The breeding success of males born to mothers above median rank was greater than that of females (means: males, 5.14; females, 3.03; $t_{52}=2.12$, $P<0.05$), while females born to mothers of below median rank tended to be more successful than males (means: males, 2.00; females, 3.08; $t_{46}=1.69$, $0.1>P>0.05$).

Although the breeding success of sons increases with their mothers' rank, a substantial proportion of variance is unaccounted for by this analysis. In part, this is a consequence of calf mortality, which occurs throughout the range of maternal rank and accounts for the majority of zero scores. Rutting injuries also contribute to variance in male success. Six stags were permanently injured before they completed their reproductive lives and five of these were less successful than expected. Six others were born to mothers that failed to conceive in the year following their birth and who continued to suckle their offspring throughout their first year of life—unlike mothers who conceived again, who weaned their sons at between 6 and 8 months⁹. All six stags whose mothers failed to conceive in the year following their birth were more successful than was predicted on the basis of their mother's rank (binomial test, $P<0.032$).

Table 1 Measures of breeding performance in hinds above median rank versus those below it

	Subordinate	Dominant	
Median age of first breeding (yr)	3.90 (60)	3.48 (52)	$G=4.32$, $P<0.05$
Fecundity rate (yr^{-1})	0.65 (46)	0.68 (43)	$G=0.01$, NS
% Conceiving before median conception date	38 (55)	58 (50)	$G=4.91$, $P<0.05$
% Changing into winter coat before 1 November	35 (37)	62 (37)	$G=5.48$, $P<0.02$
Median weight of calves at birth (kg)	6.4 (55)	6.8 (45)	$G=14.38$, $P<0.001$
% Calf mortality during first year of life	45 (55)	28 (50)	$G=3.45$, $0.1>P>0.05$
Mean lifespan (yr)	9 (14)	11 (14)	Fisher's exact probability, $P<0.05$
Median lifetime reproductive success (calves reared to 1 yr old)	2.3 (14)	6.0 (15)	Fisher's exact probability, $P<0.05$

Data from cohorts born between 1967 and 1978. Sample sizes of mothers (shown in parentheses) differ between measures since not all variables were available for all individuals. The analyses control for the effects of age as well as for geographical variation in reproductive performance within the study area. All P values are for two-tailed t -tests.

Table 2 Sex ratio of calves in relation to mother's rank

<i>a</i>	Hind dominance rank			<i>b</i>	Upper (11)		Kilmory (37)		Intermediate (28)		Samhnsan Insir (22)			
	Low (34)	Medium (29)	High (35)		Sub.	Dom.	Sub.	Dom.	Sub.	Dom.	Sub.	Dom.		
Males	61	90	149	Males	10	24	35	80	26	56	30	39		
Females	69	77	97	Females	13	11	34	60	33	37	26	29		
% Males	46.9	53.9	60.6	% Males	43.4	68.6	50.7	57.1	44.1	60.2	53.6	57.4		
<i>c</i>	Year of hind's birth													
	1966 (6)		1967 (8)		1968 (8)		1969 (5)		1970 (8)		1971 (10)		1972 (10)	
Males	Sub.	Dom.	Sub.	Dom.	Sub.	Dom.	Sub.	Dom.	Sub.	Dom.	Sub.	Dom.	Sub.	Dom.
Females	10	21	14	19	12	13	13	19	7	10	13	17	12	15
% Males	50.0	65.6	51.9	61.3	46.2	56.5	46.4	67.9	53.8	83.3	56.5	60.7	50.0	56.2

a, All births 1970–82 from mothers born between 1957 and 1974; *b*, analysed separately for each of the four geographical subdivisions of our study population¹⁰; and *c* analysed separately for hinds belonging to each of the cohorts born between 1966 and 1972. Numbers of hinds in each category are shown in parentheses. In the first analysis (*a*) hinds were divided into three equal divisions on the basis of rank. The minor inequalities in sample size were a consequence of tied values of rank. In *b* and *c*, sample sizes within categories were small and hinds were divided into two categories: above median rank for their segment of the population (dominant, dom.) and below it (subordinate, sub.).

The superior body condition and larger body size of dominant mothers may explain why their sons are more successful than those of subordinates: in red deer, the breeding success of stags depends on their fighting ability and body size⁹ which, in turn, are related to growth and nutrition during the first 18 months of life^{9,16,17}. Maternal rank may have a lesser effect on the reproductive success of daughters both because early growth and adult size are less important to females¹⁶ and because differences in nutrition during the first year of life have a weaker influence on growth in females⁹.

The mechanism underlying the association between rank and the sex ratio is unknown. In domestic ruminants, attempts to manipulate the sex ratio have been unsuccessful¹⁸, although significant trends have been previously reported in white-tailed deer¹⁹⁻²¹. In red deer, the absence of any difference in calving rate between dominant and subordinate hinds once breeding has begun (Table 1) suggests that variation in the sex ratio is unlikely to be due to differences in zygote mortality unless these occur sufficiently soon after conception for the hind to conceive again in the same breeding season.

In contrast to these results, recent studies of baboons and macaques have shown that dominant mothers produce significantly female-biased sex ratios while subordinates tend to produce more sons than daughters⁶⁻⁸. It is suggested that because female primates typically remain in their natal troops and inherit their mother's rank whereas males disperse after adolescence, maternal rank may exert a stronger influence on the breeding success of daughters than on that of sons⁸. Unfortunately, no quantitative evidence of the comparative effects of maternal rank on the breeding success of male and female offspring in primates has yet been published^{4,5}. However, the available evidence indicates that, in primates, body size may not be as important a determinant of male breeding success as in ungulates²²⁻²⁶, suggesting that early growth and parental investment may also be less important to male primates. Conversely, female dominance hierarchies are more clearly defined among primates and a female's rank is more strongly influenced by the status of her mother than in red deer²⁷⁻³¹; it would not be surprising, therefore, if in primates a mother's rank exerted a stronger influence on the breeding success of her daughters than in red deer.

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Hyperpolarization of fish retinal horizontal cells by kainate and quisqualate

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Kainic (KA) and quisqualic (QA) acids have a potent depolarizing action on a variety of neurones of the central nervous system¹⁻⁴, including retinal horizontal cells^{5,6}. We now report the novel finding that at low concentrations (1-3 μ M), these 'excitatory' amino acids hyperpolarize horizontal cells of the fish retina. We show that the hyperpolarizing effects of both KA and QA are reversed by the γ -aminobutyric acid (GABA) antagonist bicuculline^{7,8}, whereas a second GABA antagonist, picrotoxin⁹, reverses the effects of KA, but not of QA. Neither GABA antagonist influences horizontal cell depolarization by 50 μ M KA or 50 μ M QA, thus the excitatory (depolarizing) and inhibitory (hyperpolarizing) effects of the amino acids involve independent mechanisms. We provide evidence that the hyperpolarizing effects are not mediated by the dopaminergic pathways associated with retinal horizontal cells¹⁰.

Retinal horizontal cells in cyprinid fish have large cell bodies and are organized into layers of interconnected neurones¹¹. In the dark, their resting potential is -20 mV to -40 mV and, in the main, they hyperpolarize in response to light, although C-type cells are depolarized by some stimulus wavelengths^{12,13}. It is proposed that in darkness, photoreceptors release a neurotransmitter which depolarizes the horizontal cells, and that light reduces the rate of transmitter release¹⁴, causing hyperpolarization of the horizontal cells. Depolarization of C-type cells is attributed to a GABAergic feedback connection between horizontal cells and photoreceptors^{15,16}. Horizontal cells are depolarized by $\geq 10 \mu$ M concentrations of KA and QA, but are hyperpolarized by a third excitatory amino acid, *N*-methyl-D-aspartate, and in each case, the light-evoked responses (S-potentials) are suppressed¹⁷. We now report that at low concentrations, KA and QA hyperpolarize horizontal cells, apparently through a GABAergic pathway.

Retinas dissected from the excised eyes of dark-adapted cyprinid fish (roach, *Rutilus rutilus*) were placed receptor side up in a perfusion chamber and firmly held by a clamping ring and coarse-mesh net¹⁷. The individual retina was superfused at a rate of 1-4 ml min⁻¹, producing rapid changes in response to drugs. Microelectrodes (d.c. tip resistance of 80-150 M Ω) were introduced from above the retina, which was stimulated from below with 300-ms light flashes. All data refer to L-type units which hyperpolarize for all stimulus wavelengths. Figure 1a illustrates hyperpolarization of the horizontal cells and reduction of their S-potentials by 1 μ M and 3 μ M KA. The average change in membrane potential induced by 3 μ M KA was -10.0 ± 1.2 mV (± 1 s.e.), with the S-potential amplitude changed by a factor of 0.43 ± 0.07 (31 cells from 17 retinas). The corresponding values for 3 μ M QA are -9.7 ± 1.0 mV and 0.42 ± 0.06 (13 cells from 11 retinas). The figures exclude values for the first two or three applications of the amino acids, which were usually ineffective, and those for some 10% of the retinas in which