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# This Week's Citation Classic®

**Clutton-Brock T H, Guinness F E & Albon S D.** *Red deer: behavior and ecology of two sexes*. Chicago, IL: University of Chicago Press, 1982. 378 p.

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This book focusses on the evolution of differences between the sexes, summarising our work on red deer carried out between 1972 and 1982 on the Isle of Rum. First, it compares the social and reproductive behaviour of the two sexes. Second, it investigates the adaptive significance of these differences by comparing the determinants of breeding success in males and females. And finally, it explores the consequences of the contrasting breeding behaviour of males, relating sex differences in energy expenditure, food selection, habitat use, growth, and survival back to the contrasting reproductive strategies of males and females. In particular, we were able to show that juvenile males suck more frequently than females and that rearing sons depresses the reproductive success of mothers more than rearing daughters. [The *SCI*® indicates that this book has been cited in more than 475 publications.]

## The Ecology of Two Sexes

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**Having worked on the social behaviour of colobus monkeys in Tanzania and Uganda for my PhD, I had had enough of trying to investigate the behaviour of animals living 50 feet up in leafy trees. Scottish red deer, which are conspecific with American elk and live in a landscape now almost totally devoid of trees, seemed sensible animals for a study of social behaviour and population dynamics. Though their demography and feeding ecology had been recently studied, there had been no substantial study of their social behaviour since Frank Fraser Darling's classic but nonquantitative 1937 study.[1] Moreover, I was able to inherit a study population where virtually all the animals were already individually recognisable, thanks to previous work by Fiona Guinness, who came back from an expedition to Indonesia to join me in 1973 and has lived on Rum ever since. In 1976, Fiona and I were joined by Steve Albon, who came to manage the growing data sets and take charge of computing work.**

**Though it had not been my intention to focus on the evolution of sex differences, the behaviour of the deer rapidly propelled us down this line. In red deer (as in many other ungulates) mature males live separately from females and the two sexes show little interest in each other for 11 months a year. During this time, one might almost be looking at two different species. But they make up for it in the October rut when stags compete intensely for harems of up to 20 or more hinds. The contrasts in behaviour between stags and hinds were thus very obvious, while the excellent visibility combined with Guinness's ability to recognise all two- to three-hundred animals using the study area meant that it was possible to measure individual differences in breeding success and survival very accurately. We were also fortunate that most females only copulate once with a single stag so it was reasonable to assume that observational measures of mating frequency gave a reasonable indication of a male's breeding success. Nearly 20 years later, we were able to demonstrate that this was the case using DNA fingerprinting[2]—though our observational methods proved to underestimate the breeding success of the most successful stags.**

**Our focus on the ecology and evolution of sex differences in behaviour was timely, for interest in sexual selection was growing.[3,4] In particular, Bob Trivers's influential 1972 paper[5] drew attention to the close connection between sex differences in reproductive behaviour and sex differences in growth, survival, and metabolism. The red deer study provided a detailed example of these differences, supported by some of the most extensive data on individual variation in reproductive success then available. I'd like to think that this is why it has been widely quoted, but I suspect that there is probably another reason.**

**The red deer study continues to this day. Since 1982, when this book appeared, we have used the Rum study to investigate a variety of other topics in behaviour and ecology, publishing a further 26 papers on red deer. Results from these papers are commonly attributed to the 1982 book, even those that appeared several years later. This is presumably because it is quicker and more convenient to use a blanket reference (even if it's the wrong one) than to attribute results to specific papers. So the cost of a successful monograph may be that your previous and (more worrying) your subsequent papers are seldom cited!**

1. **Darling F F.** *A herd of red deer*. London: Oxford University Press, 1937. 215 p. (Cited 185 times since 1945.)
2. **Pemberton J M, Albon S D, Guinness F E & Clutton-Brock T H.** Countervailing selection in different fitness components in female red deer. *Evolution* 45:93-103, 1991.
3. **Campbell B,** ed. *Sexual selection and the descent of man*. Chicago, IL: Aldine, 1972. 378 p.
4. **Glucksman A.** Sexual dimorphism in mammals. *Biol. Rev. Cambridge Phil. Soc.* 49:423-75, 1974.
5. **Trivers R L.** Parental investment and sexual selection. (Campbell B, ed.) *Sexual selection and the descent of man*. Chicago, IL: Aldine, 1972. p. 136-79. (Cited 1,430 times.)

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