Red Deer Data Illuminate Sexual Selection

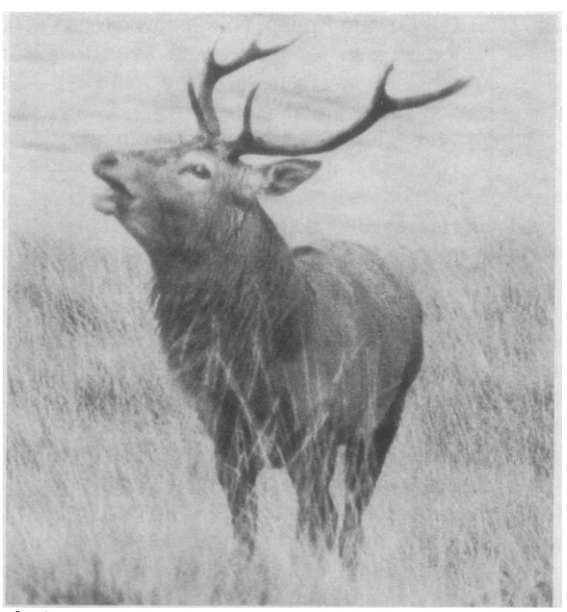
It is the effects of traits on reproductive success, not the variation in success, that determine the differences between males and females

The phenomenon of sexual selection is responsible for layer upon layer of variability, both subtle and dramatic, in the living world. And yet, as British biologist John Maynard Smith recently pointed out, the topic has been much neglected since Charles Darwin introduced the concept, first in *The Origin of Species* and then in greatly expanded form in *The Descent of Man*. The recent publication by The University of Chicago Press of *Red Deer, Behavior and Ecology of Two Sexes*, which is the culmination of a major field project in Scotland, is an important contribution to the study of sexual selection.

The project's importance, perhaps surprisingly, stems from its presentation for the first time of data on the lifetime reproductive success of individual male and female animals in a single species. Compilation of individual lifetime reproductive success, that is, the number of surviving offspring produced, might sound simple, but it is not. Yet, without such information one cannot calculate variance in reproductive success separately for males and females in a population. And without accurate measures of variance, investigation of many aspects of sexual selection is at best questionable.

The authors of *Red Deer*, Tim Clutton-Brock, Fionna Guinness, and Steven Albon, are the core of a large team of researchers who, during the past 12 years, have closely monitored the population of *Cervus elaphus* in the northern section of the Isle of Rhum, a few miles off the west coast of Scotland. The project, which has its academic base at the University of Cambridge, England, continues; but with its longevity now matching the average lifespan of hinds, an important milestone has been reached.

"Everyone pays lip service to the idea that you have to measure differences in lifetime breeding success," says Clutton-Brock, "but virtually no one measures it. For very good reasons. There are very few species of animal in which you can watch individuals for long periods and eventually measure reproductive parameters." A recent heroic effort by Margaret McVey of Rockefeller University has achieved this goal with male dragonflies. Similar information, much of it still unpublished, has now been collected for two monogamous birds, the great tit, by Christopher Perrins and John Krebs at Oxford University, and the kittiwake, by John Coulson at the University of Durham, England. For larger animals, however, the literature is full of studies that represent fragments of lifetimes of fragments of populations.



A stag roars

Before fighting, stags engage in intense roaring bouts.

Clutton-Brock identifies a number of potential traps in these partial studies. For instance, during the October rut, red deer stags attempt to hold harems, and their success in doing so is crucial to their eventual breeding success. The size of the harem is subject to quite large hourly and daily fluctuations, the result perhaps of something as simple as a change in wind direction that might unfavorably transform a previously sheltered locality. "Measurements on these animals over a short period of time might lead to overestimates of variation of reproductive success compared with the true long-term figure."

A second problem, which leads to underestimates of variance in breeding success, is particularly pertinent to polygynous species. Males that fail to win harems may skulk around the fringes of a population and may not be particularly obvious to a field observer, who may be concentrating on the breeding animals. Calculations from such observations lead to underestimates of the variance and overestimates of the mean of reproductive success. "In red deer, such short-comings would roughly double the mean and half the variance," observes Clutton-Brock.

A third complication derives from the effect of immediate reproductive success on an individual's future. In some species, such as mountain sheep, reproductive success can jeopardize a male's long-term survival, while in others, such as *Drosophila melonogaster* and red deer, successful males appear to live longest. There are of course exceptions to both these observations, but the overall implication is clear. Measures of instantaneous breeding success are not necessarily secure long-term predictors.

Last, age can be a crucial factor in determining an individual's performance at any particular time, especially in polygynous males that strive to maintain harems. For instance, red deer stags attain a breeding peak, principally through fighting ability, between the ages of 7 and 10 years. Extrapolation of short-term data over all individuals "grossly overestimates variation in lifetime success," says Clutton-Brock.

All in all, there appears to be no good substitute for going into the field and recording the fate of a population of individuals and their offspring throughout their entire lives. The red deer of Rhum offer a particularly suitable subject for such a study. Stags usually die between the ages of 9 and 11 years and hinds between 11 and 13 years. The animals' habitat is virtually treeless, and so visibility is generally good. Compared with the rather mobile large mammals of East Africa for instance, the red deer of Rhum are relatively easy to track: they spend 65 percent of their time within an

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area of less than 1 square kilometer. And last, but by no means least, the deer concentrate most of their mating efforts in a brief but intense rut in mid-October, a habit that considerably eases the logistics of collecting valuable research data. The hinds calve the following June.

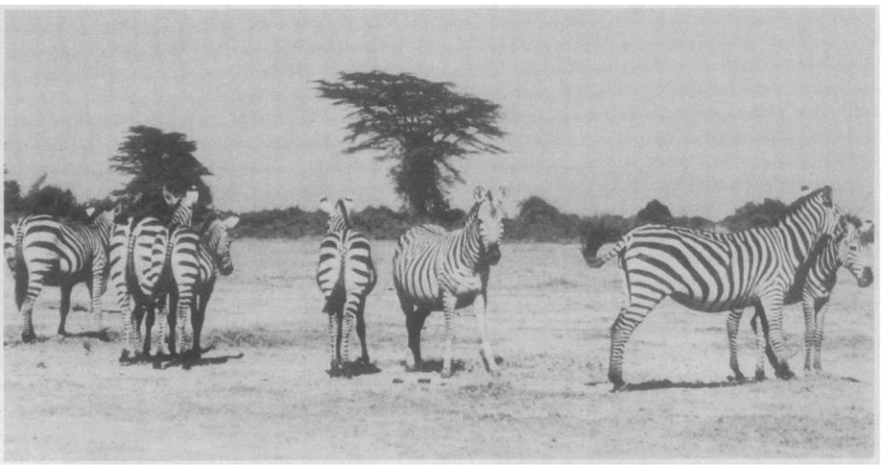
So, given at least 12 years commitment to the project, it becomes possible to determine what factors affect reproductive success in the two sexes, which is what Clutton-Brock, Guinness, Albon and their colleagues have done. It has been possible for the first time with any large animal to evaluate the selection pressures underlying some of the physical differences between the sexes.

Darwin recognized that the reason why males and females might differ physically in certain characters, sometimes substantially so, must result from the fact that contrasting selection pressures affect males and females. And, he suggested, such characters might be particularly elaborated in males because they experience especially intense selection. Why? Although the costs of reproduction in females might be high, for males it is often very low, involving just the costs of fertilization. An individual male can therefore father many offspring if he can monopolize the attention of the females. It is for that monopoly, or as near to it as they can attain, that males compete so intensely. Hence the greater selection pressure for traits that affect competitive abilities among males than among females and the fact that, generally, males are larger, stronger, and more elaborately decorated.

A simple equation has emerged out of this, but it is one that Clutton-Brock has come to question, as he explained at the Darwin Centenary Meeting held at Darwin College, Cambridge, earlier this year. The equation says that the extent to which males and females differ "will depend on the extent to which reproductive success varies among males relative to variation among females." The more variation there is in reproductive success in one of the sexes, the greater will be the opportunity for selection to act, thus enhancing the physical differences between the sexes.

Drawing on the results of the red deer project, Clutton-Brock proposes a simpler relationship, as will become clear. "It is the effects of phenotypic traits on reproductive success in males and females that will determine the degree of dimorphism," he suggests, "not the amount of variation in reproductive success per se."

The theory of sexual selection has led to four common predictions, and these are illuminated by the data from Rhum.



Burchell's zebra

Although, like red deer stags, male Burchells hold harems, there is virtually no size difference between the sexes. Perhaps this is because zebras fight with their teeth and hooves, not by the trial of strength pursued by red deer stags.

The first prediction is that "variation in reproductive success should be greater in males than in females in polygynous species but similar in the two sexes in monogamous ones." The red deer data in general fit well with this statement, but with some surprises. Stags, for instance, vary in their lifetime reproductive total from zero to about 30 calves that survive to at least 1 year of age. For hinds the figures are from zero to about 12. Although stags do have a wider variation, the difference between males and females is not as marked as might have been expected.

Although successful stags frequently hold harems of 20 or more hinds, they typically sire only six or seven calves in the season, partly because not all the females conceive and partly because an individual stag rarely holds a harem intact throughout the whole breeding season. Compounding the lower-than-expected range of success is a stag's typical expectation of only four or five productive breeding seasons. For hinds, the range of zero to 12 surviving offspring is greater than expected, mainly because individuals tend consistently to fail or succeed throughout their many reproductive years.

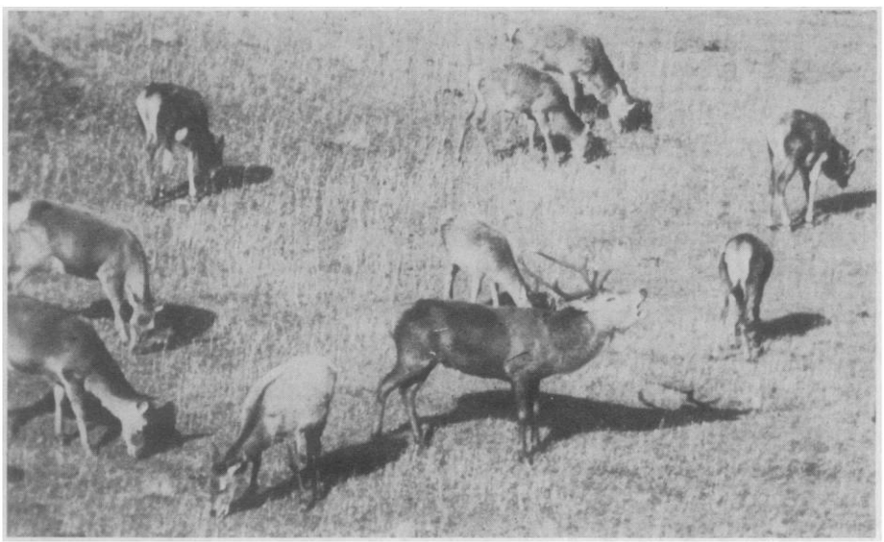
The second prediction is that "variation in reproductive success should be greater among males of polygynous species than among males of monogamous ones." Comparison of the red deer with kittiwakes, a monogamous species for which there are good lifetime data, produces a surprise. Although variation in reproductive success of male and female kittiwakes is similar, thus conforming with the first prediction, the figure for the male birds is comparable with that for the male red deer. This surprise stems, apparently, from the kittiwakes' relatively long life-span, up to 20 years, during which a population of animals can build up a lot of variation.

The comparison between kittiwakes and red deer is clearly not one between equals, but, as Clutton-Brock points out, "it emphasizes how misleading it can be to assume that the breeding sex ratio necessarily reflects the extent to which male reproductive success varies."

The third prediction says that "direct competition for mates will be more intense among males of polygynous species than among males of monogamous ones." Data to test this are not readily available, but Clutton-Brock warns that it is unwise to ignore the possibility that monogamous males might compete as intensely in securing a good quality single mate or good quality territory as polygynous males do in securing as many mates as possible.

The fourth prediction suggests that "sexual dimorphism will be most developed among strongly polygynous species and least developed among monogamous ones." There is a general association between polygyny and sexual dimorphism, and the red deer display an aspect of this well: males are twice as big as females. Features that are used in combat, such as canines in primates and antlers in deer, are also generally more developed in polygynous as against monogamous species. But there are many exceptions too. For instance, in Burchell's zebra, a polygynous species, males and females show virtually no dimorphism. And in two other polygynous animals, spotted hyena and Weddell seals, females are bigger than males.

The overall picture should be viewed, suggests Clutton-Brock, keeping in mind that it is the effect of traits on reproduc-



A harem in the October rut

The physical differences between the sexes are particularly striking during the rut.

tive success that is important, not the actual degree of variation in reproductive success. "Sexual dimorphism in size is likely to evolve where variation in male success is greater than female success and a given increment in body size has the same effect on breeding success in both sexes," he says. "But it will also evolve if variation in reproductive success is similar in both sexes but size has a greater influence on success in males." Similarly, size dimorphism is unlikely to arise if body size has no effect on reproductive success, no matter how great is the difference in reproductive success between the sexes.

If this is indeed the case, one can legitimately ask why there is a relation between sexual dimporphism and polygyny at all. "The most likely explanation is that the factors affecting breeding success in males and females tend to be most similar in monogamous species and most different in polygynous species." One of the most important results from the Rhum study is the clear distinction between the factors affecting reproductive success in hinds and stags.

For stags, fighting ability is the predominant factor in determining breeding success, for unless an individual can establish and maintain a harem it will sire no offspring. The victors in the frequent contests between mature males are principally those with the biggest bodies, plus some talent in maneuvering during the intense antler-to-antler pushing bouts. Adult body size is pretty much predetermined by the time an individual reaches 1 year, the result of frequent and good-quality suckling.

Reproductive success in females, by contrast, is influenced by an individual's longevity, the survival rate of its offspring, and the quality of its home range. This last factor, which a young hind inherits from its mother in the red deer's matrilocal society, underlies the others.

The sharpness of the distinction in influences on reproductive success in stags and hinds came as something of a surprise to the Rhum researchers, but it surely helps explain the adaptive significance of many of the physical features that separate the sexes. Body size is the most striking feature, being of prime importance to stags and of comparatively little consequence in hinds. A stag's bulk helps it in the many rutting contests it will face, as do it antlers, mane, and the seasonal development of neck muscles. It is not surprising that these characters do not occur in hinds, which do not fight in the same way or to the same extent.

There is good reason to believe that red deer are not atypical of polygynous species in the distinction in the factors that are important to the breeding success of the two sexes. This therefore helps to explain the general association between dimporphism and polygyny. Although there are as yet no good data on this point for large monogamous animals, Clutton-Brock suspects that the situation in such species is different. "While it is clear that [the factors affecting lifetime success] will not be identical in males and females, it is reasonable to suppose that, especially among species that pair for life, they are likely to be more similar than in polygynous species." A closer coincidence of factors influencing breeding success between the sexes of monogamous species will limit the evolution of dimorphism.

An obvious consequence of the race for growth in young male red deer is that, initially at least, it appears that male offspring are more costly to produce. On average, male calves weigh a pound more than female calves and gestation for them is two days longer. Male calves suckle longer and more frequently, which is a further drain on a mother's resources. The costs of giving birth to and rearing males are reflected in the mother's performance in the following season. She is more likely to be barren than a mother who has borne a female calf, and if she does conceive the birth is delayed on average by 11 days.

According to theory, the substantial extra investment made by mothers in male offspring should affect the ratio of males to females produced in the population. There will be a bias toward the least expensive progeny, predicts the theory. With red deer, however, this is not the case, and the reason for the apparent disparity has recently become clear from the Rhum data.

Although preweaning investment is greater in male young than in female, postweaning investment is the reverse. Young males leave their mother's group between the ages of 2 and 4 to join stag groups, whereas young females remain with their mothers throughout their lives. The young females might benefit from the relationship through inheriting good-quality home ranges, but the mother might suffer, as reproductive success appears to be depressed as the number of relatives in the group increases. Lifelong association between mother and daughter therefore represents a substantial postweaning cost for the mother. Overall, extra preweaning investment in sons appears to be balanced by extra postweaning investment in daughters, a result that could not have been determined by a short-term study.

The investment in the Rhum project has been great, in terms of time, money, and research effort. But, as Maynard Smith notes, the investment is sound: "The answers that emerge make the effort worthwhile." It is, however, only a beginning. "If we wish to fulfill Charles Darwin's ambition of understanding the reasons for the distribution of differences between the sexes," Clutton-Brock said at the Cambridge meeting, "we shall need to examine the causes of variation in lifetime breeding success among males and females in other natural populations."—**ROGER LEWIN**

Additional Reading

1. T. H. Clutton-Brock, F. E. Guinness, S. D. Albon, *Red Deer, Behavior and Ecology of Two Sexes* (Univ. of Chicago Press, Chicago, 1982).
2. T. H. Clutton-Brock, "Selection in relation to sex," in *Evolution from Molecules to Man*, D. S. Bendall, Ed. (Cambridge Univ. Press, New York, in press).