Deer destiny determined by density

Andrew Cockburn

Theory predicts that socially dominant females will produce more sons than daughters. But when times are hard, the higher growth rate of males means that proportionately more will die during development. New work shows that, in red deer, these effects can operate in concert.

When friends or relatives have a new baby, we inevitably ask about its weight and sex and expect the answers to be followed by the qualitative observation that mother and baby are "doing well". The relationship between offspring condition and sex, and maternal condition, lies at the heart of one of evolutionary biology's most famous predictions — the contention by Trivers and Willard[1] that, in polygynous mammalian societies (where some males can mate with many females), mothers in good condition should produce sons, whereas mothers in poor condition should produce daughters. This hypothesis has been difficult to test, but Loeske Kruuk and her colleagues[2] have now used superb long-term data from red deer (*Cervus elaphus*; Fig. 1) to cast the Trivers–Willard hypothesis in a new light. Their results, reported on page 459 of this issue, may help to explain the inconsistency among previous studies of mammalian sex ratios[3].

The Trivers–Willard hypothesis is conceptually straightforward, as long as the mother produces one infant at a time. A mother can allocate a certain amount of resources to her child, and she should not breed if she does not have at least the minimum resources required by her baby. But what if she has more than this minimum? The optimum sex for her offspring will then depend on the relationship between the extra resources given to her child and the number of offspring the child produces, which, in turn, determines her number of grandchildren. The sex of the offspring is significant here because, in polygynous mammals such as antelopes, elephants, seals and some primates, sons will often have much more variable reproductive success than daughters.

Some sons gather large harems because they are more attractive or better fighters than other males. These sons have the potential to be exceptionally successful, as they can sire the offspring of many females each year. But, as a corollary, this may mean that other sons never acquire a mate. By contrast, most daughters will be able to find a mate and rear young, but there is a limit to maximum productivity — their reproductive lifespan. So, according to the Trivers–Willard hypothesis, if the enhanced condition from heavy maternal investment is maintained by the infant into adulthood, such investment will be most beneficial to sons. This is because a heavily provisioned son will have a good chance of enjoying the bonanza associated with holding a harem (Fig. 2a). Mothers in poorer condition, on the other hand, can allocate fewer resources to their offspring so should prefer the less variable return they obtain from daughters.

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Figure 1 Dense deer — the red deer (*Cervus elaphus*). Kruuk and colleagues[2] have found that the sex ratios of offspring are affected by population density.

The most compelling support for the Trivers–Willard hypothesis comes from long-term studies of the red deer living on the Scottish island of Rum. Here, in the 1980s, Tim Clutton-Brock and his colleagues demonstrated all the separate elements of the hypothesis[4,5]. Some female deer are dominant to others, and this dominance enhances the lifetime reproductive success of their offspring. However, higher rank increases the reproductive success of sons much more rapidly than that of daughters. As predicted, Clutton-Brock and colleagues found that dominant females are more likely to produce sons, whereas low-ranking females are more likely to produce daughters.

This influential work has inspired many studies of other species, from elephants and bison to mice and shrews. But support for the hypothesis has, at best, been inconsistent, or based on data that provide only some of the links in the chain of logic. Unfortunately, such partial support may be inconclusive. Even when almost all the links are present, we cannot necessarily assume that the chain will be completed[6]. Moreover, there are alternative explanations for certain sub-components of the Trivers–Willard hypothesis, which are not always acknowledged. For example, it is often reported that mothers in poor condition are more likely to have daughters, without showing that those in good condition produce sons. In this case, overproduction of daughters can be explained by an alternative hypothesis.

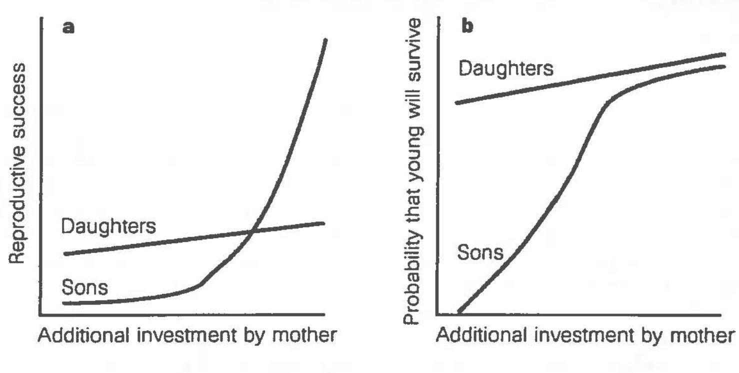

Figure 2 Two theories to explain the observed sex ratios in red deer populations on the island of Rum. a, The Trivers–Willard hypothesis states that, as mothers invest more heavily, they will gain a more rapidly increasing return (number of grandchildren) from sons than from daughters. So, there should be a point at which they switch from preferring daughters to preferring sons. In red deer, this point is associated with female dominance rank. b, An alternative hypothesis predicts that males may have a disadvantage early in their life because they grow rapidly, predisposing them to fetal mortality when resources available to their mother are in short supply. Attempts to breed by dominant red deer are unaffected by increasing density, which may predispose some high-ranking females to carry sons that die *in utero*.

Because large size assists males in the competition for females, rapid growth of males will be favoured by selection. So, sons may be more likely to die, either in the womb or during infancy, if their mothers find themselves in adverse conditions and cannot provide additional investment[7] (Fig. 2b).

Kruuk and colleagues[2] have now revisited the red deer on Rum. On certain areas of the island the population of red deer has increased because culling is not allowed. The authors found that, as the population density has increased in these areas, so the tendency of high-ranking females to produce sons has disappeared. Not only that, but the birth sex ratio as a whole is now biased towards females. A direct relationship to density seems likely because the correlation between condition of the mother and sex of her offspring persists elsewhere on the island, where culling is permitted and the population density remains low[8].

How does this change with density relate to the Trivers–Willard hypothesis? It may be associated with increased vulnerability of male fetuses to mortality. In dense populations there will be increased competition for limited food and other resources, and, in red deer, the growth of male fetuses is much more sensitive to such changes in environmental conditions than that of female fetuses[9]. Kruuk and colleagues found that high-ranking females tend to reproduce each year, even in areas of high population density. So, more of these females may fall into the realm where fetal mortality is high (Fig. 2b), masking their tendency to conceive more sons. Such interactions may explain some of the inconsistent results in the literature. For example, Kruuk and colleagues point out that there has never been positive support for the Trivers–Willard hypothesis from high-density populations of hoofed mammals.

Unsurprisingly, some questions remain. Why do dominant females breed every year, irrespective of population density? And what is the relationship between a mother's dominance and the lifetime reproductive success of her offspring now that density is high? Perhaps most important, the goalposts for tests of the Trivers–Willard hypothesis have been pushed back even further. The ability to match data on lifetime reproductive success with those on population density will be rare, except when studies persist through the lives of many generations of offspring — well beyond the term of a research grant or PhD. Indeed, where would the study of mammalian sex ratios stand if the red deer study had started when densities were already high, or it had terminated prematurely, before the effects of density could be appreciated? □

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Display technology

Glowing developments

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If you are a regular reader of *Nature*, the following description may sound familiar. A group of researchers have reported the discovery of an unusual physical phenomenon, the characterization of which promises new understanding of an important scientific question. At the end of the paper, however, the authors also raise the tantalizing possibility that the same phenomenon may find widespread application in a technological context. As so few of these promised applications seem to materialize, it could be argued that they represent little more than wishful thinking on the part of the authors. But occasionally a seemingly far-fetched claim of practical relevance does indeed live up to expectations, and does so quickly. One of these success stories was celebrated, by both academia and industry, at a conference last month*.

The phenomenon under discussion was the electrically driven emission of light (electroluminescence) from non-crystalline organic materials — both polymeric and low-molecular-weight systems — the discovery of which was announced barely ten years ago[1,2]. The proposed application is in flat-panel light-emitting displays, several impressive prototypes of which were exhibited at the meeting (Fig. 1).

Electroluminescence is usually harnessed in a device structure called a light-emitting diode (LED): essentially a thin film of a semiconductor (or several semiconductors) sandwiched between two electrodes. On applying a voltage, electrons enter from one electrode, positively charged 'holes' from the other. Recombination of an electron and a hole, within the body of the semiconductor, produces a photon, and so leads to the emission of light. LEDs based on crystalline inorganic semiconductors have a long history, and their performance has improved steadily since their creation. It is when viewed in this context that the recent progress made with semiconducting organic materials seems so remarkable (Fig. 2).

Consider the electroluminescent polymers. The first[2] polymer LED emitted green-yellow light with a quantum efficiency (photons emitted per electron injected) of no more than 0.05%. Even when driven by a relatively high voltage (> 10 V), one needed to be in a darkened room to stand a chance of seeing the glow. Moreover, the early devices were extremely short-lived, usually lasting no more than a few minutes. Hardly a promising basis for the displays of the future! But only nine years later, operational voltages of < 5V, efficiencies of several per cent (the devices can be almost too bright to look at) and lifetimes of order 1,000–10,000 hours appear to be the norm. And the range of colours now available effectively spans the entire visible spectrum.

This remarkable advance in performance can be traced to progress on several fronts. First, to achieve the efficient — and balanced — injection of electrons and holes required to obtain a high photon yield, control of the electronic properties of the semiconductor–electrode interfaces has proved crucial (M. Schwörer, Bayreuth). This has invariably led to the introduction of at least one additional organic layer within the device structures, to facilitate the injection and transport of the charged species (usually the holes) against which the light-emitting material is predisposed. The introduction of such a layer has the additional advantage of moving the zone of emission into the body of the device, and so away from an electrode interface, where impurities can trap the charges and enable them to recombine non-radiatively. (See ref. 3 for a review.)

Second has been the marked increase in device lifetime, the key to which has been to understand and control the degradation processes within the organic materials. In the case of the polymers, systematic studies have helped to characterize the nature of any structural defects within the polymer chains resulting from undesirable reactions in the polymerization process; such information has then guided the development of improved syntheses (H. Becker, Covion). More generally, the expansion in material production from laboratory to industry scales has reduced chemical impurities to levels more commonly associated with the pharmaceuticals industry.

Second International Conference on Electroluminescence of Molecular Materials and Related Phenomena (ICEL-2). Sheffield, UK, 12–15 May 1999.