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**Citation for published version:**
Pemberton, JM, Kruuk, L & Clutton-Brock, TH 2022, 'The unusual value of long-term studies of individuals: The example of the Isle of Rum red deer project', *Annual Review of Ecology, Evolution, and Systematics*, vol. 53, pp. 327-351. https://doi.org/10.1146/annurev-ecolsys-012722-024041

**Digital Object Identifier (DOI):**
10.1146/annurev-ecolsys-012722-024041

**Link:**
Link to publication record in Edinburgh Research Explorer

**Document Version:**
Peer reviewed version

**Published In:**
Annual Review of Ecology, Evolution, and Systematics

# The Unusual Value of Long-Term Studies of Individuals: the Example of the Isle of Rum Red Deer Project

**Josephine M. Pemberton**
**Institute of Evolutionary Biology**
**School of Biological Sciences**
**University of Edinburgh**
**EH9 3FL**
**UK**
**j.pemberton@ed.ac.uk**

**Loeske E.B. Kruuk**
**Institute of Evolutionary Biology**
**School of Biological Sciences**
**University of Edinburgh**
**EH9 3FL**
**UK**
**Loeske.Kruuk@ed.ac.uk**

**Tim Clutton-Brock**
**Department of Zoology**
**University of Cambridge**
**CB2 3EJ**
**UK**
**thcb@cam.ac.uk**

## Abstract

Long-term studies of individuals enable incisive investigations of questions across ecology and evolution. Here, we illustrate this claim by reference to our long-term study of red deer on the Isle of Rum, Scotland. This project has established many of the characteristics of social organization, selection and population ecology typical of large, polygynous, seasonally-breeding mammals, with wider implications for our understanding of sexual selection and the evolution of sex differences, as well as for their population dynamics and their implications for population management. As molecular genetic techniques developed, the project has pivoted to investigate evolutionary genetic questions, also breaking new ground in this field. With ongoing advances in genomics and statistical approaches, and development of increasingly sophisticated ways to assay new phenotypic traits, the questions that long-term studies such as the red deer study can answer become both broader and ever more sophisticated. They also offer powerful means of understanding the effects of ongoing climate change on wild populations.

**Key words:** deer, fitness, population density, sexual selection, climate change, inbreeding, heritability,

## Introduction

Field studies that track the complete lives of individuals can provide unique insights into the ecological and evolutionary processes that govern wild animal populations (Clutton-Brock and Sheldon 2010, Festa-Bianchet, et al. 2017, Hayes and Schradin 2017). The combination of field observations with measurements of physiology, phenology and growth as well as with estimates of parentage and relatedness from molecular data make it possible to address a wide range of questions in ecology and evolutionary biology with unusual precision. Recognition of individuals and life-time monitoring reveal the effects of sex and age on individual performance at different life stages. Data on complete lifespans – from birth to death, through all reproductive events – generate measures of the lifetime breeding success of individuals that can be used to assess variation in fitness. Analyses of the extent of these differences reveals the operation of natural and sexual selection and make it possible to explore the social, environmental and genetic causes of this variation. Continuous records across individuals' lifetimes can also identify the consequences of events at earlier stages of life on growth, breeding success, health and survival at later stages, and hence the costs and benefits of differences in development on reproduction and survival throughout life, including the process of senescence. At a population level, such studies allow analyses of population dynamics to distinguish between the demographic effects of variation in fecundity, mortality and dispersal. Finally, by their nature, long-term field studies provide invaluable information on the effects of current climate change on natural populations, and the mechanisms driving responses to changing environmental conditions.

## Study species, project history and methods

The study of red deer (*Cervus elaphus*) on the Isle of Rum in the Inner Hebrides, Scotland, is one of a small number of individual-based field studies of free-ranging mammals that began in the early 1970s and is still running today (Clutton-Brock 2021). The red deer is a medium-sized ungulate native to Europe, North Africa and Asia, closely related to other *Cervus* species of the Old World and North America. It shows pronounced sexual dimorphism driven by sexual selection through male-male competition, with adult males being on average 50% heavier than females (Figure 1a). Males also develop weaponry in the form of antlers, which are cast and regrown each year. Red deer are highly seasonal breeders, with an autumnal mating season and females giving birth to single offspring in late spring. Males play no part in parental care, instead being under intense selection to acquire matings. Scotland holds the largest concentration of red deer in Europe, and whereas the species is thought to have evolved in forest or forest edge, much of the Scottish population resides in open hill habitat dominated by heaths and bogs (Clutton-Brock and Albon 1989).

The Isle of Rum (57°N; 6°20'W'; Figure 1b) was purchased by the UK Nature Conservancy for use as a nature reserve and open-air laboratory in 1957 (Eggeling 1964). At the time, the ~100km$^2$ island carried a red deer population of around 1,500 animals, and between 1958 and 1972 deer in all parts of the island were regularly culled in line with standard management of deer populations across Scotland. Research by ecologists from the UK's then Institute of Terrestrial Ecology investigated red deer growth and reproduction (Mitchell, et al. 1976), population structure (Lowe 1969) and habitat use (Charles, et al. 1977), providing a basis for much of our subsequent work. From 1966 to 1972, a Cambridge-based project led by Roger Short and Gerald Lincoln also explored the physiological mechanisms controlling reproduction in both sexes (Guinness, et al. 1971, Lincoln, et al. 1972) and the antler cycle in males (Lincoln, et al. 1972). This project identified most of the individual males using the 12km$^2$ 'North Block' of the island (Figure 1c). In 1969, it was joined by Fiona Guinness, who learned to recognise the sixty-odd females as well as the males using the North Block, and recorded the movements and breeding success of individuals until 1972.

In 1972, Tim Clutton-Brock obtained funding from the UK's Natural Environment Research Council (NERC) for a study of social organisation, life histories and population regulation in red deer. The Nature Conservancy also agreed to terminate the annual cull there to allow the deer to habituate to the presence of observers (though study deer continued to be shot if they ranged outside the area). Census routines were developed to measure the activity, habitat use, distribution and association patterns of all individuals using the study area. Fiona Guinness returned to Rum in late 1973, resuming her records of the life histories of individuals and the first of a series of PhD students joined the project to work on reproductive and social behaviour in the following year (Gibson 1978, Hall 1978). In 1976, Steve Albon joined, first as a research assistant then as a PhD student and post doc, taking charge of data management and statistical analyses. In 1984, Josephine Pemberton joined the project to explore genetic variation in the population and in 1997, Loeske Kruuk arrived to develop research on quantitative genetics and life history evolution. By 2005, the project's research was concentrating principally on evolutionary genetic questions and it moved from the University of Cambridge to the University of Edinburgh.

*Figure 1 about here*

Since 1974, we have continuously monitored the distribution, habitat use, behaviour, annual reproductive success and survival, of all individual deer regularly using the North Block in weekly censuses of the population. Each year, around 90% of calves born in the study area are caught, marked (Figure 1d), weighed and sampled for genetic analysis. Unlike several other studies of ungulates (see (Hamel, et al. 2016)), we do not routinely catch individuals later in life and so do not have regular access to variation in body weight. Cast antlers are collected each spring and most can be attributed to individual males from their form, photographs and DNA profiling. At the end of each winter, we search the study area for carcasses, collecting and storing skeletal material. Since 1981, vegetation indices including standing crop and productivity have been measured on the grasslands, and since 2010, we have collected faecal samples for a range of analyses. As a result of genetic studies, we now have pedigree and life history records for over 4,000 individuals that have passed through the population (either as core members, or more briefly) since 1972 (Huisman, et al. 2016).

## Social organisation

The project's earliest work provided a quantitative description of social organisation, habitat use, and reproductive behaviour in the deer, building on the qualitative studies of red deer in Torridon by Frank Fraser Darling in the 1930's (Darling 1937). Females adopt home ranges overlapping those of their mother and older sisters, aggregating with them in unstable groups, and temporary groups frequently include members of several matrilineal groups with overlapping ranges (Clutton-Brock, et al. 1982b, Conradt and Roper 2000). Females have well-defined home ranges and the ability to dominate or displace other females falls when individuals move outside their own home range (Thouless and Guinness 1986). As in many other social mammals, females in the same matrilineal group establish dominance relationships early in life and an individual's dominance status is affected by its birth weight and its mother's social rank as well as by its age (Clutton-Brock, et al. 1984). Social rank in females is, in turn, positively associated with access to resources, reproductive success and longevity (Clutton-Brock, et al. 1988, Thouless 1990, Thouless and Guinness 1986).

For most of the year, male red deer live in loose groups in areas peripheral to those used by females (Clutton-Brock, et al. 1982b). Males leave their natal range and form bachelor groups when they are 2-3 years old. Like females, they have well-defined dominance relationships that are associated with their access to resources (Appleby 1980, Appleby 1982). Due to their larger body size, males have greater energy requirements and spend more time than females grazing in areas where food is more abundant but of lower quality, avoiding areas heavily grazed by females (Clutton-Brock and Albon 1989, Conradt, et al. 1999).

In September, male groups break up and mature males move into female areas and defend 'harems' of females against each other, roaring frequently to discourage rivals and attract females (Clutton-Brock and Albon 1979). Work with captive deer has shown that females are attracted to males that roar frequently and that roaring advances oestrus dates in females (McComb 1987, McComb 1991). Males mate with females as they come into oestrus, which usually lasts for less than 24 hours. While mature males defend harems, younger males try to chase females out of harems in order to mate opportunistically (Clutton-Brock, et al. 1979) – though males less than five years old rarely sire calves. Around the time of their oestrus, females are more mobile, moving between harems, partly due to fights and disturbance but also in some cases apparently by choice (Stopher, et al. 2011, unpublished data). Unlike females, males virtually cease feeding during the rut and defend their harems day and night, with the result that they rapidly lose weight (Mitchell, et al. 1976) and are eventually displaced by fresher rivals (Clutton-Brock, et al. 1982b). Males engage in 'roaring contests', and do not escalate fights with individuals that they are unlikely to beat (Clutton-Brock and Albon 1979, Reby, et al. 2005). Despite this, escalated fights between mature males are frequent and dangerous, commonly resulting in injury and occasionally in death (Clutton-Brock, et al. 1979).

<u>Female life histories</u>

The red deer study provided some of the first insights into the extent and causes of variation in lifetime reproductive success in female mammals in wild populations (Clutton-Brock, et al.

1988). On Rum most female red deer breed for the first time at three or four years old, and then continue breeding until they are eleven or twelve years old, when their fecundity begins to fall (Figure 2a; (Mitchell, et al. 1976, Nussey, et al. 2009)). Offspring birth weight, offspring survival and adult survival initially increase with age, plateau in mid-life between the ages of five and eight years, and then decline (Figure 2b; (Clutton-Brock, et al. 1982b, Nussey, et al. 2009)). Older females do not range as widely as younger ones and reductions in range size are associated with increased mortality (Froy, et al. 2018). The energy costs of lactation are high: in deer culled on Rum, mothers that rear calves in a given year enter the following winter at lower body weights than those that either fail to conceive or lose their calves shortly after birth (Mitchell, et al. 1976). A mother that successfully rears a calf is more likely to die in the following winter (Clutton-Brock and Albon 1989, Froy, et al. 2016). If she survives, she is less likely to bear a calf the following spring, and if she does breed the following year, she will on average, give birth later and to a lighter calf (Albery, et al. 2021a, Clutton-Brock, et al. 1982b). Following recent monitoring of parasitic helminth egg counts in faecal samples, we now know that these costs of reproduction are in part due to lactating females experiencing higher parasite burdens (Albery, et al. 2021a).

*Figure 2 about here*

As data on individual life histories accumulated, the study explored the correlates of individual differences in reproductive success, both within years and across the entire lifespans of individuals (Clutton-Brock, et al. 1988). We distinguish here between lifetime breeding success (LBS; Figure 3a), the number of offspring that a female gives birth to across her lifetime, and lifetime reproductive success (LRS), the number of offspring that survive to two years. Differences in the survival of offspring through their first year and in the lifespan of females make larger contributions to differences in total LRS between females than differences in their annual fecundity and standardized variance in LRS is greater than in LBS (Clutton-Brock, et al. 1988). Some females consistently fail both to breed and to rear calves, and our recent quantitative genetic analyses have shown that female fecundity and offspring survival rates are positively correlated, both phenotypically and genetically (Morrissey, et al. 2012).

Differences in reproductive success between females are associated both with aspects of their own phenotype and with the characteristics of their matrilineal group. Early work showed that reproductive success was positively correlated with a female's social rank as well as with her mother's rank, and that both daughters and sons born to dominant females had higher reproductive success than those born to subordinate mothers (Clutton-Brock, et al. 1984, Clutton-Brock, et al. 1986). Aspects of the early development of individuals are also important: females that experience challenging environmental conditions in their first two years of life show faster rates of ageing and reduced reproductive performance in the second half of their lives than those reared under more favourable conditions (Nussey, et al. 2007). Individuals that breed early in their lives senesce faster, indicating the presence of trade-offs between early and late breeding success (Moyes, et al. 2006, Nussey, et al. 2006), although there is no clear support for a genetic basis to this trade-off (Nussey, et al. 2008). The reproductive success of females is also affected by the characteristics of their matrilineal groups. Members of female groups with superior ranges (e.g. those that include grassland fertilised by gull colonies) show higher reproductive performance than those with inferior ranges (Iason, et al. 1986). In addition, members of large matrilines compete more frequently for access to resources and associate with each other less frequently, and the reproductive success of females falls as matrilineal group size increases (Clutton-Brock, et al. 1982a).

*Figure 3 about here*

## Male life histories and sexual selection

Analyses of the extent and causes of variation in breeding success between males provided new insights into the operation of sexual selection in polygynous species. Initially, the breeding success of different males was estimated by back-dating from the birth date of each calf, using a standard gestation length to identify which male's harem a female had been in when she conceived (Clutton-Brock, et al. 1988, Guinness, et al. 1978). These analyses indicated that breeding success was largely confined to mature males, and that there were large differences in breeding success between individuals within and across seasons (Clutton-Brock, et al. 1988). Both these conclusions were later confirmed by analyses of male success based on DNA fingerprinting (Pemberton, et al. 1992) and other genetic parentage assignment techniques (Figure 3b; see below).

Individual differences in breeding success among males are associated with their fighting success and body size (Clutton-Brock, et al. 1988) and their early development is also important: the most successful males are those that are born early and heavy (Kruuk, et al. 1999b). Breeding competition is intense and few individuals breed successfully until they are seven or eight years old. The average breeding success of males declines rapidly after the age of around eleven, with the result that the effective breeding lives of males are much shorter than those of females (Figure 2b). Comparisons with other polygynous mammals, like land-breeding seals, show that sex differences in the duration of breeding are a common feature of polygynous, dimorphic species where individual males compete to guard access to groups of females (Clutton-Brock and Isvaran 2007, Le Boeuf and Reiter 1988, Lukas and Clutton-Brock 2014). Adult males experience higher levels of mortality than females (Figure 2b; (Clutton-Brock, et al. 1988, Nussey, et al. 2009)) and, as in females, there is a trade-off between early reproductive effort (in terms of harem-holding), and later senescence in harem-holding (Lemaitre, et al. 2014). As expected for a strongly polygynous species, (standardised) variance in male lifetime breeding success is substantially higher for males than for females (9.80 vs 1.73, data as in Figures 2 & 3). However, sex differences in individual variation in breeding success or reproductive success are often substantially smaller if they are calculated across the lifespans of individuals than if they are based on measures of individual variation in success within particular seasons, which are often used to assess the potential strength of sexual selection in polygamous animals (Clutton-Brock 1983, Lukas and Clutton-Brock 2014).

Sex differences in survival are not confined to adults. Both in red deer and in some other sexually dimorphic mammals, the faster growth rates of juvenile males are associated with higher energy requirements and with lower survival rates in juvenile males compared to juvenile females when food is scarce or weather conditions are unfavourable (Clutton-Brock,1991b; Clutton-Brock et al 1885a). Sex differences in survival can also occur before birth in sexually dimorphic mammals (Clutton-Brock,1991a). In red deer, males are born around 8% heavier than females, indicating that male fetuses grow slightly faster than female fetuses during gestation (Clutton-Brock,1991) and comparisons of birth sex ratios between years show that the percentage of males born declines when population density is high or climatic conditions are unfavourable, suggesting that adverse conditions during gestation are probably associated with higher mortality of male fetuses compared to female fetuses (Kruuk et al 1999a)

Several lines of evidence also indicate that male offspring are more costly to rear than females. Both in red deer and in several other sexually dimorphic mammals, male infants suck from their mothers more frequently than female infants (Clutton-Brock 1991, Clutton-Brock, et al. 1981), extracting more milk (Landete-Castillejos, et al. 2005, Trillmich 1986). Early studies showed that red deer mothers who had reared a male calf were less likely to breed in the subsequent year than those that had a female (Clutton-Brock, et al. 1981) and that subordinate females were more likely to die if they had reared sons (Gomendio, et al. 1990). Later work based on a larger data set found that across all females, survival and fecundity were both depressed in females after they had reared a son to when they had reared a daughter, though the effect was not large (Froy, et al. 2016).

Since the costs of raising sons are greater than those of raising daughters, we investigated whether the additional costs of raising males might affect the sex ratio of young produced by different mothers. Early analyses showed that the dominance status of mothers was a stronger predictor of the fitness of their sons than that of their daughters and that dominant females produced more males than subordinate females (Clutton-Brock, et al. 1984, Clutton-Brock, et al. 1986), as sex ratio theory predicts (Trivers and Willard 1973). A separate study of deer culled in other parts of Rum showed that females in better condition were more likely to be carrying male embryos and suggested foetal loss of male embryos in poorer condition females as a likely mechanism (Flint, et al. 1997). Similar sex ratio biases have been reported in some other polygamous mammals (Clutton-Brock and Iason 1986, Sheldon and West 2004) but they are often unstable. In the Rum deer, the relationship between maternal dominance and offspring birth sex ratio did not persist after the population reached carrying capacity and the reproductive performance of females fell (Kruuk, et al. 1999a).

## Density-dependent and density-independent effects on population dynamics.

Social organisation and reproductive competition have important consequences for the demography and dynamics of populations. In the eight years following the cessation of culling of the study population in 1972, increases in recruitment led to a tripling of the number of females regularly using the North Block study area (Figure 4; (Albon, et al. 2000, Clutton-Brock, et al. 1982b, Clutton-Brock, et al. 1985b)). The size of matrilineal groups increased, feeding competition within them became more intense, and females from the same matrilineal group ranged more widely and spent less time together (Albon, et al. 1992). Despite this, the number of females emigrating from the North Block remained low (Clutton-Brock, et al. 1997). The changes were associated with reductions in the proportions of females that calved as three-year-olds and that calved after raising a calf in the previous year (Clutton-Brock, et al. 1985b). Average calving dates became later and calf mortality in the first winter increased, while average birth weights showed no directional change (Clutton-Brock, et al. 1987b). Adult mortality rose and longevity declined (Clutton-Brock, et al. 1987b, Clutton-Brock, et al. 1997). After the first ten years, female density did not continue to increase as rapidly, fluctuating between years in relation to winter weather conditions (Albon, et al. 2000, Coulson, et al. 1999) and variation in the winter mortality of calves and adults became the principal factors responsible for changes in population size (Albon, et al. 2000).

*Figure 4 about here*

The increase in female numbers had important consequences for the number of resident males. As female numbers rose, birth sex ratios became (slightly) less male-biased (Kruuk, et al. 1999a) and the survival of male calves and yearlings declined (Clutton-Brock, et al. 1985b), as did the growth of first antler spikes in yearlings (Schmidt, et al. 2001) and adult antler size (Clutton-Brock and Albon 1989). An increasing proportion of males of all ages dispersed from the study area, while permanent immigration of males from neighbouring areas declined (Clutton-Brock, et al. 1997). These trends led to progressive changes in the sex ratio of adults resident in the study area, which became increasingly biased towards females (Clutton-Brock, et al. 1985b, Clutton-Brock, et al. 1997) (Figure 4). Similar changes in adult sex ratios have occurred in other red deer populations (Albon and Clutton-Brock 1988) as well as in populations of other dimorphic ruminants at carrying capacity or subject to adverse environmental conditions (Clutton-Brock and Albon 1989).

The long-term monitoring of the Rum population has also shown how fluctuations in weather conditions in spring influence growth, survival and breeding success in red deer. Late springs, dry summers and cold, wet autumns and winters all reduce primary production, while high levels of rainfall in autumn or winter can increase heat loss and depress condition and survival (Albon and Clutton-Brock 1988, Albon, et al. 1987) and delay calving dates the following spring (Nussey, et al. 2005). Adverse weather conditions have disproportionate consequences for weaker animals, including the young, the old and males, all of which experience increased mortality after cold, wet winters (Albon, et al. 1987, Clutton-Brock, et al. 1987a).

Fluctuations in temperature generate substantial differences in growth, breeding success and survival between cohorts. By delaying the onset of grass growth, low temperatures in late winter and early spring reduce the prenatal growth and postnatal survival of calves, and females born after late springs produce light calves that often fail to survive over the rest of their lives (Albon et al 1987). These effects generate pronounced differences in reproductive success between cohorts (Albon, et al. 1987) though their magnitude declines as cohorts age (Hamel, et al. 2016). As with increases in population density, adverse weather conditions affect males disproportionately, generating larger reductions in juvenile and adult survival and lifetime breeding success in males than in females (Rose, et al. 1998).

The longevity of the study since carrying capacity was reached has enabled us to explore the consequences of anthropogenic climate change (e.g. (Bonnet, et al. 2019, Coulson, et al. 2003, Moyes, et al. 2011)). Over the last few decades, winters on Rum have become milder and wetter, temperatures have risen and the number of days when conditions have permitted grass growth has steadily increased (Moyes, et al. 2011). These changes in climate have had substantial effects on the dates of the start and end of the rut, oestrus, calving, antler cleaning and antler casting , all of which have advanced by 5-12 days (Bonnet, et al. 2019, Moyes, et al. 2011), while antler size has also increased (Moyes, et al. 2011). In part, these changes are a consequence of phenotypic plasticity, with individuals’ phenology changing between years in response to variation in climate (Bonnet, et al. 2019, Clements, et al. 2010, Clements, et al. 2011a, Clements, et al. 2011b, Froy, et al. 2019, Stopher, et al. 2014). However recent analyses indicate that evolutionary changes have also occurred at least in calving dates ((Bonnet, et al. 2019); see below).

## Molecular analyses

Since 1982, we have collected tissue samples from all deer captured or found dead, and cast antlers. These samples have been analysed using a range of molecular techniques as they developed, from allozyme electrophoresis (Pemberton, et al. 1988) through DNA fingerprinting (Pemberton, et al. 1992), microsatellites (Marshall, et al. 1998) to single nucleotide polymorphisms (SNPs) (Huisman, et al. 2016). The drive to infer paternity in the Rum deer using microsatellite markers inspired one of the most widely-used parentage inference programs for wild populations, CERVUS (Marshall, et al. 1998). More recently, we developed the SEQUOIA program which uses SNP data to reconstruct multiple different pedigree relationships simultaneously (Huisman 2017). The technique both confirms all field-based maternal links and provides incontrovertible assignments of paternity (Huisman, et al. 2016). Our pedigree of deer now stretches over 64 years (since it includes some individuals tagged in preceding studies), and includes 7811 mother-offspring and father-offspring links and a maximum depth of 11 generations. Combining this information with measures of phenotypes opened up two major avenues of investigation: on the occurrence and implications of inbreeding, and on the heritable genetic basis of variation of phenotypic traits.

## Inbreeding and inbreeding depression

The social organisation and mating system of the deer leads to extensive low-level inbreeding. As described earlier, female deer have characteristic home ranges, and the ranges of matrilineally related females often coincide. Individual males often attempt to (or end up) rutting in the same locations across years and so often mate with multiple members of the same female group within and between years and sometimes with the same female across years. This behaviour increases the average relatedness between individuals in the population (Stopher, et al. 2012a). In addition, although not resident in the study area throughout the year, a high proportion (75%) of males that rut in the study area were born there, possibly because it has one of the highest concentrations of females on the island. Together these patterns promote inbreeding (Stopher, et al. 2012a). However, close inbreeding is relatively rare: just 11 cases of first-degree relatives breeding have occurred over the years, all of which were cases of fathers mating with their daughters (Huisman, et al. 2016). Such matings can only occur if a male is successful in the same area at time points at least three years apart and if a daughter matures early, both of which are relatively rare events.

Successive improvements to estimating individual inbreeding coefficients have yielded increasing evidence of very strong inbreeding depression. Both non-pedigree, microsatellite-based estimates of heterozygosity (Coulson, et al. 1998, Slate, et al. 2000) and pedigree inbreeding coefficients (Walling, et al. 2011) found inbreeding in some fitness components and related traits, but the full picture has only emerged with the much greater precision afforded by the SNP-refined pedigree and genomic inbreeding coefficients ($F_{grm}$, Yang, et al. 2011) based on genome-wide SNPs. Inbreeding depresses birth weight, juvenile survival (to two years of age) independently of birth weight, and annual breeding success in both sexes (Huisman, et al. 2016). More remarkably, even though inbreeding depression in juvenile survival reduces the number of inbred females who survive to adulthood and become mothers, the calves of inbred mothers survive less well than those of non-inbred mothers (Huisman, et al. 2016). As a consequence of these effects, inbreeding depression across the lifespan is high: a female with $F_{grm} = 0.125$ (equivalent to the offspring of a mating between half sibs) or more has a 75% reduction in LBS compared with an average female with $F_{grm} = 0$, and a 79% reduction in her LRS. A male with $F_{grm} = 0.125$ has a 95% reduction in LBS compared with an average male with $F_{grm} = 0$ (Huisman, et al. 2016).

While mechanisms to avoid inbreeding have evolved in many species, this is not a universal expectation, since there are trade-offs between the costs and benefits of avoidance (Kokko and Ots 2006, Szulkin, et al. 2013). Despite the severe inbreeding depression, it is not clear that the deer have evolved inbreeding avoidance. To investigate the issue, it is necessary to examine the mating behaviour of prospective parents, not their potentially inbred offspring (Reid, et al. 2015). In the deer, the relatively short breeding lifespans of males and the changing membership of female groups mean that the probability that females will mate with a close relative is low. The act of mating with a relative (or not) has low repeatability in both sexes and hence is likely to have negligible heritability, so although there is some evidence for selection on this trait in males (but not females), an evolved response is unlikely (Troianou, et al. 2018). Given that many males never sire a calf despite surviving to adulthood (Figure 3b), it is also likely that siring any offspring at all is more important to males than the low probability of mating with a close relative, and is the main driver for male mating behaviour. In this regard our findings parallel those of the intensively studied Mandarte Island song sparrows (Reid, et al. 2015).

## The additive genetic basis of phenotypic variation

'Quantitative genetic' analyses combine measurements of individual phenotypes with information on individuals' relatedness to each other, to estimate heritabilities and levels of genetic variance of quantitative (continuous) traits. In 1999 and 2000, a trio of papers from long-term studies of ungulates, including Rum deer, presented the first application of a quantitative genetic technique developed in animal breeding known as the 'animal model' to studies of wild populations, specifically for bighorn sheep in the Rocky Mountains of Canada (Reale, et al. 1999), Soay sheep on St Kilda, Scotland (Milner, et al. 2000), and the Rum red deer (Kruuk, et al. 2000). The animal model is a form of mixed model that includes a random effect for individual genetic merit (or 'breeding value'), and hence estimates the additive genetic variance in breeding value, as well as information on other components of phenotypic variance, such as those due to maternal effects or shared environmental conditions (Kruuk and Hadfield 2007, Wilson, et al. 2010). The technique spawned a surge of interest in 'wild quantitative genetics', the study of which has to date relied almost exclusively on long-term, individual-based studies with multi-generational pedigrees such as Rum (Charmantier, et al. 2014). Expansion to a broader range of studies and taxa will hopefully occur as genomic data provide means of estimating relatedness without the need for pedigrees (Bérénos, et al. 2014, Gienapp, et al. 2017) – but long-term studies will always be necessary for robust estimation of temporal environmental heterogeneity and maternal effects.

The first analysis of heritability of multiple traits in the Rum red deer population revealed substantial genetic variance for multiple aspects of fitness, ranging from birth weight up to LBS (Kruuk, et al. 2000). This multi-trait comparison tested the widely-held expectation that traits under stronger selection should have lower levels of genetic variance. Although the observation of lower heritability in such traits appeared to support the expectation, the pattern was driven by higher levels of other components of variance, with little indication of lower genetic variance (Kruuk, et al. 2000). The importance of other components of overall phenotypic variance for different phenotypic traits has been further explored in analyses of levels of maternal genetic or environmental variance (Gauzere, et al. 2020) or shared home-ranges (Stopher, et al. 2012b). The results from these studies nicely reflect the ecology of the deer, with maternal effects (similarity between maternal relatives) typically being larger for female offspring than males (Kruuk, et al. 2000), and larger for early-life than late-life traits (Gauzere, et al. 2020). From an analytical perspective, the red deer study has also repeatedly illustrated the extent to which estimates of genetic variance may be inflated by effects of relatives sharing environments if these are not corrected for (Kruuk and Hadfield 2007, Stopher, et al. 2012b).

Evolutionary responses to selection are only possible within a population if there is genetic variance for fitness (Fisher 1930, Morrissey, et al. 2010, Walsh and Lynch 2018). Recent analysis using zero-inflated Poisson generalised linear mixed models indicates substantial genetic variance in LBS in the red deer, our estimate of ‘fitness’ (Bonnet, et al. in press). By Fisher’s Fundamental Theorem of Natural Selection, the additive genetic variance in fitness is the change in mean fitness from one generation to the next due to a genetic response to natural selection (Fisher 1930) – in other words, the per-generation rate of evolutionary adaptation in a population. The observed levels of additive genetic variance in fitness in the deer thus indicate ongoing genetic adaptation, and hence that the population is not at an evolutionary equilibrium (Bonnet, et al. in press). The fact that we do not see change in mean fitness at the phenotypic level may imply concurrent environmental deterioration, counteracting the genetic evolution (Bonnet, et al. in press). This result is an important indication, firstly, of the potential for adaptive evolutionary responses to selection within the population (including response to climate-change-induced selection). Secondly, it highlights the need to understand the drivers of the environmental deterioration. These may be related to climate change, but ‘environmental deterioration’ may also include improvements in the competitive ability of interacting individuals, leading to deterioration in the social environment (Fisher and McAdam 2019, Hadfield, et al. 2011).

A second important line of investigation has been the constancy of genetic variance. As described above, the deer population experiences substantial levels of environmental heterogeneity due to the effects of population density and weather. We expected that these might affect the expression of genetic variance underlying quantitative traits, generating genotype-by-environment interactions. However, to date, we have found no evidence of these. For example, the best-documented traits of birth date and birth weight are heavily dependent on temperature at conception and during gestation, and yet there is no evidence of variation between females in their response to temperature (i.e. no IxE interactions, or variation in individual reaction norms, Froy, et al. 2019). A lack of phenotypic variance in plasticity means no possibility of genotype-environment, or GxE, interactions (Froy, et al. 2019). This lack of GxE mirrors results from several other studies of natural populations (reviewed in Hayward, et al. 2018). Null results obviously raise concerns about statistical power, but power analyses indicate that there is easily sufficient power to detect biologically meaningful GxE with data-sets such as these (Froy, et al. 2019, Hayward, et al. 2018). However, in marked contrast to the analyses of GxE in relation to climatic conditions, the expression of genetic variance increases for several traits with individuals' age (Nussey, et al. 2008), supporting the notion of increased genetic variance at older ages (Wilson, et al. 2008).

### Evolutionary dynamics

Quantitative genetic analyses also allow us to test if evolution is constrained, and genetic variance maintained, by genetic trade-offs between different traits. Whilst the existence of trade-offs between different life-history components is a corner-stone of much of behavioural ecology, demonstrating that such trade-offs occur at a genetic level has been persistently challenging in wild populations (Teplitsky, et al. 2014). Our analyses of the Rum deer data reflect this, indicating only some evidence of constraint. For example, the structure of the genetic variance-covariance matrix **G** for a suite of female life-history traits reduces the expected rate of adaptation to 60% of the rate predicted if traits were entirely independent (Morrissey, et al. 2012). Similarly, considering **G** for life-history traits (survival and fecundity) of both sexes deflects a predicted response to selection away from the direction of fastest adaptation (in multivariate space) to a moderate, but not substantial, degree (Walling, et al. 2014). There is moderate if not strong evidence of antagonistic covariance between early- vs late-life performance in female reproductive traits (Nussey, et al. 2008), but no indication of antagonistic covariance between direct and maternal genetic effects on offspring birth weight (Gauzere, et al. 2020). Whether these limited conclusions reflect lack of statistical power in demanding analyses, lack of appropriate measures of phenotype, or a true paucity of multivariate genetic constraint remain challenging avenues to be explored.

Given the study's long-standing interest in sexual dimorphism (see above), one of the most interesting aspects of multivariate analyses involves cross-sex genetic associations. Genetic variance in a population will be sustained, and evolutionary responses constrained, by antagonistic cross-sex covariance in genetic effects, as seen for example in *Drosophila* (Chippindale, et al. 2001). Initial analyses of a measure of individual fitness called 'de-lifing' (a measure of fitness aimed at estimating individuals' contribution to population growth (Coulson, et al. 2006)) indicated that successful males had less successful female relatives, implying the existence of sexually-antagonistic genetic variance (Foerster, et al. 2007). However, subsequent analyses have failed to uphold this initial conclusion, with little evidence of sexually-antagonistic covariance. For example, there is little support for constraint through sexually-antagonistic genetic covariances between different life-history components in the two sexes (Walling, et al. 2014), and our most recent analysis of lifetime breeding success using zero-inflated Poisson models shows no evidence of antagonistic cross-sex genetic covariance (T. Bonnet, pers. comm.). The development of these conclusions illustrates both the complexity of measuring fitness appropriately, and the value of being able to return to earlier questions with superior methods and extended datasets.

Finally, a major aim of evolutionary analyses using long-term data from wild populations has been to understand temporal change in phenotypic traits, and the extent to which these can be predicted from responses to natural selection. This has been challenging, with frequent examples of directional selection on heritable traits apparently not generating the expected change in phenotype (Brookfield 2016, Merila, et al. 2001). Even when mean phenotypes are changing, evidence of underlying genetic change has been notoriously hard to prove, with arguably too little attention being paid to separating evolutionary change from effects of phenotypic plasticity in response to a changing environment (Charmantier and Gienapp 2014). In the red deer, calf birth weight shows substantial genetic variance, and is also under positive directional selection (via positive associations firstly between an individual's birth weight and its lifetime breeding success, and secondly between a female's lifetime breeding success and her offspring's birth weight (Gauzere, et al. submitted)). However, in a classic example of the 'paradox of stasis', there is no evidence of either phenotypic or genetic change in average birth weight over the study period (Figure 5a & b). Similarly, antler size is heritable, but has shown no evidence of evolutionary response to the directional selection apparently favouring larger antlers (Kruuk, et al. 2014, Kruuk, et al. 2002). In this case, the apparent phenotypic selection is probably due to a confounding association of both antler size and male breeding success with environmental conditions. This generates the appearance of selection, but in the absence of any genetic covariance between antler size and fitness, it will not generate any evolutionary response (Kruuk, et al. 2014).

In contrast, calf birth date has shown a strong temporal trend, advancing by 4.2 days per decade over the study period (despite becoming later in the early years as density rose; Figure 5c). This change is in the direction predicted both by an evolutionary response to selection and by phenotypic plasticity in response to climate change (Bonnet, et al. 2019). Whilst a substantial component of the phenotypic shift is due to plasticity in response to warming temperatures, there is also evidence of genetic change (Figure 5d). Such genetic change could be an adaptive response to the observed directional selection favouring earlier birth dates, supported by genetic covariance between a female’s parturition date and her lifetime breeding success. However we cannot yet rule out that it may be due to genetic drift. In addition, we also cannot yet say that this is an evolutionary *response to climate change*, because it is not yet clear whether the selection favouring earlier calving is driven by warming temperatures.

*Figure 5 about here*

## Genetic architecture of quantitative traits

Knowledge of the loci underpinning of quantitative traits enables better understanding of responses to selection. For example, a major quantitative trait locus (QTL) affecting horn size in Soay sheep shows heterozygote advantage, which provides an explanation for the persistence of small-horned males in the population despite their very low breeding success (Johnston, et al. 2013). Our studies of the Rum red deer have been in the vanguard of attempts to determine the genetic architecture of quantitative traits in wild populations, and also in showing that finding QTL is remarkably hard in nature.  Soon after the first genetic map relevant to red deer was established (Slate, et al. 2002a), we genotyped 90 microsatellites in a single extended pedigree of 364 Rum deer, mapped the markers and conducted linkage mapping of birth weight, finding three regions potentially containing QTL (Slate, et al. 2002b). More recently, we refined the red deer genetic map using 38,000 single nucleotide polymorphisms (SNPs) and the pedigree, demonstrating that in this species, unusually, the genetic map is longer in females than males (Johnston, et al. 2017). Using these markers in a genome-wide association study (GWAS) of birth weight in 2,200 individuals, the three regions initially suggested by linkage mapping were not replicated (J. Gauzere, pers. comm.). Similarly, a recent GWAS analysis of various antler traits using the 38K SNP markers did not find any genome-wide significant QTL, indicating a highly polygenic architecture for antler traits (Peters, et al. 2022). Another trait we have been able to derive from analysis of the pedigree is individual autosomal recombination rate (ARR). ARR is heritable in females and, using regional heritability analysis, the variation maps to a genomic region containing the genes *REC8* and *RNF212B,* adding to the evidence that these genes control variation in recombination rate in mammals (Johnston, et al. 2018). The recent assembly of a high quality genome from a Rum deer will greatly assist in future genetic mapping studies (Pemberton, et al. 2021). However, a relative lack of statistical power due to sample sizes that are low compared to studies of human or livestock populations will probably remain a limitation of these studies in the Rum and other wild populations.

## Long term studies of individuals – wider issues

### Replication

Experimental manipulation is the gold standard for proving causation in ecology and evolution, but long-term studies, including ours, yield most findings by correlation using individuals as the unit of analysis, for two main reasons. First, successful manipulations, by their very nature, change the performance of individuals and therefore have the potential to disrupt population dynamics and trait time series. Manipulations therefore need to be recorded meticulously and dealt with appropriately in all subsequent statistical analysis. Second, not all species lend themselves to manipulation. In the deer it would be difficult to give supplementary food or anthelmintics (say) to specific individuals and cross-fostering would be totally impractical, since females are aggressive towards each other’s calves.

Ecological and evolutionary phenomena vary in time and space and type 1 error exists, so if experiments are not tenable then replication is desirable. With the exception of some bird and primate species, long-term studies including ours lack replication in terms of multiple study populations of the same species. On the other hand, they have accumulating time series. We believe such studies have a duty to re-analyse earlier findings at intervals to confirm them or determine whether effects have changed and if so why. In our account above, we have documented several instances of repeated analyses. In many cases, findings have proved robust. For example the costs to a mother of rearing a calf from birth into the winter have persisted in all the analyses conducted (Albery, et al. 2021a, Clutton-Brock, et al. 1989, Clutton-Brock, et al. 1983, Froy, et al. 2016), as has evidence of the higher costs of raising males (Clutton-Brock, et al. 1981, Froy, et al. 2016, Gomendio, et al. 1990). The associations between spring temperature, birth weight and female lifetime breeding success first found by (Albon, et al. 1983) were repeated in both subsequent analyses (Kruuk, et al. 1999b, Stopher, et al. 2014) and advancing calving dates are consistently related to weather in the summer preceding conception (Bonnet, et al. 2019, Froy, et al. 2019, Stopher, et al. 2014).

Other findings have changed, become more nuanced or unrepeatable in later analyses. In some cases, this may be due to changing conditions as the population reached carrying capacity. For example, in the early data, when the population was expanding, dominant females produced more sons than subordinates (Clutton-Brock, et al. 1984), but in later years after the population had reached carrying capacity, there was no longer a significant association between maternal dominance and the sex of her offspring, though fewer males were born after winters when population density or rainfall were high (see above (Kruuk, et al. 1999a)). In other cases, findings may change as a result of improvements in analytical methods. Antagonistic cross-sex genetic correlations were found in one analysis (Foerster, et al. 2007) but not in a second which used a more conservative analytical approach (Walling, et al. 2014)

Another way to investigate the robustness of results is to compare findings across studies of different species via meta-analyses. Increasing numbers of analyses are being published that include multiple long-term studies of individuals, to which we contribute data. For example, red deer data have contributed to understanding that sex differences in juvenile mortality are commonly associated with sex differences in early growth and adult mass (Clutton-Brock, et al. 1985a); that senescence is widespread in the animal kingdom (Jones, et al. 2008, Jones, et al. 2014); to the overwhelming evidence for changing phenology (Thackeray, et al. 2016, Thackeray, et al. 2010); to evidence that there is selection on phenology which is partly offset by plasticity (de Villemereuil, et al. 2020); and to evidence for additive genetic variance for fitness (Bonnet, et al. 2019).

Public benefits

The project has provided insights for those managing red deer and other sexually selected ungulates. These include the role of variation in weather and population density in affecting growth, survival and breeding success; patterns of distribution and dispersal in both sexes; and optimal culling levels and decisions about selective culling. We have published many popular articles and pamphlets and given many talks to the Scottish deer management community summarizing our findings in relation to such issues (e.g. Pemberton and Kruuk 2015) and have also published a book summarizing of research on the ecology of red deer across the Scottish Highlands (Clutton-Brock and Albon 1989). A key message is that in sexually dimorphic species like red deer, the effects of increasing density fall disproportionately on males, leading to a female-biased adult sex ratio (Figure 4). If guest stalking is the management objective, more males, with higher body weights and larger antlers can be harvested from populations held below carrying capacity (Clutton-Brock, et al. 2002, Clutton-Brock and Lonergan 1994). We have also addressed another widespread management objective, the conservation of upland plant communities, which commonly exist as mosaics of highly-preferred and less preferred patches. Capitalizing on the different deer densities present in the five management blocks of Rum (Figure 1c) we showed that simply by shooting free-ranging deer it would be hard to achieve optimal condition of all plant communities, because deer focus on highly nutritious swards that need intense grazing to maintain their high species richness, but their grazing behavior means that their impacts spill over onto adjacent, less nutritious swards that can be damaged by overgrazing (Moore, et al. 2015, Moore, et al. 2018). The manager then has to compromise between different conservation objectives. Culling deer inevitably involves orphaning calves, a rare event in nature, and calves of both sexes, especially males, have low survival and poor performance after orphaning (Andres, et al. 2013).

Long-term projects offer great opportunities for training in scientific methods and the public understanding of science. Apart from the PhD and MSc students who have worked on the project for their theses, many undergraduate projects have been conducted on the deer data, and we estimate between 150 and 200 people have been short-term helpers at the field site – formerly volunteers but nowadays paid. Many of these people first learned about systematic fieldwork at the field site or cut their teeth analysing the deer data, and many have subsequently pursued careers in conservation and teaching as well as in academia. The deer also make excellent subjects for documentary film-makers, photo-journalists and university, college and school field trips, and we regularly host such visitors.  For visiting members of the public, we also have a visitor hide overlooking one of the richest feeding grounds, posters and leaflets.

Challenges

Of course, running long term studies of individuals also has its challenges (Festa-Bianchet, et al. 2017), chief among which is funding. Since 1972, the Rum project has been continuously supported by research grants, mainly from NERC. Like most such studies, the project has rarely had guaranteed research funding for more than three years, imposing on us a relentless cycle of proposal-writing, reviews, responses and outcomes. Successive applications to funding agencies need to ask novel, cutting-edge questions that can be answered within the duration of each grant, and further field data collection must be explicitly justified every time – even if the subject of the proposal is a long-term process such as the response to climate change. A research grant scheme open to universities that explicitly acknowledges the benefits of long-term field data collection would be highly beneficial but has never been implemented in the UK.

Long-term studies of individuals necessarily take place in specific places where the animals live; they cannot be moved about like populations of lab organisms. Thus changing land management policies can pose challenges to continuity.  In the case of Rum, while the island was originally bought for research, many of its plant communities are now designated under the EU Habitats Directive and its post-Brexit equivalent. A general prescription for such habitats is for deer numbers to be reduced by culling, though the grazing preferences of deer do not guarantee this will have the desired effect as grazing behavior is also affected the spatial arrangement of habitats (Moore, et al. 2015, Moore, et al. 2018).  If applied to our study area this would have major impacts in terms of lost habituation, reduced sample sizes and a sudden reduction in density and change of selection regime causing loss of the signals of the response to climate change for many years.

### The future

Colleagues (and relatives) often ask whether we know enough about deer or have invested enough resources in the project by now.  We argue that as data accumulate and technologies develop, our project can ask ever more sophisticated questions about how the natural world works.  Here we outline four areas where we see future development.

First, the combination of high-density genomic information (genome-wide SNPs or whole genome sequencing), pedigrees and fitness data for individuals has yet to be fully exploited. For example, at the whole-genome level, the technique of 'genomic prediction', originally developed in animal breeding  (Meuwissen, et al. 2001), is not yet widely applied in evolutionary studies, but has substantial promise (Ashraf, et al. 2021, Bosse, et al. 2017, Stocks, et al. 2019). In particular, genomic prediction may provide a clearer picture of genetic trends underpinning trait change than is available from pedigree estimates (Hunter, et al. 2022).

Second, in the last few years we have collected faecal samples non-invasively from individual deer. These samples can be used to assay hormones (Pavitt, et al. 2016, Pavitt, et al. 2015), antibodies and parasite propagules (Albery, et al. 2019, Albery, et al. 2018, Albery, et al. 2021a, Albery, et al. 2020) and in principle, to quantify aspects of diet and nutrition and the taxonomic diversity of bacteria (the microbiome), nematodes (nemabiome) and protozoa in the gut via metabarcoding, with implications for understanding how gut health plays into fitness (Wilmanski, et al. 2021). These techniques are currently opening up a wealth of information on gut ecosystems in natural populations, and offer potential for further understanding of the ecology of fitness in the red deer population.

Third, we are increasingly interested in the social networks of the deer, which are not wholly determined by their spatial behaviour (Albery, et al. 2021b). There are important questions to be asked about the relationship between measures of individual sociality, fitness and ageing (Albery, et al. in press), and also whether variation in individual sociality can explain spatial variation in the distribution of parasitism and immunity in the population (Albery, et al. 2019)

Finally, only long-term projects can assess the effects of current anthropogenic climate change on natural environments, and individual-based projects with genetic back-up are best placed to tease apart the processes underpinning observed responses. For example, while there are many long-term sampling-based projects which have documented changes in phenology (Thackeray, et al. 2016, Thackeray, et al. 2010), there are far fewer individual-based studies that have been able to explore the underlying mechanisms. And if there are impacts on demography and population dynamics, these processes will be best understood through the study of individuals. We therefore believe that the scientific potential of long-term studies such as the Rum red deer is not diminished by time, but rather offers increasing potential for continued, multi-disciplinary expansion. If they can maintain continued funding and access to their field sites, long term individual-based studies will continue to generate ground-breaking research and novel insights into the ecology and evolution of natural populations far into the future.

## Acknowledgements

For a project spanning five decades we cannot possibly include all the thanks we would like to here, but instead can only write a synopsis. We thank all the assistants and volunteers who have collected field data on Rum through thick and thin, especially Fiona Guinness, Callan Duck, Jerry Kinsley, Angela Alexander, Callum Duck, Jerry Kinsley, Colleen Covey, Derek Thomson, Ailsa Curnow, Sean Morris, Alison Morris and Martyn Baker. We also thank the 19 postdoctoral and graduate research assistants and 22 PhD students who have collected, analysed and published data from the red deer project, among whom Steve Albon's contributions have been particularly important. Ian Stevenson has been a champion of data management. There have also been many inspiring collaborators over the years. We are immensely grateful to NatureScot and its antecedents for allowing the project to take place and for not culling animals within the study area. We also thank members of the Rum community for their support over the years. Finally, we thank the funding agencies, chiefly

NERC, but also the UK's Biotechnology and Biological Sciences Research Council, the European Research Council, the Leverhulme Trust and the Royal Society of London for supporting the study, and the many, many anonymous reviewers who have supported our proposals and papers over the years: they know who they are.

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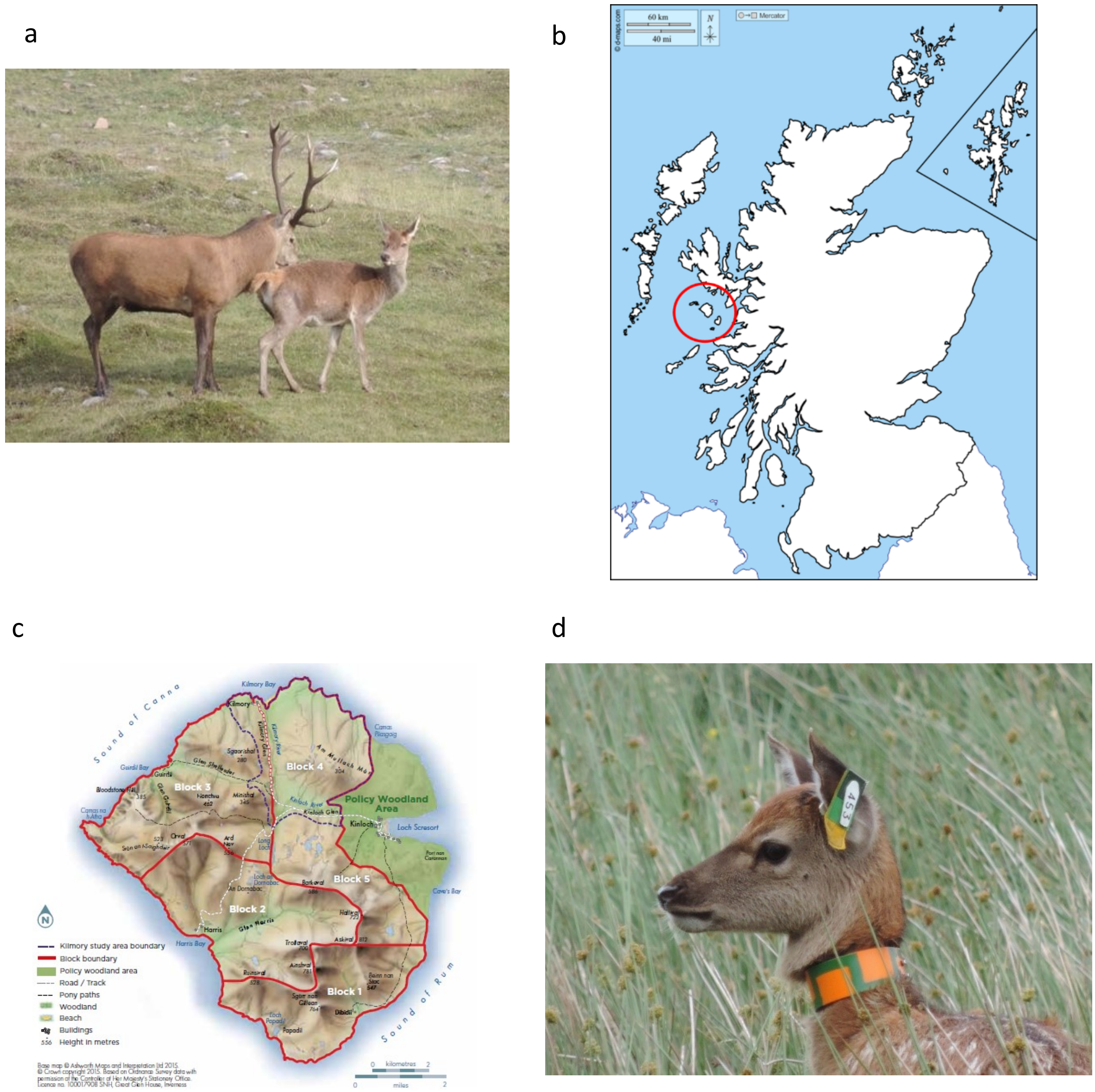

*Figure 1 (a) Male red deer (left) are about 50% larger than females (right) (Photo Alison Morris); (b) Location of the Isle of Rum, 30km west of mainland Scotland; (c) Map of Rum showing the deer management blocks; the study area, or North Block, is shown as Block 4 (courtesy NatureScot); (d) A marked female calf with tags, coloured plastic ear flashes held in by tags and an expanding collar made from the mouldable plastic Darvic (Photo Alison Morris).*

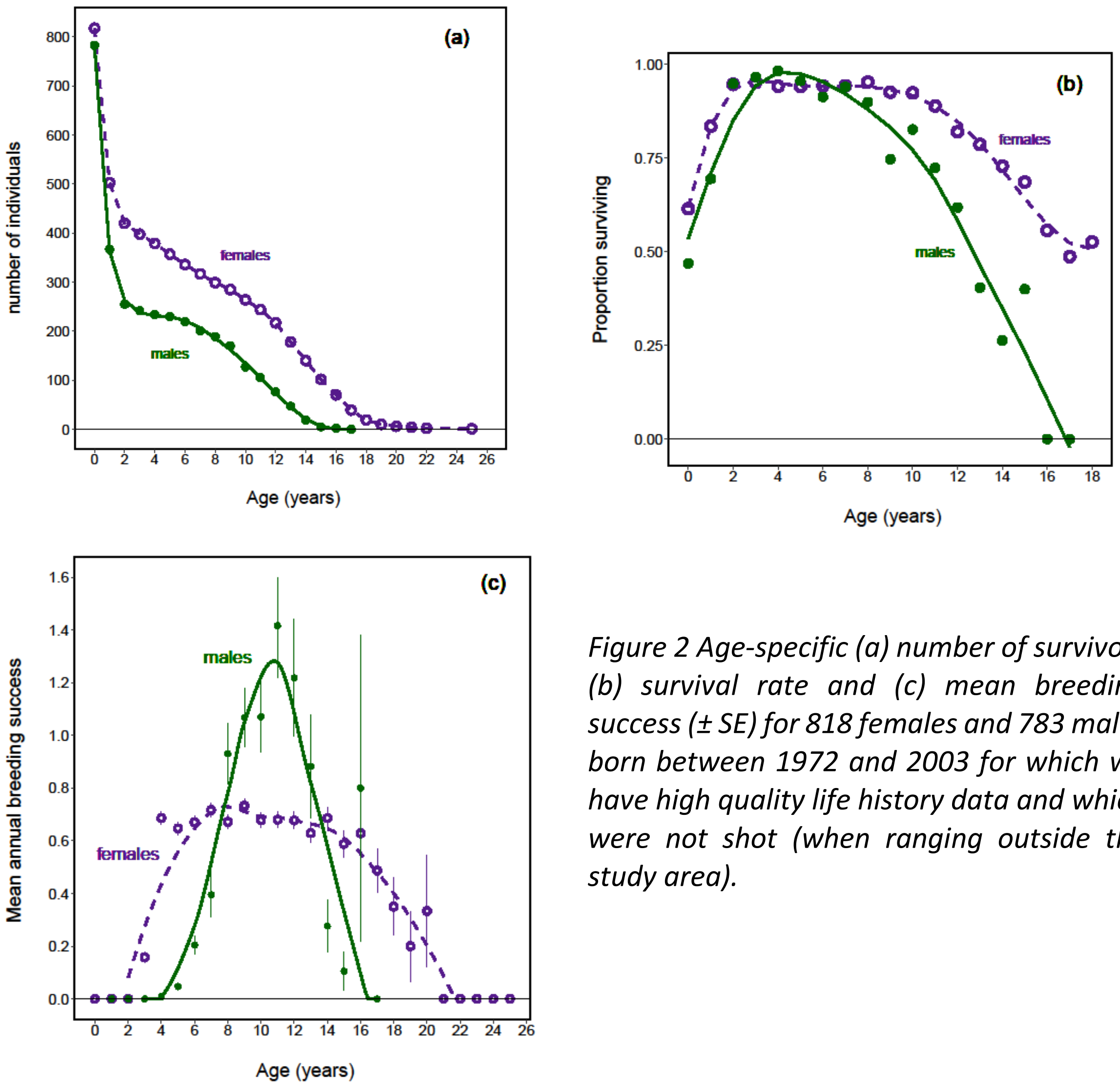

*Figure 2 Age-specific (a) number of survivors (b) survival rate and (c) mean breeding success (± SE) for 818 females and 783 males born between 1972 and 2003 for which we have high quality life history data and which were not shot (when ranging outside the study area).*

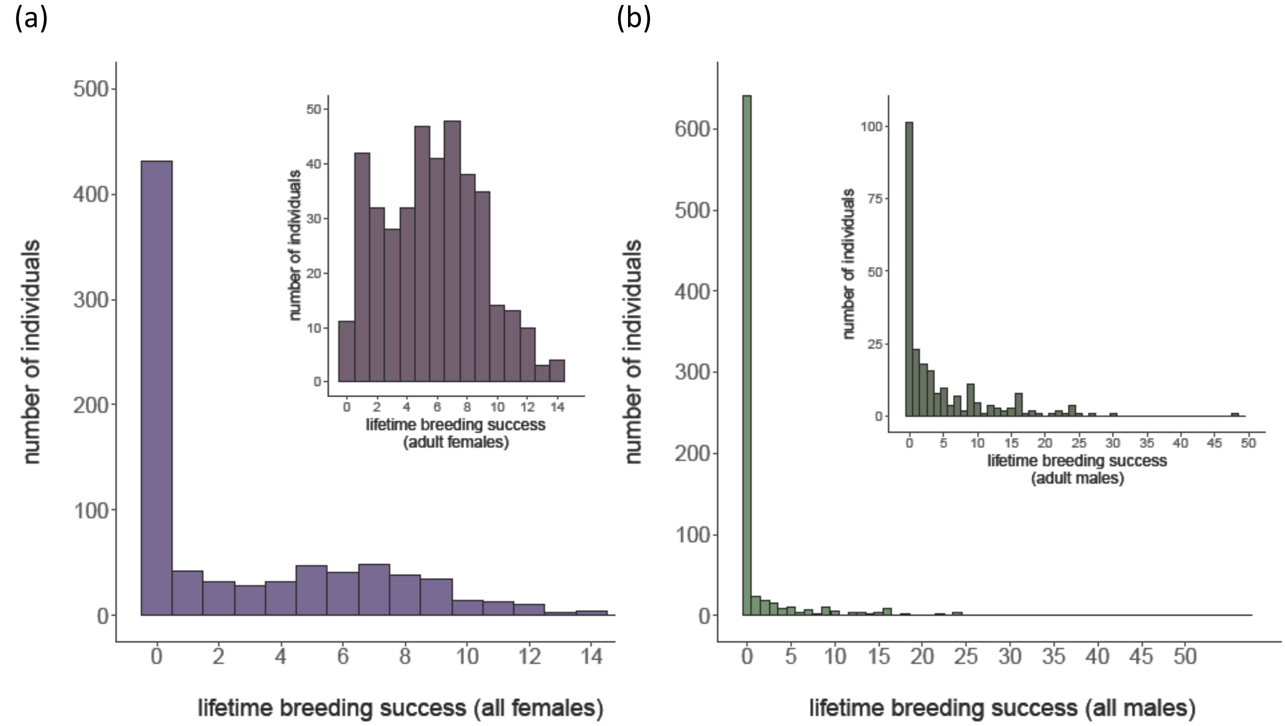

*Figure 3. Lifetime breeding success (number of calves born or sired) for (a) female and (b) male red deer. Inset plots show the same data for those individuals that survived to age three, demonstrating that while nearly all adult females breed, many adult males never sire a calf. Data selection as for Figure 2.*

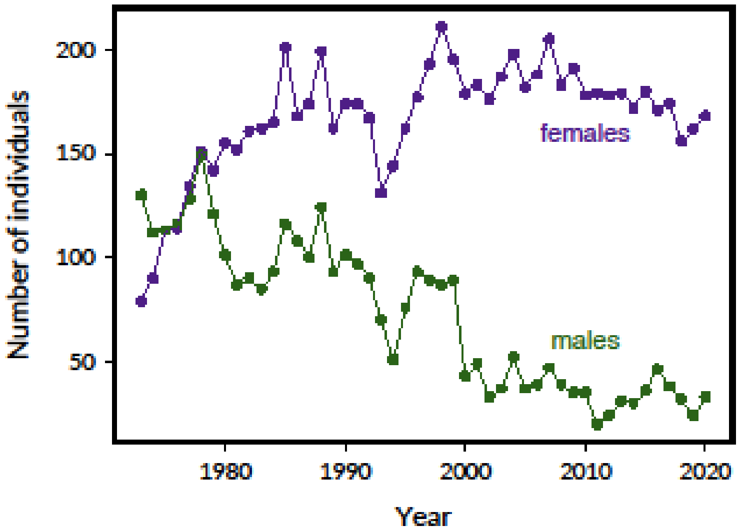

*Figure 4. The number of females and males older than one year regularly using the study area in each year since our censusing programme began. To be counted as resident, an individual has to be seen in at least 10% of study area censuses between January and May of a given year.*

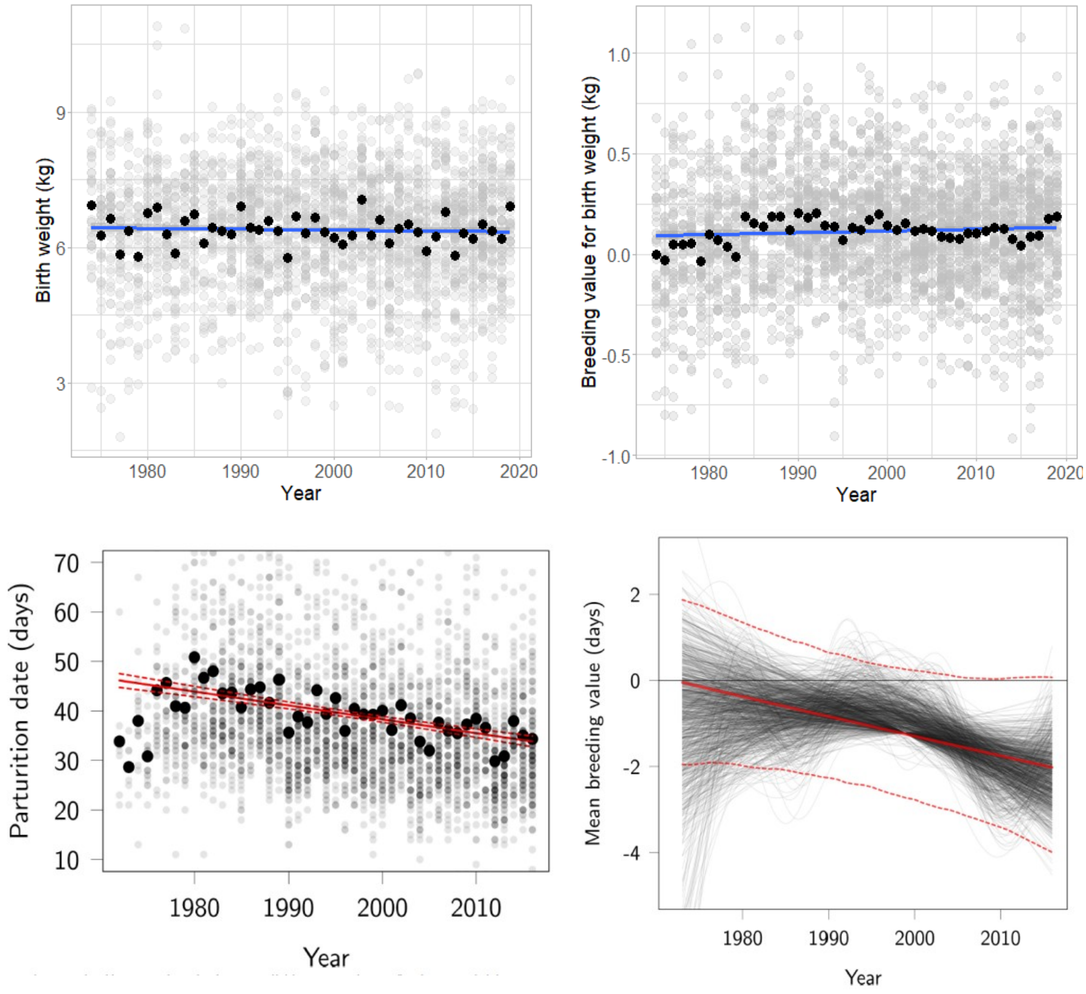

*Figure 5. (a) and (c) phenotypic and (b) and (d) breeding value trends in birth weight and birth date from recent quantitative genetic analyses. The phenotype and the breeding values are not changing for birth weight, whereas both are changing for birthdate.*