

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

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## Keywords

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## 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 population management. As molecular genetic techniques have 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 the 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.

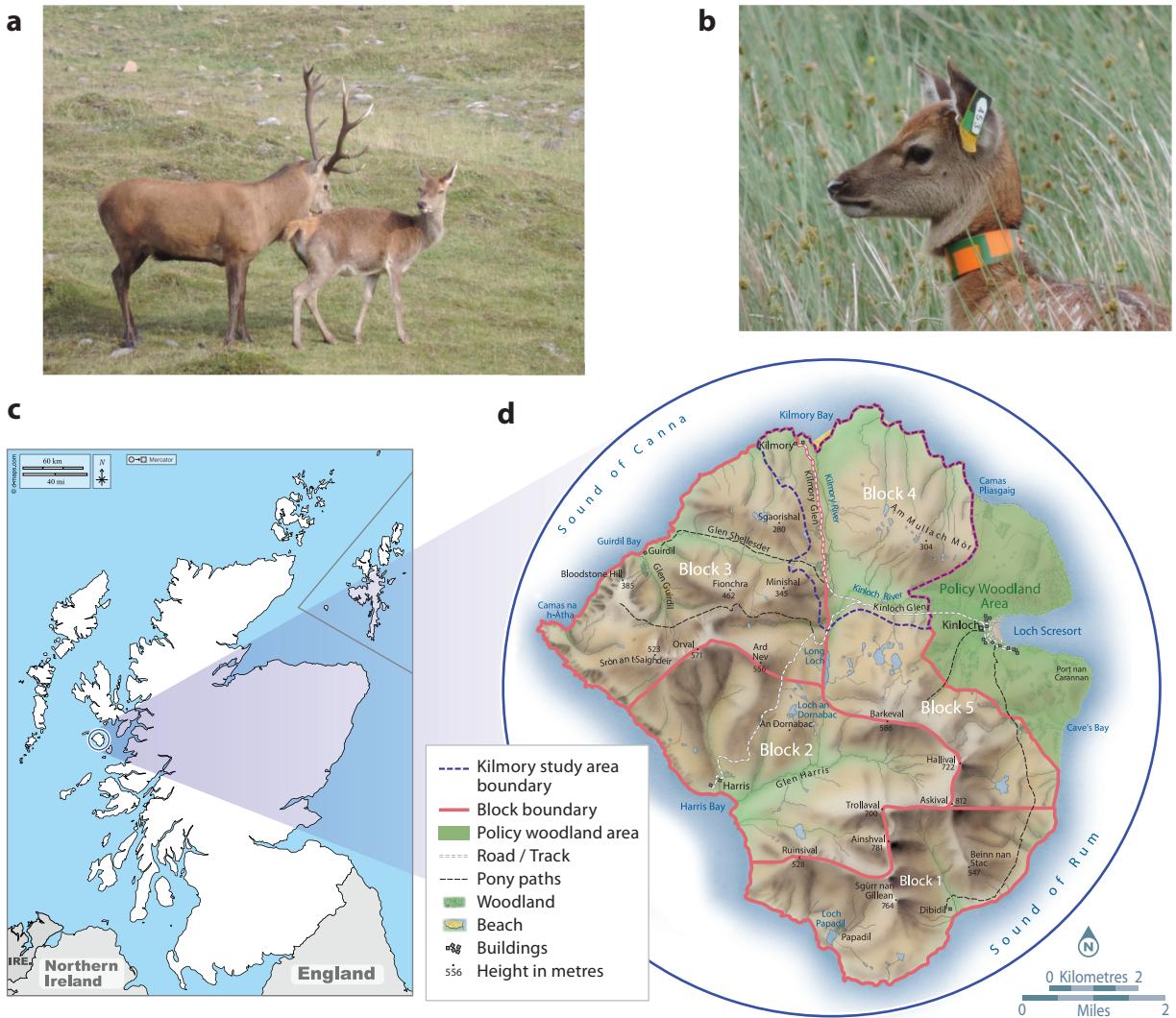
## INTRODUCTION

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 & Sheldon 2010, Festa-Bianchet et al. 2017, Hayes & 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 life spans—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 reveal 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. In addition, 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*) (Figure 1a,b) 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 and is 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 habitats, much of the Scottish population resides in open-hill habitat dominated by heaths and bogs (Clutton-Brock & Albon 1989).

The Isle of Rum ( $N57^{\circ}$ ,  $W6^{\circ}20'$ ) (Figure 1c) 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  $\sim 100 \text{ km}^2$  island carried a red deer population of approximately 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 12- $\text{km}^2$  North Block of the island (Figure 1d). In 1969, it was joined by Fiona Guinness, who learned to recognize



**Figure 1**

(a) Male red deer (*left*) are approximately 50% larger than females (*right*). (b) A marked female calf in the study population with tags, colored plastic ear flashes held in by tags, and an expanding collar made from the moldable plastic Darvic. (c) Location of the Isle of Rum, NW Scotland. (d) Map of Rum showing the deer management blocks; the study area, or North Block, is shown as Block 4. Photos in panels *a* and *b* reproduced with permission; copyright Alison Morris. Map in panel *c* adapted from d-maps, copyright, [https://d-maps.com/carte.php?num\\_car=15868&lang=en](https://d-maps.com/carte.php?num_car=15868&lang=en). Map in panel *d* reproduced with permission from NatureScot.

the approximately sixty 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 organization, life histories, and population regulation in red deer. The Nature Conservancy also agreed to terminate the annual cull in the study area 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 behavior in the following year (Gibson 1978, Hall 1978). In 1976, Steve Albon joined, first as a research assistant, then as a PhD student and postdoctoral researcher, 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.

Since 1974, we have continuously monitored the distribution, habitat use, behavior, annual reproductive success, and survival of all individual deer regularly using the North Block in weekly censuses of the population. Each year, approximately 90% of calves born in the study area are caught, marked (**Figure 1b**), 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 fecal 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 ORGANIZATION

The project's earliest work provided a quantitative description of social organization, habitat use, and reproductive behavior in the deer, building on the qualitative studies of red deer in Torridon by Frank Fraser Darling in the 1930s (Darling 1937). Females adopt home ranges overlapping those of their mother and older sisters, aggregating with them in unstable groups, and temporary groups that frequently include members of several matrilineal groups with overlapping ranges (Clutton-Brock et al. 1982b, Conradt & 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 & 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 her birth weight and her mother's social rank, as well as by her 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 & Guinness 1986).

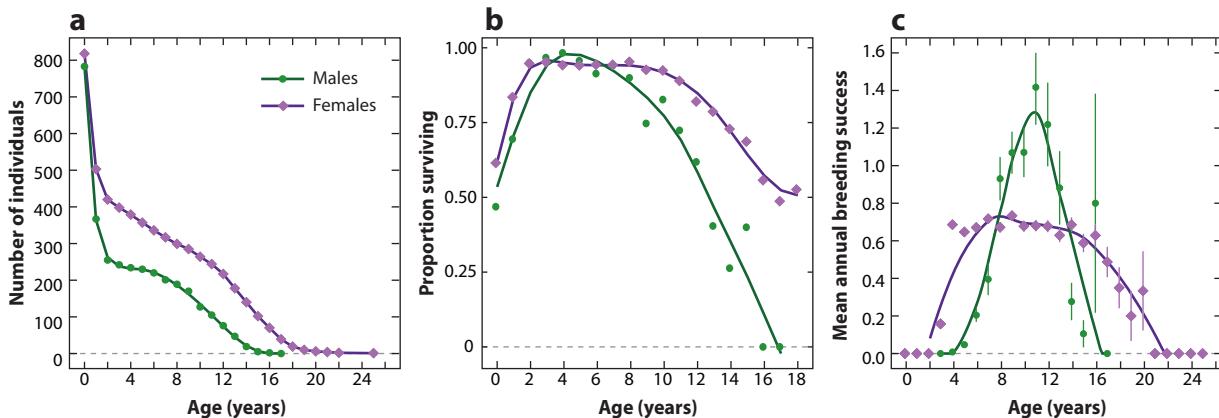
For most of the year, male red deer live in loose groups in areas peripheral to those used by females (Clutton-Brock et al. 1982b). Males leave their natal range and form bachelor groups when they are 2–3 years old. Like females, they have well-defined dominance relationships that are associated with their access to resources (Appleby 1980, 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 & 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 & Albon 1979). Work with captive deer has shown that females are attracted to

males that roar frequently and that roaring advances estrus dates in females (McComb 1987, 1991). Males mate with females as they come into estrus, 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 5 years old rarely sire calves. Around the time of their estrus, 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; J. Huisman & J. Pemberton, 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 & 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).

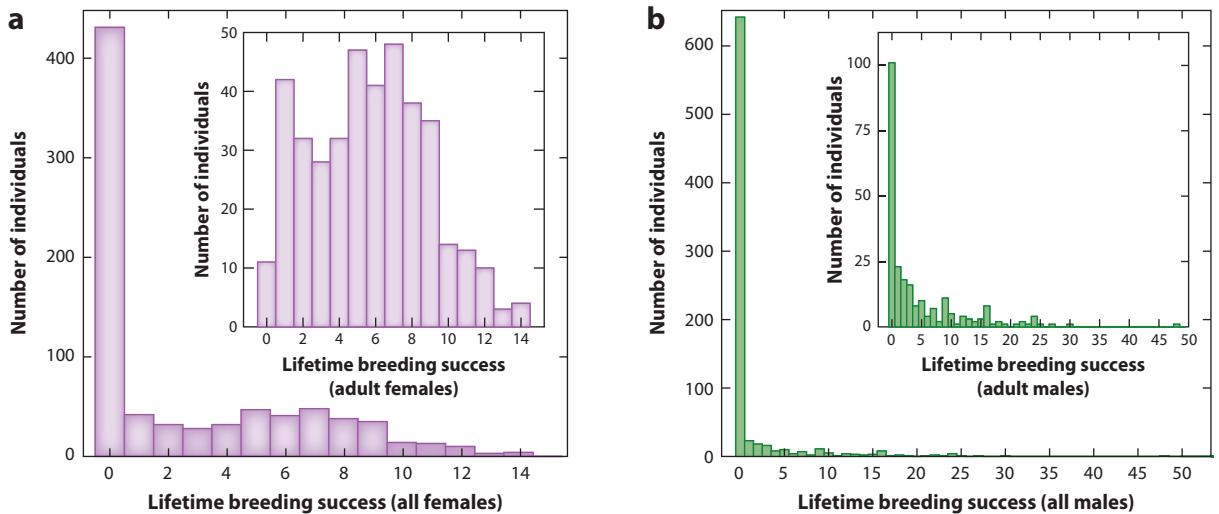
## FEMALE LIFE HISTORIES

The red deer study provided some of the first insights into the extent and causes of variation in 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 3 or 4 years old and then continue breeding until they are 11 or 12 years old, when their fecundity begins to fall (Mitchell et al. 1976, Nussey et al. 2009) (Figure 2c). Offspring birth weight, offspring survival, and adult survival initially increase with age, plateau in mid-life between the ages of 5 and 8 years, and then decline (Clutton-Brock et al. 1982b, Nussey et al. 2009) (Figure 2b). 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 & 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 fecal samples, we



**Figure 2**

Age-specific (a) number of individuals, (b) survival rate, and (c) mean annual breeding success ( $\pm$  SE) for 818 female and 783 male born red deer in the study area on the Isle of Rum, NW Scotland, between 1972 and 2003 for which we have high-quality life-history data and that died of natural causes (i.e., they 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 are for 818 females and 783 males born in the study area on the Isle of Rum, NW Scotland, between 1972 and 2003 for which we have high-quality life-history data and that died of natural causes (i.e., they were not shot when ranging outside the study area).

now know that these costs of reproduction are in part due to lactating females experiencing higher parasite burdens (Albery et al. 2021a).

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 life spans 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 2 years (not shown). Differences in the survival of offspring through their first year and in the life span 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 that 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, 1986). Aspects of the early development of individuals are also important: Females that experience challenging environmental conditions in their first 2 years of life show faster rates of ageing and reduced reproductive performance in the second half of their lives than those reared under more favorable 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 fertilized by

gull colonies) have higher LRS 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).

## 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 backdating 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 the section titled Molecular Analyses).

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 7 or 8 years old. The average breeding success of males declines rapidly after approximately the age of eleven, with the result that the effective breeding lives of males are much shorter than those of females (**Figure 2c**). 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 & Ivaran 2007, Le Boeuf & Reiter 1988, Lukas & Clutton-Brock 2014). Adult males experience higher levels of mortality than females (Clutton-Brock et al. 1988, Nussey et al. 2009) (**Figure 2a,b**) and, as in females, there is a trade-off between early reproductive effort (in terms of harem holding) and later senescence in harem holding (Lemaître et al. 2014). As expected for a strongly polygynous species, (standardized) variance in LBS is substantially higher for males than for females (9.80 vs. 1.73) (estimated from the data shown in **Figure 3**). However, sex differences in individual variation in breeding success or reproductive success are often substantially smaller if they are calculated across the life spans 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 & Clutton-Brock 2014).

Sex differences in survival are not confined to adults. In red deer and some other sexually dimorphic mammals, the faster growth rates of juvenile males are associated with higher energy requirements and with lower survival rates compared to juvenile females when food is scarce or weather conditions are unfavorable (Clutton-Brock 1991b, Clutton-Brock et al. 1985a) (**Figure 2a,b**). Sex differences in survival can also occur before birth in sexually dimorphic mammals (Clutton-Brock 1991a). In red deer, males are born approximately 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 unfavorable, suggesting that adverse conditions during gestation are associated with higher mortality of male fetuses compared to female fetuses (Kruuk et al. 1999a).

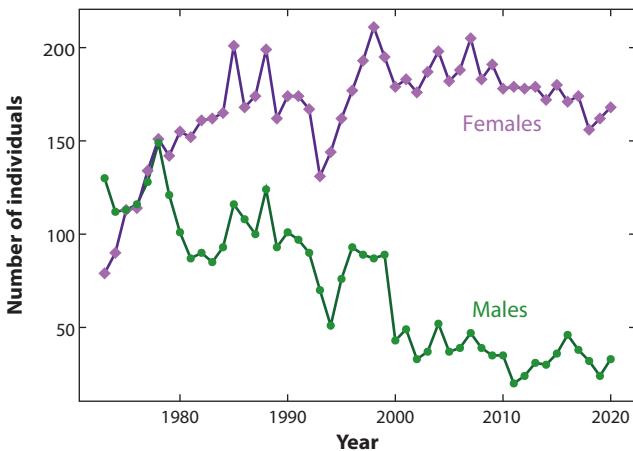
Several lines of evidence also indicate that male offspring are more costly to rear than females. In red deer and in several other sexually dimorphic mammals, male infants suck from their mothers

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 relative to when they had reared a daughter, although 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, 1986), as sex-ratio theory predicts (Trivers & 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 fetal 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 & Iason 1986, Sheldon & 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 organization and reproductive competition have important consequences for the demography and dynamics of populations. In the 8 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 (Albon et al. 2000, Clutton-Brock et al. 1982b, 1985b) (Figure 4). The size of matrilineal groups increased, feeding competition within them became more intense,



**Figure 4**

The number of female and male red deer older than 1 year regularly using the study area on the Isle of Rum, NW Scotland, in each year since our censusing program began. To be counted as resident, an individual must be seen in at least 10% of study area censuses between January and May of a given year.

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 at 3 years old 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, 1997). After the first 10 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).

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 & Albon 1989). An increasing proportion of males of all ages dispersed from the study area, while permanent immigration of males from neighboring 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 toward females (Clutton-Brock et al. 1985b, 1997) (**Figure 4**). Similar changes in adult sex ratios have occurred in other red deer populations (Albon & Clutton-Brock 1988), as well as in populations of other dimorphic ruminants at carrying capacity or subject to adverse environmental conditions (Clutton-Brock & 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 & 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 over the rest of their lives, females born after late springs produce light calves that often fail to survive (Albon et al. 1987). These effects generate pronounced differences in reproductive success between cohorts (Albon et al. 1987), although 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 LBS 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, estrus, 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, 2011a, 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 the section titled Evolutionary Dynamics).

## MOLECULAR ANALYSES

Since 1982, we have collected tissue samples from all deer captured or found dead and extracted bone from cast antlers. These samples have been analyzed using a range of molecular techniques as they developed, from allozyme electrophoresis (Pemberton et al. 1988) through DNA fingerprinting (Pemberton et al. 1992) and 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 7,811 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 organization 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 rut (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 behavior 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 attracted to the area 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 occur only if a male is successful in the same area at time points at least 3 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 nonpedigree, 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 emerged only with the much greater precision afforded by the SNP-refined pedigree and inbreeding coefficients based on the genomic relationship matrix derived from genome-wide SNPs ( $F_{\text{grm}}$ ) (Yang et al. 2011). Inbreeding depresses birth weight, juvenile survival (to 2 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 noninbred mothers (Huisman et al. 2016). As a consequence of these

effects, inbreeding depression across the life span is high: A female with  $F_{\text{grm}} = 0.125$  (equivalent to the offspring of a mating between half sibs) or more has a 75% reduction in LBS compared with an average female with  $F_{\text{grm}} = 0$  and a 79% reduction in her LRS. A male with  $F_{\text{grm}} = 0.125$  has a 95% reduction in LBS compared with an average male with  $F_{\text{grm}} = 0$  (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 & 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 behavior of prospective parents, not the fitness of their potentially inbred offspring (Reid et al. 2015). In the deer, the relatively short breeding life spans of males and the changing membership of female groups mean that the probability that females 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 this is the main driver for male mating behavior. 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 in order 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 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 & 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 are always 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 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) and 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 & 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 & Lynch 2018). Recent analysis using zero-inflated Poisson generalized linear mixed models indicates substantial genetic variance in LBS in the red deer, our estimate of fitness (Bonnet et al. 2022). 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, meaning that the population is not at an evolutionary equilibrium (Bonnet et al. 2022). The fact that we do not see a change in mean fitness at the phenotypic level may imply concurrent environmental deterioration, counteracting the genetic evolution (Bonnet et al. 2022). 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 & McAdam 2019, Hadfield et al. 2011).

A second important line of investigation has been the constancy of genetic variance. As described above (see the section titled Density-Dependent and Density-Independent Effects on Population Dynamics), 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 ( $G \times E$ ). 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 individual-by-environment interactions, or variation in individual reaction norms) (Froy et al. 2019). A lack of phenotypic variance in plasticity means no possibility of  $G \times E$  (Froy et al. 2019). This lack of  $G \times E$  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  $G \times E$  with data sets such as these (Froy et al. 2019, Hayward et al. 2018). However, in marked contrast to the analyses of  $G \times E$  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

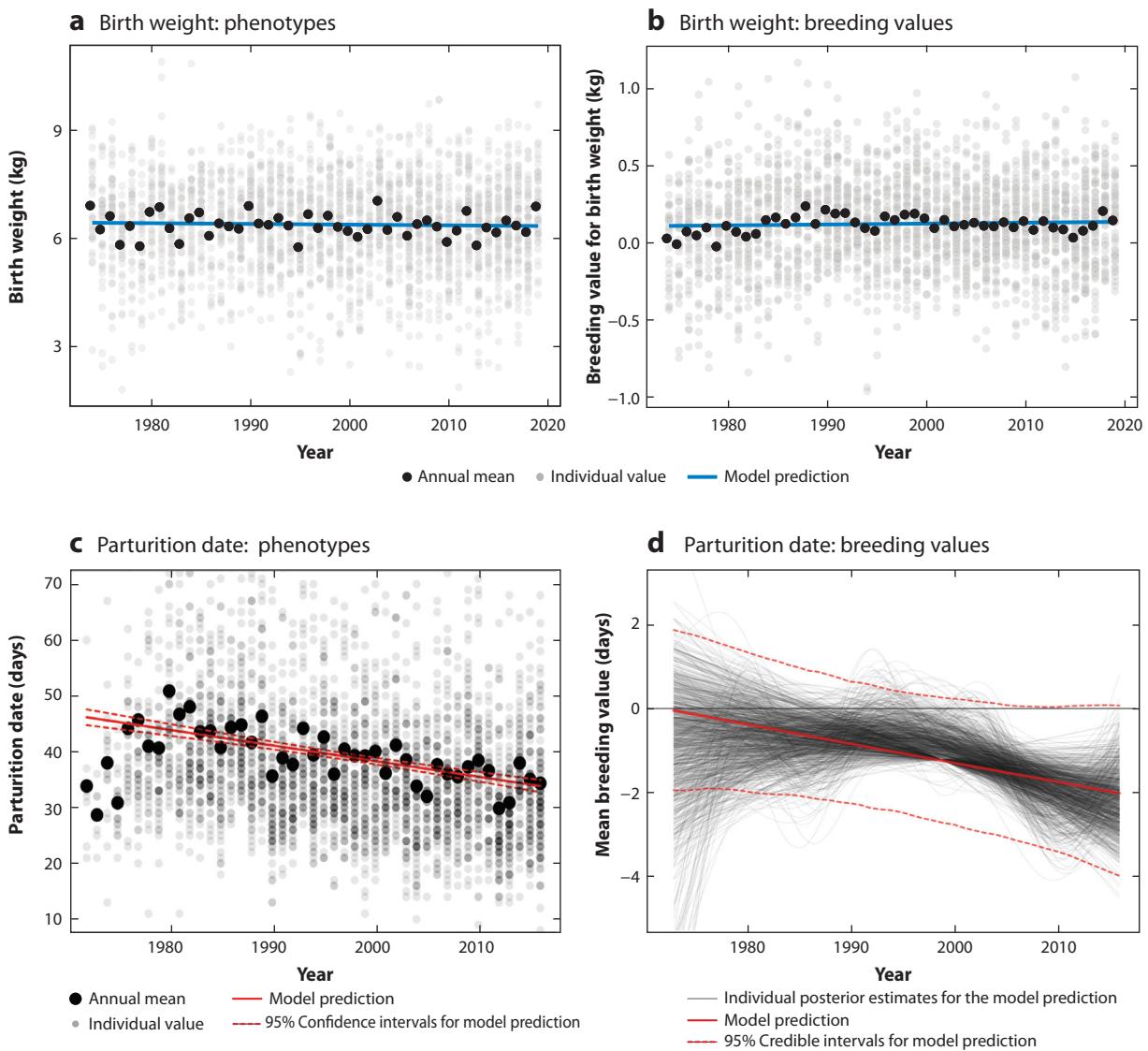
Quantitative genetic analyses also allow us to test whether evolution is constrained, and genetic variance maintained, by genetic trade-offs between different traits. While the existence of trade-offs between different life-history components is a cornerstone of much of behavioral ecology, demonstrating 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- versus 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 a lack of statistical power in demanding analyses, a 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 the section titled Male Life Histories and Sexual Selection 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 delifing [a measure of fitness aimed at estimating individuals' contributions 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 LBS using zero-inflated Poisson models shows no evidence of antagonistic cross-sex genetic covariance (T. Bonnet, personal communication). 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 data sets.

Additionally, 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 & 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 LBS and secondly between a female's LBS and her offspring's birth weight (Gauzere et al. 2022)]. 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 favoring larger antlers (Kruuk et al. 2002, 2014). 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 does not generate any evolutionary response (Kruuk et al. 2014).

In contrast, calf birth dates have 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). While a substantial



**Figure 5**

(*a*) Phenotypic and (*b*) breeding values for birth weight (kg) over time and (*c*) phenotypic and (*d*) breeding value trends in parturition date (days from May 1) for red deer on the Isle of Rum, NW Scotland, from recent quantitative genetic analyses. The phenotype and the breeding values are not changing for birth weight, whereas both are changing for birth date. Panels *a* and *b* reproduced from Gauzere et al. (2022); panels *c* and *d* adapted from Bonnet et al. (2019).

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 favoring earlier birth dates, supported by genetic covariance between a female's parturition date and her LBS. 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 favoring earlier calving is driven by warming temperatures.

## GENETIC ARCHITECTURE OF QUANTITATIVE TRAITS

Knowledge of the loci underpinning 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 QTLs 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 QTLs (Slate et al. 2002b). More recently, we refined the red deer genetic map using 38,000 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, personal communication). Similarly, a recent GWAS analysis of various antler traits using the 38K SNP markers did not find any genome-wide significant QTLs, 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 the 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. For example, in the deer, it would be difficult to give supplementary food or anthelmintics to specific individuals, and cross-fostering would be totally impractical, since females are aggressive toward 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 reanalyze earlier findings at intervals to confirm them or determine whether effects have changed and, if so, why. In several sections above, we have documented 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. 1983, 1989; 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 LBS 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 or 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, although fewer males were born after winters when population density or rainfall were high (see the sections titled Female Life Histories and Male Life Histories and Sexual Selection 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 that 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 and 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), to recognizing that senescence is widespread in the animal kingdom (Jones et al. 2008, 2014), to the overwhelming evidence for changing phenology (Thackeray et al. 2010, 2016), to evidence that there is selection on phenology that is partly offset by plasticity (de Villemereuil et al. 2020), and to evidence for additive genetic variance for fitness (Bonnet et al. 2022).

## 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 & Kruuk 2015) and have also published a book summarizing research on the ecology of red deer across the Scottish Highlands (Clutton-Brock & 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 & 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 1d**), 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, 2018). The manager then has to compromise between different conservation objectives. Culling female 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 for 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 as volunteers but nowadays paid. Many of these people first learned about systematic fieldwork at the field site or cut their teeth analyzing 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; photojournalists; 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, as well as posters and leaflets.

## Challenges

Of course, running long-term studies of individuals 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 3 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. Therefore, 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 European Union 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 by the spatial arrangement of habitats (Moore et al. 2015, 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 fecal samples noninvasively from individual deer. These samples can be used to assay hormones (Pavitt et al. 2015, 2016), antibodies, and parasite propagules (Albery et al. 2018, 2019, 2020, 2021a) and, in principle, to quantify aspects of diet and nutrition and the taxonomic diversity of bacteria (the microbiome), nematodes (the 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 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 behavior (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. 2022) 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 backup are best placed to tease apart the processes underpinning observed responses. For example, while there are many long-term sampling-based projects that have documented changes in phenology (Thackeray et al. 2010, 2016), 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 are best understood through the study of individuals. We therefore believe that the scientific potential of long-term studies such as the Rum red deer project is not diminished by time but rather increases, offering 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 groundbreaking research and novel insights into the ecology and evolution of natural populations far into the future.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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