

Genetic and behavioural estimates of reproductive skew in male fallow deer

L. SAY, F. NAULTY and T. J. HAYDEN

Mammal Research Group, Department of Zoology, National University of Ireland Dublin, Belfield, Dublin 4, Ireland

Abstract

Populations of fallow deer, in general, have low genetic diversity. Nevertheless, we screened 39 microsatellite loci and identified 20 that were polymorphic and suitable to determine paternity of fallow deer. To date, paternity has been studied for 87, 110 and 152 fallow deer fawns born between 2000 and 2002. Our results confirm the existence of a strong polygynous mating system in our population and confirm that the number of copulations performed by males is globally a good estimator of their reproductive success: males which performed the largest proportion of matings fathered the largest proportion of fawns. Nevertheless, we report some differences between the two measurements of the males' reproductive success: measures of copulatory success underestimated the variance of the males' reproductive success. On average, males whose copulatory score exceeded their paternity had mated with a higher proportion of younger females. Young females may be more likely to lose the conceptus, or their offspring may suffer high postnatal mortality.

Keywords: *Dama dama*, fallow deer, mating system, microsatellite, reproductive success

Received 1 April 2003; revision received 6 June 2003; accepted 27 June 2003

Introduction

Mating systems are the consequence of the reproductive strategies and tactics of individuals rather than innate characteristics of a population or species (Clutton-Brock 1989; Lott 1991). Tactics may vary according to the physiological, physical, or social characteristics of an animal (Hrdy & Williams 1983; Rees & Harvey 1991; Herrera & Macdonald 1993; Koprowski 1993) and according to environmental conditions (e.g. spatial and temporal availability of resources) or social context (density and intensity of intrasexual selection; Emlen & Oring 1977; Gosling 1986; Clutton-Brock 1989; Rees & Harvey 1991). Therefore, alternative reproductive tactics can appear and lead to intraspecific variability of mating systems in different populations (Zabel & Taggart 1989; Lott 1991; Davies 1992; Say *et al.* 1999). The payoff to alternative reproductive tactics is nevertheless often difficult to estimate using behavioural data alone and molecular data have shown that behavioural data may under- or overestimate the true reproductive success of males (Hughes 1998; Coltman *et al.* 1999).

Thus, variance in male reproductive success can be predicted from behavioural observations in some cases (e.g. Pemberton *et al.* 1992; Hoelzel *et al.* 1999; Røed *et al.* 2002) but not in others (e.g. Amos *et al.* 1993; Coltman *et al.* 1999; Worthington Wilmer *et al.* 2000; Gemmill *et al.* 2001). In particular, behavioural predictions of male reproductive success are more likely to be unreliable when males fail to guard females, when males do not constrain mate choice by females or when females mate with more than one partner. In such cases, paternity assessment appears to be the only way to study male reproductive success (Pemberton *et al.* 1992; Hughes 1998).

In this study, we present a genetic analysis of paternity in a fallow deer (*Dama dama*) population in a large urban park in Dublin, Ireland. The fallow deer is a dimorphic ungulate species with typically, a polygamous mating system (Clutton-Brock *et al.* 1988; Apollonio *et al.* 1992; Moore *et al.* 1995). In the study population, breeding behaviour may be observed between late August and December. Most matings occur during the rut from mid-October until the beginning of November (McElligott *et al.* 1998, 1999). Fawns are born from the beginning of June to July after a gestation period of 234 days (O'Connell 1993). Mating tactics of fallow deer are highly variable. They include defence of areas containing resources of interest to

Correspondence: L. Say. Fax: 00-353-1-716-1152; E-mail: ludovic.say@ucd.ie

females and defence of dispersed (stands) or aggregated (leks) areas for display and mating. Alternatively, they may use nonterritorial tactics characterized by harem holding, dominance hierarchy among multi-male groups, or by following groups of females in search of oestrous individuals (Langbein & Thirgood 1989; Moore *et al.* 1995). Often one particular mating tactic predominates and other males may pursue different tactics during the rut, with sometimes no clear difference in copulatory success among mating tactics (Apollonio *et al.* 1992). In our population, while a small number of males defend territories, the large majority of males (over 90%) pursue a follower tactic during the rut and access to females is based largely on dominance relationships (Moore *et al.* 1995). The reproductive skew in males is high: often the five most successful males, which are also individuals of high social status, attained more than 70% of matings (McElligott *et al.* 1998).

The objectives of this study were (i) to determine the degree to which behavioural observations (copulatory success) agree with male mating success determined genetically and (ii) to confirm that the high skew in male copulatory success translates to a similar skew in paternity score. Although around 15% of females mate more than once and, in the large majority of cases, with a different male (Farrell 2001), we expected, because of the intensive field observation schedule, a strong correlation between genetic and behavioural data.

Material and methods

Study site and population

The study population is enclosed in the Phoenix Park, west of Dublin city Ireland. This park covers 709 ha, of which 569 ha are available to the deer. Eighty per cent of the park area is covered by grassland, 20% by woodland. The population was founded when the park was enclosed in 1662. There have been a number of documented introductions since then but none since 1906 (Harrel 1898; Hayden *et al.* 1992). Population size reached 700 individuals in 1924, but deer were almost entirely culled during the Second World War. The current population comes from less than 40 individuals that survived. During our study, population size was over 600 individuals and was characterized by a slightly female-biased sex ratio. Annual tagging of fawns began in 1971 and all individuals were caught and tagged between 1991 and 1992. Since this date, a large proportion (up to 80%) of fawns born each year are ear tagged with coloured and numbered tags shortly after birth. The mothers of tagged fawns are identified by recording suckling interactions between July and October each year. Most deer are individually recognizable and of known age. Intensive observations of this population began in 1988. This study took place between October 1999 and August 2002.

Copulatory success

Observations of male behaviour began in late August and continued until late November each year. From four to 12 observers were present in the field from dawn to dusk every day. Observers noted all matings observed and identified both males and females. For this they used Kowa telescopes (27× and 40× lens magnification) mounted on Manfrotto tripods. Observers were in radio contact (Ascom LA140) to prevent duplicate recording of the same behavioural events. Mating sequences were video recorded using Sony Hi 8 video cameras.

Parentage analysis

Three cohorts were studied. Samples of ear tissue from 110 and 152 fawns, caught and tagged shortly after birth in 2001 and 2002, respectively, were analysed. These would all have been conceived in October 2000 and 2001. 73% of the 2001 cohort and 82% of the 2002 cohort had been matched to their mothers. Furthermore, many of the mothers had been recorded mating in the previous rut. In addition, 87 individuals were examined from the 2000 cohort. These were mainly ($n = 76$) individuals that had not been tagged at birth but were found dead from natural causes or were culled within 18 months of birth. Consequently, since we did not know the identities of their mothers we could not assign a putative father to each fawn, although we had a measure of copulatory success for each male in the population. This cohort was included to examine the relationship between reproductive success (paternity) revealed by an analysis of individuals of uncertain provenance and copulatory success from behavioural observations of males in the previous rut.

Tissues were conserved in alcohol until used for genetic paternity analysis. In addition, hair samples were collected from males recorded mating at least once in the ruts of 1999, 2000 and 2001. They were anaesthetized by administration of a mixture of etophine hydrochloride (18–20 µg/kg, C-Vet Veterinary Products) and xylazine (360–420 µg/kg, Rompun Dry Substance-Bayer) delivered by a syringe-dart fired from a compressed-gas rifle. They were released after an antidote injection [mixture of diprenorphine hydrochloride (24–28 µg/kg, C-Vet Veterinary Products) and antipamozole hydrochloride (50 µg/kg, Antisedan-Pfizer)]. No samples were available for adult females.

Genomic DNA was isolated using the Chelex protocol. Skin or hair samples (more than 50 hairs with follicles attached, were used in each extraction) were placed in 500 µL 10% Chelex resin, 30 µL extraction buffer (pH = 8, 0.1 M ethylenediaminetetraacetic acid, 0.05 M Tris-HCl, 1% sodium dodecyl sulphate) and 15 µL proteinase K (20 mg/mL) in a 1.5-mL tube. The mixture was incubated for 45 min at 56 °C. Extracts were centrifuged at 12 000 g for

2–3 min, then incubated for 20 min at 100 °C. Selective amplification was thereafter carried out for 39 microsatellite loci isolated in cattle, sheep and roe deer using the polymerase chain reaction (PCR). PCR were conducted using a PTC-225 DNA Engine Tetrad thermal cycler. Final volumes were 12 µL. Each primer solution was 0.15 mM (one of the locus-specific flanking primers was labelled with a fluorophore), 1.6 µL of Pharmacia Biotech dNTP (2 mM of each nucleotide), 2 µL GibcoBRL 10× buffer, 1 µL GibcoBRL MgCl₂ (50 mM), 0.1 µL GibcoBRL DNA polymerase (5 U/µL), and 1 µL DNA extract. Amplification was carried out by 25 cycles of PCR. A typical cycle was composed of a denaturing step at 94 °C, an annealing step at 45, 50, or 55 °C, depending on the locus, and an extension step at 72 °C. Each of the three steps lasted 30 s. PCR temperature cycles were preceded by a denaturing step of 3 min at 94 °C and finished by an extension step of 10 min at 72 °C. PCR products were resolved on a SureFill™ 6% denaturing polyacrylamide gel (VISIBLE Genetics inc.) on a Long-Read Tower™ System automatic sequencer (VISIBLE Genetics Inc.) at 53 °C. Internal size markers for 104, 160 and 260 base pairs were included in each analysis. Data collection and analysis, as well as automatic sizing of bands, were performed using the GENEOBJECTS™ software supplied with the sequencer.

Twenty microsatellite loci presented more than two alleles and were used for paternity analysis. Paternity was assessed using the program CERVUS, version 2.0 (Marshall *et al.* 1998). This program calculates the log-likelihood (LOD) of each putative parent being the true parent relative to an arbitrary individual. The most likely candidate parent is the candidate parent with the highest LOD score. To determine the reliability of the paternity assignment, the program CERVUS 2.0 calculates the LOD score difference (Δ LOD) between the two most likely parents. The significance of this Δ LOD score is estimated by comparison with a Δ LOD distribution obtained by simulation as follows. Critical Δ LOD-values were generated assuming both parents were unknown and that the number of putative fathers was 25, all of which were sampled for all loci. While no allelic drop out was highlighted (data not shown), we incorporated an error rate of 1% into the simulation. Ten thousand iterations were performed for the simulation. Paternity was assigned both with 95% and 80% confidence levels. In addition, we used the program CERVUS 2.0 to estimate the discrepancy from the expectation of the Hardy–Weinberg equilibrium model and to determinate the combined power of paternity exclusion of the set of loci, under the condition that both parents are unknown.

Statistical analysis

Male copulatory success for each male was defined as the proportion of the total number of copulations, observed

during daylight hours, in the population achieved by that male. We used this measure since in general, males mate only once with each female. For example in the ruts of 2000 and 2001 combined, of 304 copulations between males and tagged females, only seven represented a repeat copulation by the same pair. The reproductive success of a male was defined as the proportion of genotyped fawns that were sired by that male. In this analysis, we only took into account males recorded copulating at least once and all tests were performed separately for the three cohorts of fawns. To test if observed matings provide a good estimate of reproductive success, we used Spearman rank correlation and Kolmogorov–Smirnov tests. Non-parametric tests were preferred here because data were not normally distributed.

A discrepancy between copulatory score and paternity might arise in a number of circumstances. The probability of observing a mating by a male with little copulatory success is lower than that of catching the resultant fawn. A mating sequence lasts, on average, less than 4 min while there are many opportunities to catch a fawn. If some males were more likely to copulate at the beginning and end of the rut and at the same time if sampling effort of fawns was lower early and late in the birth season then this would produce a higher copulatory than paternity score. For other males, the reverse would be the case. Therefore, we compared the daily distributions of matings and of fawns conceived (assuming that conception occurs 234 days before birth) using the Kolmogorov–Smirnov test. For this test, we pooled all the data for cohorts born in 2001 and 2002. Particular consort associations between males and females may also explain underestimation or overestimation of a male's true reproductive success from behavioural data. Therefore, we classified females into three age classes: 1–3 years, 4–8 years, and more than 8 years. We then used a contingency cross-table to analyse if males with paternity scores higher than the copulatory scores had copulated disproportionately more with females older than 3 years and thus that are more likely to have bred successfully before.

Results

Copulatory success

Respectively 147, 180 and 225 copulations were recorded in the ruts of 1999, 2000 and 2001. Only 21 males were observed mating in 1999, 23 males in 2000 and 27 males in 2001. This corresponds to 21%, 26% and 33% of the socially mature males (4 years or older) present in the population in successive years. Among males that mated at least once, variance of mating success was high. The most successful male had a copulatory score of 0.34 (50 matings) in 1999 and 0.44 (80 matings) in 2000. The two most successful

Table 1 Variance (Var.), median (Med.), minimal (Min.) and maximal (Max.) value of male copulatory success (i.e. the proportion of the total number of copulations achieved by males) and reproductive success (i.e. the proportion of genotyped fawns that were sired by males)

		Var.	Med.	Min.	Max.
1999	Copulatory success	0.595	0.014	0.007	0.340
	Reproductive success	1.120	0	0	0.449
2000	Copulatory success	0.809	0.017	0.006	0.444
	Reproductive success	1.590	0	0	0.596
2001	Copulatory success	0.465	0.009	0.005	0.267
	Reproductive success	0.791	0	0	0.343

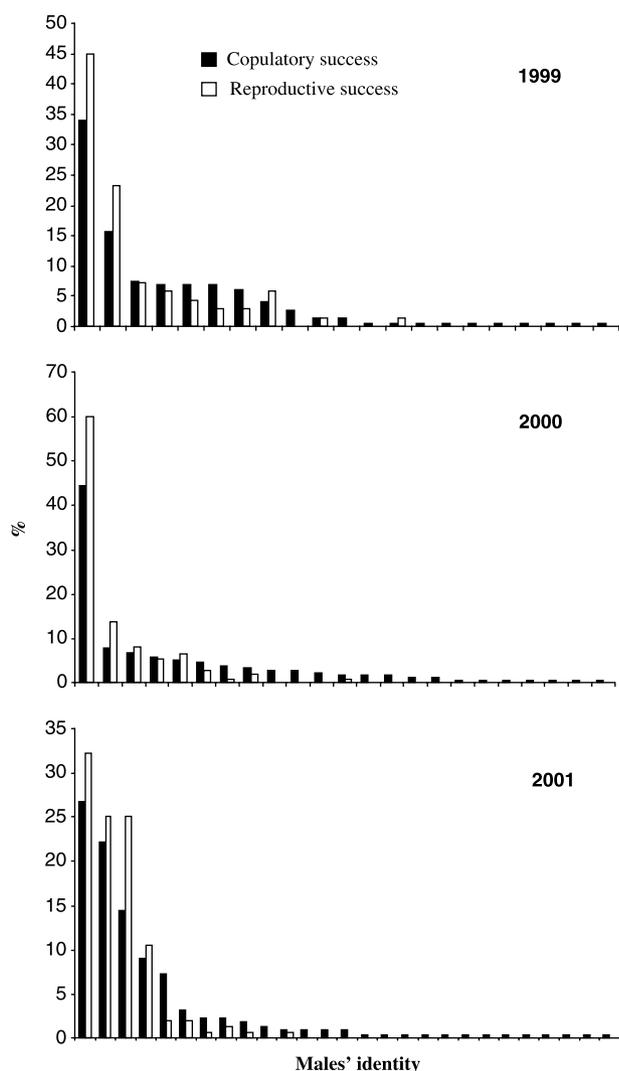


Fig. 1 Distributions of reproductive success (proportion of fawns sired) and copulatory success (proportion of matings achieved) for each reproductive male in 1999, 2000 and 2001.

Table 2 Details of polymorphic markers used in the analysis of fallow deer population: name of locus, number of alleles per locus (nb), observed (H_O) and expected (H_E) heterozygosity, exclusion probability for each locus for one-parent [Excl(1)] tests and result of the Hardy–Weinberg Equilibrium test (HW)

Locus	nb	H_O	H_E	Excl(1)	HW
INRA121	3	0.395	0.488	0.118	NS
TGLA127	4	0.286	0.307	0.047	NS
BM4208	2	0.227	0.264	0.034	NS
BM4513	4	0.500	0.543	0.148	NS
SR-CRSP24	2	0.487	0.476	0.112	NS
ILST30	7	0.551	0.636	0.227	NS
HAUT27	5	0.429	0.476	0.114	NS
TGLA122	6	0.269	0.372	0.070	NS
BM4505	4	0.160	0.202	0.020	NS
FCB193	2	0.244	0.297	0.044	NS
BM1818	4	0.233	0.266	0.035	NS
HEL1	4	0.714	0.680	0.258	NS
BMC1009	3	0.271	0.284	0.040	NS
ILST011	2	0.303	0.387	0.074	NS
ILST029	4	0.697	0.636	0.202	NS
Roe9	3	0.437	0.455	0.103	NS
SR-CRSP1	4	0.739	0.674	0.246	**
Roe1	3	0.437	0.434	0.093	NS
MAF70	5	0.807	0.731	0.321	NS
BMS119	2	0.294	0.286	0.041	NS

The primer sequences can be found in the web sites <http://www.nlh.no/ihf/Genkartstorfe> or <http://www.projects.roslin.ac.uk> except for SR-CRSP-1 (Arevalo *et al.* 1994), SR-CRSP24 (Yeh *et al.* 1997), Roe1 and Roe9 (Fickel & Reinsch 2000).

males in 2001 (0.27 and 0.22, respectively), performed between them 110 matings (Table 1, Fig. 1).

Reproductive success

We used 20 microsatellite loci that presented more than one allele in the present paternity analysis. No departure from Hardy–Weinberg equilibrium was detected in any locus except SR-CRSP1, suggesting that the effect of null alleles was negligible in our analysis (Table 2). The number of alleles and expected heterozygosity ranged, respectively, from 2 to 7 (mean 3.65) and from 0.20 to 0.73 (mean 0.39) according to the locus (Table 2). The exclusion probability ranged from 0.02 to 0.50 according to the locus and the cumulative power of exclusion for the 20 loci reached 0.93 for the one-parent test (Table 2). Paternity simulations showed that 78% and 100% of the parentage should be resolved, respectively, with 95% and 80% levels of confidence. In fact, those proportions were slightly lower, probably because of the relatedness among males. Paternity was assessed for 62% ($n = 216/349$) of tested fawns with

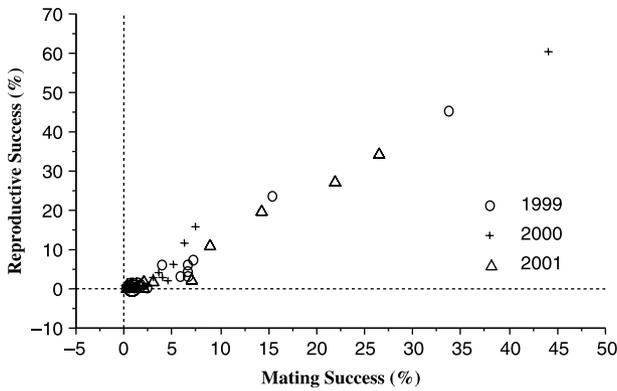


Fig. 2 Correlation between the reproductive success and the copulatory success of male fallow deer.

a 95% level of confidence and for 92% ($n = 321/349$) with an 80% level of confidence. In all but five cases where paternity was not resolved, the two most likely parents had a positive but identical LOD score value and belonged to the same cohort. According to the paternity analysis with 80% level of confidence, the most successful males sired 37/83 fawns (0.45) in 1999, 56/101 fawns (0.60) in 2000 and, 47/137 fawns (0.34) in 2001, confirming the high reproductive skew suggested by behavioural data (Fig. 1, Table 1). Among mother–fawn match-ups recorded in 2000 and in 2001, 147 involved both a tagged female and her tagged fawn. In 84 cases, females have been seen mating with only one male and the identity of the male was known. Genetic paternity was attributed to another male in 13 (16%) of these cases.

Comparison of behavioural and genetic measures of male reproductive success

Copulatory success of males is a good estimator of their reproductive success. Copulatory success was highly correlated with reproductive success in the 2001 and 2002 cohorts (Spearman correlation test: $\rho = 0.86$, $P < 0.0001$ for the 2001 cohort and $\rho = 0.84$, $P < 0.0001$ for the 2002 cohort, Fig. 2). A similar significant relationship was detected for the 2000 cohort (Spearman correlation test: $\rho = 0.90$, $P < 0.0001$ for the 2000 cohort; Fig. 2).

Nevertheless, we report some differences between the two measurements as applied to individual males (Kolmogorov–Smirnov tests: $\chi^2 = 10.24$, $P = 0.01$ for the 2000 cohort; $\chi^2 = 17.04$, $P = 0.0004$ for the 2001 cohort and $\chi^2 = 18.97$, $P = 0.0002$ for the 2002 cohort). Behavioural observations of copulatory success underestimated the variance of the males’ reproductive success. Some males had a higher copulatory success than reproductive success whereas for others the reverse was true. The daily distributions of copulations and conceptions (estimated dates) of fawns were identical (Kolmogorov–Smirnov tests: $\chi^2 = 5.76$,

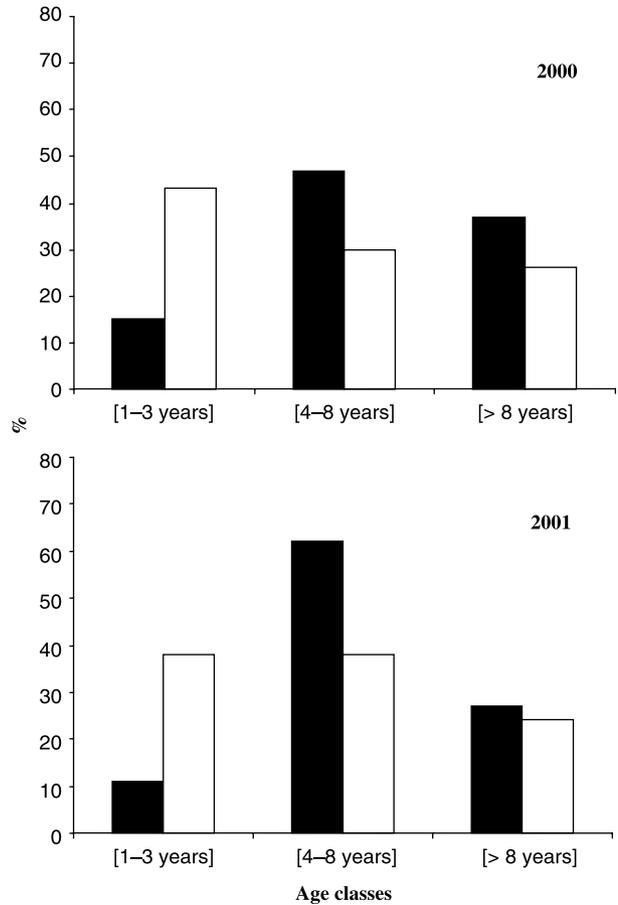


Fig. 3 Proportion of recorded matings of males with higher copulatory success than reproductive success (white) and of males with higher reproductive than copulatory success (black) with females belonging to the three following age classes: 1–3 years, 4–8 years, and more than 8 years.

$P = 0.11$). Males with higher copulatory than reproductive success mated with more young females (43% of females aged 1–3 years in 2000; 38% in 2001) than did other males (15% of females aged 1–3 years in 2000; 11% in 2001; $n = 141$, $\chi^2 = 12.77$, $P = 0.002$ for 2000 and $n = 207$, $\chi^2 = 10.22$, $P = 0.006$ for 2001; Fig. 3).

Discussion

Our results suggest that the copulatory success of males is a good estimator of their reproductive success in our population of fallow deer. Paternity assessment using genetic data confirms the existence of a polygynous mating system characterized by a high skew in male reproductive success associated with dominance rank (Moore *et al.* 1995; McElligott & Hayden 2000). This relationship was also apparent in a cohort of fawns of unknown parentage. Our analysis confirms multiple mating by females (Farrell 2001). In 16% (13/84) of cases in which a fawn, its mother and the

male that was the only observed mate of its mother were all tagged, genetic paternity was attributed to another male. The fact that those matings were not observed in spite of the large observer effort in the field suggests that some copulations occur during the night. Nevertheless, as daylight copulatory success was highly correlated with reproductive success, we argue that copulations during the night were not frequent or that the distribution of copulations between males during the night was the same as during the daylight. Finally, we found that the most successful males mated disproportionately with females aged 4 years or older.

Genetic diversity at the 39 tested loci was lower than that reported for populations of other ungulate species for the same loci (e.g. Goodman *et al.* 2001 for *Cervus nippon*; Williams *et al.* 2002 and Polziehn *et al.* 2000 for *Cervus elaphus*, Gaillard unpublished data for *Capreolus capreolus*). This is in agreement with the polymorphism found in other European populations of fallow deer (Pemberton & Smith 1985; Hartl *et al.* 1986; Randi & Apollonio 1988; for allozyme loci; Poetsch *et al.* 2001 for microsatellite loci). The overall low genetic diversity found in fallow deer has mainly been attributed to the domestication process and to the selection for tameness and coat colour (Randi & Apollonio 1988). More specifically, in our population, the low genetic diversity may be a consequence of a relatively small number of founders although this has not yet been confirmed. It was certainly influenced by the severe bottleneck through which the population passed in 1942. Furthermore, there have been no introductions from other captive or feral populations since at least 1906. In spite of this low polymorphism, the cumulative power of exclusion for the set of 20 selected loci was suited for parentage analysis in this population.

Different types of behavioural data have been used to estimate the reproductive success of polygynous males (e.g. the number of days that a male holds a given female in his harem, Pemberton *et al.* 1992). The most revealing measure is probably the number of females with which a male copulates. This further assumes that all matings are recorded or at least that those observed are representative of all the mating tactics used by males. For example, in several species of pinnipeds, the number of females with which a male copulated on land was a poor predictor of overall reproductive success because the extent of aquatic mating had been under-estimated (Worthington Wilmer *et al.* 2000; Gemmill *et al.* 2001). Furthermore, even if all matings are recorded, the number of females with which a male copulates can still fail to estimate reproductive success if females are polyandrous or mate repeatedly with the same male. Multiple mating by females is common in mammals (e.g. Travis *et al.* 1995; Sillero-Zobiri *et al.* 1996; Goosens *et al.* 1998; Say *et al.* 1999) and leads to sperm competition, sperm precedence, or even sperm choice

(Reynolds 1996; Hughes 1998). However, data in cervids are not numerous, probably because of the paucity of identifiable females and the difficulty of observing matings in natural populations. Here, we analysed 84 cases in which a fawn, its mother and the male that was the sole mate of its mother were all tagged. In 16% (13/84) of these cases genetic paternity was attributed to another male. With the average of 15% of females observed mating more than once in the same oestrus (Farrell 2001), this leads to one of the highest rates of multiple mating reported in cervids (Clutton-Brock *et al.* 1988; Geist 1990; Bartos & Perner 1998; Endo & Doi 2002). However, the rate of multiple mating could, in part, be the result of the fact that this is an enclosed population. In spite of the potential benefits of multiple mating for females and the consequences on male reproductive success via both sperm competition and female mate choice (see Reynolds 1996; Hoogland 1998), detailed investigation of the consequences of multiple mating in fallow deer has not yet been carried out.

Although not all matings are recorded and some females have a tendency to polyandry, the agreement between behavioural and genetic estimates of reproductive success is high. This is probably the result of the high proportion of matings recorded and the fact that polyandry may be lower than 20%. As for other studies (e.g. McCann 1981; Dewsbury 1982; Cowlshaw & Dunbar 1991; Haley *et al.* 1994; Ellis 1995; but see, e.g. Pereira & Weiss 1991; Berrard *et al.* 1993; Say *et al.* 2001; for opposite results), the skew in male fallow deer reproductive success is associated with dominance rank. The most successful male in each year studied here was also the most socially dominant, his copulatory success ranged from 0.27 to 0.44 of matings recorded that year and he sired from 0.45 to 0.60 of fawns. The effect of social rank on male reproductive success may be reinforced by the behaviour of females if they tend to avoid matings with immature males and to copulate with the dominant individuals (McElligott *et al.* 1998; Farrell 2001). Nevertheless, so far, we have insufficient observations ($n = 22$) to test if the discrepancy between the observed mate and confirmed sire of the offspring of a small number of females can be explained by the relative dominance rank of the males involved. Moreover, differences in female fertility may have contributed to the reproductive skew (Garnier *et al.* 2001) and explain the lower variance of the males' copulatory success obtained using behavioural data than the one reported using paternity assessment. We found that the most successful males mated disproportionately with females aged 4 years or older. Young females may be less likely successfully to implant and maintain the conceptus (e.g. Whelan & Hayden 1993 for badger *Meles meles*, Putman 2003 for fallow deer). Offspring of younger females may be over-represented in neonatal mortality (Clutton-Brock *et al.* 1982; Langbein & Putman 1992). Consequently, males that mated with

young females may achieve a lower rate of success than males that mated with older females.

To conclude, the present data have shown that the success of low-ranking male fallow deer was low. Dominant males sired the majority of young, leading to a high skew in male reproductive success. While dominant males are not usually able to maintain their dominance throughout two successive reproductive seasons, such skewed male reproductive success may affect strongly the effective population size (Kelly 2000; Maekawa *et al.* 2001). This, together with the bottleneck through which the population passed in 1942, may have led to the low genetic diversity in this population.

Acknowledgements

This work was financially supported by a Basic Research Award from Enterprise Ireland (L.S., F.N.) and by Dúchas, The Heritage Service. We are grateful to the Superintendent Mr J. McCullen and the Deerkeeper Mr D. Doran of the Phoenix Park for their support and encouragement. We thank Mr J Walsh MRCVS who captured the adult males, the members of the Mammal Research Group as well as many others volunteers who assisted in field work during the rut and in capturing and tagging fawns and two anonymous referees for constructive comments.

References

- Amos W, Twiss SD, Pomeroy PP, Anderson SS (1993) Male mating success and paternity in grey seals, *Halichoerus grypus*, a study using DNA fingerprinting. *Proceedings of the Royal Society of London B*, **252**, 199–207.
- Apollonio M, Festa-Bianchet M, Mari F, Mattioli S, Sarno S (1992) To lek or not to lek: mating strategies of male fallow deer. *Behavioural Ecology*, **3**, 25–31.
- Arevalo E, Holder DA, Derr JN *et al.* (1994) Caprine microsatellite dinucleotide repeat polymorphism at the SR–CRSP–1, SR–CRSP–2, SR–CRSP–3, SR–CRSP–4, and SR–CRSP–5 loci. *Animal Genetics*, **25**, 202.
- Bartos L, Perner V (1998) Distribution of mating across season and reproductive success according to dominance in red deer. *Folia Zoologica*, **47**, 7–12.
- Berrard JD, Nurnberg P, Epplen JT, Schimidke J (1993) Male rank, reproductive behavior and reproductive success in free-ranging rhesus macaques. *Primates*, **24**, 481–489.
- Clutton-Brock TH (1989) Mammalian mating systems. *Proceedings of the Royal Society of London B*, **236**, 339–372.
- Clutton-Brock TH, Guinness FE, Albon SD (1982) *Red Deer*. University of Chicago Press, Chicago.
- Clutton-Brock TH, Green D, Hiraiwa Hasegawa M, Albon SD (1988) Passing the buck: resource defense, lekking and mate choice in fallow deer. *Behavioural Ecology and Sociobiology*, **23**, 281–296.
- Coltman DW, Bancroft DR, Robertson A, Smith JA, Clutton-Brock TH, Pemberton JM (1999) Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology*, **8**, 1199–1209.
- Cowlishaw G, Dunbar IM (1991) Dominance rank and mating success in male primates. *Animal Behaviour*, **7**, 1045–1056.
- Davies NB (1992) *Duncock Behaviour and Social Evolution*. Oxford University Press, Oxford.
- Dewsbury DA (1982) Dominance rank, copulatory behaviour, and differential reproduction. *Quarterly Review of Biology*, **57**, 135–159.
- Ellis L (1995) Dominance and reproductive success among non-human animals: a cross-species comparison. *Ethology and Sociobiology*, **16**, 257–333.
- Emlen ST, Oring LW (1977) Ecology, sexual selection and evolution of mating systems. *Science*, **197**, 215–223.
- Endo A, Doi T (2002) Multiple copulations and post-copulatory guarding in a free-living population of sika deer (*Cervus nippon*). *Ethology*, **108**, 739–747.
- Farrell ME (2001) Courtship, multiple mating and reproductive synchrony in female fallow deer (*Dama dama* L.). PhD Thesis, The National University of Ireland, Dublin.
- Fickel J, Reinsch A (2000) Microsatellite markers for the European Roe deer (*Capreolus capreolus*). *Molecular Ecology*, **9**, 994–995.
- Garnier JN, Bruford MW, Goossens B (2001) Mating system and reproductive skew in the black rhinoceros. *Molecular Ecology*, **10**, 2031–2041.
- Geist V (1990) *Mule Deer Country*. North Word Press Incorporated, Minocqua.
- Gemmell N, Burg T, Boyd I, Amos W (2001) Low reproductive success in territorial male Antarctic fur seals (*Arctocephalus gazella*) suggests the existence of alternative mating strategies. *Molecular Ecology*, **10**, 451–460.
- Goodman SJ, Tamate HB, Wilson R, *et al.* (2001) Bottlenecks, drift and differentiation: the population structure and demographic history of sika deer (*Cervus nippon*) in the Japanese archipelago. *Molecular Ecology*, **10**, 1357–1370.
- Goossens B, Graziani L, Waits LP, *et al.* (1998) Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behavioural Ecology and Sociobiology*, **43**, 281–288.
- Gosling LM (1986) Selective abortion of entire litters in the coypu: adaptive control of offspring production in relation to quality and sex. *American Naturalist*, **127**, 772–795.
- Haley MP, Deutsch CJ, Le Boeuf B (1994) Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Animal Behaviour*, **48**, 1249–1260.
- Harrel WV (1898) *The Fallow Deer of the Phoenix Park*. New Ireland Review, Dublin.
- Hartl GB, Schleger A, Slowak M (1986) Genetic variability in fallow deer, *Dama dama* L. *Animal Genetics*, **17**, 335–341.
- Hayden TJ, Moore NP, Kelly PF (1992) The fallow deer of Phoenix Park: an evolving management plan. In: *Management, Welfare and Conservation of Park Deer* (eds Bullock DJ, Goldspink CR), pp. 27–45. UFAW, Potters Bar, UK.
- Herrera EA, Macdonald DW (1993) Aggression, dominance and mating success among capybara males (*Hydrochaeris hydrochaeris*). *Behavioural Ecology*, **4**, 114–119.
- Hoelzel AR, Le Boeuf BJ, Reiter J, Campagna C (1999) Alpha-male paternity in elephant seals. *Behavioural Ecology and Sociobiology*, **46**, 298–306.
- Hoogland JL (1998) Why do Gunnison's prairie dogs copulate with more than one male? *Animal Behaviour*, **55**, 351–359.
- Hrdy SB, Williams GC (1983) Behavioural biology and the double standard. In: *Social Behaviour of Female Vertebrates* (ed. Wasser SK), pp. 3–17. Academic Press, New York.
- Hughes C (1998) Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology*, **79**, 383–399.

- Kelly M (2000) Lineage loss in Serengeti cheetahs: consequences of high reproductive variance and heritability of fitness on effective population size. *Conservation Biology*, **15**, 137–147.
- Koprowski JL (1993) Alternative reproductive tactics in male eastern gray squirrels: 'making the best of a bad job'. *Behavioural Ecology*, **4**, 165–171.
- Langbein J, Thirgood SJ (1989) Variation in mating system of fallow deer (*Dama dama*) in relation to ecology. *Ethology*, **83**, 195–214.
- Langbein J, Putman R (1992) Reproductive success of female fallow deer in relation to age and condition. In: *The Biology of Deer* (ed. Brown RD), pp. 293–297. Springer-Verlag, New York.
- Lott DL (1991) *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge University Press, Cambridge.
- Maekawa K, Koseki Y, Igushi K, Kitano S (2001) Skewed reproductive success among male white-spotted charr land-locked by an erosion control dam: implications for effective population size. *Ecological Research*, **16**, 727–735.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7**, 639–655.
- McCann TS (1981) Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*. *Journal of Zoology, London*, **195**, 295–310.
- McElligott AG, Hayden TJ (2000) Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). *Behavioural Ecology and Sociobiology*, **48**, 203–210.
- McElligott AG, Mattiangeli V, Mattiello S, Verga M, Reynolds CA, Hayden TJ (1998) Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. *Ethology*, **104**, 789–803.
- McElligott AG, O'Neill KP, Hayden TJ (1999) Cumulative long-term investment in vocalization and mating success in fallow bucks, *Dama dama*. *Animal Behaviour*, **57**, 1159–1167.
- Moore NP, Kelly PF, Cahill JP, Hayden TJ (1995) Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behavioral Ecology and Sociobiology*, **36**, 91–100.
- O'Connell JM (1993) Reproduction in fallow does (*Dama dama*; Linnaeus, 1758) and fawn survival in Phoenix Park, Dublin. MSc Thesis, The National University of Ireland, Dublin.
- Pemberton JM, Smith RH (1985) Lack of biochemical polymorphism in British fallow deer. *Heredity*, **55**, 199–207.
- Pemberton JM, Albon SD, Dover LE (1992) Behavioural estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behavioural Ecology*, **3**, 66–75.
- Pereira ME, Weiss ML (1991) Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, **28**, 141–152.
- Poetsch M, Seefeldt S, Maschke M, Lignitz E (2001) Analysis of microsatellite polymorphism in red deer, roe deer, and fallow deer — possible employment in forensic applications. *Forensic Science International*, **116**, 1–8.
- Polzieln RO, Hamr J, Mallory FF, Strobeck C (2000) Microsatellite analysis of North American wapiti (*Cervus elaphus*) population. *Molecular Ecology*, **9**, 1561–1576.
- Putman R (2003) *The Deer Manager's Companion*. Swan Hill Press, Shrewsbury.
- Randi E, Apollonio M (1988) Low biochemical variability in European fallow deer (*Dama dama* L.): natural bottlenecks and the effects of domestication. *Heredity*, **61**, 405–410.
- Rees JA, Harvey PH (1991) The evolution of mating systems. In: *Mating and Marriage* (ed. Caryl VH), pp. 3–45. Cambridge University Press, Cambridge.
- Reynolds JD (1996) Animal breeding system. *Trends in Ecology and Evolution*, **11**, 68–72.
- Røed K, Holand O, Smith ME, Gjostein H, Kumpula J, Nieminen M (2002) Reproductive success in reindeer males in a herd with varying sex ratio. *Molecular Ecology*, **11**, 1239–1243.
- Say L, Pontier D, Natoli E (1999) A genetic analysis of male reproductive success in two contrasted environments in the domestic cat (*Felis catus* L.). *Proceedings of the Royal Society of London B*, **266**, 2071–2074.
- Say L, Pontier D, Natoli E (2001) Influence of oestrus synchronization on male reproductive success in the domestic cat (*Felis catus* L.). *Proceedings of the Royal Society of London B*, **268**, 1049–1053.
- Sillero-Zobiri C, Gottelli D, Macdonald DW (1996) Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behavioural Ecology and Sociobiology*, **38**, 331–340.
- Travis SE, Slobodchikoff CN, Keim P (1995) Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. *Behavioural Ecology*, **7**, 95–100.
- Whelan R, Hayden TJ (1993) The reproductive cycle of the female badger (*Meles meles* L.) in east Offaly. In: *The Badger* (Ed. by Hayden TJ), pp. 64–77. Royal Irish Academy, Dublin, Ireland.
- Williams CL, Serfass TL, Cogan R, Rhodes OE (2002) Microsatellite variation in the reintroduced Pennsylvania elk herd. *Molecular Ecology*, **11**, 1299–1310.
- Worthington Wilmer J, Overall AJ, Pomeroy PP, Twiss SD, Amos W (2000) Patterns of paternal relatedness in British grey seal colonies. *Molecular Ecology*, **9**, 283–292.
- Yeh CC, Kogi JK, Holder MT, Guerra TM, Davis SK, Taylor JF (1997) Caprine microsatellite dinucleotide repeat polymorphism at the SR–CRSP–21, SR–CRSP–22, SR–CRSP–23, SR–CRSP–24, SR–CRSP–25, SR–CRSP–26 and SR–CRSP–27 loci. *Animal Genetics*, **28**, 380–381.
- Zabel CJ, Taggart SJ (1989) Shift in red fox (*Vulpes vulpes*) mating system associated with El Niño in the Bering Sea. *Animal Behaviour*, **38**, 830–838.

Ludovic Say is a postdoctoral researcher studying the consequences of mating tactics on reproductive success and the effects of mating systems on the genetic structure of populations. Favel Naulty is currently completing a PhD on conflict strategies, dominance and fitness of male fallow deer. Tom Hayden is a senior lecturer in Zoology and directs the Mammal Research Group that addresses questions on the phylogeny and behavioural ecology of several species of mammals.
