

# Estimating the prevalence of inbreeding from incomplete pedigrees

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A previous review of inbreeding in natural populations suggested that close inbreeding (inbreeding coefficient  $f = 0.25$ ) is generally rare in wild birds and mammals. However, the review did not assess rates of moderate inbreeding ( $f = 0.125$ ), which may make a rather larger contribution to overall inbreeding in a population. Furthermore, previous studies may have underestimated the prevalence of inbreeding in wild populations with incomplete pedigrees. By categorizing inbreeding events by the relationship of the parental pair, we suggest a simple method for estimating rates of close and moderate inbreeding from incomplete pedigree data. We applied this method to three wild populations of ruminants: red deer on Rum, Scotland, Soay sheep on Hirta, Scotland and reintroduced Arabian oryx on the Jiddat-al-Harasis, Oman. Although paternal half-sib pairs were the most common category of inbreeding in all three populations, there was considerable variation among populations in the frequencies of the various categories of inbreeding. This variation may be largely explained by differences in population size and dynamics, in maternal and paternal sibship size and in the overlap of reproductive lifespan of consecutive generations. Close and moderate inbreeding appear to be a routine part of breeding behaviour in these ruminant populations.

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## 1. INTRODUCTION

Inbreeding and its consequences have long been a concern of medicine (Seemanová 1971; Bittles *et al.* 1991), animal and plant breeding (Darwin 1876; Abplanalp 1990; Falconer & Mackay 1996), evolutionary biology (Charlesworth & Charlesworth 1987) and conservation (Ralls *et al.* 1979). The study of inbreeding is important because in most species of animals and plants the offspring of closely related parents have lower fitness than the offspring of less related parents, a phenomenon known as 'inbreeding depression' (Charlesworth & Charlesworth 1987). Many studies of wild animals and plants have demonstrated a negative association between inbreeding and components of fitness such as survival, growth or reproduction (reviewed by Crnokrak & Roff 1999; see also Coltman *et al.* 1999b; Marshall & Spalton 2000; Slate *et al.* 2000a), and one study of the Glanville fritillary butterfly (*Melitaea cinxia*) suggests that inbreeding depression may be sufficient to cause local population extinction (Saccheri *et al.* 1998).

Inbreeding may be used to describe the behaviour of individuals or of whole populations. In this study we

define inbreeding as mating between individuals with one or more known common ancestors. More specifically we define close inbreeding as mating between full-sibs or parent and offspring, resulting in progeny with an inbreeding coefficient of  $f = 0.25$ , and moderate inbreeding as mating between half-sibs, uncle and niece, aunt and nephew, grandparent and grandchild or double first cousins, resulting in progeny with  $f = 0.125$ .

Ralls *et al.* (1986) reviewed 28 studies of wild populations of birds and mammals and found that close inbreeding generally accounted for only 0–6% of all matings. Given data available at the time, Ralls *et al.* were not able to include moderate inbreeding in their survey. Furthermore, some of the data cited by Ralls *et al.* involved very small samples (African wild dogs, *Lycaon pictus* and red deer, *Cervus elaphus*) while others were based on behavioural inference of paternity subsequently found by molecular techniques to be erroneous (splendid fairy wrens, *Malurus splendens*; Brooker *et al.* 1990; *Antechinus* spp.; Shields 1993). For species in which behavioural observation of parentage is difficult or inaccurate, DNA-based parentage analysis techniques, developed since Ralls *et al.*'s (1986) review, greatly assist investigation of inbreeding by generating reliable pedigree data.

Conventionally an inbreeding coefficient is calculated from a pedigree using a computer program such as FASTINB (Boyce 1983), but the inbreeding coefficient generated by such a procedure does not identify the routes

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Table 1. Summary of population and life-history parameters.

(For red deer and Soay sheep, whole-island populations are shown—in both cases, the study populations represent approximately one-third of the whole-island populations. Mating success statistics are based on lifetime estimates for red deer and Soay sheep; in the absence of lifetime data, cumulative mating success estimates were used for Arabian oryx. In all cases only animals surviving to breeding age were considered. For red deer and Soay sheep, not all offspring were sampled for paternity testing and, of those tested, not all could be assigned paternity with 80% confidence. Hence in both cases mean male mating success is underestimated; the true mean values are approximately twice the values shown.)

	red deer		Soay sheep		Arabian oryx	
mean population size	1457 (years 1971–1996)		1191 (years 1985–1996)		112 (years 1987–1993)	
population dynamics (size range)	stable (1175–1724)		fluctuating (694–1826)		increasing (31 ⇒ 206)	
	males	females	males	females	males	females
mean age at first breeding (years)	6.9	4.2	1.5	1.8	4.2	2.4
mean age at last breeding (years)	9.6	9.8	2.0	3.2	7.5	9.3
mating success (mean ± s.d.)	4.36 ± 4.08	5.06 ± 3.01	3.03 ± 3.20	4.45 ± 3.57	4.05 ± 3.97	2.40 ± 1.83
standardized variance of mating success	0.88	0.38	1.11	0.64	0.96	0.58

by which inbreeding occurs. This is problematic because in an incomplete pedigree, unknown individuals are implicitly presumed to be unrelated. Hence, low inbreeding coefficients may arise from a lack of pedigree information rather than an absence of inbreeding. Relatively few gaps in the pedigree can dramatically reduce the ability to calculate accurate inbreeding coefficients.

In this paper we introduce a more rigorous, detailed approach to calculating rates of inbreeding. Crucially it is necessary not only to identify inbreeding events themselves but also to count the number of cases in which particular types of inbreeding events could have been detected. If a pedigree is incomplete, this counting exercise must be repeated separately for each category of inbreeding (e.g. full-sib, paternal half-sib, maternal half-sib, etc.). Using this approach, we estimate the frequency of each type of close and moderate inbreeding event in three free-living ruminant populations: red deer on the Isle of Rum, Scotland, Soay sheep (*Ovis aries*) on Hirta in the St Kilda archipelago, Scotland, and reintroduced Arabian oryx (*Oryx leucoryx*) on the Jiddat-al-Harasis (Arabian Oryx Sanctuary, AOS), Oman.

Each category of close or moderate inbreeding involves a different combination of related individuals, and calculating rates of inbreeding separately for each category permits analysis of the demographic and life-history factors affecting the occurrence of inbreeding. An obvious prediction is that the recently reintroduced Arabian oryx, with small founder number, will have higher rates of inbreeding than red deer and Soay sheep. But in our study populations we can examine more detailed predictions: (i) the level of intragenerational inbreeding (e.g. between sibs or cousins) will be affected by sibship size, and (ii) the level of intergenerational inbreeding (e.g. parent–offspring, uncle–niece, aunt–nephew, grandparent–grandchild) will be affected by the degree of overlap of reproductive lifespan between generations.

## 2. MATERIAL AND METHODS

### (a) Study populations

Summary demographic and life-history statistics for our three study populations are shown in table 1. Each population is described briefly below.

#### (i) Red deer on Rum

The red deer is found in northern temperate regions in most parts of the world. The species probably occurred naturally on the Isle of Rum, but the current population is descended from a series of introductions from other parts of Britain that began in 1845. During the October rut, males fight for harems of females; individual females are generally mated once during a short oestrus. Detailed study of red deer in the North Block of Rum began in 1971, and culling ceased in the study area around this time. Study area population density, in particular the number of resident females, rose until 1982 and has remained relatively stable since, regulated by a combination of natural mortality and annual culling. The adult sex ratio in the study area is female biased due to male-biased mortality especially in the juvenile period. A detailed account of the study is available in Clutton-Brock *et al.* (1982).

#### (ii) Soay sheep on St Kilda

The Soay sheep is a primitive domestic breed brought to the St Kilda archipelago at least 1000 years ago. The Soay sheep were later replaced by more modern breeds on the larger and more accessible islands of the archipelago but survived on the 99 ha island of Soay, the population from which all contemporary Soay sheep are derived. In 1932, 107 Soay sheep were transferred from Soay itself to the largest island, Hirta (637 ha), from which humans and domestic stock had been evacuated in 1930. During the November rut, larger males attempt to form consorts with individual oestrous females. However, the mating system is highly promiscuous, and most females are mated by multiple males during a two-day oestrus (Coltman *et al.* 1999a). The current study of the population in Village Bay began in 1985. The population on Hirta is characterized by periodic population crashes, during which up to 60% of the population may die. The adult sex ratio is strongly female biased due to heavily male-biased mortality during population crashes. Detailed accounts of the population are available in Jewell *et al.* (1974), Clutton-Brock *et al.* (1991) and Coltman *et al.* (1999a).

#### (iii) Arabian oryx in Oman

The Arabian oryx formerly inhabited most of the desert regions of the Arabian peninsula but went extinct in the wild in 1972 due to hunting. The population now present in the AOS in central Oman is descended from animals bred in captivity in the USA and the Middle East. Reintroduction began in 1982

Table 2. Summary of genetic data used for parentage analysis.

(For red deer and Soay sheep, genetic data included some allozyme loci as well as microsatellites; for Soay sheep, different panels of loci were typed for paternity analysis of the 1986–1994 and the 1995–1997 cohorts. A full description of the parentage inference method can be found in Marshall *et al.* (1998); further details of the parentage analyses can be found in Marshall *et al.* (1998, 1999) and Pemberton *et al.* (1999).)

	red deer	Soay sheep (1986–1994)	Soay sheep (1995–1997)	Arabian oryx
number of loci	12	15	11	6
mean number of alleles	7.1	4.2	6.7	3.8
mean expected heterozygosity	0.67	0.58	0.71	0.47

and, for the first few years, the population size was relatively small. Social structure was heavily influenced by the initial release of animals in two groups (numbering 10 and 11 individuals, respectively), both of which were dependent on supplementary feed at the release site. In June 1986, a three-year drought was broken, supplementary feeding was discontinued, both herds left the release site and thereafter the social structure became increasingly dynamic as the population increased. There is no discrete breeding season: males form consorts with females with new-born calves, and, providing females are in good condition, they mate at first oestrus, about 10 days *post partum*. The data presented here are based on calves born in the wild in the period 1987–1993. Over this time the population grew at a rate of 31% per year, from 31 at the beginning of 1987 to 206 at the end of 1993. A further 20 captive-bred oryx were released during this period. Accounts of the Omani reintroduction are available in Stanley Price (1989) and Spalton (1999).

### (b) Pedigree data

In all populations maternity was assigned by behavioural observation. Genetic testing (table 2) confirmed that behavioural assignment of maternity was very accurate: more than 99% confidence for red deer and Soay sheep and *ca.* 95% confidence for Arabian oryx (Marshall *et al.* 1998, 1999; Pemberton *et al.* 1999). However, behavioural assignment of paternity is known to be unreliable in red deer (Marshall 1998) and Soay sheep (Coltman *et al.* 1999a). For these species paternity was inferred with 80% confidence using microsatellite and allozyme data analysed with the likelihood-based parentage inference package CERVUS (Marshall *et al.* 1998; Pemberton *et al.* 1999). While it would have been desirable to use higher confidence for molecular paternity inference (e.g. 95%), adopting such a threshold would have led to a crash in sample size and hence to very poor estimates of rates of inbreeding.

In Arabian oryx, analysis of sampled individuals using CERVUS indicates that behaviourally determined paternities in the Arabian oryx pedigree have an average confidence of 95% (Marshall *et al.* 1999). However, sampling was very incomplete and available microsatellite loci were insufficiently polymorphic for large-scale paternity inference. Therefore paternity was inferred by behavioural observation both in captivity (data from Dolan & Sausman 1992) and in the field (J. A. Spalton, personal observation).

### (c) Estimating rates of inbreeding

In this analysis, we categorized inbreeding events as shown in table 3, and counted the number of offspring born for whom each type of inbreeding event could have been detected. For an individual to be included, both parents had to be known, plus additional relatives of the parents shown in table 3. Close

inbreeding ( $f = 0.25$ ; Ralls *et al.* 1986) can arise via three pedigree routes, while moderate inbreeding ( $f = 0.125$ ) can arise via 11 pedigree routes.

In general we assume that, for each category of inbreeding, the available data in the pedigree give an unbiased estimate of the prevalence of inbreeding in the population as a whole. In the case of red deer, there is a possible bias in the analysis because an average of 26% of sexually active males in the study area are immigrants of unknown ancestry. In our pedigree-based analysis immigrants are not excluded from being common ancestors themselves, but are systematically excluded from being descendants because they lack ancestry data. In order to allow for the presence of immigrants in red deer, we calculated adjusted rates of inbreeding,  $f'_j$ , as

$$f'_j = f_j(p_i)^n, \quad (2.1)$$

where  $f_j$  is the frequency of inbreeding event  $j$  (father–daughter, mother–son, full-sib, etc.),  $p_i$  is the proportion of males that are residents as opposed to immigrants, and  $n$  is the number of male descendants of the common ancestor(s) required in the pedigree to detect inbreeding event  $j$  (relatives are listed in table 3).

### (d) Combining rates of inbreeding

It is not immediately obvious how to combine rates of inbreeding to derive overall frequencies of close or moderate inbreeding. However by assuming rates of inbreeding  $f_j$  are small, a crude estimate of overall inbreeding frequency,  $f_{\text{tot}}$ , can be calculated as

$$f_{\text{tot}} = 1 - \prod(1 - f_j) \quad (2.2)$$

This estimate assumes that rates of inbreeding  $f_j$  are independent of one another. While it is known that some combinations of inbreeding are in fact impossible, and hence values  $f_j$  cannot be truly independent of one another, by assuming small values of  $f_j$ , the expected frequencies for pairwise (and greater) combinations of inbreeding events are very small and the assumption of independence of rates of inbreeding  $f_j$  is reasonable. The estimate also assumes that individuals have parents (and hence category of inbreeding) selected at random from the population. Note also that if any one rate  $f_j$  is large, it will tend to dominate  $f_{\text{tot}}$  whatever the remaining values of  $f_j$ .

## 3. RESULTS AND DISCUSSION

### (a) Calculating the frequency of inbreeding

We found that 19 red deer, 10 Soay sheep and 26 Arabian oryx were closely or moderately inbred (table 4). Taking account of the number of cases in which we could have detected each of these inbreeding events, we esti-

Table 3. Close and moderate inbreeding events, and the relatives required in the pedigree in order to detect them.

male parent	female parent	inbreeding coefficient ( $f$ ) of offspring	relative(s) of male parent needed to detect inbreeding event	relative(s) of female parent needed to detect inbreeding event
close inbreeding				
father	daughter	0.25	—	father
son	mother	0.25	mother	—
full brother	full sister	0.25	both parents	both parents
moderate inbreeding				
paternal half-brother	paternal half-sister	0.125	father	father
maternal half-brother	maternal half-sister	0.125	mother	mother
grandson	paternal grandmother	0.125	paternal grandmother	—
grandson	maternal grandmother	0.125	maternal grandmother	—
paternal grandfather	granddaughter	0.125	—	paternal grandfather
maternal grandfather	granddaughter	0.125	—	maternal grandfather
full paternal uncle	full niece	0.125	both parents	paternal grandparents
full maternal uncle	full niece	0.125	both parents	maternal grandparents
full nephew	full paternal aunt	0.125	paternal grandparents	both parents
full nephew	full maternal aunt	0.125	maternal grandparents	both parents
double first cousin	double first cousin	0.125	all grandparents	all grandparents

mated the combined frequency of close and moderate inbreeding to be 13.2% for red deer (9.8% when adjusted for the presence of immigrant males), 5.4% for Soay sheep and 21.7% for Arabian oryx.

If, on the other hand, we had used the total number of individuals with known mother and father to calculate the frequency of close and moderate inbreeding, the values would have been 3.4% (19 out of 553) for red deer, 1.1% (10 out of 898) for Soay sheep and 21.3% (26 out of 122) for Arabian oryx. For red deer and Soay sheep, this approach would have substantially underestimated the true frequency of close and moderate inbreeding. It is therefore important to estimate the frequency of close and moderate inbreeding in incomplete pedigrees by calculating frequencies separately for each category of inbreeding based on the number of inbreeding events in that category which could have been detected.

In this paper we have used a simple method for combining rates of inbreeding  $f_j$  to derive an estimate of overall inbreeding  $f_{\text{tot}}$  in order to permit comparison with previously published estimates. Although our three study populations fulfil the key assumption of this calculation (that all inbreeding rates  $f_j$  are small), the method is not ideal because it does not take account of the differing confidences in inbreeding rates  $f_j$  caused by differing sample sizes. There is need for a more general method for estimating overall rates of inbreeding from incomplete pedigrees that takes account of differing sample sizes and would give meaningful results even when individual rates  $f_j$  are large.

### (b) Sources of bias

Our approach for calculating the prevalence of inbreeding depends on obtaining an unbiased set of inbreeding events from the pedigree. The approach would be biased if inbred individuals were preferentially excluded from the pedigree because of a lack of observations or sampling, if substantial numbers of immigrant animals were breeding, or if the parentage assignment technique was biased when related parents were considered. We discuss each of these possible sources of bias in turn below.

First, in all study populations newborn individuals must have maternity assigned in order to form part of the pedigree. In the case of Soay sheep, a small number of neonates died each year before maternity could be assigned. We were unable to determine if these individuals tend to be more inbred than those that survive, but, if so, population rates of inbreeding based on this latter group may be underestimates. Additionally for red deer and Soay sheep, all individuals except matriarchs must be sampled for paternity analysis to be included in the pedigree. Most individuals are sampled as neonates but samples from many remaining individuals were collected later in life from both live and dead animals. We do not believe sampling is biased against inbred individuals. In Arabian oryx, paternity analysis depends only on field observations of the parents and we have no reason to believe these observations are biased against inbred offspring. We conclude that there is a possible source of bias due to inbreeding depression in Soay sheep but not in red deer or Arabian oryx; in practice poor maternal nutrition is the primary cause of neonatal mortality in Soay sheep.

Second, in both red deer and Soay sheep, females are philopatric and so there is almost no immigration of females. However, for red deer, immigrant males account for on average 26% of all males present during the rutting season. Taking account of the sampling bias caused by the systematic exclusion of immigrants from parts of the pedigree (see § 2), the adjusted rate of close and moderate inbreeding was 9.8%, somewhat lower than the unadjusted figure of 13.2%. However the adjusted rate is conservative because the adjustment assumes that all immigrants are unrelated to residents, which is probably untrue. In a few cases immigrants may be unmarked individuals who were born in the study area and emigrated as juveniles, later to return to the study area, unrecognized, as adults. For Soay sheep, immigrant males represent a much smaller proportion of all males present during the rutting season, so any overestimate of inbreeding rates due to immigrants is likely to be small. In Arabian oryx, new individuals of both sexes added to the population during

Table 4. Percentage of matings resulting in live birth classed as close or moderate inbreeding events.

(The sample size given at the top of each column is the number of individuals for which both parents were known. The number of offspring tested for each inbreeding event is the number of individuals for which all the necessary relatives were known in order to infer whether or not a given inbreeding event had occurred (see table 3). In many cases, the number of offspring tested is much less than overall sample size because of missing pedigree data. Note that the total percentages shown are not direct summations of the individual percentages—see § 2 for a description of the calculation. In the case of red deer, both raw rates of inbreeding and adjusted rates of inbreeding are shown—the adjustment corrects for the presence of immigrant males in the population and is also described in § 2.)

male parent	female parent	inbreeding coefficient ( <i>f</i> ) of offspring	red deer ( <i>n</i> = 553)		Soay sheep ( <i>n</i> = 898)	Arabian oryx ( <i>n</i> = 122)
			raw	adjusted		
close inbreeding						
father	daughter	0.25	1.5% (3/195)	1.1%	0% (0/339)	2.7% (3/113)
son	mother	0.25	0% (0/440)	0%	0.5% (2/429)	2.5% (3/122)
full brother	full sister	0.25	0% (0/102)	0%	0% (0/131)	4.8% (5/104)
moderate inbreeding						
paternal half-brother	paternal half-sister	0.125	10.7% (11/103)	7.9%	3.0% (4/131)	6.7% (7/104)
maternal half-brother	maternal half-sister	0.125	0.9% (4/428)	0.7%	0.7% (2/293)	2.5% (3/122)
grandson	paternal grandmother	0.125	0% (0/84)	0%	0% (0/104)	0% (0/111)
grandson	maternal grandmother	0.125	0.3% (1/314)	0.2%	1.2% (2/161)	0% (0/122)
paternal grandfather	granddaughter	0.125	0% (0/21)	0%	0% (0/72)	0% (0/111)
maternal grandfather	granddaughter	0.125	0% (0/72)	0%	0% (0/92)	0% (0/113)
full paternal uncle	full niece	0.125	0% (0/8)	0%	0% (0/38)	1.0% (1/102)
full maternal uncle	full niece	0.125	0% (0/44)	0%	0% (0/40)	1.0% (1/103)
full nephew	full paternal aunt	0.125	0% (0/17)	0%	0% (0/9)	1.9% (2/103)
full nephew	full maternal aunt	0.125	0% (0/23)	0%	0% (0/15)	0.9% (1/108)
double first cousin	double first cousin	0.125	no data	no data	no data	0% (0/97)
total measured inbreeding			13.2%	9.8%	5.4%	21.7%
close inbreeding			1.5%	1.1%	0.5%	9.6%
moderate inbreeding			11.8%	8.8%	4.9%	13.3%
intragenerational inbreeding			11.5%	8.6%	3.7%	13.4%
intergenerational inbreeding			1.9%	1.4%	1.7%	9.5%

the course of the study were all of known ancestry, and the population is otherwise completely isolated, so there is no possible bias due to immigrants of unknown ancestry entering the population. We conclude that immigrant males are a source of bias in red deer, but not in Soay sheep or Arabian oryx.

Third, with the exception of immigrant males discussed above, maternity was known with near certainty for almost all red deer and Soay sheep in the study populations. By contrast, the method used to assign paternity in red deer and Soay sheep does not assign paternity to all individuals tested, and when paternity is assigned, the average confidence is 80%. However, because the paternity assignment method is not biased towards assignment of paternity to males related to the mother except under extreme conditions—for example, when there are many full-sibs of the mother among the candidate males (Marshall *et al.* 1998)—false paternity assignments are expected to misidentify inbred individuals as outbred and outbred individuals as inbred with approximately equal frequency. A recent reanalysis of a subset of the red deer paternity data using a large number of additional microsatellite markers confirmed the accuracy of the method (Slate *et al.* 2000*b*). In Arabian oryx, maternity was known for all individuals in the population while paternity was assigned by behavioural observation for 70% of individuals; both maternity and paternity were identified with 95% confidence in

those individuals for whom genetic testing could be carried out (Marshall *et al.* 1999). Since paternity assignment was dependent on observation rather than genetic sampling we believe that the available pedigree is a random sample of the population with respect to inbreeding; in any case more than half of the population was tested for all 14 categories of close and moderate inbreeding. We therefore conclude that estimates of inbreeding rates are unlikely to be biased by the parentage assignment method used for any of the three species.

(c) **Influence of population size and population dynamics on frequency of inbreeding**

Close and moderate inbreeding was most common in Arabian oryx and least common in Soay sheep. The Arabian oryx population had very few founders, grew rapidly and, before 1990, breeding was dominated by a small number of males. By contrast, the red deer and Soay sheep populations were comparatively large throughout the study period (table 1). For the Arabian oryx population, which on average was an order of magnitude smaller than the other two populations, the number of alternative mates was low and the probability that a given mate was closely or moderately related was high. This population size effect is presumably the primary reason why close and moderate inbreeding was more common in Arabian oryx than in red deer and Soay sheep.

In the larger red deer and Soay sheep populations, moderate inbreeding was almost an order of magnitude more common than close inbreeding, whereas in the smaller oryx population, close inbreeding was almost as common as moderate inbreeding (table 4). Thus, in the two larger populations, moderate inbreeding contributed four to five times as much to the overall average inbreeding coefficient as did close inbreeding, and this pattern may be true for many natural populations (see also Keller 1998).

In both red deer on Rum and Soay sheep on Hirta, the study area populations represent around one-third of the whole-island populations, and male dispersal between the study areas and other parts of the islands occurs routinely. We therefore believe that the frequency of close and moderate inbreeding on Rum and Hirta is indicative of what would be found on mainland populations of many mammals, and is not an artefact of the island setting of these populations. On the other hand the Arabian oryx population on the Jiddat-al-Harasis is small and isolated, and the high level of close and moderate inbreeding found here may be more characteristic of isolated, highly endangered populations.

#### (d) *Influence of life history on frequency of inbreeding*

Intragenerational inbreeding, between sibs or half-sibs, accounted for the majority of close and moderate inbreeding in all three populations (table 4). All three species are polygynous, with a higher standardized variance in male reproductive success than female reproductive success (table 1). Consequently paternal half-sibship size tends to be larger than maternal half-sibship size. Furthermore, reproductive lifespan of males is shorter than that of females in all three species and, within their reproductive lifespan, annual reproductive success tends to be more sharply peaked in males than in females. Therefore paternal half-sibs are more likely to be reproducing concurrently than maternal half-sibs. In all three populations, paternal half-sib mating was the most common form of close or moderate inbreeding (table 4), particularly so for red deer and Soay sheep.

The extent to which the reproductive lifespan of different generations overlap controls the opportunity for intergenerational inbreeding (i.e. parent-offspring, uncle-niece, aunt-nephew and especially grandparent-grandchild matings). In all three populations reproduction overlaps between generations, primarily because females start reproducing at a young age and have long reproductive lifespans. The overlap is greatest for Arabian oryx (table 1), and may explain why intergenerational inbreeding was more common in this species than in red deer or Soay sheep (table 4). This may also be another factor, in addition to population size, explaining why close and moderate inbreeding was most common in Arabian oryx.

#### (e) *Close and moderate inbreeding in birds and mammals*

Ralls *et al.* (1986) summarize their review of inbreeding in wild birds and mammals by saying that *close* inbreeding ( $f=0.25$ ) generally occurs at a frequency of 0–6%, with over one-half of studies yielding a figure of less than 2%. Our study suggests that red deer (which were also included in Ralls *et al.*'s analysis, though based on a very

small sample) and Soay sheep both fall within this category, but Arabian oryx do not. Ralls *et al.* cite two species with close inbreeding at a frequency greater than 6%: a natural population of splendid fairy-wrens in Western Australia (19.4%), and a small introduced population of European mute swans (*Cygnus olor*) in the USA (9.8%). However, subsequent genetic work on the splendid fairy-wren population revealed that extra-pair copulation is extremely frequent (Brooker *et al.* 1990), and that close inbreeding is probably rare. The European mute swans are therefore the most inbred population included in Ralls *et al.*'s (1986) review. Interestingly, both the European mute swans and the Arabian oryx were introduced populations initiated with a small number of founding individuals. Other studies, published since Ralls *et al.* compiled their review, suggest that some small mammal species can tolerate very high levels of close inbreeding (meadow voles *Microtus pennsylvanicus*; Pugh & Tamarin 1988; naked mole-rats *Heterocephalus glaber*; Reeve *et al.* 1990). We conclude that while close inbreeding may be rare in most birds and mammals, a relatively high frequency of close inbreeding may occur if there is a lack of alternative mates (mute swans and Arabian oryx) or a high cost of dispersal (meadow voles and naked mole-rats; see also Bengtsson 1978).

Although close inbreeding may be generally rare, *moderate* inbreeding may be rather more common. In our study populations, we estimate that the combined frequency of close and moderate inbreeding accounted for between 5.4% and 21.7% of matings. Two other large-scale studies of wild vertebrates, both of which used molecular methods to validate behavioural observations of parentage, offer minimum estimates of the frequency of close and moderate inbreeding. Keller (1998) reported that 51 of 671 pairs (7.6%) of an island population of song sparrows (*Melospiza melodia*) were closely or moderately related, while Hoogland (1992) reported that 36 of 770 copulations (4.7%) of black-tailed prairie dogs (*Cynomys ludovicianus*) were between closely or moderately related pairs (note that our definitions of close and moderate inbreeding differ from those used by Hoogland, who described both  $f=0.25$  and  $f=0.125$  as close inbreeding). In both species the true frequency of close and moderate inbreeding is likely to be higher because pedigrees were incomplete, and when calculating inbreeding rates the authors did not account for incomplete pedigrees by using a method such as the one described in this paper. For song sparrows, additional data in the paper suggest that the true frequency of close and moderate inbreeding was more than 10%. Whereas for prairie dogs in 1988, a year in which pedigree data were particularly complete, 6 of 69 pairs (8.7%) were closely or moderately inbred. There are also comparable data from humans. One category of moderate inbreeding, uncle-niece unions, account for 21.0% of Hindu marriages and 10.2% of Christian marriages in the Karnataka region of southern India, and even among Muslims in Karnataka, for whom uncle-niece marriages are proscribed by the Koran, 3.7% of marriages are of this type (Bittles *et al.* 1991).

Based on our data and those in the literature, we suggest that moderate inbreeding is likely to be a relatively common occurrence in wild mammal and bird populations, and we believe that Ralls *et al.*'s (1986) conclusions about

the rarity of close inbreeding in most natural populations of wild mammals and birds do not extend to moderate inbreeding, at least in mammals. Tentatively we suggest that for wild mammals, close and moderate inbreeding may generally account for 5–15% of matings and in some circumstances may exceed 20% of matings.

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