

The influence of parental relatedness on reproductive success

W. Amos^{1*}, J. Worthington Wilmer^{1†}, K. Fullard¹, T. M. Burg^{1‡}, J. P. Croxall², D. Bloch³ and T. Coulson¹

¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

²British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, UK

³Natural History Museum, Fátalág 100, Tórshavn, Faeroe Islands

The relationship between fitness and parental similarity has been dominated by studies of how inbreeding depression lowers fecundity in incestuous matings. A widespread implicit assumption is that adult fitness (reproduction) of individuals born to parents who are not unusually closely related is more or less equal. Examination of three long-lived vertebrates, the long-finned pilot whale, the grey seal and the wandering albatross reveals significant negative relationships between parental similarity and genetic estimates of reproductive success. This effect could, in principle, be driven by a small number of low quality, inbred individuals. However, when the data are partitioned into individuals with above average and below average parental similarity, we find no evidence that the slopes differ, suggesting that the effect is more or less similar across the full range of parental similarity values. Our results thus uncover a selective pressure that favours not only inbreeding avoidance, but also the selection of maximally dissimilar mates.

Keywords: inbreeding depression; outbreeding; mate choice; pilot whale; grey seal; albatross

1. INTRODUCTION

Offspring born to closely related parents commonly show reduced fitness (Crnokrak & Roff 1999; Husband & Schemske 1996; Keller 1998; Ralls *et al.* 1979; Saccheri *et al.* 1996), particularly under stressful conditions (Dahlgaard & Hoffmann 2000; Hauser & Loeschke 1996). This phenomenon has long been recognized and is referred to as inbreeding depression (Darwin 1868; Charlesworth & Charlesworth 1987), and is thought to be one of the primary selective forces opposing the build-up of deleterious recessive mutations (Lynch 1993). Avoidance of inbreeding has probably played a major role in the evolution of dispersal and breeding behaviours (Brooker *et al.* 1990; Clutton-Brock 1989; Dobson *et al.* 1997; Goosens *et al.* 2001; Keane 1990), and has implications for many areas of biology including conservation (O'Brien 1994; Hedrick & Kalinowski 2000) and human health (Bellamy *et al.* 2000).

The term inbreeding depression often carries with it an unstated assumption that the majority of effects involve loss of fitness in those few matings that occur between close relatives. Conversely, most individuals in a population are usually considered unaffected by inbreeding depression, particularly once they have successfully reached adulthood. Indeed, there is some evidence that genetic incompatibility (Tregenza & Wedell 2000) and other factors can reduce the fitness of dissimilar pairs, a possibility referred to as outbreeding depression. By implication, there is some optimal intermediate level of parental similarity, which confers maximal fitness (Bateson 1982, 1983).

Despite the wealth of data from laboratory studies, there is as yet relatively little information about the incidence of inbreeding depression in natural populations. A primary reason for this relates to the need for accurate, deep pedigrees in order to assess the level of inbreeding associated with any given individual. Suitable data can be obtained from intensive long-term studies, for example the Mandarte Island song sparrows (Keller 1998; Keller *et al.* 1994) or the red deer on Rum (Pemberton *et al.* 1992), or from known family sizes in metapopulations (Saccheri *et al.* 1998), but these are the exceptions not the rule. Similarly, while in plants it is possible to conduct experimental crosses between individuals of contrasting relatedness (Sheridan & Karowe 2000), for most species of animal this is difficult.

Until recently, genetic methods for estimating parental relatedness were rather crude, being based on simple heterozygosity. However, two new genetic measures have been developed, which are very much more sensitive. First, mean d^2 is a measure based on the mutational difference between microsatellite alleles, and is calculated as the squared difference in length between the alleles at a locus averaged across all loci considered (Coulson *et al.* 1998). Second, standardized heterozygosity (SH) is a method of calculating heterozygosity in which the score for each locus is weighted by the average heterozygosity at that locus (Coltman *et al.* 1999).

Applied to natural populations of mammals, these new genetic methods are revealing a picture in which parental similarity influences offspring fitness for many different traits and appears to affect essentially all individuals in the population. Thus, parental similarity influences birth weight and juvenile survival in red deer (Coulson *et al.* 1998, 1999) and harbour seals (Coltman *et al.* 1998), and explains significant variation in parasite load of sheep (Coltman *et al.* 1999), which in turn impacts on adult survival. The latest study shows that adult reproductive

*Author for correspondence (w.amos@zoo.cam.ac.uk).

†Present address: Department of Biology, 5 Cummington Street, Boston University, Boston, MA 02215, USA.

‡Present address: N122 Ramaley, Campus Box 334, Department of EPOB, University of Colorado, Boulder, CO 80309, USA.

success of red deer is also negatively correlated with parental similarity, particularly among males (Slate *et al.* 2000). In general, this would have remarkable implications for individual fitness and the maintenance of genetic variability, and would shift the emphasis of inbreeding effects from mortality among inbred individuals to enhanced success among relatively outbred individuals.

Although fascinating, the red deer study leaves two key questions unanswered. First, the Rum population is currently small and isolated, and has a strongly polygynous breeding system in which inbreeding effects might be particularly strongly felt. It is possible that less extreme breeding systems and less isolated populations will show little or no effect. Second, it remains unclear whether the relationship between parental similarity and fitness extends across all matings or is instead driven by a small number of low-quality individuals born to exceptionally closely related parents, i.e. classical inbreeding depression. While this is an interesting possibility, it does not have the same evolutionary consequences as a system in which increased partner dissimilarity brings benefits at all levels. This is because inbreeding depression alone selects only for the avoidance of mating with relatives, whereas a more general relationship would favour patterns of mate choice in which dissimilarity to self is a key factor.

To examine the generality of the influence of parental similarity on adult reproductive success we analysed large genetic datasets from natural populations of three additional species with contrasting breeding systems, none of which is strongly polygynous. We are able to show that the trend is general and appears to extend across the full range of parental similarity values.

2. METHODS

(a) *Datasets*

We used data from three large genetic studies in which parental similarity can be determined and over which reproductive success has been measured over many years. Dataset 1 is based on a 13-year study of grey seal (*Halichoerus grypus*) breeding behaviour at two Scottish breeding colonies, North Rona and the Isle of May (Amos *et al.* 1995; Worthington Wilmer *et al.* 1999). Breeding behaviour was until recently described as polygynous. However, recent molecular studies have shown that dominant males are not as successful as they appear (Amos *et al.* 1993b), with as few as 1% of males fathering above average numbers of pups (Worthington Wilmer *et al.* 1999), and that some level of partner fidelity exists (Amos *et al.* 1995). Male reproductive success was determined by paternity-testing 288 North Rona males sampled over 12 years against 524 pups born to sampled mothers over an 11-year study period. Corresponding figures for the Isle of May are 167 males sampled over 7 years tested against 319 pups sampled over 7 years. Some males were alive for the entire study period, but others inevitably either died during the study or only became adult after the study began. Paternities were assigned using the program NEWPAT, which allocates each pup either to a single matching male, or to which of several males is most closely related (Queller & Goodnight 1989) to the pup. Genuine paternities are included with high confidence, but the large number of pairwise comparisons results in significant numbers of type I errors, with some 35% of assignments being spurious (Worthington Wilmer *et al.*

1999). Female reproductive success was estimated from sighting records, using the assumption that females who were not seen in a particular year did not produce a pup. Since some females undoubtedly died or left the colony during the study period, sighting records were taken as ending at the last sighting. All seals were genotyped for nine polymorphic microsatellites with a mean heterozygosity of 74% (Allen *et al.* 1995; Worthington Wilmer *et al.* 1999).

Dataset 2 comprises 735 long-finned pilot whales, *Globicephala melas*, from 11 complete or near-complete social groups, that were caught in the Faeroese drive fishery between 1986 and 1988 (Amos *et al.* 1993a). Male breeding behaviour in this species is thought to involve males from one group fertilizing females from another, with no single male dominating (Amos *et al.* 1991, 1993a; Fullard 2001). More recent analysis suggests that single males very rarely father more than one offspring in a group (K. J. Fullard and W. Amos, unpublished data). All individuals were genotyped for 16 highly variable microsatellite loci, including one locus with 70 alleles (Fullard 2001). Ages for ca. 80% of animals were determined by tooth sectioning (Bloch & Lockyer 1993). Maternal relationships were assigned using the program NEWPAT (Worthington Wilmer *et al.* 1999) to find genetically compatible pairs of animals with at least a 5-year age difference and where the older animal was female. With such a large number of loci, some of which are extraordinarily polymorphic, we estimate only a 3–5% offspring assignment error, which is unlikely to distort the overall pattern of maternal reproductive success.

Dataset 3 comprises pairs of wandering albatrosses (*Diomedea exulans*) on Bird Island. Additional data from two other species of albatross (*Thalassarche chrysostoma* and *T. melanophris*) were also used. Albatrosses are considered the classical example of a monogamous species, and individual pairs produce a maximum of one egg per breeding attempt. All samples were genotyped for seven microsatellites. However, one locus in the wandering albatross showed a strong homozygote excess due to sex-linkage, and was excluded from the analysis for this species. No evidence of either null alleles or sex-linkage was detected in other species or at other loci. Since albatrosses have biparental care (Cobley *et al.* 1998; Croxall *et al.* 1990), in addition to examining the effect of parental similarity on reproductive success of males and females separately, it is also possible to test the influence of parental similarity on the success of pairs. For each pair, parental similarity is taken as the average similarity of the two parents. Also, reproductive success can be measured in terms of either the number of eggs that successfully hatch, or the number of offspring that survive to fledge. As with the grey seals, sighting records for particular pairs varied greatly, from one season up to 14. With three species of albatross, three measures of parental similarity and two measures of offspring number, a total of 18 testable relationships was possible.

(b) *Estimation of parental similarity*

Previously published methods for assessing parental similarity include mean d^2 , heterozygosity and SH. Mean d^2 depends on long-term mutational differences and hence may be better suited to situations involving population admixture rather than effects present in otherwise homogeneous populations (Pemberton *et al.* 1999). SH is an improvement over heterozygosity because scores at each locus are weighted by the heterozygosity at that locus. Better still would be a measure based on allele sharing where the frequency of every allele counts towards the final score, thereby allowing the sharing of rare alleles to be weighted more than the

Table 1. Relationships between parental similarity and reproductive success.

(Significant relationships are highlighted in bold. Three measures of parental relatedness are compared: internal relatedness (IR), standardized heterozygosity (SH) and mean d^2 (see §2b). Depending on the species, analyses were performed on males (M), females (F) or on average score for both parents (B).)

species	n	sex	trait	error	term	IR value			SH			mean d^2		
						slope	χ^2	p	slope	χ^2	p	slope	χ^2	p
grey seal, North Rona	68	F	offspring	binomial		-1.629	7.65	<0.01	1.259	4.8	<0.05	1.58	0.76	n.s.
grey seal, North Rona	288	M	offspring	Poisson		-1.285	10.9	<0.001	0.82	5	<0.05	-0.54	0.20	n.s.
grey seal, Isle of May	49	F	offspring	binomial		-0.703	2.5	n.s.	1.116	1.6	n.s.	1.78	0.65	n.s.
grey seal, Isle of May	167	M	offspring	Poisson		0.375	0.4	n.s.	-0.901	2.7	n.s.	-3.17	2.80	n.s.
pilot whales	251	F	offspring	Poisson	age	-0.948	8.3	<0.005	0.729	5.9	<0.025	0.36	0.10	n.s.
wandering albatross	178	B	fledged	binomial		-0.874	12.4	<0.001	0.827	12.1	<0.001	0.42	0.10	n.s.
	178	F				-0.445	7.3	<0.01	0.402	7.6	<0.01	-0.129	0	n.s.
	178	M				-0.417	5	<0.05	0.359	5.3	<0.025	0.633	0.40	n.s.
	178	B	hatched	binomial		-0.278	0.9	n.s.	0.295	1.4	n.s.	-0.34	0.10	n.s.
	178	F				-0.102	0.3	n.s.	0.117	0.4	n.s.	0.02	0	n.s.
	178	M				-0.187	0.7	n.s.	0.202	1.1	n.s.	-0.4	0.10	n.s.
grey-headed albatross	121	B	fledged	binomial		-0.307	0.4	n.s.	0.624	2	n.s.	1.86	1	n.s.
	121	F				0.136	0.2	n.s.	0.099	0.1	n.s.	0.43	0.20	n.s.
	121	M				-0.398	1.4	n.s.	0.434	2.3	n.s.	1.21	0.90	n.s.
	121	B	hatched	binomial		-0.87	2.4	n.s.	1.101	4.8	<0.05	0.83	0.20	n.s.
	121	F				-0.344	0.7	n.s.	0.453	1.7	n.s.	0.59	0.20	n.s.
	121	M				-0.484	1.6	n.s.	0.527	2.6	n.s.	0.01	0	n.s.
black-browed albatross	82	B	fledged	binomial		-0.228	0.1	n.s.	0.224	0.2	n.s.	1.73	0.90	n.s.
	82	F				0.286	0.3	n.s.	-0.08	0	n.s.	1.19	0.70	n.s.
	82	M				-0.62	1.3	n.s.	0.43	0.8	n.s.	0.78	0.30	n.s.
	82	B	hatched	binomial		-1.24	2.53	n.s.	0.884	1.8	n.s.	-0.27	0	n.s.
	82	F				-0.762	1.8	n.s.	0.603	1.5	n.s.	-0.12	0	n.s.
	82	M				-0.662	1.1	n.s.	0.466	0.73	n.s.	-0.18	0.01	n.s.

sharing of common alleles. Queller & Goodnight (1989) have developed just such a measure of relatedness, based on the genetic correlations between two individuals. Although usually applied to comparisons between pairs of individuals, their method can also be applied to data in which, at each locus, two alleles rather than two pairs of alleles are compared. In this special case their basic formula simplifies to:

$$\frac{(2H - \sum f_i)}{(2N - \sum f_i)}, \tag{2.1}$$

where H is the number of loci that are homozygous, N is the number of loci and f_i is the frequency of the i th allele contained in the genotype. No adjustment is made to the allele frequency estimates for the alleles carried by the individual concerned (Queller & Goodnight 1989). When calculated over several loci, the resulting value shares the same attractive properties as r -values, being approximately normally distributed and centred more or less on zero for individuals born to ‘unrelated’ parents, with negative values suggesting relatively ‘outbred’ individuals and high positive values being suggestive of inbreeding. Since the quantity being measured is between parental half-genotypes within an individual, we refer to the measure as internal relatedness (IR). All three measures were assessed for their abilities to explain a significant proportion of the observed variation in reproductive fitness. Since d^2 values vary greatly between loci, a simple arithmetic mean will give undue weighting to loci with large allele size ranges. For this study we attempted to achieve a more even weighting by dividing all d^2 values by the maximum observed value at the same locus. The resulting values never exceed one and were averaged across loci to yield a measure we term ‘standardised mean d^2 ’.

(c) **Statistical analysis**

Relationships between parental similarity and reproductive success were analysed using generalized linear models (GLMs). Where reproductive success was expressed in terms of the proportion of breeding attempts that were successful (female grey seals, albatrosses), a binomial error structure was used. Where success was measured in terms of number of attributable offspring (male grey seals, female pilot whales) a Poisson error structure was used. In all cases, number of progeny was fitted as the dependent variable and parental similarity as the independent variable. Each model was fitted to n observations and yields a slope with standard error and deviance explained (χ^2). For pilot whales, an age covariate was fitted. Parental similarity values were calculated using an EXCEL macro written in VISUAL BASIC, and statistical analyses were conducted using GENSTAT (GENSTAT 5 Committee 1995).

3. RESULTS

Our results are summarized in table 1. In all three primary studies (in bold: grey seals of both sexes on North Rona, pilot whales and wandering albatrosses based on fledged offspring) significant relationships exist between parental similarity and reproductive success, measured as IR (negative trends) and SH (positive trends), indicating that individuals born to dissimilar parents tend to grow up to become successful adults. Of the 19 remaining relationships for IR, all but three have a negative slope. Thus, even though most tests do not show significantly non-zero slopes and in no case does IR explain more than 5% of the variance in fitness, overall

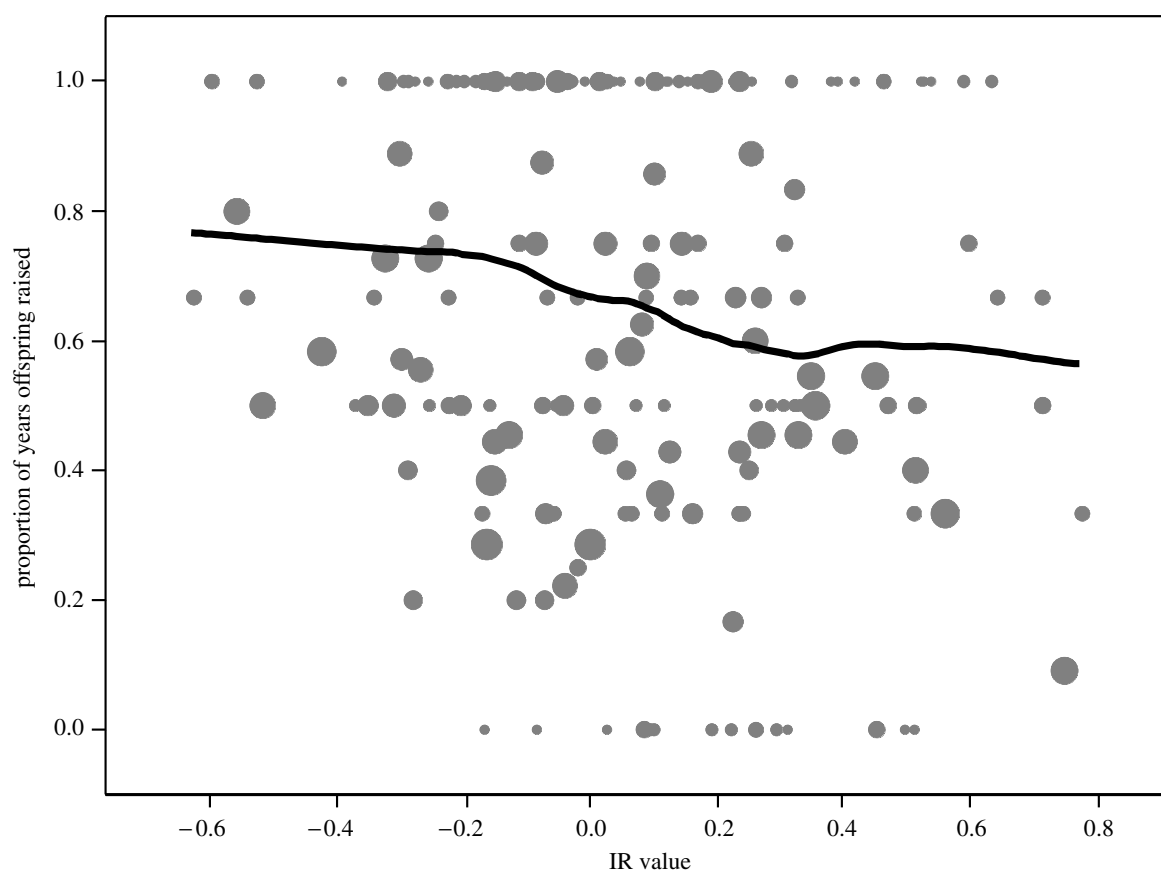


Figure 1. The relationship between proportion of chicks fledged and mean parental IR value for the wandering albatross. The fitted line is a local regression fit and indicates that the slope of the association between the proportion of fledged chicks and the IR value is approximately constant across the range of IR values. Point sizes represent the total sample sizes used to calculate the proportion, with large points representing large sample sizes.

we can reject the null hypothesis of no relationship with high confidence (H_0 = equal numbers of positive and negative slopes, $p \sim 0.004$, binomial exact). Furthermore, all counter-trend slopes are borderline, accounting for three of the smallest five χ^2 -values. An essentially identical pattern is seen for SH, with all but two slopes being positive. Finally, at the Isle of May, only 5 out of 167 males fathered more than three pups and these successful males dominate the relationship. Removal of these males reveals a significant negative trend (slope = -0.59 , $p = 0.02$).

To test whether the generally negative relationships could be driven by the presence of small numbers of unsuccessful individuals born to related parents ('inbred'), the data were further subdivided into individuals with above mean parental similarity and those with mean or below-mean parental similarity. As expected with smaller sample sizes, levels of significance fall. However, the proportion of negative relationships remains high (below-mean 15/21 negative, mean slope = -0.65 ± 0.33 s.e.m.; based on individuals with above-mean parental similarity, 17/21 relationships yield a negative slope, mean slope = -0.38 ± 0.22 s.e.m.). Since neither the mean slope nor the proportion of negative slopes differs among the two groups, parental similarity appears to influence reproductive success over its entire range. This is supported by local regressions (see figure 1 for a typical example), which show no evidence that the local slope changes consistently with either increasing or decreasing parental similarity. Also, in none of our studies do we see evidence of optimal outbreeding (Bateson

1982, 1983) where highest fitness is associated with intermediate IR values. By implication, our study populations do not encompass a sufficiently large range of parental similarity values for negative outbreeding effects to become important.

Comparing the three measures of parental similarity, it is noticeable that mean d^2 explains less variability in fitness than the other two measures (table 1), and is less strongly correlated with them (figure 2). Thus, in no case does mean d^2 explain significant variation in fitness, and in every case where the other measures yield significant χ^2 -values, mean d^2 explains significantly less variation in fitness. The measures IR and SH are highly correlated and both perform well. In the only case where one measure explains significantly more variation in fitness than the other (grey seal males at North Rona), IR explains more variation in fitness than SH. Moreover, if the slope of the IR–success relationship (as a surrogate for strength of effect) is plotted against difference in χ^2 -value between IR and SH, a significant relationship is found ($r = 0.61$, $n = 23$, $p < 0.01$), indicating that the stronger the effect, the better IR performs relative to SH.

For the albatross datasets, two independent inbreeding effects could affect fledging success, namely the effect we are looking at (parental quality as influenced by the relatedness of the parents' parents) and the inherent quality of the chicks, in terms of their own inbreeding coefficients (Bensch *et al.* 1994). Although not the focus of the current study, we also fitted inter-parent relatedness (measured as

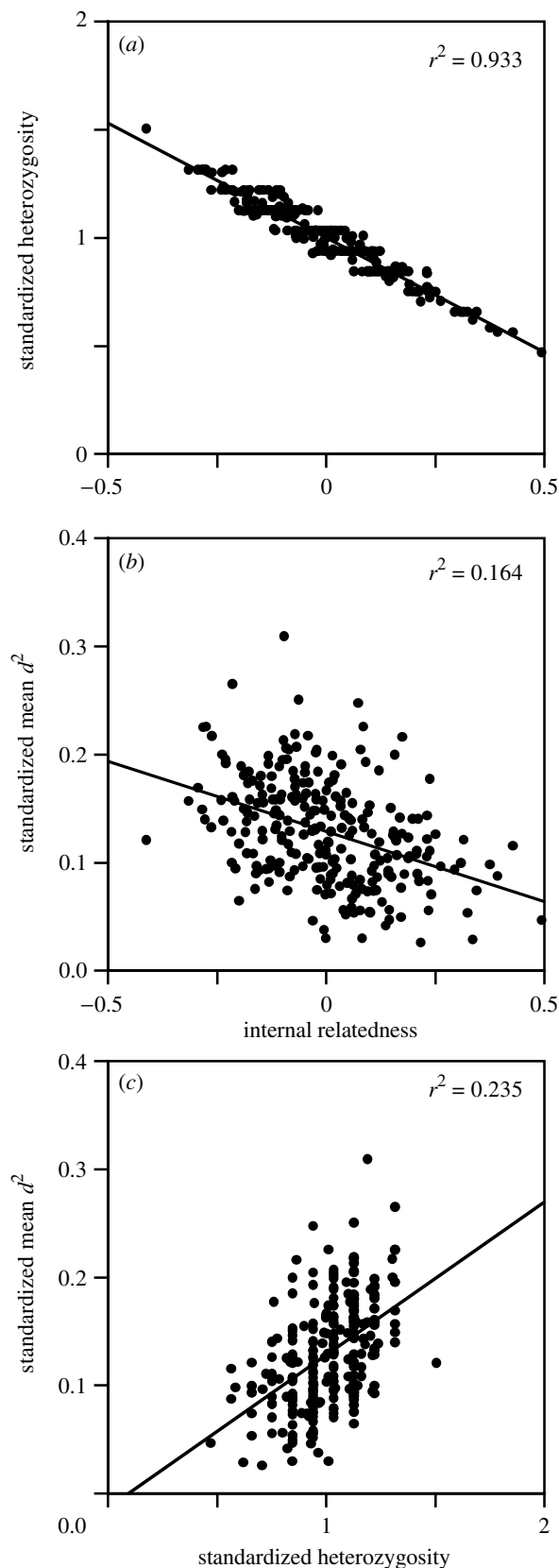


Figure 2. Relationship between three measures of parental similarity applied to 735 long-finned pilot whales. Measures are standardized heterozygosity (Coltman *et al.* 1999), internal relatedness (see § 2b) and standardized mean d^2 (see § 2b; Coulson *et al.* 1998). Similar degrees of correlation are seen in all other species examined. (a) Standardized heterozygosity against internal relatedness; (b) standardized mean d^2 against internal relatedness and (c) standardized mean d^2 against standardized heterozygosity.

Queller and Goodnight r) as an extra explanatory variable in each species. Only the mean IR–fledging success models were tested. In all three species, increased relatedness between the parents tended to reduce fledging success, the effect being significant in grey-headed, borderline in wanderer and non-significant in black-browed albatrosses (data not shown).

4. DISCUSSION

In this paper we use a new genetic measure of parental relatedness to show that reproductive success in two marine mammals and three species of albatross is related to parental similarity such that individuals born to genetically dissimilar parents tend to produce greater than average numbers of offspring. There is no evidence that these relationships are due mainly to small numbers of poor quality ‘inbred’ individuals, but instead the slopes appear homogeneous over the entire range of individuals.

We show that in the vast majority of all tests conducted, parental similarity is negatively related to adult reproductive success, and that, wherever sample sizes are large, the relationships become significantly negative. However, some caution is needed when interpreting the male grey seal results, where success is measured by paternity testing and where genuine paternities are ‘diluted’ by spurious assignments due to type I errors affecting the large number of pairwise comparisons. Heterozygous males will tend to match more pups by chance compared with homozygous males, giving rise to an ascertainment bias. This bias is likely to explain some of the effect we observe, although it is interesting that the most successful males on the Isle of May have high IR values, with greater than average homozygosity. Data for the pilot whales, where errors in maternity assignment are rare, and for female grey seals and albatrosses, where success is determined by observation rather than by genetic testing, are not affected by this bias.

Among the three measures of parental similarity we compared, mean d^2 proved substantially less effective than SH, as reported previously (Coltman *et al.* 1998; Slate *et al.* 2000). SH was itself marginally less effective than our new measure, IR. This rank order agrees with *a priori* expectations. Mean d^2 is based on long-term mutational divergence between alleles, has a large variance and will be best suited to situations where population admixture has occurred (Pemberton *et al.* 1999). Measures of heterozygosity capture information about the number of homozygous loci in an individual relative to the number expected by chance. SH makes allowance for variation in variability between loci, but within each locus a simple binary homozygote–heterozygote classification is used. IR goes one step further, weighting each genotype by the frequencies of the alleles involved, such that rare allele homozygotes are given more weight than homozygotes for common alleles.

Previous studies using genetic measures to explore the relationship between inbreeding and fitness exploited intensively studied island populations of sheep and deer (Coltman *et al.* 1999; Coulson *et al.* 1998, 1999; Pemberton *et al.* 1996), where many key variables such as parental body weight, birth year and birth date could all be controlled statistically. By contrast, our studies were conducted on small subsections of much larger populations, for the most

part precluding such detailed monitoring and such reliable paternity analysis. For example, while some grey seal males were reproductively active over the whole 13-year study period, others may have appeared for only part of a single season, yet because presence could not be accurately quantified, all males had to be treated as potentially present for the whole study period. This has the disadvantage that the strength of the effects that we see may be underestimated or even not detectable. On the positive side, any patterns we do find are likely to be in reality even stronger. Also, a possible criticism of studies based on small, isolated, polygynous populations is that a single successful male could dominate the analysis. For example, one of the most successful of all Rum stags had a Rum mother but a mainland father (Slate 1999), making it difficult to determine whether he and his many offspring were successful because they were outbred, or because they inherited 'good genes' from their high-quality father.

Two recent studies suggest that inbreeding effects can impact negatively on adult reproductive success. First, experimentally inbred mice ($F_i=0.25$) released into a semi-natural environment proved less fit than competing outbred controls (Meagher *et al.* 2000). Second, individual SH and reproductive success are positively correlated in red deer, particularly among males (Slate *et al.* 2000). However, neither of these studies explicitly distinguished between an effect due to the presence of a small proportion of inbred individuals with low success and a more general pattern in which greatest success consistently goes to individuals born to maximally dissimilar parents, though the deer data suggest strongly that maximally outbred males are unusually successful. This is an important distinction, which would determine the extent to which breeding behaviours might go beyond simple incest taboos to evolve mechanisms of selecting maximally dissimilar partners. Our study suggests that effects are felt across the full range of parental similarity, and hence that, all other things being equal, females can increase their fitness by seeking out dissimilar mates. Ultimately, too much dissimilarity will of course result in outbreeding depression (Bateson 1983; Marshall & Spalton 2000). However, our study provides no evidence that this limit is reached in natural populations.

Our observations identify a continuum of effect ranging from the most 'inbred' to the most 'outbred' individuals. In this context, the terms 'inbreeding' and 'outbreeding' begin to appear somewhat artificial. For example, are the fittest individuals successful because they are less inbred or because they are more outbred? Unless a clear mechanistic distinction can be made between the two ends of the spectrum, perhaps a more neutral term such as 'parental similarity' might be preferable.

The relative strengths of the relationships between fitness and parental similarity in the albatross datasets suggest two aspects of the species' biology that may be particularly important. First, the χ^2 -values for average parental IR and SH values are significantly larger than those for either fathers or mothers alone. By implication, pairs comprising two average parents tend to outperform pairs with one 'inbred' and one 'outbred' parent. This subtle distinction emphasizes the known importance of biparental care in albatrosses. Second, the strongest trends are found for the number of fledged chicks rather

than for the number of hatched eggs. This implies that parental 'quality' is better reflected in a bird's ability to guide chicks through to fledging than simply in the ability to lay fertile eggs.

If relatively outbred individuals within a population generally enjoy enhanced reproductive success, there would be implications for many areas of evolutionary biology. First, it would tend to increase the effective size of a population, promoting higher levels of variability and increasing the advantage of dispersal, sperm selection and other mechanisms of inbreeding avoidance. This accords with increasing numbers of reports describing mate choice in favour of dissimilar partners (Amos *et al.* 2001; Kelley *et al.* 1999; Olsson *et al.* 1996; Stockley 1999). Second, statistical removal of the effects of parental similarity might enhance the informativeness of studies of natural populations looking at heritable components of fitness such as body weight and sexually selected traits. This would be particularly important if, as seems to be the case, inbreeding effects are felt most strongly in traits directly associated with fitness (DeRose & Roff 1999). Finally, our observation provides a fascinating added complexity to the question of what makes a high-quality mate. In general terms, greater success among dissimilar pairs would provide a selective force acting against evolutionary patterns that tend to increase mean relatedness, such as polygyny and strong directional selection. Amusingly, this also seems to offer a possible basis for sayings such as 'opposites attract' and a reason why the stereotypical attractive man is not only 'tall and dark', but also 'a stranger'!

We thank B. Charlesworth, J. Pemberton, D. Coltman, J. Slate, P. Bateson and T. Clutton-Brock for discussion and comments on the manuscript. This work was funded by the Natural Environment Research Council (grant no. GR3/10084), a Commonwealth Scholarship to T.B. and a Bradlow Foundation Scholarship to F.F. We are grateful to the large number of people who contributed to sample collection for this project, and in particular to P. Pomeroy and S. Twiss for the grey seal samples.

REFERENCES

- Allen, P. J., Amos, W., Pomeroy, P. P. & Twiss, S. D. 1995 Microsatellite variation in grey seals (*Halichoerus grypus*) shows evidence of genetic differentiation between two British breeding colonies. *Mol. Ecol.* **4**, 653–662.
- Amos, W., Barrett, J. A. & Dover, G. A. 1991 Breeding behaviour of pilot whales revealed by DNA fingerprinting. *Heredity* **67**, 49–55.
- Amos, W., Schlötterer, C. & Tautz, D. 1993a Social structure of pilot whales revealed by analytical DNA typing. *Science* **260**, 670–672.
- Amos, W., Twiss, S. S., Pomeroy, P. P. & Anderson, S. S. 1993b Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proc. R. Soc. Lond. B* **252**, 199–207.
- Amos, W., Pomeroy, P. P., Twiss, S. D. & Anderson, S. S. 1995 Evidence for mate fidelity in the grey seal. *Science* **268**, 1897–1899.
- Amos, W., Worthington Wilmer, J. & Kokko, H. 2001 Do female grey seals select genetically diverse mates? *Anim. Behav.* **62**, 157–164.
- Bateson, P. 1982 Preferences for cousins in Japanese quail. *Nature* **295**, 236–237.
- Bateson, P. 1983 Optimal outbreeding. In *Mate choice* (ed. P. Bateson), pp. 257–277. Cambridge University Press.

- Bellamy, R. (and 15 others) 2000 Genetic susceptibility to tuberculosis in Africans: a genome-wide scan. *Proc. Natl Acad. Sci. USA* **97**, 8005–8009.
- Bensch, S., Hasselquist, D. & Von Schantz, T. 1994 Genetic similarity predicts hatching failure—non-incestuous inbreeding in the great reed warbler. *Evolution* **48**, 317–326.
- Bloch, D. & Lockyer, C. 1993 Age and growth parameters of the long-finned pilot whale off the Faeroe Islands. *Rep. Int. Whal. Comm.* (Special Issue 14), 163–207.
- Brooker, M. G., Rowley, I., Adams, M. & Baverstock, P. R. 1990 Promiscuity: an inbreeding avoidance mechanism in a socially monogamous species. *Behav. Ecol. Sociobiol.* **26**, 191–199.
- Charlesworth, D. & Charlesworth, B. 1987 Inbreeding depression and its evolutionary consequences. *A. Rev. Ecol. Syst.* **18**, 237–268.
- Clutton-Brock, T. H. 1989 Mammalian mating systems. *Proc. R. Soc. Lond. B* **236**, 339–372.
- Cobley, N. D., Croxall, J. P. & Prince, P. A. 1998 Individual quality and reproductive performance in the grey-headed albatross *Diomedea chrysostoma*. *Ibis* **140**, 315–322.
- Coltman, D. W., Bowen, W. D. & Wright, J. M. 1998 Birth weight and neonatal survival of harbour seal pups are positively correlated with genetic variation measured by microsatellites. *Proc. R. Soc. Lond. B* **265**, 803–809.
- Coltman, D. W., Pilkington, J. G., Smith, J. A. & Pemberton, J. M. 1999 Parasite-mediated selection against inbred Soay sheep in a free-living island population. *Evolution* **53**, 1259–1267.
- Coulson, T. N., Pemberton, J. M., Albon, S. D., Beaumont, M., Marshall, T. C., Slate, J., Guinness, F. E. & Clutton-Brock, T. H. 1998 Microsatellites reveal heterosis in red deer. *Proc. R. Soc. Lond. B* **265**, 489–495.
- Coulson, T. N., Albon, S., Slate, J. & Pemberton, J. 1999 Microsatellite loci reveal sex-dependent responses to inbreeding and outbreeding in red deer calves. *Evolution* **53**, 1951–1960.
- Crnokrak, P. & Roff, D. A. 1999 Inbreeding depression in the wild. *Heredity* **83**, 260–270.
- Croxall, J. P., Rothery, P., Pickering, S. P. C. & Prince, P. A. 1990 Reproductive performance, recruitment and survival of wandering albatrosses *Diomedea exulans* at Bird Island, South Georgia. *J. Anim. Ecol.* **59**, 775–796.
- Dahlggaard, J. & Hoffmann, A. A. 2000 Stress resistance and environmental dependency of inbreeding depression in *Drosophila melanogaster*. *Conserv. Biol.* **14**, 1187–1192.
- Darwin, C. R. 1868 *The variation of animals and plants under domestication*. London: John Murray.
- DeRose, M. & Roff, D. A. 1999 A comparison of inbreeding depression in life-history and morphological traits in animals. *Evolution* **53**, 1288–1292.
- Dobson, F. S., Chesser, F. K., Hoogland, J. L., Sugg, D. W. & Foltz, D. W. 1997 Do black-tailed prairie dogs minimise inbreeding? *Evolution* **51**, 970–978.
- Fullard, K. J. 2001 microsatellite analysis of long-finned pilot whales. PhD thesis, University of Cambridge, UK.
- GENSTAT 5 Committee 1995 *GENSTAT for Windows reference manual*. Oxford: Clarendon Press.
- Goosens, B., Chikhi, L., Taberlet, P., Waits, L. P. & Allaine, D. 2001 Microsatellite analysis of genetic variation among and within Alpine marmot populations in the French Alps. *Mol. Ecol.* **10**, 41–52.
- Hauser, T. P. & Loeschke, V. 1996 Drought stress and inbreeding depression in *Lychnis flos-cuculi* (Caryophyllaceae). *Evolution* **50**, 1119–1126.
- Hedrick, P. W. & Kalinowski, S. T. 2000 Inbreeding depression in conservation biology. *A. Rev. Ecol. Syst.* **31**, 139–162.
- Husband, B. C. & Schemske, D. W. 1996 Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* **50**, 54–70.
- Keane, B. 1990 Dispersal and inbreeding avoidance in the white-footed mouse, *Peromyscus leucopus*. *Anim. Behav.* **40**, 143–152.
- Keller, L. 1998 Inbreeding and its fitness effects in an insular population of song sparrows (*Melospiza melodia*). *Evolution* **52**, 240–250.
- Keller, L. F., Arcese, P., Smith, J. N. M., Hochachka, W. M. & Stears, S. C. 1994 Selection against inbred song sparrows during a natural population bottleneck. *Nature* **372**, 356–357.
- Kelley, J. L., Graves, J. A. & Magurran, A. E. 1999 Familiarity breeds contempt in guppies. *Nature* **401**, 661–662.
- Lynch, M. 1993 The mutational meltdown in asexual populations. *J. Hered.* **84**, 339–344.
- Marshall, T. C. & Spalton, J. A. 2000 Simultaneous inbreeding and outbreeding depression in reintroduced Arabian oryx. *Anim. Conserv.* **3**, 241–248.
- Meagher, S., Penn, D. J. & Potts, W. K. 2000 Male–male competition magnifies inbreeding depression in wild house mice. *Proc. Natl Acad. Sci. USA* **97**, 3324–3329.
- O'Brien, S. J. 1994 A role for molecular genetics in biological conservation. *Proc. Natl Acad. Sci. USA* **91**, 5748–5755.
- Olsson, M., Shine, R., Madsen, T., Gullberg, A. & Tegelström, H. 1996 Sperm selection by females. *Nature* **383**, 585.
- Pemberton, J. M., Albon, S. D., Guinness, F. E., Clutton-Brock, T. H. & Dover, G. A. 1992 Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behav. Ecol.* **3**, 66–75.
- Pemberton, J. M., Smith, J. A., Coulson, T. N., Marshall, T. C., Slate, J., Paterson, S., Albon, S. D. & Clutton-Brock, T. H. 1996 The maintenance of genetic polymorphism in small island populations: large mammals in the Hebrides. *Phil. Trans. R. Soc. Lond. B* **351**, 745–752.
- Pemberton, J. M., Coltman, D. W., Coulson, T. N. & Slate, J. 1999 Using microsatellites to measure the fitness consequences of inbreeding and outbreeding. In *Microsatellites, evolution and applications* (ed. D. B. Goldstein & C. Schlötterer), pp. 151–164. Oxford University Press.
- Queller, D. C. & Goodnight, K. F. 1989 Estimating relatedness using genetic markers. *Evolution* **43**, 258–275.
- Ralls, K., Brugger, K. & Ballou, J. 1979 Inbreeding and juvenile mortality in small populations of ungulates. *Science* **206**, 1101–1103.
- Saccheri, I. J., Brakefield, P. M. & Nichols, R. A. 1996 Severe inbreeding depression and rapid fitness rebound in the butterfly *Bicyclus anynana* (Satyridae). *Evolution* **50**, 2000–2013.
- Saccheri, I. J., Kuussaari, M., Vikman, P., Fortelius, W. & Hanski, I. 1998 Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491–494.
- Sheridan, P. M. & Karowe, D. N. 2000 Inbreeding, outbreeding and heterosis in the yellow pitcher plant, *Sarracenia flava* (Sarraceniaceae), in Virginia. *Am. J. Bot.* **87**, 1628–1633.
- Slate, J. 1999 Mapping genes for birth weight in a wild population of red deer (*Cervus elaphus*). PhD thesis, University of Edinburgh.
- Slate, J., Kruuk, L. E. B., Marshall, T. C., Pemberton, J. M. & Clutton-Brock, T. H. 2000 Inbreeding depression influences lifetime breeding success in a wild population of red deer (*Cervus elaphus*). *Proc. R. Soc. Lond. B* **267**, 1657–1662.
- Stockley, P. 1999 Sperm selection and genetic incompatibility: does relatedness of mates affect male success in sperm competition? *Proc. R. Soc. Lond. B* **266**, 1663–1669.
- Tregenza, T. & Wedell, N. 2000 Genetic compatibility, mate choice and patterns of parentage. *Mol. Ecol.* **9**, 1013–1027.
- Worthington Wilmer, J., Allen, P. J., Pomeroy, P. P., Twiss, S. D. & Amos, W. 1999 Where have all the fathers gone? An extensive microsatellite analysis of paternity in the grey seal (*Halichoerus grypus*). *Mol. Ecol.* **8**, 1417–1430.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.