

Inbreeding depression and male fitness in black grouse

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The male lifetime lekking performance was studied, and related to inbreeding–outbreeding in a wild population of black grouse (*Tetrao tetrix*) in central Finland between 1989 and 1995. Inbreeding was measured as the mean heterozygosity and mean d^2 of 15 microsatellite loci. We found a significantly positive relationship between mean d^2 and lifetime copulation success (LCS), while the relationship between heterozygosity and LCS was close to significant. We also found that males that never obtained a lek territory had significantly lower mean heterozygosity than males that were observed on a territory at least during one mating season in their life. Furthermore, among males that were successful in obtaining a lek territory, LCS and mean d^2 were highest for those males that held central territories. We suggest that inbred males have a disadvantage (or outbred males have an advantage) in the competition for territories that may explain the relationships with LCS and inbreeding. Furthermore, the fact that mean d^2 was positively correlated with LCS whereas heterozygosity was not when we restricted the analysis to territorial males, suggests that mean d^2 provides more information about levels of inbreeding–outbreeding than heterozygosity alone, and potentially highlights the effects of heterosis. To our knowledge, this is the first time that measures of inbreeding and lifetime fitness have been linked in a non-isolated population. This is important in establishing that the relationships found in previous studies are not artefacts of low gene flow created by limited dispersal but a general feature of wild vertebrate populations.

Keywords: inbreeding; inbreeding depression; lifetime copulation success; microsatellites; heterozygosity; mean d^2

1. INTRODUCTION

The detrimental effects of inbreeding (inbreeding depression) on traits relating to individual fitness and population persistence have been investigated for several decades. Inbreeding depression reflects the consequences of increased homozygosity for alleles that affect fitness, and may be manifest either through superior performance of heterozygote over homozygote genotypes, and/or the effects of recessive deleterious alleles (Charlesworth & Charlesworth 1987, 1999). When two inbred lines are crossed it is commonly observed that fitness increases in the outbred F_1 generation, an effect termed heterosis.

There is ample evidence of inbreeding depression in captive vertebrate populations from a range of taxa (see Ralls *et al.* 1988; Lacy *et al.* 1993, and references therein), but few studies have involved natural populations (Keller 1998; Crnokrak & Roff 1999). This is due, in part, to the difficulties associated with identifying parameters that reflect lifetime reproductive success (LRS) and the ability to monitor these in natural populations, and, also, an inability to establish the required pedigrees among individuals for a classical inbreeding analysis (Wright 1969).

Moreover, the majority of studies on inbreeding have focused on early life-history stages. Inbreeding studies that examine only juvenile stages in captive or semi-captive populations probably underestimate the effects of inbreeding because they ignore the effects of deleterious alleles that affect adult life-history stages, and also cannot properly mimic the natural conditions that are likely to reveal conditionally deleterious alleles (see Meagher *et al.* 2000, and references therein).

Recent developments in DNA marker-based methods for detecting inbreeding have now made it possible to study inbreeding without pedigrees, using surrogate estimators such as heterozygosity and mean d^2 (Bierne *et al.* 1998; Coltman *et al.* 1998; Coulson *et al.* 1998, 1999; Fisher & Mathies 1998; Pemberton *et al.* 1999; Saccheri *et al.* 1998). Such approaches have shown, for example, a negative relationship between inbreeding and male and female LRS in red deer (*Cervus elaphus*) (Slate *et al.* 2000), and a positive relationship between outbreeding and offspring survival in the horseshoe bat (*Rhinolopus ferrumequinum*) (Rossiter *et al.* 2001). In addition, the effects of inbreeding are enhanced by male–male competition in semi-natural populations of the house mouse (*Mus domesticus*) (Meagher *et al.* 2000). With the gradual accumulation of studies using genetic markers to study inbreeding effects, the predictions of inbreeding theory are confirmed: offspring born to genetically dissimilar partners seem to show above average general fitness, regardless of

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whether the effects are due to the negative effects of inbreeding depression or the positive effects of heterosis (Amos *et al.* 2001a,b).

A common feature of previous studies that use molecular markers to examine levels of inbreeding (Coltman *et al.* 1999; Slate *et al.* 2000; Rossiter *et al.* 2001) is that they are carried out on island, or isolated populations, where the effects of inbreeding may be more demonstrable. This is because dispersal to, and from, isolated populations may be hampered or impossible for extended time-periods, and the effective population size is often small in isolated populations. We describe the effects of inbreeding on LRS in black grouse (*Tetrao tetrix*) from a population in a continuous taiga habitat where extensive dispersal of individuals is possible (Höglund *et al.* 1999). Our previous study showed that, at a local scale, this population is moderately structured as a consequence of male philopatry but that female natal dispersal is extensive (see also Willebrandt 1988), a pattern common to all grouse species studied (Jamieson & Zwickel 1983; Small & Rausch 1989; Pierney *et al.* 1998). Black grouse have a lek mating system whereby males gather to display and females come to mate but subsequently nest elsewhere, away from the male (Höglund & Alatalo 1995). We propose that, assuming competitive interactions between males at a lek are designed to advertise fitness (Alatalo *et al.* 1991), those males that are successful in attaining a territory on a lek, and also having the highest reproductive success among territory holders, are predicted to be the fittest, possibly because of reduced inbreeding effects.

2. MATERIAL AND METHODS

(a) Study area and population

We studied a population of black grouse from a nature reserve near Petäjävesi, Central Finland (62°10' N, 25°05' E) from 1989 to 1995, where hunting is prohibited. Males were caught at feeding sites during winter using traps baited with oats, or during the mating season, by cannon netting. A blood sample was taken from the wing vein for subsequent DNA analysis. Males were ringed with a metal ring for permanent identification and three colour rings for identification at a distance. We subsequently studied the lekking behaviour of males annually at their traditional lek sites during the main part of the breeding season in April and May. Briefly, we recorded the identity, territorial position, display behaviour and annual copulatory success of individual males. We defined longevity as the number of years any male was observed to be present in the study area, and male lifetime copulation success (hereafter LCS) as the observed cumulative number of copulations by any given male throughout his lifetime. Our measure of longevity is probably a conservative underestimate in cases in which males were still alive at the termination of the study. The timing of copulations in black grouse are exceptionally synchronized in that the majority of the annual copulations take place within one week, and we have been unable to detect any significant proportion of copulations taking place outside the leks (Alatalo *et al.* 1996; Rintamäki *et al.* 2001). As all males at all leks each year were observed for the entire lekking period, there was no need to standardize copulations for differences in observation period per male. A previous study using multilocus DNA fingerprinting indicated that observed copulation in most instances is a reliable measure of male reproductive success (Alatalo *et al.* 1996). Details of the

field procedures and the study area are available in Rintamäki *et al.* (2001).

(b) Microsatellite genotyping and genetic estimates of inbreeding

DNA was extracted from blood using standard phenol/chloroform extraction procedures (Sambrook *et al.* 1989). Microsatellite allele length variation was determined at 15 microsatellite loci, 10 of which were specifically cloned from black grouse (BG primer pairs; Pierney & Höglund 2001), three loci were cloned from capercaillie (*Tetrao urogallus*) (TUT1–3 primers; Segelbacher *et al.* 2000) and two loci were cloned in red grouse (*Lagopus lagopus scoticus*) (LLST1 and 3 primers; Pierney & Dallas 1997). PCR reaction conditions and temperature profiles followed the original publications. In all cases, PCR fragments were separated by electrophoresis on 6% denaturing polyacrylamide gels and visualized using silver staining.

The mean d^2 was calculated as the squared difference in repeat units between two alleles at a locus averaged over all loci at which an individual was scored (Coulson *et al.* 1998; Pemberton *et al.* 1999; Slate *et al.* 2000) such that

$$\text{mean } d^2 = 1/n \sum (i_a - i_b)^2,$$

where i_a and i_b are the lengths in repeat units of alleles a and b at locus i , and n is the total number of loci. The mean heterozygosity was determined as the proportion of typed loci for which an individual was heterozygous while standardizing for the heterozygosity at any given locus (Coulson *et al.* 1998; Slate *et al.* 2000). We chose not to standardize the mean d^2 , as this enhances the contribution of less variable loci on mean d^2 , whilst reducing the contribution of highly variable loci. For example, if the relationship between locus-specific variance in mean d^2 and number of alleles at each locus is exponential, as in black grouse, standardization for locus-specific variance overemphasizes the contribution of loci with a few alleles (J.H. and J. Dannewitz, unpublished data).

(c) Statistical analyses

The relationship between LCS and other traits described in §2b were analysed using generalized linear models (McCullagh & Nelder 1989). In all models, we used a Poisson error structure and a log-link function because the large number of males with LCS = 0 violates the assumptions of standard linear regression. All analyses were performed using GENSTAT, v. 4.1 (Genstat 5 Committee 1993).

3. RESULTS

A total of 139 males were genotyped at 11.3 ± 3.3 (mean \pm s.d.) microsatellite loci. Males with data from seven loci or less were excluded from the analysis. For all individuals, both mean d^2 and mean heterozygosity were positively related to LCS, although only the former was significant (mean $d^2 \chi_1^2 = 18.81$, $p < 0.001$; heterozygosity $\chi_1^2 = 3.78$, $p = 0.052$).

Assuming that male black grouse need to obtain a territory to become a member of the reproducing population, we examined whether there were any differences in the genetic variables between males that were observed as permanent territory holders during at least one reproductive season, and those that were never observed on territories.

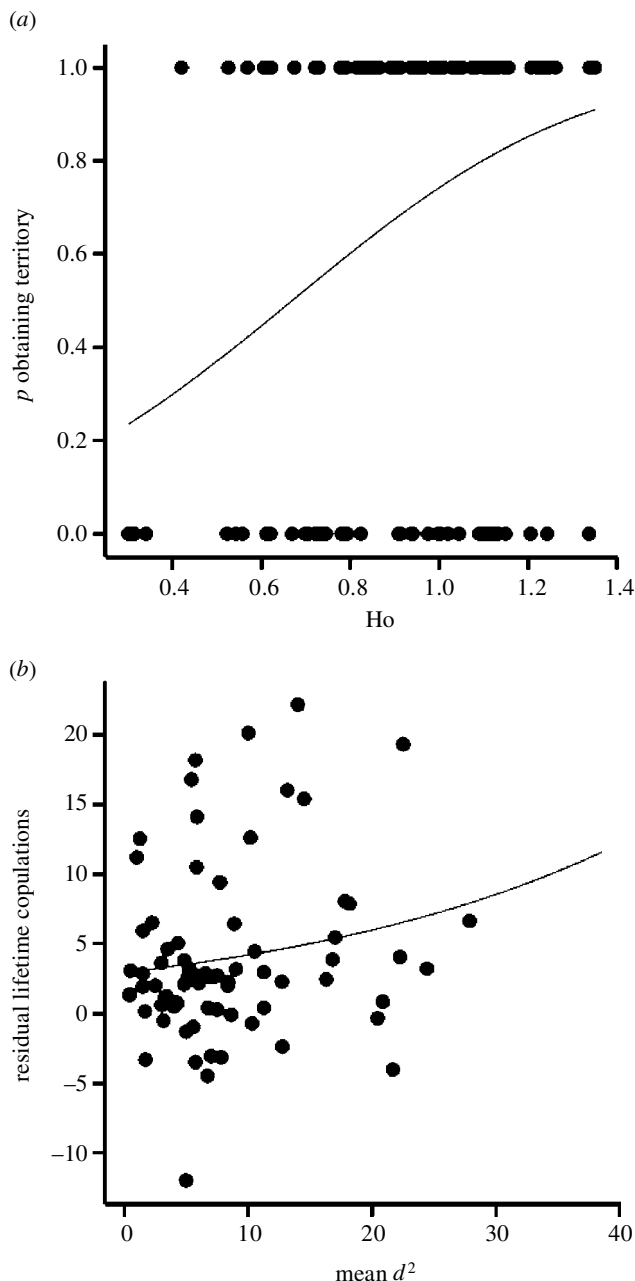


Figure 1. (a) Territoriality (data points: 0, never observed on a territory; 1, observed on a territory at least once during lifetime) against mean standardized heterozygosity, Ho. The fitted relationship is the predicted outcome of the logistic regression $E(\text{Territorial} | \text{Ho}) = -1.73 + 2.68 \text{ Ho}$. (b) Residual lifetime copulation success (when the effects of territorial centrality, longevity and attendance are controlled for) plotted against mean d^2 .

In this analysis, we only included males from the main part of the study area where we had complete data on male territoriality. Therefore, this is a conservative test as some of the males that were assigned as non-territorial may have dispersed out of the study area and have occupied territories where we could not observe them. There was no effect of mean d^2 on the probability of territory ownership (logistic regression: $F_{1,101} = 1.44$, n.s.) but a significant effect of mean heterozygosity (logistic regression: $F_{1,101} = 2.51$, $p = 0.012$, figure 1a).

Table 1. Full general models of lifetime copulation success in male black grouse. In the first model (a), we used mean d^2 as the genetic variable (mean deviance ratio = 59.48, d.f. = 4, 43, $p < 0.001$). In the second model (b), we used mean heterozygosity (mean deviance ratio = 37.79, d.f. = 4, 43, $p < 0.001$).

term	<i>t</i>	<i>p</i>
(a)		
attendance	4.92	<0.001
territorial centrality	-3.23	<0.001
longevity	3.08	0.002
mean d^2	4.69	<0.001
(b)		
attendance	4.70	<0.001
territorial centrality	-4.37	<0.001
longevity	2.39	0.017
mean heterozygosity	0.81	n.s.

Table 2. Relationships between genetic variables ((a) mean d^2 , (b) mean heterozygosity) and other variables explaining a significant proportion of the variance in lifetime copulation success for territorial males. $N = 43$ in all cases.

term	<i>t</i>	<i>p</i>
(a)		
attendance	1.43	n.s.
territorial centrality	-3.84	<0.001
longevity	2.34	0.019
(b)		
attendance	0.27	0.785
territorial centrality	1.89	0.059
longevity	0.72	0.474

For males that achieved territorial status in the main study area, we ran generalized multiple regression models to examine the effect of the genetic variables together with other sources of variance in LCS. Male attendance at the lek, a measure of territorial centrality, longevity and mean d^2 all independently explained some of the variance in LCS, but we could not detect any significant residual effect of mean heterozygosity (figure 1b, table 1). The only variables that were significantly correlated with any of the genetic variables were territorial centrality and longevity, which were significantly correlated with mean d^2 (table 2). Mean d^2 and heterozygosity were positively correlated but the relationship levelled off at high values of mean d^2 (figure 2), such that the variance among the data was significantly better explained by a logarithmic relationship than by a linear relationship ($p < 0.001$ and n.s., respectively).

4. DISCUSSION

We have established that, among male black grouse, an individual's position on the inbreeding-outbreeding continuum affects reproductive fitness. Overall, LCS was positively correlated with both mean d^2 and heterozygosity, and those males that were successful in securing a territory on a lek at least once during their lifetime had a higher heterozygosity than males that never obtained a territory. Moreover, among territorial males, those found

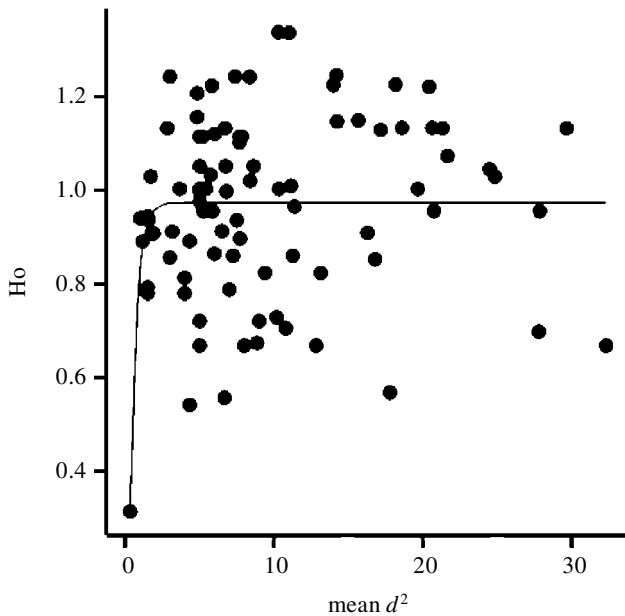


Figure 2. Mean heterozygosity (H_o) plotted against mean d^2 . The fitted line is the predicted relationship from $H_o = 0.97 - 1.09 \times 0.14 \text{ mean } d^2$, $F_{2,117} = 8.14$, $p < 0.001$.

on central, and hence more successful, territories had a higher mean d^2 . As increasing heterozygosity and mean d^2 reflect a higher degree of outbreeding, our results indicate that more inbred individuals have reduced competitive abilities. As the majority of studies that have detected detrimental inbreeding effects have tended to focus on early life-history stages (Ralls *et al.* 1988; Lacy *et al.* 1993; Crnokrak & Roff 1999), and we did not examine fertilization success, embryo mortality or the relative success of chicks and juveniles, the importance of inbreeding in defining the overall fitness of individual black grouse may be even more pronounced.

The competitive interactions between black grouse at a lek are designed to advertise their fitness to potential mates (Alatalo *et al.* 1991). A demonstration that the highest reproductive success is associated with reduced inbreeding highlights that these advertisements are honest and reflect a component of overall genomic quality rather than just single-locus effects. In this case, the positive associations between mean d^2 , heterozygosity and LCS seem to be mediated through an effect on territoriality. Meagher *et al.* (2000) highlighted the reduced competitive ability of more inbred mice in agonistic interactions during territory establishment. Given the intense competition for territory acquisition that has been observed in black grouse (Höglund & Alatalo 1995), a similar effect is entirely plausible.

One particular concern over the use of mean d^2 to measure an individual's position in the inbred–outbred continuum is the lack of congruence between associations of fitness with the mean d^2 and heterozygosity. Hedrick *et al.* (2001) examined the predictive power of both heterozygosity and mean d^2 for measuring levels of inbreeding in a captive population of wolves (*Canis lupus*) of known pedigree. They found that the mean d^2 was less predictive of the known inbreeding coefficient than heterozygosity, and hence carried no more information than heterozygosity about the levels of inbreeding or outbreeding. They

therefore state that it is unclear whether studies that find fitness associations with mean d^2 , especially in the absence of association with heterozygosity, are a reflection of high statistical power rather than biological reality. By contrast, Coulson *et al.* (1998) suggested that differences are due to the mean d^2 reflecting processes associated with heterosis following population admixture, whereas heterozygosity provides an indication of the negative effects of inbreeding depression.

In black grouse, the acquisition of a territory is essential for recruitment to the adult population and subsequent reproductive potential. As we found an association between ability to get a territory and heterozygosity, this means that individuals with low heterozygosity are automatically excluded from subsequent examination of fitness effects on LCS (lower left portion of figure 2). As such, a low level of variation in heterozygosity among territory holders makes it difficult to find significant association with other fitness parameters measured subsequently. By contrast, there is still considerable variation in the mean d^2 among territory holders, and hence more scope for detecting fitness associations. We feel that this is a more probable explanation for a lack of congruence between heterozygosity and mean d^2 for measuring fitness associations among territory holders, rather than inferring that inbreeding depression affects fitness prior to territory acquisition, and that heterosis underpins LCS.

As with the majority of bird species, male black grouse are philopatric, whereas females display natal dispersal (Willebrandt 1988; Höglund *et al.* 1999). This creates a socially induced population structure with related males and unrelated females (Sugg *et al.* 1996). As such, the only potential for incestuous breeding occurs if females reproduce with their sons in subsequent years. The observation that two-year-old, or older, females mate with their mate from the previous year if he is still alive (Rintamäki *et al.* 1995) suggests a possible inbreeding avoidance mechanism. However, as male mortality can be high and inbreeding effects were observed in this study, some females may have been forced to mate with relatives or face yet another dispersal phase. Future studies should address whether females have more subtle mechanisms for inbreeding avoidance, such as disassortative mating based on parasite resistance (Coltman *et al.* 1999) and immunocompetence genes (Penn & Potts 1999; Grahn 2000).

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