Genetic similarity and hatching success in birds

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The ecological correlates of fitness costs of genetic similarity in free-living, large populations of organisms are poorly understood. Using a dataset of genetic similarity as reflected by band-sharing coefficients of minisatellites, we show that bird species with higher genetic similarity experience elevated hatching failure of eggs, increasing by a factor of six across 99 species. Island distributions and cooperative breeding systems in particular were associated with elevated genetic similarity. These findings provide comparative evidence of detrimental fitness consequences of high genetic similarity across a wide range of species, and help to identify ecological factors potentially associated with increased risk of extinction.

Keywords: birds; comparative analysis; cooperative breeding; genetic similarity; hatching success; minisatellites

1. INTRODUCTION

High degrees of genetic similarity among adults should result in higher levels of reproductive failure owing to the effects of deleterious alleles (Charlesworth & Charlesworth 1987; Roff 1997). These fitness costs include increased risks of spontaneous abortion, reduced offspring survival and reduced mating success of offspring (Ralls *et al.* 1979; Saccheri *et al.* 1998; Crnokrak & Roff 1999). In the extreme case of breeding between close relatives, such reductions in fitness are known as inbreeding depression (Charlesworth & Charlesworth 1987; Roff 1997). Levels of inbreeding are usually considered to be low in large populations (Charlesworth & Charlesworth 1987) because the probability of two closely related individuals being in the same location at the time of reproduction is low. Field estimates of the negative fitness effects of genetic similarity are often based on isolated populations, such as those on islands (Ralls *et al.* 1979; Keller *et al.* 1994; Slate *et al.* 2000). Such populations generally have limited possibilities for dispersal, providing restricted opportunities for mating with unrelated individuals and hence for avoidance of inbreeding. Whether similar phenomena apply to large populations that have not passed through equally severe population bottlenecks and where the choice of partners is less constrained remains largely unknown (Crnokrak & Roff 1999; Hedrick & Kalinowski 2000; Keller & Waller 2002), and there is a need to search for general patterns in the incidence of fitness costs of elevated genetic similarity (Keller & Waller 2002).

In birds, one of the best-established fitness costs of elevated genetic similarity is a high proportion of hatching failure, involving eggs that are not predated or deserted during incubation but fail to hatch owing to infertility or embryo mortality. Average hatching success across birds is *ca.* 90% of eggs laid (Koenig 1982), but there is substantial variation among species. Elevated hatching failure is a common characteristic of endangered or insular species with small population sizes (e.g. Pletschet & Kelly 1990; Jamieson & Ryan 2000). Clear relationships between increased genetic similarity between pair members and hatching failure have also been demonstrated in isolated populations of common and widespread species (van Noordwijk & Scharloo 1981; Bensch *et al.* 1994; Keller 1998) and in rare incidences of inbred matings in outbred populations (Kruuk *et al.* 2002; but see Kempenaers *et al.* 1996). Yet, whether hatching failure is also pervasive in non-incestuous matings within outbred populations remains unknown.

First, we use a comparative analysis to test the prediction that high levels of genetic similarity among adults, as estimated from minisatellite molecular markers (Wetton *et al.* 1987; Reeve *et al.* 1990; Hoelzel 1992; Papangelou *et al.* 1998), are associated with reduced hatching success in birds. Because estimates of genetic similarity were extracted largely from the paternity literature, most species were well-studied, common and widespread; some, however, are well-known models in studies of inbreeding depression (e.g. *Picoides borealis*, *Loxioides bailleui*) and were disproportionately represented among those species with exceptionally high (greater than 0.5) band-sharing values. Hence, to avoid any bias caused by known rare or declining species, we repeat all analyses excluding species listed as threatened (six species) or endangered (one species) in BirdLife International (2000). We also repeat analyses with island-dwelling species (six species, of which four are threatened or endangered) removed to preclude any bias introduced by atypical conditions on islands. Second, we determine ecological factors associated with high levels of genetic similarity to identify taxa that are likely to suffer the most from the negative fitness consequences of reduced genetic variability. Third, we test whether any deleterious effects of elevated genetic similarity may be counterbalanced by life history. Because genetic variability is expected to be related to population size and hence inversely related to adult survival and body mass, any reductions in hatching success might be relatively less important for species with long-lived life histories involving many possible breeding attempts. We test

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this by examining the relationship between hatching success and body mass, which has repeatedly been shown to be positively related to adult survival (e.g. Lindstedt & Calder 1981; Saether 1989; Brawn *et al.* 1995). If life history has the potential to alleviate the consequences of hatching failure, then we expect negative relationships between body mass and band-sharing, and between body mass and hatching success.

2. MATERIAL AND METHODS

Information on genetic similarity and hatching success was obtained from an extensive search of the paternity literature on birds (dataset and sources are reported in electronic Appendix A, available on The Royal Society's Publications Web site). Genetic similarity was estimated as the band-sharing coefficient between adults in a population (usually dyads of pair members, but in cases where dyads of random adults in the population were also compared results were very similar), which is an estimate of the number of shared minisatellite bands in relation to the total number of bands among adults (Wetton *et al.* 1987). A high band-sharing coefficient implies that many bands are shared among unrelated individuals and hence that the genetic similarity in the population is relatively high. Band sharing has been used extensively as a measure of genetic similarity among individuals within a species (e.g. Reeve *et al.* 1990; Hoelzel 1992; Blomqvist *et al.* 2002). In this study, we use species-specific mean band-sharing values for comparative purposes. This is supported firstly by the highly significant repeatability (Becker 1984) of band-sharing coefficients among studies of the same species using the same probe, based on 25 studies of nine species in the present dataset ($R = 0.55$ (s.e. $= 0.20$), $F = 3.90$, d.f. $= 8,16$, $p = 0.0099$). Though the relatively low statistical power of the test should be borne in mind, this result suggests that band-sharing estimates are consistent between populations of the same species. Second, a review of 129 published studies of 70 species has shown that mean band sharing between dyads of unrelated individuals from populations or species defined as outbred on the basis of independent evidence was *ca.* 50% lower than that for populations defined as small or inbred (Papangelou *et al.* 1998). Furthermore, mean band sharing between dyads of unrelated individuals in small or inbred populations was similar to that for dyads of first-order relatives in outbred populations (Papangelou *et al.* 1998). This implies that mean band-sharing coefficients of populations consistently reflect whether there is a high degree of genetic similarity within a species, and that these estimates are likely to be comparable among species.

Between one and three fingerprinting probes were used per study, with different studies using different probes (largely probe numbers 33.15 and 33.36, but also per, M13 and others), potentially causing heterogeneity among analyses. Multiple probes were employed in cases where paternity exclusion could not be achieved with fewer probes. However, the repeatability of band-sharing coefficients among probes used in the same study, based on 47 studies of 20 species, was highly significant ($R = 0.86$ (s.e. $= 0.06$), $F = 17.16$, d.f. $= 19,27$, $p < 0.0001$), suggesting that multiple probes should not introduce bias with respect to the hypotheses under test. If anything, multiple probes should have the effect of decreasing band sharing in species with little genetic variability, hence rendering our test conservative.

Hatching success was estimated as the proportion of eggs incubated to term that hatched, thus excluding hatching failure

owing to nest desertion and nest predation. Many published estimates of hatching success do not make this distinction, and unless hatching success was explicitly defined as above, we only included estimates confirmed by the authors to conform to our definition. Although band-sharing and hatching success estimates sometimes derived from different populations, any related inconsistencies should only make our findings conservative with respect to the hypothesis under test.

We investigated the relationship between hatching success and band-sharing coefficients using the software CAIC (Purvis & Rambaut 1995), assuming a gradual model of evolution to estimate branch lengths (Grafen 1989). This software allows tests of the hypothesis that two continuous characters coevolve, while taking the phylogenetic relationships between species into account. In multivariate analyses, cooperative breeding and coloniality scores were treated as continuous, as intermediate states are biologically meaningful. For bivariate analyses involving cooperative breeding and island distributions, CAIC's BRUNCH algorithm for discrete variables was used. The hatching success estimates and band-sharing coefficients were square-root arcsine-transformed before analysis. For the analyses, we used a composite phylogenetic hypothesis, reported in electronic Appendix B and mainly based on Sibley & Ahlquist (1990) and Barker *et al.* (2002). Tests of the statistical and evolutionary assumptions of the continuous comparative procedure (Garland *et al.* 1992) revealed, in some cases, significant negative relationships between absolute standardized contrasts and their standard deviations, and positive ones with their estimated nodal values. To reduce the consequent problem of heterogeneity of variance, (i) two outliers (contrasts with Studentized residuals of greater than 3) were excluded from subsequent analyses (Jones & Purvis 1997); and (ii) analyses were repeated with the independent variable expressed in ranks. In neither instance did these analyses change any conclusions.

Species were classified as mainland-living or as island endemics (restricted to a single island or archipelago), as solitary or colonial (if ever colonially breeding), and as having a cooperative or other breeding system based on information in handbooks, mainly Cramp *et al.* (1977–1994) and Poole & Gill (1992–2002). Koenig (1982) found that social species and species with cooperative breeding have reduced hatching success. Body mass (mean of male and female masses where these differed) was also obtained from handbooks, principally Dunning (1993), and was $\log_{10}$-transformed.

3. RESULTS

Average hatching success was 89.1% (s.e.m. $= 0.86$, range of 45–100.0%) across 99 species. Average band sharing was 0.246 (s.e.m. $= 0.012$, range of 0.051–0.685), where the expected band-sharing between first-order relatives is $0.50 \times (1 + \text{band-sharing})$ and between second-order relatives is $0.25 \times (1 + \text{band-sharing})$. Hatching success was significantly negatively correlated with band-sharing coefficients across species (figure 1*a*; $F = 22.52$, d.f. $= 1,97$, $R^2 = 0.188$, $p < 0.001$, slope(s.e.) $= -0.423$ (0.089)). This relationship was similar when calculations were based on phylogenetically independent contrasts (Purvis & Rambaut 1995; Grafen 1989) (figure 1*b*; $F = 24.56$, d.f. $= 1,94$, $R^2 = 0.207$, $p < 0.001$, slope(s.e.) $= -0.389$ (0.078)). According to the linear regression based on species, hatching success decreased from 96.2% to 76.0% across the range of band-sharing coefficients.
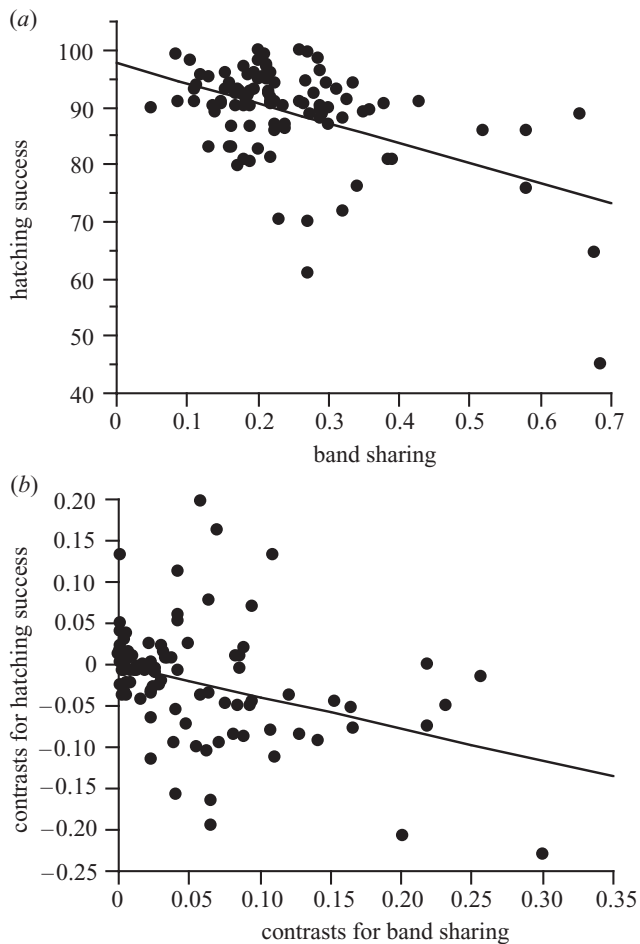
Figure 1. Hatching success (%) in birds in relation to band-sharing coefficients based on minisatellites. (*a*) Species-specific values as data points. (*b*) Statistically independent contrasts as data points. The lines are the regression lines with the equations (*a*) $y = 97.69 - 34.97x$ and (*b*) $y = -0.389x$. Note that (*a*) is plotted on untransformed axes for ease of interpretation; transformation reduced heteroscedasticity, and results were also qualitatively unchanged if Spearman rank correlation was instead applied ($r_S = -0.331$, $p = 0.0008$). Similarly, exclusion of the data point at the bottom right of (*b*) affected neither the significance nor the direction of the regression line.

After removing the seven species recognized as threatened or endangered (BirdLife International 2000), the relationship between band sharing and hatching success remained qualitatively unchanged when considering either species ($F = 11.48$, d.f. = 1,90, $R^2 = 0.113$, $p = 0.001$, slope(s.e.) = -0.327 (0.096)) or contrasts ($F = 24.50$, d.f. = 1,86, $R^2 = 0.222$, $p < 0.001$, slope(s.e.) = -0.392 (0.079)) as independent data points. Similarly, conclusions were unchanged after removing the six island-endemic species (species: $F = 6.42$, d.f. = 1,91, $R^2 = 0.066$, $p = 0.013$, slope (s.e.) = -0.252 (0.099)); contrasts: $F = 12.60$, d.f. = 1,87, $R^2 = 0.127$, $p < 0.001$, slope(s.e.) = -0.288 (0.081)).

Cooperatively breeding species had an average band-sharing coefficient of 0.340 (s.e.m. = 0.045, $n = 17$), whereas species with other mating systems had an average band-sharing coefficient of 0.227 (s.e.m. = 0.010, $n = 82$), and this was confirmed in an analysis taking phylogenetic similarity into account, using CAIC's BRUNCH method for discrete variables ($F = 7.07$, d.f. = 1,12, $R^2 = 0.37$,

$p = 0.021$). Similarly, island populations had higher band-sharing coefficients than mainland populations (islands: 0.453 (s.e.m. = 0.090), $n = 6$, mainland: 0.233 (s.e.m. = 0.010), $n = 93$). A lack of statistical power precluded a BRUNCH analysis with this dataset; however, a pairwise comparison of sister taxa with island and continental distributions has already revealed higher band sharing in island taxa (Møller 2001).

Breeding sociality and cooperative breeding have previously been shown to be associated with reduced hatching success (Koenig 1982) and are potentially confounding. In this study, cooperative breeding was again found to be significantly associated with reduced hatching success (BRUNCH: $F = 6.42$, d.f. = 1,12, $R^2 = 0.35$, $p = 0.026$), but a multiple linear regression with hatching success as the dependent variable and band-sharing coefficient, cooperative breeding and coloniality as independent variables only revealed a significant effect for band sharing (table 1*a*). Hence, the effect of genetic similarity on hatching success was statistically independent of these ecological factors.

Hatching success was weakly positively related to body mass, though this relationship only became statistically significant after controlling for phylogenetic similarity (species as data points: $F = 0.05$, d.f. = 1,97, $R^2 < 0.001$, $p = 0.83$; independent contrasts as data points: $F = 5.52$, d.f. = 1,93, $R^2 = 0.056$, $p = 0.021$, slope(s.e.) = 0.087 (0.037)). A weak positive relationship was detected in a species regression between band sharing and body mass, but this disappeared after taking phylogeny into account (species: $F = 4.28$, d.f. = 1,97, $R^2 = 0.042$, $p = 0.041$, slope(s.e.) = 0.037 (0.18); independent contrasts: $F = 0.05$, d.f. = 1,95, $R^2 < 0.001$, $p = 0.816$). When body mass was entered into a multiple regression with ecological factors, the conclusions remained unchanged (table 1*b*).

Finally, if deleterious recessive alleles causing infertility have been removed by selection in species with high band sharing, we would expect relatively high hatching success in such species and hence nonlinearity in the relationship plotted in figure 1. However, there is no evidence that this relationship is nonlinear (second-order polynomial regression, based on species, model: $F = 13.49$, d.f. = 2,96, $R^2 = 0.219$, $p = 0.001$, band sharing: $F = 1.05$, $p = 0.308$, band sharing squared: $F = 3.81$, $p = 0.054$; based on contrasts, model: $F = 12.35$, d.f. = 2,93, $R^2 = 0.210$, $p < 0.001$, band sharing: $F = 2.18$, $p = 0.143$, band sharing squared: $F = 0.33$, $p = 0.566$).

4. DISCUSSION

This study shows that high levels of genetic similarity are associated with reduced hatching success across a wide range of bird species, even when breeding may not occur among close relatives. Across the range of band-sharing coefficients encountered in different species of birds, hatching failure was predicted to increase from 3.8% to 24.0%, an increase by a factor of six. This is a serious fitness cost. The effect of genetic similarity on hatching success was statistically independent of the potentially confounding effects of breeding sociality and cooperative breeding, which had previously been suggested to be associated with hatching success (Koenig 1982), and of any

Table 1. Predictors of hatching success in birds.
(Multiple linear regressions with square-root arcsine-transformed hatching success as the dependent variable, and as independent variables in (*a*) square-root arcsine-transformed band-sharing coefficient, and untransformed cooperative breeding and coloniality scores. In (*b*), body mass is also included in the model. Independent observations used in the calculations are contrasts, and regression is hence through the origin.)

independent variable	F	slope (s.e.)	p
(*a*) model: $F = 9.40$, d.f. $= 3{,}92$, $R^2 = 0.235$, $p < 0.0001$			
band-sharing coefficient	15.68	-0.337 (0.085)	< 0.001
cooperative breeding	3.22	-0.061 (0.034)	0.076
coloniality	0.17	-0.017 (0.042)	0.683
(*b*) model: $F = 8.20$, d.f. $= 4{,}91$, $R^2 = 0.265$, $p < 0.0001$			
band-sharing coefficient	15.62	-0.331 (0.084)	< 0.001
body mass	3.74	0.069 (0.036)	0.056
cooperative breeding	5.13	-0.079 (0.035)	0.026
coloniality	0.33	-0.024 (0.042)	0.568

potential bias introduced by studies of known threatened species and of island endemics. Hence, certain species of birds live under conditions that reduce their hatching success considerably. The linear relationship demonstrated in this study also implies that genetic purging (Waller 1993) has not generally reduced the deleterious effects of elevated genetic similarity in birds.

How can free-living populations with high genetic similarity be maintained? Species with high band-sharing coefficients often have cooperative breeding systems or island distributions (this paper and Møller 2001). Elevated levels of genetic similarity on islands are likely to arise as a consequence of genetic bottlenecks during establishment, subsequent inbreeding and reduced dispersal (see Grant 1998 for a review). However, genetic bottlenecks are an unlikely explanation for the observation that cooperative breeders exhibited elevated levels of band sharing, given that the majority of cooperative species included in this study are common and widespread. This suggests that bottlenecks alone cannot account for the variation in genetic similarity reported in this study, or for the diversity of species in which this is associated with hatching success. Dispersal, particularly sex-biased dispersal (Greenwood 1980), is a mechanism that reduces genetic similarity among individuals within a population (Clobert *et al.* 2001). Among cooperative breeders, constraints on dispersal owing to habitat limitation, in association with increased variance in reproductive success among individuals owing to high adult survival and overlap of generations, may be responsible for decreasing effective population size (Nunney 1991) and hence genetic diversity independently of any recent changes in census population size. High adult survival may also be a mechanism contributing to elevated genetic similarity in non-cooperative species that have not undergone dramatic population reductions, implying that levels of genetic similarity are not merely related to recent population size changes, but also to evolutionary history.

Might life history ameliorate the deleterious effects of high genetic similarity? If there is variance in hatching success among the breeding attempts of a single female, a given increase in hatching failure might entail a substantial change in fitness for a small, short-lived passerine, but only a small change for a large, long-lived species (e.g. a

Procellariiform seabird) in which such an effect might be absorbed by the large number of possible breeding attempts. Given that genetic diversity is expected to be related to population size and hence be lower in larger, longer-lived species, those species experiencing low hatching success might perhaps suffer least from its negative effects. However, this was clearly not the case: we took body mass to be a proxy of adult survival (Lindstedt & Calder 1981; Saether 1989; Brawn *et al.* 1995) and, contrary to the prediction above, found a weak positive relationship between body mass and hatching success. Hence, species with 'slow' life histories do not appear to be those that suffer most from hatching failure. Genetic effects on hatching failure are also likely to be consistent between clutches (e.g. Kempenaers *et al.* 1996). If this is the case, all a pair's broods should show a similar effect, and there would hence be no fitness differences between longer- and shorter-lived species, perhaps depending on patterns of divorce among years. This suggests that those species experiencing the highest levels of proportional hatching failure are likely to suffer a real fitness cost as a result. The fitness consequences of hatching failure may also be lessened if surviving fledglings benefit from decreased clutch sizes through improved parental care. However, brood size manipulation experiments typically show no enhancement in recruitment per brood from artificially reduced broods relative to broods of natural size (e.g. Gustafsson & Sutherland 1988), suggesting that viability of surviving offspring is unlikely to compensate for reduced brood sizes owing to hatching failure.

This study has identified an important general fitness consequence of elevated genetic similarity in birds, in particular in cooperatively breeding species and in species endemic to islands. Such species are also likely to suffer from other negative effects of reduced genetic variability and inbreeding. In view of these costs, it may be informative to examine inbreeding avoidance mechanisms such as sex-biased dispersal and kin recognition in relation to hatching success, once these data become available for sufficient species. It is also possible that reduced hatching success in populations with high degrees of genetic similarity has conservation consequences, and that even certain species with large mainland populations may run elevated risks of extinction because of high rates of

hatching failure. High levels of hatching failure are also important for studies of life history because analyses of optimal clutch size and comparative life-history studies attempt to assess the adaptive significance of clutch size (Roff 1992; Stearns 1992), even when a significant proportion of such clutches does not hatch.

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