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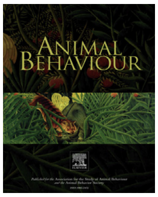

Maternal inbreeding reduces parental care in the zebra finch, *Taeniopygia guttata*

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Increased embryo mortality is the most commonly cited cause of reduced fitness in inbred organisms. Reduced embryo survival may be the result of reduced parental expenditure by inbred individuals and here we tested the hypothesis that inbreeding results in impaired incubation behaviour in captive zebra finches. We compared incubation attentiveness of inbred female zebra finches (derived from full-sibling mating) with that of control females (derived from unrelated parents) and found a statistically significant inbreeding depression of 17% in incubation attentiveness. This shows that inbreeding can significantly influence parental behaviour. Despite a reduction in the amount of time inbred females spent incubating, their partners were able to compensate for the reduced incubation attentiveness. Incubation temperature also did not differ between inbred and control females. To test for the effect of incubation behaviour, we fostered eggs laid by control females to either inbred or control females at the end of laying. Eggs that were incubated by inbred females had an 8.5% lower hatching success than eggs incubated by control females and, although based on a relatively small sample and not statistically significant, the magnitude of the difference was consistent with differences in hatching success observed in the wild under relatively benign environmental conditions. Thus, under more challenging environmental conditions usually encountered in the wild, the reduced incubation attentiveness of inbred females could provide one proximate explanation for the consistent finding of decreased hatching success with increasing maternal inbreeding in birds.

Inbreeding depression is the deleterious effect on fitness resulting from mating between relatives. Under natural conditions inbreeding depression can be biologically significant and it is important to consider it in evolutionary and conservation biology (Crnokrak & Roff, 1999; Keller & Waller, 2002). Severe inbreeding can ultimately lead to the extinction of small isolated populations (Saccheri, Kuussaari, Kankare, Vikman, & Hanski, 1998). Inbreeding increases genetic homozygosity and inbreeding depression is thought to occur mainly because of the unmasking of rare deleterious alleles, although reduced heterozygous advantage may also contribute (Charlesworth & Willis, 2009). Inbreeding may affect fitness in two ways (Margulis, 1998; Mattey, Strutt, & Smiseth, 2013). First, a mating between relatives can affect traits expressed by the offspring and lead to a reduction in fitness of the inbred offspring themselves (offspring inbreeding). Second, in species in which offspring depend on parental care, fitness of outbred offspring can also be reduced by some behavioural or physiological deficits in inbred parents (parental or intergenerational inbreeding). Although there are some examples of intergenerational inbreeding in which inbreeding of parents can have a detrimental effect on offspring fitness in birds, mammals, fish and insects (Jimenez, Hughes, Alaks, Graham, & Lacy, 1994; Keller, 1998; Mattey et al., 2013; van Noordwijk & Scharloo, 1981; Richardson, Komdeur, & Burke, 2004; Slate, Kruuk, Marshall, Pemberton, & Clutton-Brock, 2000; Szulkin, Garant, McCleery, & Sheldon, 2007) many studies of inbreeding depression confound offspring deficiencies with deficiencies in parental behaviour and physiology (Margulis, 1998) and the intergenerational effects have so far received very little attention (Mattey et al., 2013, but see Margulis, 1998). Careful consideration of the way in which inbreeding influences reproductive behaviour and physiology is essential, however, to assess the impact of inbreeding on populations (Margulis, 1998; Mattey et al., 2013).

A consistently reported deleterious effect of parental inbreeding is the reduced survival of embryos of inbred females as observed in birds, mammals, fish and insects, even if mothers are paired with an unrelated mate such that offspring heterozygosity is not reduced (e.g. Cordero, Aparicio, & Veiga, 2004; Farkas et al., 2007; Keller,

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1998; Margulis & Altmann, 1997; Marr, Arcese, Hochachka, Reid, & Keller, 2006; Mattey et al., 2013; Moura, Polastre, & Wechsler, 2000; van Noordwijk & Scharloo, 1981; Pulkkinen, Van Der Lende, Groen, Kaal, & Zonderland, 1998; Sittmann, Abplanalp, & Fraser, 1966; Su, Liljedahl, & Gall, 1996). The underlying causes of maternally mediated intergenerational inbreeding effects on embryo viability have not been identified, but could include deficiencies in the behaviour and physiology of the parents that detrimentally influence the inbred parent's capacity to raise young. Effects of inbreeding on embryo viability have been studied particularly in birds in which reduced egg quality (caused by reduced provisioning of the egg), reduced parental care in supporting development or a combination of the two can contribute to the poorer hatching success of inbred parents (for references see above). Inbred female birds can produce smaller eggs than control females (Sewalem, Johansson, Wilhelmson, & Lillpers, 1999; Sittmann et al., 1966; Wetzel, Stewart, & Westneat, 2012) and offspring from smaller eggs can have a reduced fitness (reviewed in Kirst, 2011; Williams, 1994). Avian parents must also actively maintain favourable conditions for optimal embryo development (Webb, 1987) which can be expensive in terms of both energy and time (reviewed in Reid, Monaghan, & Nager, 2002; Tinbergen & Williams, 2002). Thus incubation expenditure can be influenced by the parent's energy balance, body condition and food availability (Bryan & Bryant, 1999; Eikenaar, Berg, & Komdeur, 2003; Gorman & Nager, 2003; Reid et al., 2002). As inbred individuals may be in poorer condition (Jimenez et al., 1994; Knaepkens et al., 2002) or have less energy available to spend on other than self-maintenance activities (Ketola & Kotiaho, 2009) compared with outbred individuals, their capacity to expend resources on incubation expenditure could be lower than in outbred individuals. Low parental incubation expenditure can result in slower embryo development, birth defects due to homozygosity of deleterious alleles, increased bacterial growth in the egg and even embryo mortality (Cook, Beissinger, Toranzos, & Arendt, 2005; Tinbergen & Williams, 2002; Webb, 1987). The effects of parental inbreeding on parental care such as incubation expenditure have, however, so far been largely neglected (Mattey et al., 2013; but see Margulis, 1998).

In this study, we explored the relationships between parental inbreeding, parental behaviour and offspring viability in zebra finch females in a captive population. We compared incubation behaviour and incubation success between inbred and control females. To separate the effects of parental and offspring inbreeding we cross-fostered eggs between pairs with inbred and control females. We predicted that inbred females paired to unrelated, outbred males would spend less time incubating eggs (lower incubation attentiveness) and/or maintain eggs at a lower temperature than in pairs with control females. Because in zebra finches both parents incubate (Zann & Rossetto, 1991), we also tested whether males compensated for any reduction in their inbred partner's incubation expenditure. To assess the consequences of being incubated by an inbred mother on embryo survival and development, we compared hatching success and hatching mass of offspring produced by control females and incubated by either inbred or control females.

METHODS

Animals and Housing

Zebra finches used in this study were from the stock population kept at the University of Glasgow. Nonbreeding birds were kept at a density of six birds per cage (0.4 × 1.2 m and 0.4 m high, made of metal with a mesh front). Birds had access to four perches, two high and two low, of which at least half were flexible and tapered. Cage floors were covered with absorbent paper and hemp core (Law et al., 2010). All birds received a basic diet consisting of ad libitum water, grit and mixed dry seed, supplemented with vitamins, calcium and fresh organic greens once per week (for details see Hill, Lindström, & Nager, 2011). The room temperature was held at 23 ± 1 °C, relative humidity at 30–50% and photoperiod at 12:12 h light:dark using full-spectrum daylight fluorescent tubes (Arcadia Bird Lamp FB36, Redhill, U.K.). Birds were provided opportunities to bath twice a week.

Breeding of Experimental Birds

In the winter 2008/2009 we bred inbred and control zebra finch females from our stock of several hundred individuals with known pedigree since 2006; this stock is regularly replenished with birds from other populations in order to maintain genetic diversity. Inbreeding in captive zebra finches has been shown to be low and similar to that found in many wild avian populations (Forstmeier, Segelbacher, Mueller, & Kempenaers, 2007). To obtain inbred birds, we paired brothers with sisters; control birds were obtained by pairing males and females from our stock population that did not share any grandparents and supplemented with 10 females from another breeding stock brought into the stock just prior to this experiment that were assumed to be unrelated to any stock bird. We created 21 pairs of unrelated birds and 19 brother–sister pairs. Pairs of unrelated and related mates were randomly assigned to breeding cages (0.4 × 0.6 m and 0.4 m high) within the same bird room and experienced the same housing conditions and diet as described above for the stock birds. Cardboard nestboxes were attached to the outside of the cage and coconut fibres were provided ad libitum for nest building. Pairs were allowed to produce offspring between December 2008 and May 2009 and raised up to three broods in this period; females used in the inbreeding experiment come from either a first, second or very rarely a third brood of their parents and this was considered as the factor ‘brood number’ in subsequent analyses. The proportions of offspring that were derived from first, second or third broods were similar between the two groups (Fisher's exact test: $P = 0.550$). The probability of producing viable offspring (at least one chick that survived to independence at 35 days) was similar between control and inbred pairs (16 of 21 and 17 of 19 pairs produced viable offspring, respectively; Fisher's exact test: $P = 0.412$). All control and inbred birds were thus bred at the same time and under identical conditions. When they became independent at around 5 weeks of age they were separated from their parents and housed in cages (0.4 × 1.2 m and 0.4 m high) in same-sex groups of six birds until they were used in the inbreeding experiment.

Inbreeding Experiment

The daughters of the brother–sister pairs then became the inbred females (inbreeding coefficient $f = 0.25$), while those from the unrelated pairs became the control birds ($f = 0$, assuming no inbreeding in the stock population). Because these experimental birds were produced over an extended period and we wanted them to breed at a similar age, the experimental breeding rounds were conducted at two time points (July 2009 and October 2009), hereafter referred to as the first and second replicate, respectively. Based on a median inbreeding depression of 12% for life history traits (DeRose & Roff, 1999) and the observed distribution of incubation attentiveness of females in our population (mean ± SD = 62 ± 9%, Gorman & Nager, 2003; Hill et al., 2011) we calculated an expected Cohen's effect size of 0.82 (Nakagawa & Cuthill, 2007). For this effect size a sample size of 57 individuals would give a statistical power of 85% at $P = 0.05$ and we therefore decided to pair up 16 inbred and 16 control females in each of the two replicate breeding rounds