The evolution of infertility: does hatching rate in birds coevolve with female polyandry?

E. H. MORROW,* G. ARNQVIST* & T. E. PITCHER†

*Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen, Uppsala, Sweden
†Department of Zoology, University of Toronto, Toronto, Ontario, Canada

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Abstract

Natural levels of infertility in many taxa are often remarkably high, amounting to a considerable fitness cost which one expects to be minimized by natural selection. Several mechanisms have been proposed as potential causes of infertility, including inbreeding depression, genetic incompatibilities and selfish genetic elements. Infertility may also be an inherent result of conflict over fertilization between the sexes in polyandrous species, either because too many sperm enter the egg or because of over-efficient barriers to such polyspermic fertilizations. We generated phylogenetic independent contrasts to examine the variation in hatching success for a maximum of 58 species of birds in relation to two measures of female polyandry. Hatching success varied enormously across species (range: 61–100%), with a mean of 12% of eggs failing to hatch, but was not related to either the rate of extrapair paternity or to relative testes size. Thus, the causes of this significant fitness cost remains unclear and merits further examination by evolutionary biologists.

Introduction

The rate of infertility in natural animal populations is often remarkably high. Reviews of a wide variety of animal taxa show that an average of about 15% of the eggs produced fail to hatch (Koenig, 1982; Anderson, 1990; Eberhard, 1996). Despite the obvious fact that such high rates of zygote wastage constitutes a substantial fitness cost, primarily to the sex which invests most in gamete production, infertility as a phenomenon has not received much attention from evolutionary biologists. Hence, our understanding of the evolution of infertility is currently limited, and we know little about why the rates of developmental failure in natural populations are so high despite presumably strong selection for maximized fertility. The fact that fertility rates in some species are near 100% implies that infertility does not simply result from inexorable evolutionary constraints. Infertility may, in theory, result from several proximate mechanisms (see Table 1), of which some invoke genetic compatibilities between gametes and others rely on antagonistic coevolution between egg and sperm.

Correspondence: Edward H. Morrow, Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden.
Tel.: +46 18 4716486; fax: +46 18 4716484;
e-mail: ted.morrow@ebc.uu.se

Inbreeding is known to cause elevated rates of infertility in domesticated animals, primarily because of homozygous expression of recessive lethal alleles (Charlesworth & Charlesworth, 1987; Thornhill, 1993), and has thus been invoked to explain infertility also in natural populations (see Tregenza & Wedell, 2000 for a review). Although inbreeding depression is substantial in many species (see Keller & Waller, 2002 for a review), it is difficult to see how this could generally maintain the high rates of infertility observed in most natural populations. In theory, a low frequency of recessive and mildly deleterious alleles can certainly be maintained by a mutation-selection balance (Hedrick, 1994; Lande, 1995). However, strong natural selection should efficiently purge recessive lethal alleles from populations and the occurrence of individuals homozygous for these should thus be very low (Koenig, 1982; Hedrick, 1994; Lande, 1995; Tregenza & Wedell, 2000).

Several other forms of genetic compatibility between mates, or gametes, are perhaps theoretically more likely to contribute to infertility (see Zeh & Zeh, 1996; Jennions

Table 1 Main proximate causes of infertility and their putative mechanisms of evolutionary maintenance.

Proximate cause	Ultimate cause	Type	Reference
Embryo death: homozygous expression of rare recessive	Mutation–selection balance	Genetic*	Charlesworth & Charlesworth (1987), Thornhill (1993)
Embryo death: other forms of gamete 'incompatibility'	Frequency-dependent selection, selfish genetic elements	Genetic*	Zeh & Zeh (1996, 1997), Tregenza & Wedell (2000)
Embryo death: polyspermic fertilization of egg nucleus	Antagonistic coevolution between sperm and egg	Inappropriate fertilization†	Eberhard (1996), Rice & Holland (1997)
Embryo death: genetic eggs or material aberrations of eggs (production errors)	Stabilizing net selection on fertility (i.e. senescence)	Genetic/phenotypic	Rose (1991), Partridge & Mangel (1999)
Lack of fertilization of egg: female barriers against sperm	Antagonistic coevolution between sperm and egg	Inappropriate fertilization†	Eberhard (1996), Rice & Holland (1997)
Lack of fertilization of egg: sperm with poor fertilizing ability	Evolutionary conflict between mitochondrial and nuclear genes	Genetic	Gemmell & Allendorf (2001)
Inappropriate parental care	Stabilizing net selection on fertility (trade-offs)	Phenotypic	Webb (1987), Veiga (1992)

*Positive coevolution between polyandry and fertility predicted.
†Negative coevolution between polyandry and fertility predicted.

& Petrie, 2000; Tregenza & Wedell, 2000 for reviews). Such gametic compatibility may result from variation maintained by frequency dependent selection, which seems to be the case for the highly variable vertebrate major histocompatibility complex (MHC): females of several vertebrate species have also been shown to suffer increased infertility when mated with males with similar MHC haplotypes. Alternatively, infertility can be caused by genetic incompatibility because of various selfish genetic elements, such as segregation distorters, cytoplasmic parasites or maternal effect lethals.

Infertility could also result from a sexual conflict over fertilization of the egg in polyandrous species. A male mutation which confers a competitive advantage in sperm competition will spread in a population even if it compromises female interests, provided that the benefits accrued by a male in sperm competition outweighs the costs because of the lowered fitness of his mate (Parker, 1984). This proposal led Eberhard (1996) to suggest that infertility might result from sexually antagonistically coevolving male and female gametes. If sperm become overly efficient, as a result of sperm competition, the nucleus of each of a female's eggs will suffer a certain risk of being fertilized by more than one sperm. This phenomenon is known as polyspermy, and results in zygote mortality (Ginzburg, 1972). If overly aggressive sperm cause polyspermy, females are predicted to evolve barriers against aggressive sperm (Birkhead *et al.*, 1993). Such barriers would then favour (by sperm competition) even more aggressive sperm, leading to an antagonistic coevolutionary arms race between eggs to resist penetration by sperm and sperm to penetrate the egg as rapidly as possible (Rice & Holland, 1997). Under this scenario, females would be caught in a delicate evolutionary dilemma: the evolution of overly effective barriers against aggressive sperm might prevent fertilization altogether, whereas barriers that are too permissive will result in high rates of polyspermy and associated zygote mortality. Eberhard (1996) thus suggested that female infertility might at least partially represent this evolutionary 'walk on a tightrope' which females of sexually reproducing species are forced to embark upon. There are several lines of indirect support for this. For example, females of most species have evolved many molecular and structural adaptations which make it difficult for sperm to fertilize eggs (Birkhead *et al.*, 1993; Stricker, 1999) and proteins mediating sperm–egg interactions evolve very rapidly (Swanson & Vacquier, 2002). Moreover, rates of polyspermy increases dramatically when such female adaptations are circumvented (such as in *in-vitro* fertilizations and artificial uterine inseminations). Most importantly, reviews have shown that the average rates of polyspermy in natural populations are frequently as high as several percent, showing that overly aggressive sperm is clearly a problem for females of many taxa (e.g. Ginzburg, 1972). As the rate of polyspermy should also be associated with a similar sized risk of remaining unfertilized for each egg (Eberhard, 1996), antagonistic coevolution between sperm and egg could in theory maintain high rates of infertility. Other factors are known sometimes to contribute to infertility in natural populations (see Table 1), but these are more specific and are therefore not prime candidates as general explanations for the maintenance of infertility.

One important way to gain insights into the relative importance of various factors for the evolution of infertility is by the use of comparative studies (cf. Koenig, 1982). In particular, explanations based on genetic compatibility and those based on antagonistic coevolution make contrasting predictions with regards to the coevolution between infertility rate and mating system (see Table 1). Zeh & Zeh (1996, 1997) suggested that female polyandry

represents a strategy to evade the negative effects on fertility of genetic incompatibility. By mating with more than one male, females can use pre- or post-copulatory discrimination between males or sperm to minimize infertility because of fertilization by genetically incompatible sperm (see also Jennions & Petrie, 2000). If genetic incompatibility is responsible for infertility, we would therefore expect the evolution of polyandry to be associated with a lowered infertility rate (cf. Lifjeld, 1994). In contrast, if infertility is a product of sexually antagonistic coevolution, we would expect the evolution of polyandry to be associated with an elevated infertility rate (Eberhard, 1996). As no sperm competition occurs in monandrous species, it will be in the interest of both sperm and egg to maximize fertility within these species (cf. Holland & Rice, 1999; Arnqvist *et al.*, 2000). Thus, the basic sexual conflict which fuels antagonistic coevolution only exists in polyandrous species.

The current study represents an explicit comparative test of the *a priori* predictions discussed above. We test for correlated evolution between polyandry and infertility in birds, using standard comparative techniques to control the effects of common ancestry across species (Harvey & Pagel, 1991; Martins & Garland, 1991; Garland *et al.*, 1992).

Materials and methods

Sources of data

We used hatching failure as a measure of infertility, and both a direct and an indirect measure of female mating rate. A direct measure of female polyandry was provided by data on extrapair fertilization rates, obtained from the published literature. Reliable rates of extrapair paternity (EPP) have been widely used in several previous comparative studies as a measure of polyandry, and we obtained our measures of EPP from these, excluding those not published before 2001 (Westneat & Sherman, 1997; Petrie *et al.*, 1998; Griffith, 2000; Møller, 2000; Møller & Cuervo, 2000). Where possible, rates of hatching success were obtained by searching electronic databases of the published literature. However for some species, information on hatching success was either not explicitly given or not published, in these cases authors were contacted directly either for clarification or for unpublished data. A total of 149 species were found for which an estimate of the rate of EPP is at hand. Of these, data on hatching success was only available for 64 species (see Appendix). Hatching success for each species was defined as the proportion of eggs that failed to hatch relative to the total number of eggs laid, but excluding those eggs lost to predation or desertion of the nest. This precluded a great many studies because often the proportion of eggs laid and subsequently lost to predation were not distinguished from those that simply failed to hatch. As both data on the rates of EPP and hatching success are by nature proportional, they were arcsine square-root transformed prior to use in the comparative analysis (Sokal & Rohlf, 1995).

A second and indirect measure of female mating rate was estimated from data on testes size. Testes mass for each species was obtained from published compilations (Møller, 1991; Møller & Briskie, 1995; Stutchbury & Morton, 1995) or from museum specimen tags (see Acknowledgements), which consisted of testis length and width measurements. Testes mass was estimated from these measurements using Møller's (1991) corrected formula: testis mass (g) $= 2 \times 1.087$ g cm^{-3} 1.33π $[a\ (\mathrm{cm})]^2 b$ (cm), where a and b are the width and length of each testis (see also Møller & Briskie, 1995). In cases where more than one estimate was available for the same species we used the average of available estimates. Testes mass was calculated as the mean testes value from at least 20 breeding males, but typically 30 or more breeding males were used (e.g. Møller, 1991; Møller & Briskie, 1995). Because of extreme seasonal variation in testes size (Murton & Westwood, 1977; Wingfield, 1984), testis size was only recorded for adult specimens with breeding status indicated on the specimen tag in order to exclude data from the nonbreeding season.

Phylogenetic relationships

The phylogenetic relationships among the majority of species used were obtained from Sibley & Ahlquist (1990). Several authors have questioned this phylogeny (Krajewski, 1991; O'Hara, 1991; Raikow, 1991) although it has been confirmed by several independent data sets (reviewed by Sibley, 1994). Additional phylogenetic information was gained from the phylogeny presented by Møller & Cuervo (2000). The phylogeny used is given in an electronic file (see Supplementary material).

Comparative analysis

The possible effects of phylogenetic inertia were controlled for by using phylogenetically independent contrasts between species rather than simply the transformed data for individual species (Harvey & Pagel, 1991; Garland *et al.*, 1992). The CONTRAST program within the PHYLIP (version 3.5c) software suite was used to generate these independent contrasts for testis size, body size, rates of EPP and hatching success, with the branch lengths being kept equal (Harvey & Pagel, 1991; Martins & Garland, 1991; Felsenstein 1993). Residual testes sizes were obtained from a regression between contrasts of testes size and body size, as advocated by Garland *et al.* (1992). The contrasts were then analysed using linear regression forced through the origin (Garland *et al.*, 1992). For several variables, the absolute value of the standardized contrast was significantly correlated with the standard deviation of the contrast, indicating an inappropriate standardization (Garland

et al., 1992). To solve this problem, we transformed the sum of branch lengths prior to standardization, which rendered all the above correlations insignificant ($P > 0.05$ in all cases). It should be stressed here, however, that the choice of standardization of the contrasts, using either the square root of the sum of branch lengths or the square root of the transformed sum of branch lengths (Garland *et al.*, 1992), only very marginally affected our results quantitatively and in no case affected our conclusions qualitatively.

Results

The rates of hatching success were found to vary enormously across species: from as low as 61% in *Loxioides bailleui* (Oustalet) to over 95% in at least nine species (see Appendix), with mean hatching success being 87.65% (standard error ± 1.07).

There was no relationship between the rate of EPP and hatching success when either species data ($r^2 = 0.018$; $\beta = 0.07 \pm 0.06$, $t_{63} = 1.08$, n.s.; Fig. 1a) or contrasts were used ($r^2 = 0.04$; $\beta = 0.12 \pm 0.08$, $t_{57} = 1.58$, n.s.; Fig. 1b). Similarly, there was also no relationship between relative testes size and hatching success, using either species data ($r^2 = 0.007$; β regression coefficient $= -0.02 \pm 0.03$, $t_{53} = -0.60$, n.s.; Fig. 2a) or contrasts ($r^2 = 0.04$; β regression coefficient $= 0.49 \pm 0.34$, $t_{49} = 1.43$, n.s.; Fig. 2b). A multiple regression model, using contrast data and forced through the origin, of EPP and relative testes size as simultaneous predictor variables of hatching success was also not significant ($r^2 = 0.052$, $F_{2,51} = 1.40$, n.s.). We also carried out two multiple regression models, forced through the origin, to assess whether any of our measures of polyandry were related to hatching success when simultaneously accounting for variance in life-history variables (1982). The covariates included as simultaneous predictor variables in the multiple regressions were phylogenetically independent contrasts of: body mass, clutch size, whether the species nests colonially, whether there is male incubation, and whether the nest is open or not. However, neither EPP (n.s.) or relative testes size (n.s.) contrasts explained any variance in hatching success contrasts in these multiple regressions.

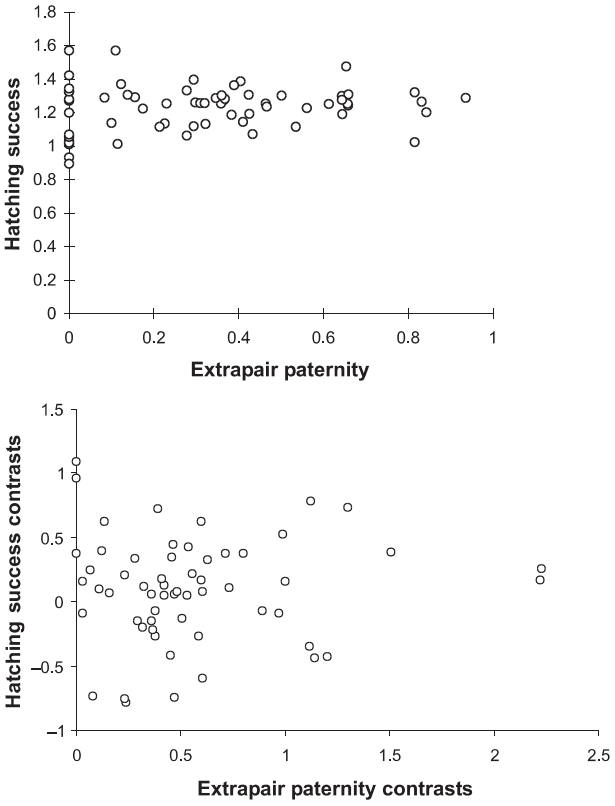

Fig. 1 The association between rates of extrapair paternity and hatching success in socially monogamous birds using either (a) species averages ($n = 64$) or (b) phylogenetically independent positivized contrasts ($n = 58$).

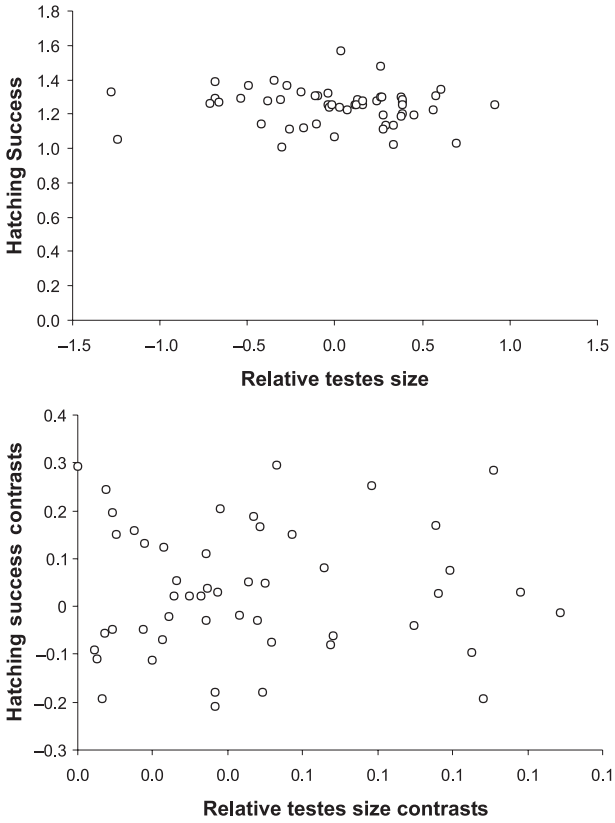

Fig. 2 The relationship between relative testes size and hatching success in socially monogamous birds using either (a) species averages ($n = 54$) or (b) phylogenetically independent positivized contrasts ($n = 50$).

Discussion

Our analyses revealed an enormous range in the proportion of eggs that fail to hatch amongst the species investigated. In many species as much as a quarter of all eggs laid fail to hatch, whereas all eggs hatch in others. Our overall estimate of an average infertility rate of 13% is comparable with similar estimates among other groups (Koenig, 1982; Anderson, 1990; Eberhard, 1996), confirming that infertility represents a highly significant and general fitness cost in natural populations. Koenig (1982) found that hatching success differed across bird species exhibiting different social systems. Unfortunately, that study did not control for the confounding effects of shared phylogenetic history among the species included. Møller & Ninni (1998) found no relationship between hatching success and EPP, but the authors only included data from six species. Using a much larger data set and methods which control for phylogeny, we failed to establish a relationship between either of our two measures of polyandry (EPP rate and relative testes size) and hatching success. This may be the result of at least five quite different possibilities, each of which will be discussed briefly below.

First, we may have been unable to detect a true relationship because of low statistical power. Although type II statistical errors can never be completely excluded, we suggest that this is an unlikely explanation for our results. We made great efforts to maximize the number of species included in our study, and power analyses do not indicate particularly low statistical power. For example, the probability of detecting a fairly weak correlation ($r = 0.3$) between infertility rate and EPP rate with our data was 0.68 (Cohen, 1988). Similarly, it could be argued that our measures of polyandry are not reliable enough estimates of the true rate of polyandry experienced by a species. However, these traits are widely accepted as reliable indicators of the rate of polyandry both over evolutionary time (testes size: Warner & Robertson, 1978; Harcourt *et al.*, 1981; Kenagy & Trombulak, 1986; Møller, 1988; Ginsberg & Rubenstein, 1990; Briskie & Montgomerie, 1992; Jennions & Passmore, 1993; Gage, 1994; Hosken, 1997; Stockley *et al.*, 1997) and in extant populations (EPP rates: Møller & Briskie, 1995; Petrie & Kempenaers, 1998; Petrie *et al.*, 1998; Griffith, 2000; Møller, 2000).

Secondly, counter to theory (see Introduction), female mating rate and infertility may be functionally unrelated, and may hence not coevolve. This seems an equally improbable explanation, in part because of the overwhelming amount of experimental data demonstrating links between female mating behaviour and various components of female reproductive fitness in many different groups (Andersson, 1994; Eberhard, 1996; Arnqvist *et al.*, 2000; Jennions & Petrie, 2000) and in part because several intraspecific studies of birds have indeed documented correlations between polyandry and infertility. For example, Wetton & Parkin (1991) first established that hatching success declined significantly with increasing rates of extrapair fertilizations across clutches in *Passer domesticus* (L.). These results cannot be attributed merely to sperm depletion, as Birkhead *et al.* (1995) found that 73% of the house sparrow eggs that fail to hatch do so because of early embryo mortality rather than a lack of sperm (see also Lifjeld, 1994). Subsequent studies of birds have presented partly conflicting evidence. Cordero *et al.* (1999) found lower hatching success and Kempenaers *et al.* (1999) found higher hatching success in nests with extrapair young, whereas Bensch (1996) failed to document a significant effect of polygyny on hatching success.

Thirdly, several different mechanisms may simultaneously but antagonistically affect correlated evolution between polyandry and infertility, one masking the effect of the other, resulting in an apparent lack of correlated evolution. We see at least two likely possibilities for such a scenario. Most obviously, any positive effects on fertility of increased polyandry resulting from genetic mechanisms may come at the cost of increased problems with infertility because of sexually antagonistic coevolution between sperm offence and ova defence (see Introduction). Both of these processes seem likely among the species studied here. Several intraspecific studies have at least indicated that some form of genetic incompatibility can cause infertility in natural bird populations (Van Noordwijk & Scharloo, 1981; Bensch *et al.*, 1994; Kempenaers *et al.*, 1996; Brown & Brown, 2001). At the same time, observations showing that embryo death in birds can result from dispermic fertilizations of the egg pronucleus (e.g. Lee *et al.*, 1990; de la Seña *et al.*, 1992) and that infertility because of a lack of fertilization also seems to occur (Birkhead *et al.*, 1994, 1995), both strongly imply that genetic incompatibility is not the only source of infertility in birds. The fact that birds, along with several other groups, are physiologically polyspermic (i.e. several sperm routinely enter the egg cytoplasm but only one fuses with the female pronucleus, Ginzburg, 1972; Jaffe & Gould, 1985) does of course not preclude the possibility that aggressive characteristics of male sperm and female resistance mechanisms are coevolving antagonistically. The supernumerary sperm pronuclei normally degenerate in physiologically polyspermic species, so the block against functional polyspermic fertilization and resulting developmental problems of the zygote acts at a relatively late stage in these species. The mechanism behind this polyspermy-avoidance strategy remains poorly understood, but it is obviously imperfect (Lee *et al.*, 1990; de la Seña *et al.*, 1992) and seems to involve substances produced either by the oocyte itself or by the zygote nucleus (Jaffe & Gould, 1985).

Fourthly, infertility in our data set almost certainly derive from several proximate sources. However, this will only mask true relationships between infertility and

polyandry if the contribution from some sources to net infertility correlate negatively with polyandry whereas others correlate positively. For example, one possibility is that positive effects on fertility of increased polyandry resulting from genetic mechanisms is masked by simultaneous negative effects because of increased rates of embryo mortality resulting from inappropriate parental care. If increased rates of polyandry among socially monogamous birds is associated with reduced paternal care, which might be the case (Møller & Birkhead, 1993; Petrie & Kempenaers, 1998), then these effects may indeed counterbalance one another. We see no possibility of testing such scenarios conclusively with data currently available. Different scenarios generate different expectations with regards to the proximate causes of infertility (see Table 1) but such data is virtually nonexistent (see Birkhead *et al.*, 1995), which is unfortunate as it would significantly promote our understanding of the evolution infertility.

Finally, sexual conflict may not relate linearly to polyandry (cf. Holland & Rice, 1999; Arnqvist *et al.*, 2000) and the regression analyses used here may therefore not be ideal. A more simple direct comparison between monandrous and polyandrous species may be more suited to testing the sexual conflict hypothesis. Unfortunately, there is simply not enough data available within the monogamous group of species to make such a comparison statistically meaningful.

In summary, we have documented a large variation in infertility across species, and showed that infertility rates are substantial in natural bird populations. Our current lack of a general understanding of the evolution of infertility is highlighted by our study, which indicates that infertility may be the result of complex interactions between several different factors. We suggest that more effort should be made towards understanding the maintenance of the high rates of infertility observed in natural populations.

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Supplementary material

The following material is available from http://www.blackwell-science.com/products/journals/suppmat/JEB/JEB445/JEB445sm.htm:

Appendix

Figure

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