PROCEEDINGS OF THE ROYAL SOCIETY B

*Proc. R. Soc. B* (2006) **273**, 2363–2368
doi:10.1098/rspb.2006.3591
*Published online* 20 June 2006

# Mother guarding: how offspring may influence the extra-pair behaviour of their parents

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In this paper we propose a novel form of social control of mate choice. Through mother guarding, offspring can help in protecting the paternity of their father by preventing their mother from engaging in extra-pair matings. We present a model that predicts the circumstances under which mothers should be selected to seek or avoid extra-pair matings, and existing offspring should be selected to prevent or promote such matings. In its simplest form, our model shows that offspring are selected to mother guard as long as the viability of extra-pair young is less than twice that of within-pair young; when the relative viability is greater, offspring are selected to promote extra-pair mating by their mother. If the existing offspring are not necessarily sired by their mother's social mate, then the potential for conflict is further reduced. We also consider whether offspring have an interest in the extra-pair reproduction of their fathers. We show that when the costs of the father's infidelity to the mother's brood are high, existing offspring are selected to prevent extra-pair mating by their father; when such costs are low, offspring are selected to promote extra-pair mating by their father. In principle, our model applies to all species where offspring show delayed dispersal and where breeding pairs raise multiple broods or litters. This situation exists in, but is not limited to, the majority of cooperatively breeding species. The significance of this model with regard to our current understanding of the evolution of extra-pair behaviour in such species is discussed.

**Keywords:** female choice; extra-pair paternity; cooperative breeding

## 1. INTRODUCTION

Behavioural and genetic studies during recent years have shown that extra-pair copulations and fertilizations are widespread among birds (reviewed by Birkhead & Møller 1995; Petrie & Kempenaers 1998; Westneat & Stewart 2003). The frequency of extra-pair paternity (EPP) varies both within and between species (Petrie & Kempenaers 1998; Griffith *et al.* 2002). Reasons for this variation are poorly understood, but are likely to be related to variation in the underlying benefits and costs of extra-pair behaviour. Extra-pair matings can provide females with direct benefits, such as material benefits (e.g. Gray 1997) and fertility assurance (e.g. Sheldon 1994), and indirect benefits, such as access to 'good genes' (e.g. Hasselquist *et al.* 1996) or 'compatible genes' (e.g. Johnsen *et al.* 2000). However, these benefits may be tempered by several costs, such as loss of the social mate's investment (see Whittingham & Dunn 2001*a* for a review) and increased risk of sexually transmitted disease (see Sheldon 1993 for a review). To fully understand variation in the frequency of EPP, we also need to consider variation in constraints on female mate choice (Petrie & Kempenaers 1998) and it is important to recognize that extra-pair mating occurs in the context of a multi-player game in which different individuals pursue their own genetic interests (Westneat & Stewart 2003).

A major constraint on a female's extra-pair activity is the behaviour of her social mate (e.g. Westneat & Stewart 2003). Because female extra-pair mating is costly for cuckolded males, male behaviour that maximizes paternity should be selected for (Trivers 1972) and such behavioural strategies may pose an important restriction on female choice (Petrie & Kempenaers 1998). In birds, such strategies by the social mate typically involve frequent copulation as well as mate guarding by close following of females (Birkhead & Møller 1992).

Although female extra-pair matings are thought to influence mainly the fitness of social mates, the fitness of other individuals may also be affected. For example, existing full offspring of a female and her social mate stand to lose in terms of their indirect genetic representation in the next generation if their mother mates with unrelated males. Therefore, there is the potential for kin selection on behavioural strategies in offspring that protect the paternity of their father by preventing their mother from engaging in extra-pair matings.

In this paper, we suggest that such selection may give rise to 'mother guarding' by close following of females by their offspring. We present a general model that explores the conditions under which we would expect offspring to be selected to influence the mate choice of their parents in relation to the costs and benefits of extra-pair mating to the reproductive female, her social mate and the offspring themselves.

## 2. THE MODEL

Imagine that the viability (i.e. the survival or reproductive chances) of extra-pair young relative to that of within-pair young is $V$, the proportion of the brood that is extra-pair is $P$ and the clutch size is $n$. Then, ignoring any costs of producing extra-pair young, the payoff to an existing member of the family from the production of such a brood is

$$B = n[r_{wp}(1-P) + r_{ep}PV], \tag{2.1}$$

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*Received* 21 March 2006
*Accepted* 16 April 2006

where $r_{wp}$ and $r_{ep}$ are the relatedness of the individual to the within- and extra-pair offspring, respectively.

In the absence of inbreeding, for the reproductive female, $r_{wp} = r_{ep} = 1/2$; hence

$$B_{female} = \tfrac{1}{2}n(1 - P + PV). \tag{2.2}$$

Assuming that any extra-pair young is produced with a male unrelated to this female's social mate, for the social mate, $r_{wp} = 1/2$ and $r_{ep} = 0$; hence

$$B_{male} = \tfrac{1}{2}n(1 - P). \tag{2.3}$$

Ignoring any possible costs of extra-pair mating, it is clear that a female benefits from increased $P$ when $V > 1$, but an increase in $P$ always decreases the payoff to her social mate. This is the reason for classical mate guarding.

The inclusive fitness of existing offspring of the pair is also affected in much the same way. For full offspring of the pair, $r_{wp} = 1/2$ and $r_{ep} = 1/4$, so

$$B_{offspring} = \tfrac{1}{2}n(1 - P + \tfrac{1}{2}PV). \tag{2.4}$$

This shows that the interests of the mother and her offspring may not necessarily coincide. Mother and full offspring are in conflict when an increment in $P$ leads to an increase in $B_{female}$ but a decrease in $B_{offspring}$, i.e. when

$$\frac{\partial B_{female}}{\partial P} > 0 \quad \text{and} \quad \frac{\partial B_{offspring}}{\partial P} < 0.$$

This happens when

$$\tfrac{1}{2}V - \tfrac{1}{2} > 0 \quad \text{and} \quad \tfrac{1}{4}V - \tfrac{1}{2} < 0.$$

Figure 1 shows that the zone of conflict is where $V$ lies between 1 and 2. For other values of $V$, either both parties lose, or both gain from an increase in $P$. This means that it generally pays full offspring to mother guard unless the viability of extra-pair young is greater than or equal to twice that of within-pair young.

This prediction is altered if the existing offspring themselves are not necessarily sired by their mother's social mate. For the mother, $r_{wp}$ remains unchanged (at 1/2), while for an existing offspring $r_{wp}$ is $(1/4)(1 + S)$, where $S$ is the probability that it was sired by the mother's social mate. Regardless of $S$, $r_{ep}$ remains unchanged for both mother and offspring (at 1/2 and 1/4, respectively, assuming that existing offspring are unrelated to their mother's extra-pair partner). The zone of conflict is now defined by $1 < V < 1 + S$, and so when $S < 1$, the potential for conflict of interest between existing offspring and their mother is reduced. For example, if existing offspring have only a 50% probability of being sired by their mother's social mate, then it pays these offspring to mother guard while $1 < V < 3/2$ (assuming that such existing extra-pair offspring do not share a sire with future extra-pair offspring). The interests of extra-pair offspring ($S = 0$ in figure 1) are coincident with those of their mother.

Conflict can occur not only between mothers and offspring but also between fathers and offspring. For example, from figure 1 one would predict that full offspring ($S = 1$) should be in conflict with their father (who always pays a cost if cuckolded) when $V > 2$. As $S$ decreases from 1, such conflict becomes increasingly likely (figure 1). Under these circumstances, we would expect adaptations in existing offspring that prevent their father from obtaining paternity with their mother's new brood.

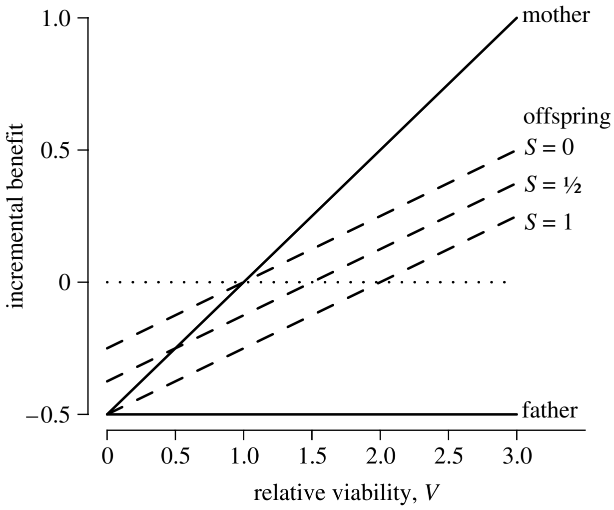


Figure 1. Incremental benefits to individuals in a family for a given increase in $P$ (i.e. $\partial B/\partial P$) in relation to the relative viability of extra-pair young. Brood size, $n$, is taken here to be 1. Extra-pair matings are favoured when the incremental benefit is positive, but are not favoured when the incremental benefit is negative (i.e. there is an incremental cost). Broken lines show the relationship for existing offspring with different probabilities of being sired by their mother's social mate ($S$). When the relative viability, $V$, is less than 1, neither mothers nor full offspring ($S = 1$) benefit from an increase in $P$. When $V > 2$, both mothers and full offspring benefit, but both are then in conflict with the father (who never benefits when his social mate seeks extra-pair fertilizations). When $1 < V < 2$, mothers benefit, but full offspring pay a cost with increasing $P$; hence mother and offspring are predicted to be in conflict. The value of $V$ at which the incremental benefit for existing offspring switches from negative to positive depends on the probability that such offspring are sired within the pair.

Clearly, there may also be costs to the reproducing female for producing extra-pair young, for example through reduced care by the cuckolded male and the existing offspring, and this may lead to a reduction in the survival of the current brood. Ignoring future costs, if costs to current reproduction increase with the proportion of extra-pair young, $P$, at the rate $c$, then the overall payoff to an individual in the family can be written as

$$W = B(1 - cP). \tag{2.5}$$

Substituting this into equation (2.1) shows that the incremental payoff, $\partial W/\partial P$, is positive when

$$V\frac{r_{ep}}{r_{wp}} > \frac{c}{1 - 2cP} + 1. \tag{2.6}$$

This means that the relative viability required to produce a positive incremental payoff is an increasing and accelerating function of $c$ and $P$. This incremental payoff is positive for mothers and negative for existing full offspring when

$$\frac{c}{1 - 2cP} + 1 < V < 2\left(\frac{c}{1 - 2cP} + 1\right).$$

The model thus predicts that conflict between mother and offspring is most likely to occur when either $c$ or $P$ or both are low.

For completeness, we can also compare the effects of extra-pair behaviour by mothers and fathers. For mothers, a relatively inflexible brood size must be apportioned between within-pair paternity and EPP. However, the extra-pair reproduction of fathers does not necessarily come at an equivalent expense of within-pair reproduction (e.g. Lessells & Parker 1999). In this way, extra-pair reproduction by the father is qualitatively different from that of the mother. The overall payoff to a member of the family from the reproduction of both the mother and the father can be written as

$$W - g(F) + r_{\text{epf}}F,$$

where $r_{\text{epf}}$ is the relatedness of that individual to the father's extra-pair offspring, $F$ is the number of such extra-pair offspring and $g(F)$ is a function describing the costs of the father's infidelity to the mother's brood (perhaps through a reduction in paternal care).

From this, it is clear that her partner's infidelity is never beneficial for the mother (because for her, $r_{\text{epf}}=0$). Fathers should be selected to pursue increasing numbers of extra-pair copulations when the marginal increase in $r_{\text{epf}}F$ is greater than that in $g(F)$, i.e. when $\mathrm{d}r_{\text{epf}}F/\mathrm{d}F > \mathrm{d}g(F)/\mathrm{d}F$, which simplifies to $r_{\text{epf}} > \mathrm{d}g(F)/\mathrm{d}F$. Existing offspring are not in conflict with their fathers if, for such offspring too, $r_{\text{epf}} > \mathrm{d}g(F)/\mathrm{d}F$, but their interests do differ from that of their fathers if $r_{\text{epf}} < \mathrm{d}g(F)/\mathrm{d}F$. Because $r_{\text{epf}}$ is 1/4 for existing offspring and 1/2 for their father, offspring should help their fathers in obtaining extra-pair copulations when an additional half-sib (through the father) costs less than 1/4 of a full-sib, but offspring should prevent their fathers from engaging in extra-pair copulations (i.e. they should 'father guard') when the cost is between 1/4 and 1/2 of a full-sib.

As earlier, the situation is altered if existing offspring may have been sired by a male other than their mother's social mate. In this case, for existing offspring, $r_{\text{epf}} = (1/4)S$. As $S$ declines from 1, the marginal benefit to offspring of the infidelity of their mother's social mate declines proportionately, until when $S=0$, the interests of existing (extra-pair) offspring coincide with that of their mother, as before.

## 3. DISCUSSION

Previously, work on the variation in the frequency of EPP has focused exclusively on the behaviour of adults, but not on that of existing offspring. Our model demonstrates that offspring are expected to be selected to influence their parent's mating behaviour under quite a wide range of reasonable circumstances, and therefore the behaviour of offspring needs to be considered to provide a more complete accounting of the factors underlying variation in EPP.

In particular, our model shows that as long as extra-pair offspring have a somewhat higher viability than within-pair offspring, mothers and their existing offspring should be in conflict, and it pays offspring to mother guard. The viability of extra-pair young relative to that of their within-pair half-sibs has not been evaluated for many species. For those in which it has been estimated, the relative viability ($V$ in our model) ranges from 1.06 to 1.31 for fledging success (Kempenaers *et al.* 1997; Whittingham & Dunn 2001*b*; Schmoll *et al.* 2003; Charmantier *et al.* 2004) and from 0.69 to 1.4 for recruitment to the next year (Kempenaers *et al.* 1997; Krokene *et al.* 1998; Lubjuhn *et al.* 1999; Schmoll *et al.* 2003; Charmantier *et al.* 2004). These estimates indicate that, at least for the species studied, extra-pair young enjoy a small-to-moderate advantage over within-pair young. However, if extra-pair offspring have a substantially higher viability than within-pair offspring, the interests of existing offspring are coincident with those of their mother and conflict would arise between offspring and their father instead. This is expected to select for adaptations in existing offspring to prevent their father from obtaining paternity in their mother's new brood, such as interference during copulation or mate guarding, or for adaptations that promote their mothers' extra-pair mating, such as helping behaviour that compensates for a reduction in parental assistance by the mother's social mate (e.g. Mulder *et al.* 1994).

Our model further shows that the potential for mother–offspring conflict may be influenced by the costs to the mother of obtaining extra-pair matings. With increasing costs to the mother of obtaining extra-pair matings, the magnitude of the viability of extra-pair offspring relative to within-pair offspring must increase in an accelerating fashion in order to generate mother–offspring conflict. However, this latter conclusion is necessarily tentative because it depends on the particular form of the relationship between the costs of producing extra-pair young and the proportion of the brood that is extra-pair (i.e. the shape of equation (2.5)).

In our model, the potential for mother–offspring conflict depends on the background average value of $S$ (the probability that they are extra-pair offspring) in the population. The range of $V$ for which mothers and offspring are expected to be in conflict decreases with the probability that existing offspring are extra-pair. Hence, it is expected that the potential for mother–offspring conflict is reduced in species with high background values of EPP. This situation changes if offspring could potentially gather information about whether or not their mother's social mate is their sire. However, because existing offspring may be extra-pair themselves, father recognition cannot simply be achieved through spatially based recognition or recognition by association; rather it could be achieved through recognition by phenotype-matching, or by recognition alleles (for review see Hepper 1991), for which as yet there is little evidence (Sherman *et al.* 1997). Alternatively, father recognition could be achieved indirectly on the basis of the male breeder's history of investment in the existing offspring, as this may reflect his perceived relatedness to the offspring (e.g. Sheldon & Ellegren 1998; Neff 2003). If such information is available to offspring, we might expect variation in mother guarding to occur within a species (and possibly even within a brood), with full offspring selected to mother guard, but extra-pair offspring selected not to. Thus, in species with effective father recognition mechanisms, mother–offspring conflict could occur even against high background values of EPP.

We also explore the conditions under which offspring should be selected to influence the extra-pair reproduction of fathers. Our model shows that when the costs of the father's infidelity to the mother's next brood are high, fathers and their existing offspring should be in conflict and it pays offspring to prevent their fathers from engaging in extra-pair copulations (i.e. 'father guarding'); whereas when such costs are low, offspring should help fathers in obtaining extra-pair copulations. Father helping could thus be a cheap way for existing offspring to gain fitness under certain circumstances. If the existing offspring themselves are not necessarily sired by their mother's

Table 1. List of cooperative breeding bird species that show delayed dispersal for which extra-pair paternity (EPP) has been determined (from appendix A in Griffith *et al*. 2002).

| species | common name | %EPP offspring (*N*) |
|---|---|---|
| *Aphelocoma coerulescens* | Florida scrub-jay | 0 (139) |
| *Dacelo novaeguineae* | laughing kookaburra | 0 (140) |
| *Turdoides squamiceps* | Arabian babbler | 0 (186) |
| *Melanerpes formicivorus* | acorn woodpecker | 0 (423) |
| *Porphyrio porphyrio* | pukeko | 0 (73) |
| *Picoides borealis* | red-cockaded woodpecker | 1.3 (80) |
| *Aphelocoma ultramarina* | Mexican jay | 1.4 (142) |
| *Campylorhynchus nuchalis* | stripe-backed wren | 1.5 (69) |
| *Camphylorhynchus griseus* | bicoloured wren | 2.3 (222) |
| *Manorina melanophrys* | bell miner | 4.2 (24) |
| *Lanius collurio* | red-backed shrike | 5.2 (19) |
| *Manorina melanocephala* | noisy miner | 5.9 (85) |
| *Sericonis frontalis* | white-browed scrubwren | 12.4 (137) |
| *Sialia mexicana* | western bluebird | 18.8 (207) |
| *Acrocephalus sechellensis* | Seychelles warbler | 38.0 (55) |
| *Malurus cyaneus* | superb fairy wren | 71.6 (1307) |

social mate, then the benefit of the infidelity of their mother's social mate declines accordingly, and the interests of extra-pair offspring are coincident with those of their mother.

Several assumptions must be made clear, the violation of which would modify our conclusions. First, our model is based entirely on genetic benefits of extra-pair fertilizations, but there may also be direct benefits. If these direct benefits favour mothers more than existing offspring, they are expected to increase the potential for conflict between mothers and offspring. Second, offspring may be able to influence the magnitude of $V$ by adjusting their degree of helping behaviour in relation to the mother's extra-pair behaviour. In parallel with species where social mates reduce their paternal effort in relation to the certainty of paternity to the brood (e.g. Sheldon & Ellegren 1998; Neff 2003), existing offspring may calibrate their helping effort according to the expected payoffs. Third, we have not considered costs of mother guarding; clearly, if the costs to future reproductive success outweigh the incremental fitness accrued through mother guarding, then the behaviour should not appear. Finally, it is clear that alleles in existing offspring have different interests depending on whether they are maternal or paternal in origin, and the interests of paternal alleles differ further depending on whether offspring are the product of within- or extra-pair mating. Payoffs to maternal alleles are identical to the payoffs to the mother (equation (2.2)), while those to paternal alleles are either identical to payoffs to her social mate (equation (2.3)) or to those of her extra-pair mate that fathered the existing offspring. Although we have concentrated on the average payoffs to existing offspring (equation (2.4)), one might expect selection for genomic imprinting such that maternal and paternal alleles promote different behaviour in the offspring (Haig 1997). Still, our model shows that genomic imprinting is not a prerequisite for mother guarding because, under certain circumstances, even unimprinted alleles in offspring should be selected to prevent extra-pair copulations by the mother.

Mother guarding and mate guarding have several predictions in common: mother guarding should only occur during the mother's fertile period (see also Birkhead 1982; Gowaty & Plissner 1987; Arvidsson 1992; Hanski 1994); mother guarding intensity should be adjusted to the risk of EPP, i.e. intrusion pressure from extra-pair males, and to female extra-pair behaviour (see also Alatalo *et al*. 1987; Møller 1987; Gray 1996); and it is likely to depend on ecological constraints (see also Birkhead & Møller 1992). Furthermore, as with paternal care, offspring helping behaviour should decrease when offspring are experimentally prevented from mother guarding as this would increase uncertainty in relatedness (see also Westneat & Sargent 1996). However, we can also make some predictions unique to mother guarding: it should depend on the relative viability of 'extra-paternal' offspring and it should depend on the likelihood that the father of the existing offspring will be the social mate of the mother in subsequent broods.

The potential inclusive fitness gains that can be accrued through mother guarding are considerable (i.e. up to 25% per offspring produced by the mother) whereas the costs of mother guarding are likely to be relatively low because they can be shared between existing offspring and only have to be incurred during the mother's fertile period. Nevertheless, to our knowledge there is no direct evidence from the literature to suggest that mother guarding occurs. However, the possibility of helpers exerting social control over their mother's mate choice because they can accrue inclusive fitness gains by protecting their relatedness to their siblings has not previously been considered, and consequently mother guarding has not yet been investigated specifically. In addition, mother guarding behaviour can easily be misinterpreted as offspring seeking food or protection, or as communal defence of a territory. Hence, the lack of direct empirical evidence could simply be a consequence of the absence of a theoretical expectation for mother guarding.

Which species are most likely to show mother guarding? An important prerequisite for the evolution of mother guarding is that offspring should physically be in a position to influence their mother's mate choice, such as in species where offspring delay dispersal and where breeding pairs have multiple broods or litters. This situation exists in, but is not limited to, the majority of cooperative breeders where offspring help to raise their non-descendant kin in their parents' subsequent broods (e.g. Koenig & Stacey 1990; Emlen 1995; Heinsohn & Double 2004). In such species, mother guarding could be considered a form of 'helping' behaviour because by guarding their mothers, offspring would effectively help their father to protect his paternity, albeit against the best interests of their mother.

We expect that mother guarding is most likely to occur in cooperatively breeding species with low or intermediate values of EPP because high values of EPP dilute the relatedness between existing offspring and male breeders. This reduces conflict between existing offspring and their mother and lowers the benefit of mother guarding. Therefore, in order to determine in which particular species mother guarding is likely to occur, information is needed with regard to both breeding system and degree of EPP. Currently, such information is most readily available from birds (Griffith *et al.* 2002). It shows that among cooperatively breeding birds with delayed dispersal and in which EPP has been assessed, low or intermediate values of EPP occur in the majority of species, including the red-cockaded woodpecker *Picoides borealis*, the noisy miner *Manorina melanocephala* and the western bluebird *Sialia mexicana* (table 1). However, as discussed earlier, father recognition may enable mother guarding even in species with high EPP rates. There is observational evidence from birds for preferential allocation of aid by helpers to breeders that are closer relatives (e.g. *Aphelocoma coerulescens*, Mumme 1992; *Manorina melanophrys*, Clarke 1984; *M. melanocephala*, Poldmaa *et al.* 1995; *S. mexicana*, Dickinson *et al.* 1996; *Acrocephalus sechellensis*, Komdeur 1994; *Aegithalos caudatus*, Hatchwell *et al.* 2001), which indicates that in such species there must be an effective mechanism for discriminating related breeders from non-related breeders. In such species, mother guarding is most likely to be exhibited only by full offspring, and could occur even when the species have high average values of EPP (e.g. *A. sechellensis*; table 1).

Cooperative breeding is an interesting and widespread phenomenon in the animal kingdom (Emlen 1997). Historically, cooperative breeding has been studied mostly in birds, where it occurs in about 8–17% of species (Heinsohn & Double 2004); but it also occurs in roughly 3% of mammals (including elephants, suricates, mole rats, canids, primates and humans) (Solomon & French 1997; Russell 2004), in several species of fishes (Taborsky 1994) and in many species of invertebrates. Because such species have traditionally served as model systems for the study of the evolution of the family, mother guarding has potentially important consequences for our understanding of family life. However, our model is not limited to cooperatively breeding species; in principle, it applies to all species where offspring remain in close proximity to their parents into adulthood. Such prolonged associations with kin are common among animals and are thought to occur when ecological factors cause dispersal costs to be high (Emlen 1994). Our model shows that when offspring delay dispersal, they have the opportunity to increase their fitness not only by helping their parents reproduce, but also by influencing their parents' mating behaviour. Through their potential impact on their parents' mating behaviour, offspring may be important in shaping the evolution of extra-pair behaviour in a wide variety of animal species.

We are very grateful to Rufus Johnstone, Nick Davies and two anonymous referees for discussion and constructive comments on the manuscript. We thank Øistein Holen, Kavita Isvaran, Rebecca Kilner, Toshinori Okuyama and Claire Spottiswoode for suggestions and help with the model.

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