Male mate choice, male availability and egg production as limitations on polyandry in the red-necked phalarope

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In sequentially polyandrous birds, a female's second mate faces a substantial risk of cuckoldry due to rapid mate switching and stored sperm. Secondary males are potentially available to females because males arrive asynchronously and/or are recycled into the breeding pool following nest predation. In a study of red-necked phalaropes, *Phalaropus lobatus*, a sex-role reversed shorebird, we tested the hypotheses that the proportion of females that become polyandrous is proximately limited by: (1) the ability of females to produce eggs, (2) the availability of males as mates and (3) male mate choice. In a colour-banded population in which rates of nest loss were manipulated by researchers, females that produced second clutches required similar lengths of time to complete clutches as those contemporaneously producing first clutches, and increased their egg size relative to their first clutch, making egg limitation unlikely. There was no correlation between an annual measure of males' availability as potential mates following nest losses and the proportion of females that were polyandrous. The majority of males that lost clutches (66%) repaired with their original female significantly more often than expected by random mate choice ($P < 0.0001$). Although 76% of polyandrous nestings involved renesting males, only 6% ($N = 46$) of renesting males changed mates if their original female was still available. Renesting males that changed mates did not select for or against females that had already produced clutches (NS). Our results suggest that the level of polyandry in this species is not constrained by the females' abilities to produce more eggs or by the number of males recycling back into the breeding pool. Instead, the proportion of females that become polyandrous is limited by males choosing to renest with their original females, thereby decreasing their probability of caring for eggs potentially fertilized by a female's previous mate.

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Polyandry as a social mating system is more common in shorebirds (Charadrii) than in other avian groups (Jenni 1974; Oring 1986; Ligon 1999). This prevalence has been attributed to common characteristics of breeding biology that facilitate uniparental care and the production of multiple clutches (Oring 1986). In territorial species, females obtain multiple mates by monopolizing resources required for successful nesting (Tarboton 1995), as in jacanas (Jenni & Collier 1972; Osborne & Bourne 1977; Emlen et al. 1998; Butchart et al. 1999) and spotted sandpipers, *Actitis macularia* (Oring & Lank 1986). In nonterritorial species, such as phalaropes and dotterels, females often precede males to the nesting grounds (Reynolds et al. 1986) and guard mates (Emlen & Oring 1977; Reynolds 1987; Colwell & Oring 1988a; Owens et al. 1995). Females that become polyandrous typically nest earlier, capitalize on the asynchronous arrival of males, and pair with males recycled into the breeding pool following clutch losses (Hildén & Vuolanto 1972; Schamel & Tracy 1977; Colwell 1986).

Early evolutionary hypotheses proposed to account for the prevalence of polyandry in shorebirds focused on energy limitation of females and the frequency of clutch losses (Erckmann 1983; Lenington 1984; Oring 1986). The 'replacement clutch hypothesis' assumes that relatively high rates of clutch loss, and subsequent renesting, favoured female emancipation from incubation to recoup energy for additional clutch production. Although a male might benefit from assuming all parental care if there is an increased probability of his mate replacing a failed clutch, this also facilitates female exploitation of additional breeding opportunities (Erckmann 1983). This idea seems applicable to temperate and tropical species, such as jacanas and spotted sandpipers, with long nesting seasons

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and high rates of clutch loss and replacement (Lank et al. 1985; Tarboton 1995; Butchart et al. 1999; Mace 2000), but less applicable to Arctic species, which have short nesting seasons and reduced rates of clutch loss and replacement (Erckmann 1983; Lenington 1984; Oring 1986).

Two detailed studies of phalaropes provide differing information about the relationship between predation/renesting and the prevalence of polyandry (Reynolds 1987; Colwell & Oring 1988a). Predation rates in a 5-year study of Arctic-nesting red-necked phalaropes, *Phalaropus lobatus*, were not high ($\overline{X} = 35\%$, annual range $18-62\%$) and renesting rates were low (18%). Nevertheless, at least 60% of second mates of polyandrous females were renesting males (Reynolds 1987). Reynolds (1987) concluded that the main constraint on polyandry was male availability, and predicted that higher nest losses, especially early in the season, should increase the operational sex ratio (OSR, expressed as available males/competing female; Emlen & Oring 1977), and thereby increase polyandry rates. In contrast, clutch losses in Wilson's phalaropes, *P. tricolor*, were higher ($68-87\%$) and a greater proportion of males renested ($24-36\%$; Colwell & Oring 1988a). However, the incidence of polyandry was low in Wilson's phalaropes (6.5% of marked females), despite apparently greater availability of males as second mates.

Whitfield (1990) suggested an additional factor that might limit polyandry. Later in the nesting season, females may differ in attractiveness to unpaired males because some females have already produced eggs and may be storing sperm from their previous mate ('C1-females': Whitfield 1990; Oring et al. 1992; Valle 1994). Recent paternity studies show that later-breeding phalarope males do indeed face a substantial risk of cuckoldry (Dale et al. 1999), but less so if they renest with the female that laid their previous clutch (their 'C1P-female': Schamel 2000). Males may therefore be choosy and avoid pairing with other C1-females (Whitfield 1990).

Following nest loss, males might avoid pairing with C1-females, if these females are energetically stressed, and therefore more likely to delay egg production or to produce smaller eggs or clutches, than are females that have not yet produced clutches that season ('C0-females': Whitfield 1990). Although egg size in phalaropes is relatively small compared with other shorebirds (Ross 1979; Liker et al. 2001), a full clutch represents 65% of female mass (Rubega et al. 2000), which is a significant investment of resources. Any preference for C0-females would make second mates more difficult for C1-females to obtain, thereby limiting the occurrence of polyandry. In the current study, we examine three factors that might affect the proportion of female red-necked phalaropes obtaining multiple mates: (1) the ability of females to produce eggs, (2) the availability of males and (3) male mate choice.

Egg Production

Polyandry might be directly limited by females' egg production capacity (Lank et al. 1985), or, more subtly, if males discriminate against C1-females because of their reduced egg production ability. We examined evidence relevant to these mechanisms by comparing the time taken by C0- versus C1-females to produce a clutch, the egg sizes in successive clutches of individuals, and the renesting interval of males that retained their previous female or switched mates after losing clutches. If egg production limitation is important, males should prefer C0-females.

Male Availability

Since males provide all parental care, the OSR in phalaropes and other polyandrous species is typically strongly female biased after the onset of incubation, suggesting that male availability limits females' opportunities to become polyandrous (Schamel & Tracy 1977; Lank et al. 1985; Colwell & Oring 1988a). We tested experimentally whether increasing mate availability, by recycling males into the breeding pool, would increase the incidence of polyandry. In 4 years, we augmented natural rates of clutch loss by removing clutches early in incubation, as part of a paternity study (Schamel 2000). We predicted a positive relation between the proportion of nest losses and the proportion of polyandrous females. While the availability of additional males is obviously necessary for sequential polyandry to occur, we tested the degree to which this is also a sufficient condition to produce higher rates, or whether other factors still limit polyandrous opportunities.

Male Mate Choice

By experimentally recycling nesting males back into the breeding pool, we increased our opportunity to determine whether such males avoided polyandrous situations. Evidence in support of this hypothesis would be obtained if males: (1) preferred to pair with a C0-female, (2) avoided C1-females formerly paired with other males, whether forming their second pair with C0- or C1P-females, or (3) left the area to renest elsewhere, rather than mate locally with a C1-female.

Methods

Phalaropes were studied at Cape Espenberg (66°30′N, 163°30′W), on the northern Seward Peninsula in western Alaska, during late May through mid-July, 1976−1979 and 1994−1999. This area is wet coastal tundra, interspersed with small ponds and wet sedge marsh (Schamel & Tracy 1987). We searched a $1-2$-km^2 area for phalarope pairs and nests, attempting to find nests early in laying by following nest-searching pairs daily. Adults were captured with hoop nets, nest traps (Schamel & Tracy 1977) or long-handled dip nets (Reynolds 1987), and received unique combinations of coloured bands (Schamel & Tracy 1977). Banding preference, in descending order, was: paired females, paired males, solo females, incubating males and solo males.

A bird was considered paired if it: (1) consistently tolerated another bird's approaches within 0.5 m and was seen associating for 2+ days, (2) mutually nest-scraped with another, or (3) was nonaggressively associated with another bird at a nest prior to clutch completion. We kept daily notes on banded birds sighted while searching for specific pairs for focal pair observations. Banded birds were scored as alone or paired. These data were used to estimate the number and status (C0-, C1-, or C1P-) of unpaired females available to previously mated males that were seeking replacement clutches following nest failure. This analysis was necessarily restricted to females of known nest history. A female who lays a male's first clutch is termed his 'primary clutch' female (C1P-female). If this clutch is lost, a 'replacement clutch' might be produced by the C1P-female, or by a C0- or other C1-female during a second pairing and nesting attempt. Cloacas of females who had not laid eggs measured 2−3 mm, whereas those of laying or postlaying females measured 5−6 mm. We calculated an annual rate of polyandry as the proportion of nesting, banded females laying clutches for more than one male.

We established nest initiation dates by finding nests during the egg-laying stage, by floating eggs to estimate their relative density (Sandercock 1998), or by backdating from hatching dates. Time between clutches was defined as the interval between clutch loss and the deposition of the first egg in the next clutch. The timing of clutch loss was determined by the sudden renewal of courtship behaviour by previously incubating males followed by confirmation of loss by a nest visit, by inspection during routine fieldwork, or by collection of eggs. Nests were included in this analysis only if we were able to estimate the interclutch interval within 6 h.

We defined 'replaceable nest losses' (Erckmann 1983) as losses occurring early enough in the nesting season such that birds had the possibility of renesting (i.e. losses prior to a seasonal cutoff date for laying, calculated as 5 days before the first egg date of the last clutch laid each season). We subtracted 5 days from the initiation of the last clutch each year because the mean time for clutch replacement for males renesting with different females was 4.8 days. Because phalaropes are nonterritorial and can move freely over a large area, we did not attempt to estimate the local OSR directly. We hypothesized that an increase in nesting males recycled into the breeding pool should provide females with increased opportunities for obtaining second mates. We calculated the proportion of nesting males recycled annually by dividing the number of replaceable nest losses by the number of nesting males.

To establish nest fate in the 1970s, we visited nests every 2 days after mid-June and examined eggs for pipping. Once eggs were pipped, we visited nests daily. Clutches that disappeared less than 17 days into incubation, or before pipping was noted, were considered depredated. We used 17 days as a cutoff because minimum incubation duration is 18 days (Rubega et al. 2000). If pipped eggs were missing on subsequent nest visits, we considered nests successful if the: (1) male was 'broody', or (2) nest bowl contained shell fragments (Mabee 1997). 'Broody' males displayed behaviours associated with tending chicks: ground distraction displays, approaching intruders and calling, and/or producing brooding vocalizations (Rubega et al. 2000). In the 1990s, we established nest initiation dates by observation of egg laying or egg flotation, and avoided revisiting nests until hatching was imminent.

We used one-way analyses of variance (ANOVAs) to examine differences between means without covariates. We used logistic regression for nest success analyses. Pairing patterns were examined with chi-square analyses. Means are reported with standard errors. Statistics were calculated using SAS (SAS 1999).

RESULTS

Egg Production

Females produced larger eggs in their second clutches than in their first clutches ($\overline{X} \pm$ SE mass: clutch 1: 6.30 ± 0.07 g; clutch 2: 6.53 ± 0.07 g; paired t test: $t_{27} = 4.34$, $N = 28$, $P = 0.0002$; $\overline{X} \pm$ SE mean volume: clutch 1: 5.99 ± 0.0 cm^3; clutch 2: 6.18 ± 0.07 cm^3; paired $t_{27} = 3.16$, $N = 28$, $P = 0.004$), suggesting that egg production for second clutches is not energetically constrained. There was no difference in mean clutch size between first and second clutches (clutch 1: 3.88 ± 0.04, $N = 87$; clutch 2: 3.95 ± 0.04, $N = 38$; one-way ANOVA: $F_{1,123} = 0.75$, $P = 0.38$).

Males obtained replacement clutches with C1P-females 4.2 ± 0.24 days ($N = 28$) following nest loss, compared with 4.8 ± 0.24 days ($N = 16$) when changing mates (ANOVA: $F_{1,42} = 3.20$, $P = 0.08$). There was no obvious difference in mean time to replace clutches when mating with C0- versus C1-females (C0: 4.5 days, range 4−5 days, $N = 2$; C1: 4.8 days, range 3.7−7.0 days, $N = 13$). If a female's ability to produce eggs is limited later in the season, we would expect a decreasing probability that males losing clutches could obtain replacements. However, there was no difference in mean loss date, standardized to first egg date each year, between clutches that were or were not replaced before the seasonal cutoff date for laying (replaced: 9.8 ± 0.8 days since first egg, $N = 69$; not replaced: 10.1 ± 1.4 days, $N = 22$; logistic regression: $\chi^2_1 = 0.03$, $P = 0.86$).

Male Availability

Nest losses were high in the 1990s compared with the 1970s (Table 1). Loss rates in 1994−1995 were natural rates (range 91−95%), whereas those in 1996−1999 also included experimental clutch removals (range 85−96%). Over 50% of nest losses occurred early enough in the nesting season to be replaced (Table 1). Combining all years, these losses recycled 44.3% (range 13.8−72.2%) of all nesting males back into the breeding pool, providing females with opportunities to obtain second mates. However, we found no relationship between the proportion of males recycled and the proportion of polyandrous females ($F_{1,6} = 0.26$, $P = 0.63$; Fig. 1).

Table 1. Nest losses, replaceable losses, proportion of males recycled and replaced losses in red-necked phalaropes

Year	Total nests	Total losses		Replaceable losses		Total males	Proportion of males recycled	Replaced losses	
		N	%	N	%			N	%
1978	39	9	23.1	5	55.5	36	0.138	3	60.0
1979	71	22	31.0	15	68.2	57	0.263	14	93.3
Total 1970s	110	31	28.2	20	64.5	93	0.215	17	85.0
1994	22	21	95.4	6	28.6	18	0.333	4	66.7
1995	22	20	90.9	14	70.0	20	0.700	8	57.1
1996*	46	44	95.6	18	40.9	34	0.529	12	66.7
1997*	52	44	84.6	24	54.5	34	0.706	21	87.5
1998*	26	24	92.3	13	54.1	18	0.722	10	76.9
1999*	29	26	89.6	10	38.5	20	0.500	9	90.0
Total 1990s	197	179	90.9	85	47.5	144	0.590	81	75.3
Overall total	307	210	68.4	105	59.5	237	0.443	98	77.1

*Loss rates include experimental removals.

Male Mate Choice

About 80% (range 57–93% annually) of potentially replaceable nest losses were replaced (Table 1). We knew the nesting history for 65 of the 81 females that replaced males' clutch losses. Males renested with C1P-females in 66% of the cases. In 86% of the 22 cases where males changed mates, the C1P-female was either paired with another male ($N = 8$) or had left the area ($N = 11$). Only 6% (3 of 46) of all renesting males changed mates when the C1P-female was in the area and unpaired. We examined the likelihood of same-pair versus different-pair renests by determining the number of banded, unpaired females available on the date of nest loss. This is a conservative estimate with respect to the probability of remaining with a mate, since it excluded unbanded females and banded females not seen recently. Even so, same-pair renests occurred significantly more frequently than expected by random pairings ($\chi^2_1 = 91.8$, $P < 0.0001$),
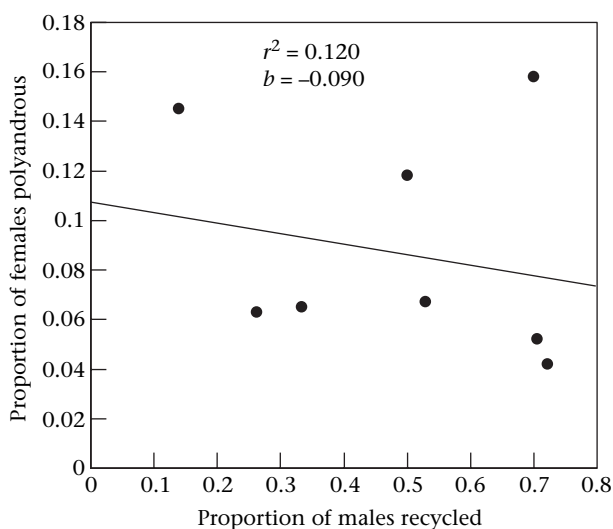
Figure 1. Proportion of female red-necked phalaropes that were polyandrous as a function of the proportion of males recycled into the breeding pool.

based upon the field of available banded females. This result was consistent with the male mate choice hypothesis. Males obtained replacement clutches significantly more often if the original female was unpaired than if she had formed a new pair bond (92 versus 61%, $N = 80$; $\chi^2_1 = 11.38$, $P = 0.0007$). C1P-females were banded in 15 of 24 potentially replaceable nest losses that were not replaced. In 73% of these cases, the female had either left the area (nine cases) or was paired with another male (two cases). The female was present and unpaired in only four instances. Three of these four males remained in the area, unpaired.

Polyandry and Renesting

We knew the local nesting histories of 18 of 23 males associated with polyandrous clutches. Renesting males accounted for 76.5% of polyandrous clutches, while newly arrived males accounted for 23.5%. In only one instance did a renesting male pair with another C1-female when his C1P-female was available. Of 15 males that changed mates and renested with females of known status, 80% paired with C1-females and 20% paired with C0-females, which was not different from the frequency expected from random pairings with available females (goodness of fit: $\chi^2_1 = 0.02$, $N = 15$, NS).

DISCUSSION

We tested predictions based on three proximal mechanisms that might regulate annual levels of polyandry in red-necked phalaropes. Our data are only consistent with the hypothesis that male mate choice limits polyandry, but the mechanism differs from that suggested by Whitfield (1990).

Egg Production

We found no evidence to support the hypothesis that C1-females are lower-quality mates because they are

energetically stressed (Whitfield 1990). There was no decline in clutch size in second clutches produced by the same female. Likewise, there was no difference in the time needed to replace a lost clutch by C0- versus C1-females, although our statistical power was low. Within females, eggs in second clutches were actually larger than those in first clutches; eggs in first and second clutches of polyandrous females are significantly larger than those of monogamous females (Schamel 2000). The similarity of mean loss dates of replaceable clutches that were replaced and not replaced is not consistent with the egg-limitation hypothesis. Our data came from females that produced multiple clutches. Eggs in second clutches of polyandrous females were significantly larger than those of females producing second clutches monogamously. In shorebirds, there is some evidence that larger eggs not only result in larger chicks, but that larger chicks have greater survival (Galbraith 1988; Grant 1991). Our evidence that poly-androus females produce larger eggs than monogamous females, and are not delayed in second clutch production, thus suggests they may be of higher quality than monogamous females (Schamel 2000). Despite this, males mostly avoided polyandrous matings (see below).

Male Availability

Ideally, we would have indexed male availability directly through OSR (e.g. Lank et al. 1985). Unfortunately, OSR in phalaropes is difficult to assess, because this is a nonterritorial species and individuals may range quickly over many square kilometres in search of prospective mates (Schamel & Tracy 1977; Reynolds et al. 1986; Colwell & Jehl 1994). Instead, we used the ratio of replaceable clutch losses (clutches lost early enough in the nesting season to be replaced) to total nesting males, to provide an index of recycled males. We reasoned that a high proportion of recycled males would provide females with increased opportunities to produce multiple clutches.

In contrast to other studies of phalaropes, a large proportion of total clutch losses in our study population were replaced (46.7%, $N = 210$; Table 1). Typically, only about 20% (range 18−27%) of total losses are replaced locally in all three phalarope species (Hildén & Vuolanto 1972; Schamel & Tracy 1977; Oring 1986; Reynolds 1987; Colwell & Oring 1988b), and one study of red phalaropes in northern Alaska found no local renests, even though 29 clutches were unsuccessful (Erckmann 1981). We found that a large percentage of potentially replaceable losses were replaced ($\overline{X} = 77.1\%$, $N = 98$; Table 1), which is comparable to the high replacement rate reported for temperate and tropical breeders such as spotted sand-pipers (Oring 1986) and jacanas (Tarboton 1995; Butchart et al. 1999).

In this study, therefore, predation provided opportunities for females to obtain second mates, by recycling males into the breeding pool. However, we failed to find a positive relationship between the proportion of males re-entering the breeding pool and the proportion of females that were polyandrous (Fig. 1), which does not support the male availability limitation hypothesis. As discussed below, males' nesting histories, as well as numbers, affected females' options.

Male Mate Choice

The ability of females to obtain second mates appeared to be limited, primarily because males showed a strong tendency to renest with their original mates (66%, $N = 65$). It is difficult to make meaningful comparisons with other studies of phalaropes because sample sizes of renesting marked pairs have generally been small ($N = 4−5$ pairs; Hildén & Vuolanto 1972; Schamel & Tracy 1977; Oring 1986; Reynolds 1987; Colwell & Oring 1988a).

Males pairing with C1-females face a larger risk of cuckoldry (50%) than males renesting with their original females (6%; Schamel 2000). For males that change mates to renest, 80% involve a higher-risk, polyandrous pairing. Their probability of caring for one extrapair fertilized (EPF) chick is 0.34, as calculated from the product of the probability of pairing with a C1-female and the probability of receiving an EPF egg from that female.

Male preference for C0- over C1-females was one outcome predicted if the risk of cuckoldry is a major consideration in mate choice (Whitfield 1990), but this was not observed, even among those males that did not renest with their C1P-female (NS). If prior nesting by females causes males to choose against pairing with them, then selection should favour behaviours in C1-females that mask their status. Indeed, successful copulation rates of C1P-pairs are higher than in either C0-pairs or C1-pairs (Schamel 2000), implying that previously paired males are able to recognize their former mates, but other males are apparently unable to distinguish between females that have and have not produced eggs in the current season.

In contrast, one study of red-necked phalaropes found increased copulation rates in C1-female pairs, and increased male aggression towards courting C1-females, compared with C0-females (Whitfield 1990), implying that males were able to distinguish between females that had and had not produced eggs in that season. In general, males were more aggressive towards C1-females, implying that they were less likely to form pairs with them. For males that did pair with a C1-female, their increased copulation rate may be interpreted as an attempt to outcompete residual sperm from a previous male.

Instead of pursuing C0-females, males achieve a lower probability of receiving EPF eggs primarily by re-pairing with their C1P- versus other C1-females (Schamel 2000). There is some evidence that previously paired females are of higher quality (produce larger eggs) than previously unpaired females (C0-females; Schamel 2000). Although re-pairing with their C1P-female protects males against incubating EPF eggs, it also carries with it an opportunity cost for their own ability to fertilize eggs in other nests (Valle 1994), which may be part of their overall mating strategy, based on copulation patterns (Schamel 2000). In the present study, when the C1P-female was not available, significantly more males left the area or failed to renest

locally than when the original female was present, as predicted if the risk of EPF is a consideration for male mate choice.

One means to lessen the EPF risk is to lengthen the prelaying period, since sperm loss may be a passive process in birds (Birkhead & Fletcher 1995). Our data suggest a possible ($P = 0.08$) 0.5-day delay in egg laying in polyandrous pairs, compared with same-pair renests, but whether males could cause this brief delay is unknown. A confounding factor is previous mate familiarity; this delay may be attributable to the time needed for mate assessment and pair formation.

There are alternative explanations why males might prefer to mate with the C1P-female. Whatever factors led to the choice of this particular female initially may still hold, although renesting males usually have numerous available females from which to select. Monogamy also reduces the potential risk of sexually transmitted diseases (Lombardo 1998; Westneat & Rambo 2000), which can adversely affect reproductive success (Sheldon & Verhulst 1996). We did not collect data to assess either of these hypotheses.

Our data show an apparent paradox. On one hand, a majority (76%) of polyandrous females replaced clutches for males. These data support the hypothesis that clutch losses can promote the frequency of polyandry in red-necked phalaropes, by releasing males back into the breeding pool. On the other hand, males chose to renest with their original females 94% of the time that these females were available. Thus, nest-loss-generated potential for polyandry is realized primarily if the original female is not available for the renesting male. These findings support Whitfield's (1990) hypothesis that polyandry in phalaropes is constrained by male avoidance of cuckoldry, but not through a simple preference for previously unmated females, as he suggested. Instead, these data suggest that the breeding system of phalaropes, like that of spotted sandpipers and jacanas, is fundamentally a renesting system that favours male incubation. However, in contrast to spotted sandpipers and jacanas, which obtain multiple mates by controlling access to resources, phalaropes obtain sequential multiple mates primarily when original females are unavailable for renesting males.

Acknowledgments

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