Conspecific brood parasitism is biased towards relatives in the Common Black-headed Gull

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Given the many detailed studies on the breeding biology of gulls, surprisingly little is known about conspecific brood parasitism (CBP) in these birds. CBP has been recorded in only a few of the roughly 60 species of *Laridae*. We studied CBP in two colonies of Common Black-headed Gull *Croicocephalus ridibundus* in northeastern Poland, during two consecutive years. We found parasitism in 22% and 10% of the monitored nests in the colonies, as determined with protein fingerprinting. Among the parasitic females we found only one that acted as both parasite and host. In both colonies, most cases of parasitism involved nests of females more related than average to the parasitic female. The rare cases of egg expulsion involved hosts with low relatedness to the parasite. We suggest that kin selection is implicated in CBP in the Black-headed Gull.

Key words: conspecific brood parasitism, *Croicocephalus ridibundus*, protein fingerprinting, relatedness

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Conspecific brood parasitism (CBP) is the phenomenon of females (parasites) laying their eggs in the nests of other females (hosts) of the same species, and so passing the costs of incubation and nestling rearing to the host (Yom-Tov 1980, Andersson 1984, Yamauchi 1993, Payne 1997). Previously it was thought that parasitic eggs appear accidentally in the nests of others, by mistake or when the nest of the parasitic female has been lost, but it is now clear that it is a rather common behaviour in many species (Yom-Tov 1980, MacWhirter 1989, Payne 1997, Schielzeth & Bolund 2010). Such behaviour has been shown to be advantageous: laying a normal clutch and being parasitic at the same time can considerably increase a female's reproductive success (Åhlund & Andersson 2001).

While clearly advantageous to the parasitic female, the effect of CBP on the host female's reproductive success varies considerably among species. The host female may either accept parasitic eggs, if having the additional eggs does not increase the costs of rearing her own brood, or should try to avoid being parasitized, if there are extra costs (Lyon & Eadie 2000, Andersson 2001). The former will be typical for precocial birds with large clutches of their own, in which the self-sufficient chicks do not need much care, and brood size is not limited by the incubation and chick-rearing capacity of the female, but rather by her ability to produce eggs. For many species of Anatidae the cost of parasitism to the host is relatively low and in some cases compensated by higher survival of chicks in mixed broods (Choudhury *et al.* 1993). Such females tend to adopt all dumped eggs, and their clutches are sometimes as large as double the usual size (Stawarczyk 1995). Host females may even benefit, if being parasitized dilutes the risk of predation of their own eggs/nestlings (Choudhury *et al.* 1993, Roy Nielsen *et al.* 2008).

Some bird species show strong natal philopatry, so if parasites nest nearby, they are likely to be related to the host. If eggs of females nesting nearby are then more likely to be accepted and females nesting farther away more likely to be chased from the host territory, kin selection can play a role in the evolution of CBP (Andersson 2001). Such patterns were observed in the Goldeneye *Bucephala clangula* and Common Eider *Somateria mollissima*, in which the costs of acceptance of parasitic eggs were relatively low and additionally compensated by kin selection (Andersson & Åhlund

2000, Waldeck *et al.* 2004). Completely different patterns of parasitic egg-laying and host responses are expected for species in which the cost of rearing an additional (altricial) nestling is high or acceptance of a parasitic egg reduces the number of the host bird's own eggs (as it can in indeterminate layers; Hamilton & Orians 1965, Kennedy 1991). The most obvious result is an arms race, as in the case of CBP in the American Coot *Fulica americana* (Lyon 1993). Parasitic females of this species attempt to lay eggs in the nests of other females, while host females try to avoid being parasitized by chasing away all the females that approach the nest, and by expelling parasitic eggs when the nest is parasitized (Lyon 2003). Under high costs of rearing chicks, parasitic females should avoid individuals they are related to, since CBP may lower their inclusive fitness (Andersson 2001). However, in such a case, parasites that avoid related females considerably increase the risk of having their egg rejected by unrelated hosts (Andersson 2001).

We studied the Common Black-headed Gull *Croicocephalus ridibundus*, a bird that usually lays three-egg clutches. Both parents care for the chicks, which are able to leave the nest soon after hatching but need feeding until fledging (Makatsch 1952). The chances of survival to fledging strongly depend on the amount of food provided to the nestlings, so the crucial factors are timing of hatching, food abundance and quality, and the parents' age, experience and quality (Morris *et al.* 1991, Monaghan *et al.* 1998, Prevot-Julliard *et al.* 2001). Experimental enlargement of broods has been shown to lower the quality of chicks, since they fledge at a lower mass than chicks from unmanipulated broods (Monaghan & Nager 1997). Moreover, the third egg of the Black-headed Gull is usually the smallest within the clutch, and the chick that hatches from this egg has the lowest chance of survival (Morris *et al.* 1991, Lee *et al.* 1993, Royle & Hamer 1998).

In studies based on detailed observations, CBP has been found in about 10% of Black-headed Gull clutches (Duda *et al.* 2003, Ležalowá-Piálková & Honza 2008). Such estimates, however, may be underestimates as compared with assessments based on biochemical analysis (Grønstøl *et al.* 2006). The frequency of parasitism in this species estimated from protein fingerprinting of egg albumen was in fact much higher as this yielded an average of 34% of clutches parasitized, sampled in three different colonies (Duda *et al.* 2008).

Many aspects of breeding biology in the gull family are described, but CBP has rarely been studied (Moynihan 1955, Pierotti 1980, Nisbet & Drury 1984, Duda *et al.* 2003, Duda *et al.* 2008, Ležalowá-Piálková & Honza 2008). Rejection and acceptance of eggs dumped in Black-headed Gull nests have not been examined in terms of host–parasite relatedness. In this paper we provide evidence based on isoelectric focusing (IEF) profiling that host females accept or reject an egg according to their relationship with the female that parasitized her nest. As experimentally exchanged eggs were accepted in the host nests, this behaviour seems to be based on adult individual recognition, rather than on egg morphology similarity.

METHODS

Field methods

The study, involving observations and albumen sampling, was conducted in two Black-headed Gull colonies in the vicinity of Siemianówka Reservoir (NE Poland, 52°56'33"N, 23°47'15"E). In 2005, 111 nests (*c.* 16%) were sampled in a colony of about 700 nests on an island (S1). In 2006, 102 nests were sampled in a colony of about 200 nests on another island (S2), 5 km southeast of S1. The position of each nest was located and stored with a GPS receiver. We extracted a small amount (around 1% of egg volume) of egg albumen as soon as each egg appeared in the nest. Afterwards the shell was glued with cyanoacrylid glue and left in the nest. If this sampling is done with enough care this is a noninvasive technique that does not reduce hatching success (Andersson & Åhlund 2000). Methods differed between the colonies. In 2005 we found a colony with nests already established. We sampled eggs from randomly selected nests in that colony. Nests at different laying stages were in the sample, so the egg-laying order was not always known. To determine the precise timing of laying parasitic eggs in the clutch, we searched through the colony site (S2) each day for nests at the single-egg stage in 2006. Such nests were included in the study, and all the eggs found in them were individually marked and albumen sampled. Nests were monitored every day until the day the eggs hatched or were depredated. The details of the sample storage conditions, electrophoresis and gel reading are given in Duda *et al.* (2008). We regarded an egg as rejected if we found a previously marked egg out of the nest cup within two days after the laying date (Ležalowá-Piálková & Honza 2008).

Egg-switching experiment

In 2006 we experimentally exchanged eggs between different nests in S2. This experiment used 20 nests in the two-egg stage, selected from the S2 nests not sampled in the work described above. One egg from each nest was reciprocally exchanged between five pairs of nests 1 m apart from each other. The same was done with five pairs of nests 25–30 m apart. The nests were checked every day for the next 12 days. On the 13th day of the experiment, 18 eggs were returned to their own nests and one egg was left in the foster nest, because the matched nest had been abandoned.

Protein profiles of females

As the albumin sample is secreted in the female's oviduct, it represents the maternal genotype only and is useful for parasitic egg identification and testing of the difference between individuals' pairwise relatedness (White 1991, Andersson & Åhlund 2000). Samples of all eggs from one nest were put on the same gel together, and the pattern of scored bands gave the protein profile of the female(s) that laid those eggs. As standard, 2 samples run on other gels were placed on both sides of each gel. The female whose eggs outnumbered the others in this nest was classified as the host (Duda *et al.* 2008). When the number of eggs in a nest from two females was equal we could not assign host or parasite status, but we used those data for estimation of the relationship coefficient between them.

To score the females' protein profiles we used the procedure described in Duda *et al.* (2008). We found a maximum of 47 different bands for all samples, and for the analyses we used only 45, as the frequencies of two of them were higher than 0.993 (Isabel *et al.* 1999). The probability that two females can share the same band pattern is x^f, where x is the mean probability that the band present in one profile is also present in another one, and f is the mean number of bands in the profile of one individual (Jeffreys *et al.* 1985ab). In our study $x = 0.425$ and $f = 18.99$, then $x^f = 8.77 \times 10^{-8}$, which is rather low. After finding cases of parasitism, the profiles of those females were double-checked by the independent researcher. A previous study based on observations of laying females, showed that protein fingerprinting correctly recognized two different females even if profiles differed in one band only (Andersson & Åhlund 2000). When profiles differed in only one faint band the eggs were scored as one female's. In 8 doubtful cases, slightly different profiles were scored as one female's, to avoid overestimation of CBP frequency, especially in cases of closely related host–parasite pairs.

Relatedness among females

We used two measures to assess the relationship between females. One was the band-sharing (BS) coefficient, that shows how many identical protein bands are shared by two females (Andersson & Åhlund 2000). The second was the r coefficient for dominant markers, calculated with SPAGeDi 1.2 software (Hardy & Vekemans 2002) and used for analysis of the correlations with geographical distance. The r-value for dominant markers does not show the real probability of having the same alleles and may have values outside the 0 – 1 range (Hardy 2003). Without standardization of calculated values according values of r of individuals of known relationship (unrelated and closely related), the utility of dominant markers for relatedness estimation is rather limited. Despite the fact that they usually overestimate relatedness between full-sibs, the estimators of relatedness coefficients are well suited to characterize spatial genetic structure (Hardy 2003). For the test we assumed a low rate of inbreeding, with 0.1 as the value of the inbreeding coefficient.

To test the assumption that females nesting in close vicinity are more related to each other than to more distant females, we compared mean relatedness within females that nest closer than 1 m with mean relatedness within females that nest more than 1 m from each other. We performed the same test to compare the second, more distant group (4 m distance) versus females nesting farther apart. Differences in mean values of relatedness between females nesting in different distance classes were tested with a two-sample randomization test (100,000 randomizations), using Rundom Pro 3.14 software (Jadwiszczak 2009).

RESULTS

We found conspecific brood parasitism in both colonies studied. Analyses of IEF profiles allowed us to find a single female that laid eggs in two nests, meaning that she acted as host and parasite simultaneously. The proportions of parasitized nests and parasitic eggs in colony S1 (22% of nests, 11% of eggs) were more than double the corresponding proportions in S2 (10% of nests, 4% of eggs) (test $\chi^2_1 = 4.04$; $P = 0.04$ for nests, test $\chi^2_1 = 6.31$; $P = 0.01$ for eggs; Table 1). There were three cases of parasitic eggs laid as the first in the empty nests, and one case only of a parasitic female laying the last egg. In this single case, one of the host's eggs was replaced in the nest by the parasitic egg. Most cases of parasitizing occurred early in the season, within the first 5 days of the population wide laying period; only two parasitic eggs were laid on the 10th or 11th day of the laying period, 4 days before we found the last egg laid in that colony. In 10 parasitized nests there were only two eggs for which we could not classify the identity of the parasitic egg.

The majority of parasitized nests (69%, 22 of 32 clutches) consisted of two host's eggs and a single parasitic one. Mixed clutches were found in all parts of the colony (central and peripheral). The mean number of eggs (2.13 ± 0.86 SD) found in the nests without CBP was higher (Mann–Whitney test: U = 2444, $P < 0.005$) than the number of eggs laid by the host in the parasitized nests (1.64 ± 0.58). Although the females that have accepted parasitic eggs incubated larger clutches (2.7 ± 0.7 compared to non-parasitized: 2.13 ± 0.86 Mann–Whitney test U = 2207, $P = 0.005$), it should be pointed out that in one case only the total number of eggs in parasitized nest exceeded three eggs. This nest was found with all four eggs already laid, two eggs were host eggs and an additional two were laid by two other females.

Only two (6%) of all parasitic eggs (one per colony) were ejected from the nest within two days after laying. This result was based on naturally occurring parasitism. Similarly in experimental clutches, only one clutch was deserted in the remaining 19 nests and all experimentally transferred eggs were incubated in the regular way.

The global BS for all females within the colony was similar for the two colonies: 0.66 (± 0.11) for S1 and 0.69 (± 0.12) for S2 ($P = 0.05$, two-sample randomization test). The corresponding values for host–parasite female pairs in S1 and S2 were significantly higher than the mean values for the colonies (0.88 ± 0.09 for S1; $P < 0.001$ and 0.79 ± 0.15 for S2; $P < 0.01$; two-sample randomization test).

Table 1. Number of sampled clutches and eggs, number of parasitized clutches and parasitic eggs in the two studied colonies of a Black-headed Gull. S1 was sampled in 2005, S2 in 2006.

Colony	Sampled clutches	Sampled eggs	Parasitized clutches	Parasitic eggs
S1	111	241	24 (22%)	26 (11%)
S2	102	236	10 (10%)	10 (4%)
Combined	213	477	34 (16%)	36 (8%)

Table 2. Average host–parasite relationship coefficient ($r_{\mathrm{H-P}}$), and relatedness between females nesting at distance up to 1 meter (r_{0-1}) and up to 4 meters (r_{0-4}). Differences were tested with two-sample randomization tests (100,000 randomizations).

Colony	$r_{\mathrm{H-P}}$	r_{0-1}	$P(r_{\mathrm{H-P}}$ versus $r_{0-1})$	r_{0-4}	$P(r_{\mathrm{H-P}}$ versus $r_{0-4})$
S1	0.87	0.14	0.0001	0.11	0.0001
S2	0.49	0.04	0.01	0.01	0.0001

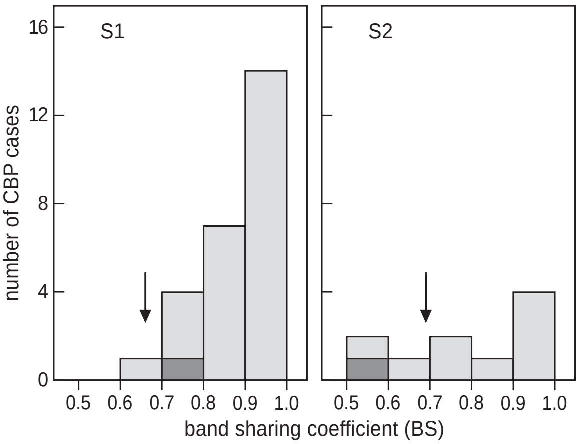

Figure 1. Band sharing coefficients of females involved in brood parasitism (light grey boxes) and egg rejection (dark grey boxes). Given for colonies S1 (2005) and S2 (2006). The arrows indicate the average band sharing coefficient for all females in the colonies.

We expected females nesting closer to each other to be more closely related than the colony mean. Indeed, for both colonies the relationship coefficient for dominant markers decreased slightly but significantly with increasing distance between nests of compared female pairs (Pearson correlation: $r = -0.14$, $P < 0.001$ for S1; $r = -0.01$, $P < 0.001$ for S2). In both colonies, however, the average relationship coefficient for dominant markers was significantly higher between host and parasite than between females nesting within 4 m, and within 1 m (Table 2).

More than half of the parasitic females were related to the host at BS > 0.9. We did not find any parasitic egg laid by a female having BS with the host lower than 0.5 (Figure 1). Parasitically laid eggs were generally accepted and incubated by the hosts, and the rare rejections were for eggs of females not related to the host (BS close to the mean BS for that colony). The accepted parasitic eggs were laid by females significantly more closely related to the host female ($n = 34$, BS = 0.87 ± 0.11) than were females whose eggs were rejected ($n = 2$, BS = 0.63 ± 0.15; two-sample randomization test, $P < 0.01$). We found three cases of possible parasitism preceding clutch initiation by the host. This might constitute cases of nest take-over. In those nests the first egg was laid and then removed from the nest, and after 3–10 days, the egg(s) of another female were found in the nest. Those females were less related to the host (BS = 0.76 ± 0.12) than females whose eggs were accepted (two-sample randomization test, *P* = 0.04).

DISCUSSION

Although previously thought rare and not even worth consideration, conspecific brood parasitism is being described in an ever-growing number of species (MacWhirter 1989, Payne 1997, Yom-Tov 2001). CBP now appears to be an important component of reproductive success, able to significantly influence an individual's fitness (Åhlund & Andersson 2001). In gulls, a well studied group of birds, parasitism within species has not been studied in detail, while other aspects, such as clutch size limitation or the influence of age on breeding success, are known quite well (Fetterolf & Blokpoel 1984, Bańbura & Zieliński 1990, Bukaciński & Bukacińska 1995, Kilpi *et al.* 1996, Heldbjerg 2001, Duda *et al.* 2008, Ležalowá-Piálková & Honza 2008). Many experiments with gull eggs have shown a general tendency for adoption of added eggs, both for real eggs and dummies (Trubridge 1980). It is now apparent that CBP operates in those birds, and we know that at least in the Black-headed Gull it is a nonrandom process, which is strongly biased towards related females.

The CBP frequency we found in the studied Black-headed Gull colonies is similar to the frequency reported for this species in the Czech Republic (Ležalowá-Piálková & Honza 2008). The frequency of CBP may differ significantly between separate populations of a given species (McRae 1997). We observed the majority of egg dumping in the first few days of the egg-laying period, and the parasitic eggs were usually the first or second in the clutch. Such behaviour may increase the parasitic eggs' chances of hatching. It is conceivable that some of these cases were the result of nest desertion or nest take-over, especially in those three cases when eggs were laid a few days after the first egg was removed, but it would be difficult to explain why the second female in such a nest usually was closely related to the female that laid the first egg. As Black-headed Gull females in good condition are able to lay clutches that exceed the usual number of 3 eggs (Nager *et al.* 2000), and as the chicks from enlarged clutches survive less well, being a parasite seems to be more profitable than enlarging a female's own clutch. Interestingly, we rarely observed enlarged clutches that were the effect of parasitism, and usually the host female that accepted a parasitic egg had fewer of her own eggs in that nest (in ten cases only one egg). It may be that parasites choose nests of females that are unable to lay the full normal complement of eggs. It could also be that the host female stops laying her own eggs when parasitized (Power *et al.* 1989), or (partly) adjusts her number of eggs to the number of eggs already present in the nest, independent of the type of eggs already present (as is typical for indeterminate layers). It is worth noting that such behaviour lowers her reproductive success but the costs of rearing the hatchlings stay the same.

In bird species other than gulls, the parasite may lay eggs in a nest that happens to be available regardless of the relationship to the host, as in American Coots (Lyon 1993), or it may prefer nests of closely related females, as in Goldeneyes or Eiders (Andersson & Åhlund 2000, Waldeck *et al.* 2004). The tactic depends on a number of factors acting in concert, such as the philopatry of the species, the ability to distinguish related from unrelated individuals, and the reaction of the host to egg laying by the parasite. In Black-headed Gulls natal philopatry is very strong, young birds that return to their natal colony for breeding tend to occupy territories close to their place of birth (Prevot-Julliard *et al.* 1998). Young gulls learn to recognize own parents from other individuals at 3–4 days of age (Charrier *et al.* 2001), they easily distinguish own siblings from other chicks in the colony (Burger 1998). As they can recognize individuals in the herd, it is not surprising that they very often migrate in closely related groups, and occupy common territories at wintering areas (Snow & Perrins 1998).

Theoretically, the parasite should tend to avoid parasitizing relatives as it may impose additional costs on the hosts, however this may maximize the chance of acceptance and they may thus choose such nests regardless of the costs (Andersson 2001). Hosts may adopt different tactics to deal with being parasitized, like chasing other females from the nest, expelling the added eggs, burying them in the nest, or accepting the parasitic eggs (Hamilton & Orians 1965, Gaston *et al.* 1993, Lopez-Sepulcre & Kokko 2002, Ležalowá-Piálková & Honza 2008).

We found that Black-headed Gull parasites lay eggs in the nests of closely related females. In the colonies studied, we observed no case of an egg being laid in the nest of a female related less than the average value for the colony. We cannot say whether this was the result of parasite choice or due to the behaviour of prospective hosts selectively declining to chase related females from the nest. In theory, however, a parasite may try to minimize the risk that her egg will be expelled when the host can distinguish related from unrelated individuals (Andersson 2001, Lopez-Sepulcre & Kokko 2002).

The results of the egg-switching experiment, and the widely known cases of adoption of eggs or egg-shaped objects (Trubridge 1980), show that gulls do not reject eggs added by researchers. In nature the mechanism by which added eggs are allowed to stay in the nest can involve recognition of related adults. Eggs of related females are accepted, and also eggs found in or near the nest bowl without any sign of the presence of other females are treated as the host's own. In Goldeneyes the females allow related females to lay eggs but chase away unrelated ones (Andersson & Åhlund 2000), and we know that gulls learn easily to distinguish their relatives from other birds in a colony (Burger 1998); vocalization seems to play the most important role here (Holley 1984). The rare instances of rejection of eggs, soon after less related females laid them, may be cases in which the host caught the parasite red-handed in the act of laying.

Kin selection theory (Andersson 2001) may explain the pattern of acceptance of parasitic eggs in our experiments. Acceptance of eggs laid by a very closely related parasite, lowers the reproductive success of the host, but may be compensated at least partially by inclusive fitness, with the loss being smaller if host–parasite relatedness is higher (Andersson 2001, Lopez-Sepulcre & Kokko 2002). We can even imagine extreme cases in which it may be profitable for the host to accept eggs laid by its sister or mother. In the studied colonies the mean clutch size was lower than the three eggs typical for the species. It may suggest that at least some females have arrived at the breeding colony in poor condition after migration and cannot lay a full clutch early in the season. A probable reason for that is the high cost of egg production, reaching almost five daily BMR expenses (Paynter 1974). As Black-headed Gulls have three brood patches, hosts that accept an additional egg, third in a clutch, may not significantly raise the overall cost of incubation (Niizuma *et al.* 2005). Moreover, Brown & Lang (1996) suggest that the female with low social status acting as a host may prevent future acts of aggression towards the hatchlings from the parasite female. It has been observed in the studied species that some hatchlings may seek actively for foster parents to adopt them (Groothuis *et al.* 2006), which may lower the costs of raising the hatchlings.

The observed average number of eggs per nest, lower than typical for the species, suggests food shortage at the beginning of the breeding season in the studied area. In all but one case accepting the parasitic eggs did not increase the brood size over three eggs. So, in general, in the parasitized nests the costs of incubation were not significantly higher than they would be without parasitism. It would be very interesting to test if a similar CBP pattern would be observed in a colony with additional feeding, where females would not have problems in gaining resources for egg production.

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SAMENVATTING

Ondanks de vele gedetailleerde studies over de broedbiologie van meeuwen is er nog vrij weinig bekend over intraspecifiek broedparasitisme bij soorten van deze groep. Zo is binnen de familie van de *Laridae* slechts bij enkele van de 60 soorten vastgesteld dat vrouwen eieren leggen in nesten van soortgenoten. In deze studie hebben de auteurs gedurende twee jaar in het noordoosten van Polen met behulp van peptide- of proteïnevingerprintkaarten de mate van broedparasitisme bestudeerd in twee kolonies van de Kokmeeuw *Chroicocephalus ridibundus*. Een peptidekaart maakt gebruik van het feit dat het eiwit in een ei slechts eiwitten bevat van de moeder. De vingerprint laat daarbij een uniek individueel patroon zien. De auteurs vonden dat in de twee populaties respectievelijk in 22% en 10% van de broedgevallen sprake was van intraspecifiek broedparasitisme. De vrouwen die hun eieren legden in de nesten van andere vrouwen, waren meer dan gemiddeld aan de geparasiteerde vrouw verwant. In slechts enkele gevallen werden vreemde eieren door de geparasiteerde vrouw verwijderd. In deze gevallen bleken de geparasiteerde en de parasiterende vrouw minder dan gemiddeld aan elkaar verwant te zijn. De auteurs stellen daarom dat bij Kokmeeuwen kin-selection hoogstwaarschijnlijk een belangrijke rol speelt bij intraspecifiek broedparasitisme.

(KvO)

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