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ORIGINAL ARTICLE

The dark side of the red ape: male-mediated lethal female competition in Bornean orangutans

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Abstract Female Bornean orangutans (*Pongo pygmaeus wurmbii*) are mainly solitary and philopatric, leading to adult female relatives sharing adjacent and overlapping home ranges. Females tend to be intolerant of unrelated females, with whom they also may have overlapping home ranges. However, fights that lead to injuries are extremely rare and lethal aggression had never been observed. Here, we report the first case of lethal female-female aggression during over 26,000 h of focal data collected on adult females at Tuanan, Central Kalimantan: A young female, who had recently lost her infant, attacked an old resident female. The interaction's unique feature was that the attacking female was supported by an unflanged male, who had been in consort with her during the week preceding the attack and was responsible for the lethal injuries to the victim. The victim received protection from a flanged male who was probably attracted to the noise generated by the fight. We conclude that even in a species in which coercion is frequently observed in male-female interactions, female leverage over males can coax males into providing services, such as coalitionary support.

Keywords Orangutan · Lethal aggression · Coalitionary attack · Female-female competition · Male support

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Significance statement In this paper, we report the first observed case of female-female lethal aggression in orangutans. This case was extraordinary because the attacking young female recruited the help of a male, who caused the injuries that eventually killed the old, resident female. The old female that was attacked subsequently received protection from a male. The males were thus in effect acting as hired guns. The effective recruitment of males into conflicts between females is novel and unique among apes. It shows an unsuspected degree of leverage of sexually attractive females over unrelated males and can coax males into providing services, such as coalitionary support, in a species otherwise better known for their sexual coercion by males.

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Introduction

Aggression serves ultimately to gain access to limiting resources (Wilson 1975). Although aggression among primates is frequent, lethal attacks are very rare. Young infants are the most likely victims of such attacks in many primate species (van Schaik 2000), whereas weaned individuals are far less likely to be a target of lethal aggression. Among adults, escalated dyadic fights can turn lethal, as when males attempt to take over a group controlled by another male (e.g., Wich and Sterck 2007), but in the majority of lethal attacks on mature conspecifics, the aggressors attack together and outnumber the victims. Indeed, such joint coalitionary attacks have been reported in chimpanzees (*Pan troglodytes*: Mitani et al. 2010; Wilson et al. 2014), red colobus (*Procolobus badius:* Starin 1994), capuchin monkeys (*Cebus* spp.: Miller 1998; Gros-Louis et al. 2003; Scarry and Tujague 2012), muriquis (*Brachyteles arachnoides*: Talebi et al. 2009), and spider

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monkeys (*Ateles geoffroyi*: Campbell 2006; Valero et al. 2006). In most cases, mature victims were killed by same-sex coalitions, and most victims were males. In the best-studied cases, involving chimpanzees, attackers greatly outnumber victims and favor unprovoked, "surprise" aggression. Both tactics serve to reduce individual risk through use of an imbalance of power (Wrangham 1999; Wrangham and Glowacki 2012). A major feature of these joint coalitional killings is that the attackers ignore victim's signals of submission and seem to be focused on inflicting wounds rather than just chasing the opponent away from the resource (e.g., food or mate).

Here, we report a case of lethal aggression in Bornean orangutans that deviates from this typical pattern of joint coalitionary attacks. Instead, males joined ongoing female-female agonistic interactions. Even though males sometimes join or interfere in such interactions in other primates (e.g., Gouzoules 1980; Seyfarth 1978), these cases have so far never been reported to result in the death of a female victim. Here, two males were involved: one provided active support for the aggressor and the other protected the victim.

Female Bornean orangutans (*Pongo pygmaeus wurmbii*) are philopatric, whereas males disperse from their natal range (Morrogh-Bernard et al. 2011; Arora et al. 2012; van Noordwijk et al. 2012). Female home ranges are relatively small (around 300 ha in Tuanan, Central Kalimantan) and stable over time (Wartmann et al. 2010). Maternally related females (mothers, daughters, half-sisters and their offspring, which know each other since birth) tend to have adjacent and overlapping ranges and form social clusters (Arora et al. 2012; van Noordwijk et al. 2012), as in Sumatran orangutans (*Pongo abelii*: Singleton and van Schaik 2002). Related females spend more time in association and are more tolerant towards each other than to unrelated females with similar home range overlap (van Noordwijk et al. 2012). Nonetheless, home ranges, as well as core areas (>50 % use) of related and unrelated females (here defined as females descended from different maternal grandmothers), may overlap to a similar degree in Tuanan (Wartmann et al. 2010; van Noordwijk et al. 2012), in apparent contrast to some other Bornean sites (Knott et al. 2008, 2010).

Although between-matriline intolerance resulted in a few observed cases of female-inflicted non-lethal injuries in Sumatran orangutans (SSUA unpublished data), only six female-female attacks with physical contact have been observed in Tuanan in 11 years of study. In one of these, both the aggressor and the victim of the encounter described here were involved. However, none of these six attacks resulted in visible injuries (current study: Table A Supplement). Given the modest intensity of aggression and low incidence of wounding when a female attacks another female independently, support by a male, with their much longer canines, may strongly increase the severity of injuries.

Methods

The lethal attack took place at Tuanan (2° 15′ South, 114° 44′ East), which is situated in the Mawas Reserve, Central Kalimantan, Indonesia. The research area consists of 750 ha of peat-swamp forest, previously subjected to commercial selective logging in the 1990s and recovering since then. The orangutans live at a density of approximately 4.5 individuals per square kilometer (van Schaik et al. 2005), which is among the highest in Borneo (Husson et al. 2009). All resident individual orangutans in Tuanan are habituated.

Orangutans are followed during nest-to-nest follows, whenever possible for a maximum of ten consecutive days, using focal animal sampling following standardized protocols (cf. van Schaik 1999; http://www.aim.uzh.ch/research/orangutannetwork/sfm.html). It was not possible to record data blind because our study involved focal animals in the field. Observers frequently conduct inter-observer reliability tests. This population has been intensively studied since 2003, and most of the individuals, especially the resident females and their offspring, have been observed since this time. Their relatedness, social relationships, and ranging patterns are already largely known (Arora et al. 2012; van Noordwijk et al. 2012; Ashbury 2013). By the time of the attack on July 13, 2014, over 26,000 h of focal data had been collected on adult females.

The participants

Four adult individuals, two females and two males, as well as one immature male were involved in the attacks reported here (Table 1). Kondor, the attacker, is a young female who was known since 2003 when she was estimated to be around 4–5 years old and still nursed by her mother. She gave birth to her first infant in February 2012, but it died 6–9 weeks before the attack. In the 2 weeks before the attack, Kondor was regularly seen in association with various flanged and unflanged males. Just before the attack, she had been followed for seven consecutive days, during the last five of which she was in a consortship with unflanged male Ekko.

Sidony, the victim, was an adult, resident female ranging in the southeastern part of the study area. To our knowledge, unlike most other females in the study population, Sidony's home range did not overlap with those of adult female maternal relatives. She had at least two daughters: the younger, adolescent one had not yet settled in her own range, while the older one, born around 1997, has not been seen with certainty since early 2006. Despite her advanced age, Sidony had a healthy 4-year-old son at the time of the attack. She spent little time in association with her unrelated female neighbors (0.3 % of her 768 h of focal time up to the attack, compared to almost 2 % on average for females with maternally related neighbors (see also Fig. 1)), despite their overlapping home

Table 1 Participants of the attack

Individual	Class	Age	Known[a] since	Role in the attack
Sidony	Adult female with infant	>35	2007	Target of the aggression; suffered fatal injuries; protected her infant and tried to escape multiple times, but did not actively defend herself
Sony	Male dependent immature	4.5	Born March 2010	Sidony's son; not the target of the attack; not injured; after Guapo arrived also involved in protecting his mother (only against Kondor)
Kondor	Young female	ca. 15	2003	Main aggressor: initiated, sustained and prolonged the aggression; inflicted a number of injuries
Ekko	Unflanged male	>25	2003	Aggressor: supported Kondor; inflicted a number of major and life-threatening injuries
Guapo	Flanged male	>35	2007	"Defender": protected the victim in an active, but non-aggressive way; his intervention kept Ekko at bay and reduced the physical aggression directed at the victim by Kondor

[a] Reliably recognized and subject to focal follows when found

ranges (van Noordwijk et al. 2012). Only two previous encounters between Sidony and Kondor were witnessed, and these occurred when Kondor was still an adolescent. During one of these encounters in 2009, Sidony chased, hit, and bit Kondor, who was repeatedly approaching Sidony's ca. 7-year-old daughter, whereas Kondor persisted in her attempts to approach. Thus, the two females had already a history of aggressive interactions.

Ekko has been regularly recorded throughout the study area since 2003, and by 2014, he was larger in body size than all known females and dominant over all other regularly seen unflanged males. Moreover, changes in his facial features as well as behavior suggest that he was already in the process of growing flanges (by August 2015, he had fully developed flanges) (cf. Dunkel et al. 2013; Marty et al. 2015). Over the years, Ekko was often observed in association with resident females (during 31.5 % of 534 h of focal follow hours on Ekko since 2003), including Sidony.

The final participant, flanged male Guapo, was first seen in the area in 2007 and again in 2012. Since then, he was recorded only rarely (on average twice a year). However, Guapo has sired two offspring with females ranging at the periphery of the study area before the start of observations in 2003. Neither Guapo nor Ekko sired any of Sidony's known offspring, and the mature participants in the attack were not related (M. Krützen, pers. comm.; see also Arora et al. 2012).

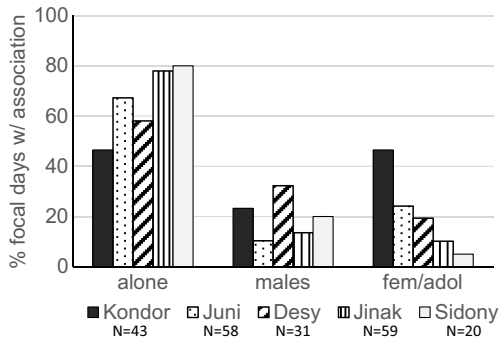

Fig. 1 Comparison of the % of nest-to-nest follow days that a female with a 0–3-year-old infant was not in association with any other independently traveling individual, with a male (unflanged or flanged) or with another female (with or without offspring) or adolescent. Females are in order of known parity: Kondor with 1 infant (died), Desy and Juni with 2, and Jinak and Sidony with more. Note on the same day a female can be in association with males and females. Kondor vs Juni days with female association $\chi^2 = 4.58$, df = 1, $P = 0.03$

Results

We distinguish two phases of the encounter: before and after the arrival of the flanged male. Figure 2 provides a timeline of the attack (see also Table B in the supplementary material for a detailed description of the encounter).

Phase I: coalitionary attack

During a focal follow of the female Kondor and the unflanged male Ekko, who were in association, they encountered (defined as an approach within 50 m) Sidony and Sony in the core area of Sidony's home range. Initially, Kondor and Ekko approached to within 10 m and Sidony did not retreat right away. After about 10 min, Ekko sexually inspected Sidony but returned to Kondor to mate with her, whereas Sidony started to move away. Kondor then interrupted her mating with Ekko, approached Sidony, and physically attacked her. Immediately, Ekko joined Kondor in the attack, which continued for 33 min (see Fig. 2) with two brief interruptions. During the first fight, Kondor and Ekko took turns attacking Sidony for 12 min. When one was involved in physical aggression, the other

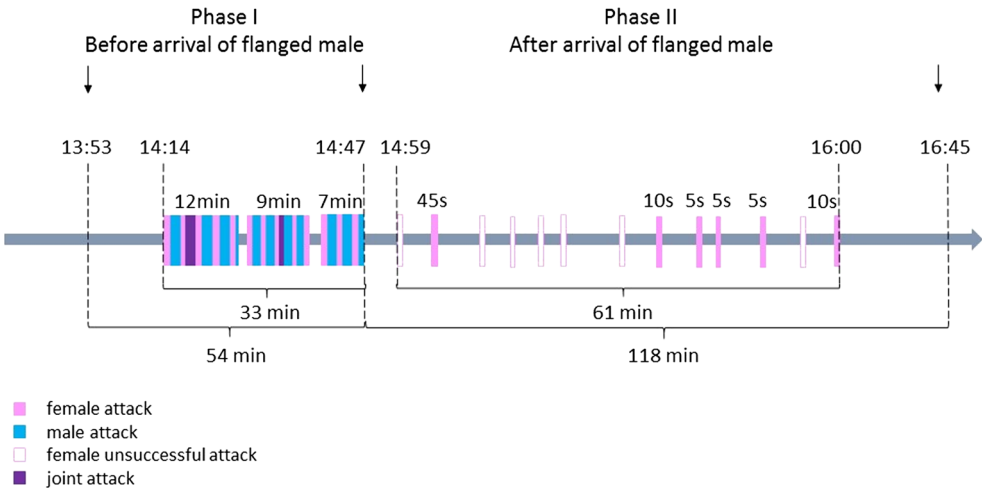

Fig. 2 Diagram of the aggression

watched and blocked the victim's escape, leaving no more than 45 s pause in between. In addition, on two occasions, Kondor and Ekko simultaneously attacked the victim. The attack therefore was coalitionary, continuous, and coordinated. Two subsequent attacks took place, lasting 9 and 7 min, respectively. All attack sessions were initiated by Kondor, but Ekko inflicted the most serious injuries and was most effective in denying Sidony the chance to escape.

Phase II: intervention

The dynamics of the fight changed when the flanged male Guapo arrived, from likely >100 m away, because Ekko retreated from the fight location (>10 but still <50 m distance). Guapo briefly chased Ekko and then mated with Sidony, while Kondor continued to harass her and even bit Sidony in her foot. Whenever Kondor attacked Sidony, Sidony would scream, which prompted Guapo to approach and either move towards Kondor, position himself between the females, or move away together with Sidony. Whereas 85 % of the attacks were physical in phase I, only 2 % were physical in phase II, after Guapo's arrival (Table 2). Moreover, all remaining attacks in phase II were by Kondor alone. Sidony sustained major injuries in phase I but only minor scratches and bites in phase II. This confirms that Ekko caused the most serious injuries and that Guapo was effective in protecting Sidony against additional damaging attacks.

About 45 min after the last attack (Fig. 2), Sidony began building a nest, while all other participants were feeding. All individuals made a nest within 50 m of each other, with Guapo in between Sidony and Kondor whereas Ekko's nest was farther away.

Subsequent events

On the morning of day 2, Kondor left her nest and immediately approached Sidony, but Guapo intervened instantly and mated with the victim. Ekko left the association in the morning. Kondor kept trying to attack Sidony, but Guapo intervened every time and interrupted physical contact between the females. Kondor left Sidony (>50 m) at the end of the day and was followed by Guapo. Both Sidony and Sony frequently groomed and licked her wounds.

Table 2 Result of flanged male intervention

	Before intervention	After intervention
Duration of aggression	33 min	61 min
Total time of physical aggression	28 min	1 min 20 s
Aggressors	Ekko, Kondor	Kondor
Type of attack	Continuous, coordinated, and coalitionary	Brief, single attacks
Type of injuries	Serious wounds resulting from bites on arms and legs; bites and scratches on the back and head	Minor bite wounds on hands and feet
Prevented and interrupted attacks	None	All
Unsuccessful attacks	None	Many

On day 3, Kondor came back to Sidony twice and tried to attack, but Guapo followed Kondor and intervened. All of his interventions were non-aggressive, as on previous occasions. Kondor eventually left, followed by Guapo. Guapo was not observed to mate with Kondor that or any other day following the attack.

On day 5, Ekko came back alone to the location of the attack, where Sidony was still present, since she had not moved. Ekko did not attack her. On day 6, Ekko revisited the location of the attack again and watched Sidony for 30 min from a distance of 15 m. He did not approach her nor was he aggressive towards her.

On day 10, Sidony's offspring Sony left and nested alone over 100 m away from his mother and did not approach within 50 m for the subsequent days. Sidony was last seen alive on day 12. She was found dead on the ground on day 16. The stage of decomposition suggested she died one or at most 2 days before she was found, about 2 weeks after the attack.

Sidony's infant Sony has been seen since the attack and was observed in March and April 2015 in association with his adolescent sister, indicating he had survived without his mother. He was around 4.5 years old at the time of her death and not yet weaned, whereas so far the youngest known immature to be completely weaned in Tuanan was 5.5–6 years (van Noordwijk et al. 2013). Kondor has frequently been seen throughout the study area since the attack. She showed clear sign of pregnancy (and a human pregnancy test was positive) in November 2014 and gave birth in early April 2015. Therefore, she conceived around the time of the attack or shortly afterwards and within only 2–3 months after losing her first offspring.

Discussion

Lethal aggression among adult primates is rare. Individual attacks that turn lethal are most likely in territorial species (Palombit 1993), but orangutans are not territorial, and aggression among males is far more likely to escalate than that among females (Table A Supplement). Male-male fights in orangutans are always dyadic and are known to lead to facial scars, missing fingers and toes, and even death (Knott 1998; Dunkel et al. 2013). In group-living species, dyadic conflicts, although much more common, are much less likely to have lethal outcomes than conflicts involving same-sex coalitions, suggesting that the greater imbalance of power produced by the numerical asymmetries is a key factor.

The orangutan case reported here in which a female was the victim does not comfortably fit the pattern of joint coalitional killings seen in other primates. The attack involved between-sex coalitions, with males providing agonistic support to the females: one supporting the aggressor and other protecting the victim. This is quite unexpected, as wild orangutan males and females have never been reported to form coalitions before. Moreover, in this population, females spend little time in association (Fig. 1) with males, except during a few months prior to conception (Mitra Setia et al. 2009), i.e., once per ca. 7 years. Although captive studies report male interventions in female conflicts, these were peaceful and tended to terminate aggression (Edwards and Snowdon 1980; Zucker 1987), whereas in another study the interventions in female-female agonism were by a female or a juvenile male (Tajima and Kurotori 2010). There are no reported cases of male intervention in female conflicts from the studies on wild orangutan populations. In fact, in Tuanan, only one other male intervention in a between-female conflict has been observed so far (B. Spillmann pers. comm.). Nonetheless, because females attacking alone are not known to severely injure other females, the explanation for the lethal outcome of the attack should be sought in its mixed-sex nature and imbalance of power during the first phase of the attack.

Fundamentally, the observed polyadic interaction is an expression of female-female competition as the aggression was initiated, prolonged, and maintained by Kondor against Sidony. Indeed, Kondor continued with physical harassment even after the departure of her male coalition partner, while her partner, Ekko, was not aggressive towards Sidony during a subsequent encounter a few days after the attack, once Kondor was no longer in association with Ekko.

Previous observations at Tuanan showed that female-female competition over range use is intense. Adult female Bornean orangutans are not territorial, i.e., they do not have an "exclusive use" area that is defended. Instead, they establish overlapping home ranges, where mothers spend much of their time alone and only in the company of their own (semi-)dependent offspring. Thus, within their overlapping ranges, females mostly do avoid close encounters especially across matrilines (van Noordwijk et al. 2012). In 2002–2003, an adult female (Sumi) with dependent offspring (Susi) lost her habitat due to logging, mining, and fires. Over a period of several years, she shifted her range into the study area where she had no maternal relatives (Arora et al. 2012). Sumi avoided close encounters by remaining very quiet and upon discovery descended to the ground and moved away as inconspicuously as possible (cf. Ashbury et al. 2015). Even though the resident females chased her whenever they discovered her, Sumi always immediately fled and physical fights were never observed. Sumi eventually died in August 2006 as a result of the attack by a clouded leopard (SSUA unpublished data).

In the current case, the female-female interaction escalated between two residents in different phases of their lives, one old and one early in her reproductive career. Kondor, a young member of the largest local matriline, had recently lost her first infant. In general, adolescent females start to explore beyond their natal home range but settle where they least encountered other females, including their own mother, before the birth of their first offspring (Ashbury 2013). However, after the birth

of her first infant, Kondor still ranged over a larger area than all other known females in similar reproductive state (AM et al. unpublished data). In addition, compared to other mothers with offspring under 3 years old during the same period (July 2010–July 2014), Kondor spent fewer days alone and she associated on many more days with other females and adolescents (Fig. 1). While social play is the major positive social interaction during associations of orangutan mother-offspring dyads (van Noordwijk et al. 2012), Kondor's high association rate was not due to more frequent social play with associates by Kondor and/or her offspring compared to other mother-offspring dyads (Kunz 2015). On the other hand, there is no evidence that Kondor was more often agonistically displaced by other females. Nevertheless, the high encounter frequency does suggest that Kondor was experiencing increased pressure from the other resident females and adolescents (mostly her known maternal relatives).

Infant mortality in wild orangutans is reported to be much lower than that in other great apes (Wich et al. 2009). In the Tuanan population, Kondor's infant is the first to have died in 1084 infant observation months (including all pre-weaned known offspring) or a rate of 0.011 deaths/infant-year. Even though the circumstances of the loss of her infant remain unclear (it seemed healthy at last sighting), it is likely that Kondor's particular condition contributed to her unusual, aggressive behavior. Her consortship with a long-known partner may have contributed to her confidence to fiercely attack the female she had occasionally encountered before and was chased and hit by on at least one occasion when Kondor had just started to roam without her mother in 2009.

Without the involvement of Ekko, it is unlikely that Sidony would have incurred such severe wounds, and the fight would probably have ended within the first 7 min (see Table B Supplement), during one of the breaks in which Sidony started to move away. Ekko's active participation in the attack on Sidony can be interpreted as his investment in the consortship with Kondor. It should be noted that at no time did Ekko attempt to copulate with the victim (he had inspected her briefly before the attack and shown no further interest), and we can therefore reject the interpretation that his injuring Sidony represented extreme force during a forced mating attempt (which have also never been reported to lead to injury). The observation that Ekko did not attack or try to mate with Sidony a few days later when he was on his own supports this argument. Thus, Ekko's participation in the lethal aggression was not due to a mating conflict with Sidony but instead elicited by the presence and actions of the consorted female.

Ekko and Kondor were ranging together for 5 days before the attack. It is likely that to maintain this association and to increase his chances to sire Kondor's next offspring, which was conceived around that time, Ekko supported her during the attack. Benefits from maintaining a tolerant association with a female may include more cooperative mating opportunities, in contrast to coerced matings more often seen during short associations (Dunkel et al. 2013). Therefore, Ekko's behavior can be explained as his investment in maintaining the association with Kondor. By supporting her and showing his fighting abilities, he could influence her choice to willingly maintain her consortship with him.

Young females are known to use sexual proceptivity as a "sexual passport" (e.g., Goodall 1986). By attracting males and associating with them, a young female gains safety to move throughout an area outside her natal range without being at risk of potential aggression from unfamiliar resident females (Ashbury 2013).

In the attack reported here, Guapo intervened in the conflict and separated the aggressors and the victim multiple times over a period of 3 days. Guapo's intervention included threatening the unflanged male, which is nothing unusual as many male agonistic interactions start in the presence of a female (Utami Atmoko et al. 2009). Guapo also approached the female aggressor, positioning himself between the two females separating them and "guarding" the victim, again something not very unusual (e.g., Edwards and Snowdon 1980). None of the actions against Kondor involved aggression on his part, but each either terminated the aggression or prevented physical contact between her and Sidony. A male's interest in securing his access to multiple females may explain Guapo's effort in protecting one female, with whom he may have had a long-term relationship without attacking the other, young one. Nevertheless, perhaps surprisingly, Guapo was not seen to mate with Kondor during or after the attack, nor did he remain in consortship with her after Guapo and Kondor left Sidony together on the third day.

Conclusion

Male-female coalitions have not been described for wild orangutans and must therefore be extremely rare. The most plausible interpretation of the lethal attack here is that males in consort with a female must not only show great tolerance, as when females take food from them (van Noordwijk and van Schaik 2009), but can also be recruited to support them in their competition with other females, including participation in attacks. This suggests that fertile females have great leverage (Lewis 2002) over males, if only because they can end the association by attracting other males, and thus can elicit male services on her behalf, in the form of food sharing or agonistic support. This is all the more remarkable because of the huge sexual dimorphism and high potential for sexual coercion in orangutans, as reflected by the high proportion of matings that are forced (Fox 2002), especially on Borneo (Knott et al. 2010).

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Conflict of interest The authors declare that they have no competing interests.

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