Social Organization and Territoriality of Giant Otters (Carnivora: Mustelidae) in a Seasonally Flooded Savanna in Brazil

by

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ABSTRACT

Giant otters live in family groups, formed by an alpha couple and their off-spring of different ages. The objectives of this research were to investigate the association between individuals, the fidelity of groups to their territories and to investigate if there were changes in the numbers of individuals and groups, and the size and distribution of their territories between two consecutive low-water seasons, in an area of the Pantanal of Brazil. We monitored giant otter groups monthly, between July/2006 and November/2007, on the Vermelho River and on one section of the Miranda River, over a total of 75.8 km. We identified 43 individuals in seven groups. Most association indices between individuals of the same group varied from 1.0 to 0.5. The association levels between the individuals in the two low-water seasons were not random; i.e. groups persisted across seasons. We observed more dispersion of individuals and establishment of new groups during the low-water seasons, and this contributed to the decrease in association of individuals. The average linear size of territories was an 11.4 km stretch of river. There was an average of 10.8 km between the centers of group territories. There was no significant correlation between group size and territory size (r=0.35, n=12). However, the number of latrines ($F_{(1,11)}$ = 13.846, P=0.003; r^2=0.56) and the number of scent-marks ($F_{(1,11)}$ = 13.236, P=0.004; r^2=0.55) increased linearly with the territory size. During the low-water season of 2007, the groups generally maintained the same territories used during the low-water season of 2006, but two of them apparently exchanged their territories. The number of groups was stable in

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the study area since 2003, suggesting that the giant otter population is near carrying capacity in the area and has recovered from depletion caused by the poaching from the 1980's in the Pantanal.

Key-words: *Pteronura brasiliensis*, association, territory size, territory fidelity.

INTRODUCTION

Formation and maintenance of social groups within populations is common in mammals (Greenwood 1980). The knowledge of the social organization of individuals is an important element of the population biology, since it influences gene flow and spatial pattern distribution and can be used in conservation actions. The frequency with which individuals interact can determine the social structure of a population (Whitehead 1997), and can predict the cohesion and maintenance of the group unit.

In most of social species, the maintenance of the group structure is influenced by the retention of individuals in the parental unity (Emlen 1982). Some mammal species are socially organized under reproductive cooperation as in wolves (*Canis lupus,* Van Ballenberghe 1983), mongooses (*Helogale parvula,* Rood 1990) and wild dogs (*Lycaon pictus,* Villiers *et al.* 2003). In these social systems, dispersion and natal philopatry can be related with favorable environmental and temporal conditions as well as individual tactics (Stacey and Ligon 1991). Most social species are spatially organized through the establishment of exclusive territories, which can vary in size and distribution according to many environmental and social factors (Doncaster & Macdonald 1991).

The giant otter (*Pteronura brasiliensis*) is a social species (Duplaix 1980, Schweizer 1992) that lives in family groups with reproductive cooperation. According Duplaix (1980), the groups are composed of an alpha couple and offspring of different ages, which live in actively defended territories. Individuals from the same social group do most of their daily activities together, displaying strong cohesion (Duplaix 1980, Carter & Rosas 1997).

Endemic to South America, the giant otter had its original distribution (from Venezuela to Argentina) reduced, and in Brazil it was restricted to the Pantanal and the Amazon basin since the 90's (Carter and Rosas 1997). The species is classified as threatened by the World Conservation Union (IUCN

2006). During the 60-80's the species was intensely hunted in the Pantanal and decreasing populations were reported in several rivers of the Pantanal, like the Paraguay River, Miranda and Vermelho (Schweizer 1992).

The objectives of this research were to investigate the association between individuals and the fidelity of groups to their territories, and to investigate if there were changes in the numbers of individuals and groups, and the size and distribution of their territories, between two consecutive low-water seasons, in an area of the Pantanal of Brazil.

MATERIALS AND METHODS

From July 2006 to November 2007, we monitored groups of giant otters in the Vermelho River and in a section of the Miranda River, in the Southern 12(he)]TJ/Span<</ActualText<FEFF0053> EFF0053> E(19o)-'n<</ActualText

Fig. 1. Representative of the Giant Otter showing distinctive chest markings by which individuals may be recognized.

also was outstanding in the defense of the group, which was lactating during the reproductive season, and which manifested more attachment to the cubs. We compared the individuals' identities with pictures registered between August/2002 and October/2003 by Ribas (2004) in the same study area. This was used to confirm the presence of the groups in the area since 2002-2003, and also to roughly estimate the age of the individuals that remained there until this study.

We registered the position of the individuals, dens, latrines (places with feces and/or urine) and scent-marks (places with strong giant otter scent, but without feces), with a GPS Etrex receptor (Garmin, Inc., Olathe, KS). We classified dens and latrines as "active" or "inactive", based on presence of damp earth, fresh feces and urine, fallen leaves and dry limbs, or the presence of the individuals.

For the association analysis, we used the half-weight index, which quantifies associations on a scale of 0 (two individuals never seen together) to 1 (two individuals always seen together). This index is generally recommended, as it is known to minimize bias due to sampling techniques (Cairns & Schwager 1987). We used the program SOCPROG (Whitehead 1999) (available at http://www.dal.ca/~hwhitehe/social.html) to do the cluster analysis (Average

linkage). To verify the fidelity of the individuals to their groups, we calculated the percentage of individuals that remained in the family group in the second low-water season, for each group.

We used the GPS TrackMaker 13.1 program (available at http://www.gpstm.com, accessed on 12 - Dec - 2007) to measure territory sizes and overlap, and the distance between the centers. Group territories were measured along the extension of the river channel, and limited by first scent-marks, dens and active latrines.

RESULTS

We identified 43 individuals in seven groups during July/2006 and November/2007. The average number of individuals per group was six (2 to 13 individuals). Considering only the individuals that we encountered, the sex ratio was 19 females: 10 males. However, we could not identify the sex of cubs (n=10) and two adults in the groups. In one case, we observed two consecutive substitutions of the alpha male that accompanied an alpha female. In this situation, we considered only one of them to calculate the sex ratio. We also registered four solitary males. Two of them were subsequently seen in groups. It was not possible to identify the other two solitary males from throat splotches, and we did not include them in the 43 giant otters that composed the groups.

Association

We used 234 encounters with giant otter groups to calculate the association index between individuals. We observed strong associations between individuals of the same group. However, these values differed between the 2006 and 2007 low-water seasons. Most of associations between individuals of the same group varied from 1.0 to 0.5. Association values smaller than 0.5 indicate a low level of association, which occurred when the individual left the group, when the group was formed during the sampling period, or when the cubs were born after the initiation of the research (Fig. 2). The average association between individuals of newly formed groups was lower than between individuals from stable groups. The values of association varied as the group composition underwent minor changes. Most of the groups changed little across seasons and retained from 62 to 100% of their individuals. However,
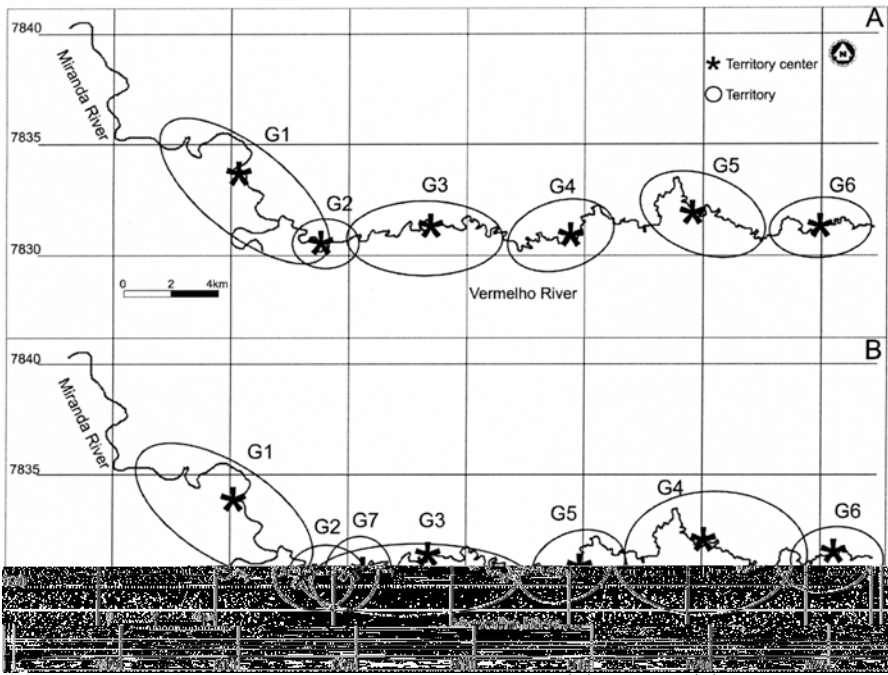
Fig. 2. Territories of giant otter groups monitored on the 2006 (A) and 2007 (B) low-water seasons. Each ellipse represents the territory size of a group (G1 to G7) between July/2006 and November/2007, on the Miranda and Vermelho Rivers, in the Pantanal of Brazil.

in one case, a group formed by just one pair changed one individual and, in another case, a group suffered major changes, retaining just two of the original six individuals.

During the high-water season we found only three groups. In each group the individuals remained strongly associated with members of the same group in the previous season (Fig. 2B). Twelve of the 15 individuals that left their groups did it during the low-water seasons, when we also witnessed the formation or attempts of formation of new groups. All these resulted in a general decrease in linkage between individuals in groups (Fig. 2A and C).

Territory

Mean territory extension (Fig.1) was 11.4 km (ranging from 5.2 to 19.7 km). The average distance between the centers of the territories of neighboring groups was 10.8 km (2.2 to 17.2 km). There was no statistically significant correlation between group size and territory size (r= 0.35, n=12). However, the number of latrines and the number of scent-marks were linearly related

to the territory size (number of latrines = territory size * 0.775 – 1.944, $F_{(1,11)}$ = 13.846, P=0.003, r^2=0.56; number of scent-marks = territory size * 1.140 – 4.746, $F_{(1,11)}$ = 13.236, P=0.004, r^2=0.55).

Some groups overlapped their territories during both low-water seasons (Fig. 3). Most overlaps occurred in an area located within 4 km of the mouth of the Vermelho River. In the 2006 low-water season, group 2, formed by a pair, overlapped about 3 km (19%) of the territory of group 1 and 1.1 km (8%) of group 3. This group remained in the area for only two months (September and October 2006). In the 2007 low-water season, group 2 returned to the same area, overlapping the territory of group 1 by 2.8 km (14%) and the territory of group 3 by 2.4 km (40%). Group 2 remained in the area for three months (June, July and August 2007) and we did not re-sight it thereafter. During the 2007 low-water season, group 4 overlapped 1.3 km (23%) with the territory of the group 6 (Fig. 3).

In the low-water season of 2007, we re-sighted all groups monitored during the low-water season of 2006. The number of individuals in the study area during both low-water seasons was 36 and 34, respectively. The structure of group 5 changed markedly, since a new male started to lead the group that included the former alpha male and two subordinate females, one of which then became dominant. The former alpha female was not sighted again, and a young female previously belonging to group 3 joined the group. Also, group 5 exchanged the position of its territory with group 4 (see Fig. 2 A and B). The other groups maintained their territory positions, with minor changes. Group 3 moved upriver on August 2007, giving its place down river to a new group (G7), with a territory length of 6.2 km. Group 1, residing on the Miranda River, moved to the Vermelho River during November and December 2006, and then returned to its original territory.

DISCUSSION

The principal element of a giant otter group is an alpha pair (Duplaix 1980, Carter & Rosas 1997). Duplaix (1980) surveyed 19 groups and registered a sex ratio of 30 males: 31 females, but she did not provide the sex of 37 subadults and 15 cubs. Ribas (2004) reported a sex ratio of 8 males: 9 females in the same area as the present study, but she did not record the sex of 13 individuals. Sex ratios near 1:1 suggest an equal dispersal probability
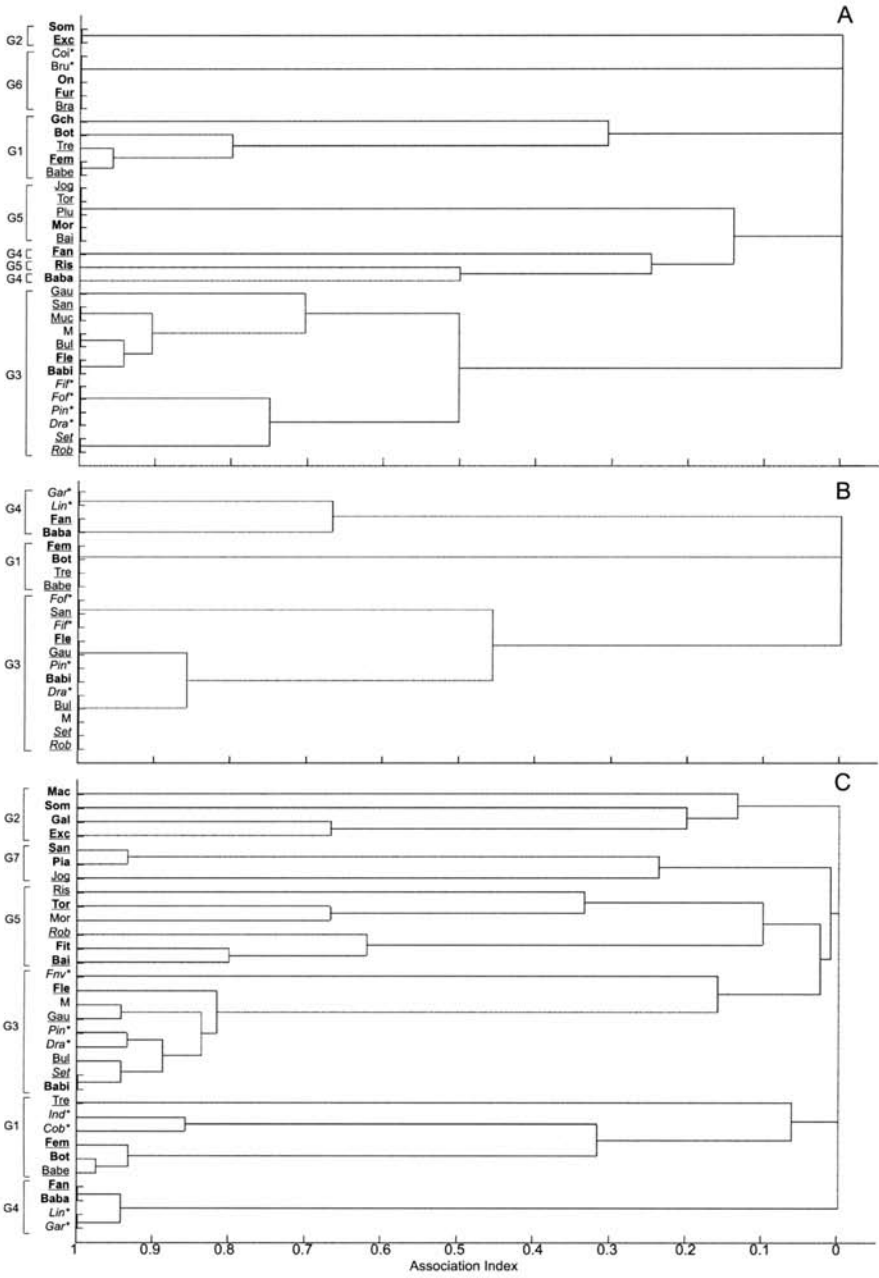
for males and females, independent of the age. Therefore, the female-biased sex ratio (10:19) found in the present study suggests that daughters are generally more philopatric than the young males. In many social mammals, such as lions (*Panthera leo*), hyenas (*Crocuta crocuta*) and white-nosed coatis (*Nasua narica*), males have a high dispersal rate, but females tend to remain in their natal territory (Schaller 1972, Gompper *et al.* 1998, Boydston *et al.* 2001). The most accepted hypothesis to explain female philopatry is that females compete for resources, and males compete for access to females (Eisenberg 1981). Therefore, it is advantageous for females to remain in their natal area, as long as there are resources available, and to gain experience in cub rearing. For males, the best choice in a monogamic system such that as described for giant otters (Duplaix 1980), would be to disperse, avoiding competition with alpha males.

Association

Giant otter social groups spend most of the day together (Duplaix 1980, Schweizer 1992, Carter & Rosas 1997). The association values we calculated between the individuals of the giant otter groups were similar to those reported for other social species such as killer whales (*Orcinus orca,* Baird & Whitehead 2000) and coyotes (*Canis latrans,* Atwood & Weeks 2003), displaying a powerful cohesion in the groups of these species. Individuals of newly formed groups had lower association averages, probably because new groups are less stable. In general the groups changed little across seasons, except in two cases. The recently formed group 2 (composed only by a pair in the 2006 low-water season) suffered frequent changes of the alpha male, and group 5 received and lost various individuals in less than 1 month. The replacement of alpha males occurs in giant otter groups when the males are senescent or inactive in relation to group defense and territory marking (Evangelista 2004). In the present study, this appeared to happen with group 1, in which an old male (≥ 6 years) was replaced by a young male (≥ 3 years).

Fig. 3 (facing page). Dendogram from cluster analysis of association matrix (Half-weight index) for all individuals from the monitored groups through the 2006 low-water season (A), high-water season (B) and the 2007 low-water season (C), between July/2006 and November/2007 on the Miranda and Vermelho rivers, Pantanal, Brazil. Alpha individuals are shown in boldface type, females are underlined and cubs are shown in italic type, and * represents unknown sex. The brackets on the left indicate group affiliation.

Table 1. Group composition observed during the study. Alpha individuals are shown in boldface type, females are underlined and cubs are shown in italic type, * represents unknown sex; birth year or, between parenthesis, a rough estimate of age in years; time within the group (period during which the individual was sighted within the group); origin (former group or known solitary origin).

Group Code	ID	Birth year (Estimated age)	Known Time within group	Origin
G1	**Fem**	(≥ 6)	Jul/2006 > Nov/2007	
	Gch	(≥ 6)	Jul/2006 – Aug/2006	
	Babe	(≥ 3)	Jul/2006 > Nov/2007	
	Tre	(≥ 2)	Jul/2006 – Mar/2007	
	Bot	(≥ 3)	Sep/2006 > Nov/2007	Solitary
	*Ind**	2007	Aug/2007 > Nov/2007	
	*Cob**	2007	Aug/2007 > Nov/2007	
G2	**Exc**	(≥ 3)	Aug/2006 > Sep/2007	
	Som	(≥ 3)	Aug/2006 – Jun/2007	
	Gal	(≥ 3)	Jul/2007 – Aug/2007	
	Mac	(≥ 3)	Aug/2007 > Sep/2007	
G3	**Fle**	(≥ 6)	Jul/2006 > Sep/2007	
	Babi	(≥ 6)	Jul/2006 > Sep/2007	
	Gau	(≥ 3)	Jul/2006 > Sep/2007	
	Muc	(≥ 3)	Jul/2006 – Nov/2006	
	San	(≥ 2)	Jul/2006 – Dec/2006	
	Bul	(≥ 3)	Jul/2006 > Sep/2007	
	M	(≥ 2)	Jul/2006 > Sep/2007	
	Rob	2006	Aug/2006 – May/2007	
	Set	2006	Aug/2006 > Sep/2007	
	*Pin**	2006	Aug/2006 – Sep/2007	
	*Dra**	2006	Aug/2006 > Sep/2007	
	*Fof**	2006	Aug/2006 – Dec/2006	
	*Fif**	2006	Aug/2006 – Dec/2006	
	*Fnv**	2007	Aug/2007 > Sep/2007	
G4	**Fan**	(≥ 3)	Aug/2006 > Sep/2007	
	Baba	(≥ 3)	Aug/2006 > Sep/2007	G5
	*Gar**	2006	Nov/2006 > Sep/2007	
	*Lin**	2006	Nov/2006 > Sep/2007	
G5	**Ris**	(≥ 3)	Jul/2006 – May/2007	
	Mor	(≥ 3)	Jul/2006 > Sep/2007	
	Plu	(≥ 3)	Jul/2006 – Aug/2006	
	Jog	(≥ 3)	Jul/2006 – Aug/2006	
	Tor	(≥ 3)	Jul/2006 > Sep/2007	
	Bai	(≥ 3)	Jul/2006 – Jul/2007	
	Fit	(≥ 3)	Jun/2007 > Sep/2007	
	Rob	(≥ 1)	Jun/2007 – Jul/2007	G3
G6	**Fur**	(≥ 3)	Jul/2006 > May/2007	
	Onc	(≥ 3)	Jul/2006 > May/2007	
	Bra	(≥ 3)	Jul/2006 > May/2007	
	Bru*	(≥ 2)	Jul/2006 > May/2007	
	Coi*	(≥ 1)	Jul/2006 > May/2007	
G7	**San**	(≥ 3)	Jul/2007 < Nov/2007	G3
	Pia	(≥ 3)	Jul/2007 < Nov/2007	Solitary
	Pin*	2006	Sep/2007 < Nov/2007	G5
	Jog	(≥ 3)	Sep/2007 < Nov/2007	G3

During this study, individuals of some groups were sighted within other groups or in newly formed pairs. According to Krebs and Davies (1993), the reproductive success of a group has a positive correlation with the number of helpers. Therefore, newly formed small groups can increase their competitiveness by accepting non-kin helpers. It is unclear how unrelated helpers increase their fitness by helping the group, although some authors (e.g. Rood 1990, Creel & Waser 1991) suggested that they could increase their reproductive chances within the group, or just use the time to obtain experience and physical conditioning prior to dispersing and then trying to establish their own territories.

Giant otters are thought to disperse from their family group when they reach maturity, at approximately two years of age (Duplaix 1980, Carter & Rosas 1997). In this study, we commonly saw subordinates three or more years old within groups, but the older individuals (i.e. ≥ 6 years) were always alpha (Table 1). We observed a 10 month old female that left her parental group and joined another group. At that time, her parental group had 13 individuals, and the high number of helpers in the group may have favored her decision to disperse (see Koenig *et al.* 1992).

Territory

The linear territories of groups were 11.4 km on average, similar to the values of 9.3 km reported by Ribas (2004), in the same study area, and 10.8 km reported by Tomás *et al.* (2000) for the Aquidauna and Miranda Rivers, in the Southern Pantanal. Duplaix (1980) found territories of 2 to 3 km extension in a river stretch for a giant otter population in Suriname. However, Duplaix described the area as good fishing water bodies with a mosaic of habitats, some of them apparently unsuitable. Therefore, the 2-3 km linear territory mentioned could represent just a linear section of a two-dimensional territory of unknown surface. Considering that giant otter groups actively defend their territories (Schweizer 1992, Ribas & Mourão 2004), the 10.8 km average distance between the territory centers of adjacent groups could be the optimal size of linear territories to minimize encounters between groups.

There was no relationship between group size and territory size, but larger territories had more latrines and scent-marks, and obviously it was more expensive to defend larger areas. Agonistic encounters between giant otter

groups and conspecific intruders, as well as infanticide, were reported for giant otters in the Pantanal (Schweizer 1992, Mourão & Carvalho 2001, Ribas & Mourão 2004) and observed during this study. Therefore, the territory size of giant otters in the Pantanal is probably related to defense ability and the pressure exercised by the neighboring groups.

We observed territory overlap during low-water seasons, mainly near the mouth of the Vermelho River. This area seems to be hotly disputed by the groups, and two agonistic encounters have been reported there (Ribas & Mourão 2004, this study). In both low-water seasons, a pair attempted unsuccessfully to establish their territory in this area.

During the high-water season, we re-sighted only three groups in the study area and, on many occasions, we saw or heard individuals in the flooded forest alongside the river banks. Utreras *et al.* (2005) reported that giant otter groups used lagoons and flooded forest during the rainy season in Equatorial Amazonia, and some of them increased their home ranges about 13 times in this period. Apparently, during the high water season, some groups can expand their usual territories to adjacent flooded areas, while other groups may disperse farther.

During the low-water season of 2007, the groups generally maintained the same territories used during the low-water season of 2006, but two of them apparently exchanged their territories. The numbers of individuals and groups, and the distribution of these groups, were almost the same as those reported for the low-water season of 2003, in the same area (Ribas 2004). In fact, in the low-water season of 2007, we observed only one more group than Ribas (2004). Even this group probably did not establish a successful territory, since it was not seen in the last surveys. The stability in the number of groups indicates that it is likely that the giant otter population has recovered from depletion caused by poaching during the 1980's in the Pantanal, reported by Schweizer (1992), and is now near carrying capacity in the Vermelho River.

ACKNOWLEDGMENTS

who assisted us in the field. Arnaud Desbiez and William Magnusson made many useful suggestions and improved the English of a draft manuscript.

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