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Patterns of Wounding in Stumptail Macaques (*Macaca arctoides*)

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ABSTRACT. A three-year study of the patterns of wounding in a group of stumptail macaques (*Macaca arctoides*) was conducted at the Yerkes Regional Primate Research Center Field Station. Wounds were classified as punctures, lacerations or abrasions. Data were analyzed to determine if patterns of wounding vary by age/sex class, body part or wound type. Results indicate that adult males receive significantly more total wounds than expected, based on their total time spent in the group. Adult males also receive more serious wounds than other age/sex classes. Low-ranking animals are wounded more often than high-ranking individuals. Moreover, the location of wounds within each age/sex class is non-random. Adult males receive a disproportionate number of wounds on the forequarters, but adult and immature females are wounded disproportionately on the hindquarters. Finally, age/sex classes differ in the number of wounds on individual body parts. Adult males receive more wounds on the head, arms and hands than other age/sex classes, but adult and immature females receive more wounds on the feet than other age/sex classes. These results demonstrate that wounding patterns are clearly non-random and depend on a variety of factors such as age, sex and dominance rank.

INTRODUCTION

Aggression and competition are normal aspects of life for many species of socially-living mammals. Theories of sexual selection predict that, in general, males should engage in more life-threatening forms of competition than females (TRIVERS, 1972), but theories of life history predict that, under some circumstances, older animals may be more likely to incur risk due to their lower reproductive value (GADGIL & BOSSERT, 1970; POPP, 1978; SCHAFFER, 1974). However, few data are available to test these propositions, particularly for nonhuman primates. Adult male primates appear to be more likely to engage in overt aggression than adult female primates (NAGEL & KUMMER, 1974). Studies of free-ranging Old World monkeys suggest that adult males are more aggressive than other age/sex classes (DITTUS, 1979; DRICKAMER, 1975; HAUSFATER, 1975; POIRIER, 1974). Among captive primates, more aggression is observed when males are artificially paired than when females are paired (THOMPSON, 1969).

However, other data suggest that males, in fact, participate less frequently in agonistic interactions than other age/sex classes (BERNSTEIN, 1971; BERNSTEIN, WILLIAMS & RAMSAY, 1983). Moreover, females may be more likely to inflict injuries than males; it has been suggested that female primates are more likely to attack without warning, but males are more likely to threaten before attacking (NAGEL & KUMMER, 1974). On the other hand, the larger size and longer canines of adult males make them better equipped to inflict serious injury.

On La Paguera and in North India, adult male rhesus macaques (*Macaca mulatta*) received more wounds than other age/sex classes (DRICKAMER, 1975; LINDBURG, 1971; VANDENBERGH & VESSEY, 1968). On Cayo Santiago, adult male rhesus macaques were wounded more than adult females during the mating season, but they did not differ from females in

frequency of wounding during the birth season (WILSON & BOELKINS, 1970). BERNSTEIN, GORDON and BALCAEN (1980) note, too, that adult males suffered a disproportionately large number of wounds in captive, group-living Old World monkeys. However, HAUSFATER (1972) reports that adult females were wounded more frequently and received more wounds on the posterior part of the body than males in the same colony, but males were wounded more severely and received more wounds on the anterior part of the body.

Little is known about the relationship between wounding and age. Old female hanuman langurs (*Presbytis entellus*) have been noted to defend infants more frequently against males than have young females or even the infants' mothers (HRDY & HRDY, 1976). POPP (1978) examined the wounds and scars on free-ranging adult male baboons (*Papio anubis*) and reports that old males had higher rates of injury than their younger counterparts.

The location of wounds on the body, although of major importance in the expression of aggression, has not been investigated systematically. BERNSTEIN and GORDON (1974) note that during introduction of conspecific intruders into existing heterosexual social groups, adult males were not injured on the throat or abdomen, but areas such as the shoulders, face, haunches, brow, tail and back were likely targets of aggressive encounters. However, little is known about the specifics of wounding patterns, and these observations could simply indicate that wounds are received on the most exposed body part.

Moreover, little is known about how gender and dominance rank influence the location and severity of injury. This paper examines patterns of wounding in captive stumptail macaques (*Macaca arctoides*). Data on wounding, collected over a three-year period, were analyzed retrospectively to determine if patterns of wounding vary by age, sex, dominance rank, body part or wound type. Observations reported previously suggest that an association exists among age, sex, dominance rank, wound type and body part. It is hypothesized that: (1) adult males will receive more wounds than other age/sex classes; (2) high-ranking animals will receive fewer wounds than low-ranking ones; (3) wounds will be inflicted on areas other than the ventral surface; and (4) non-serious wounds will be most common. Testing these hypotheses may permit conclusions to be reached about the costs of competition for individuals of different age, sex and dominance rank.

METHODS

STUDY GROUP AND HOUSING

Subjects were a group of captive stumptail macaques (*Macaca arctoides*) housed at the Yerkes Regional Primate Research Center Field Station near Lawrenceville, Georgia. Previously, they had been housed at the Wisconsin Primate Research Center's Breeding Facility [see WEISBARD & GOY (1976) for details]. The subjects were maintained in an outdoor compound measuring 28×33 m which was connected via two metal tunnels to indoor quarters measuring 4×12 m. The group consisted initially of 36 animals, including 4 adult males, 18 adult females, 1 subadult male, 3 subadult females, 3 juvenile males, 2 juvenile females, 3 immature males and 2 immature females. Eight subjects were feral born; the remainder were born in captivity. The adult animals were ranked in male and female dominance hierarchies based on supplants over food items. The study group and physical facilities are described in greater detail in SMITH and PEFFER-SMITH (1984).

During the entire 36 months of the study, no experimental manipulations were used which

were designed to increase rates of wounding. On the contrary, concern was focused on patterns of aggression as a natural feature of behavior in an intact social group. During the study, only nine animals had to be removed from the group as a result of wounds received, and they were reintroduced after medical treatment, typically either on the same day or one or two days thereafter, with little or no complications.

DATA COLLECTION

Data on wounding were collected over a three-year period. Group members were examined daily for fresh wounds. Although the animals were not trapped for examination, observers were able to record, with the aid of binoculars, the animal's identity, location of the wound and wound type. Wounds were classified, according to the degree of trauma, as abrasions (epidermis torn or removed), lacerations (dermis torn), or punctures (skull, abdomen or appendages pierced). Lacerations and punctures were considered serious wounds due to their potential life-threatening consequences; abrasions were considered non-serious wounds.

Data on aggressive behavior were based on 447 hr of observation on adult males and 60 hr of observation on adult females, collected in 15-min focal-animal samples (ALTMANN, 1974). Data were recorded on a DATAMYTE-900 (Electro-General Corp.) in the form of who, does what, to whom, when (SMITH & BEGEMAN, 1980). Data on male subjects were collected from December 1979 to December 1982; data on females were collected from July 1982 to March 1983.

ANALYSIS

Wound frequencies were tabulated for each age/sex class, wound type and wound location. These results constitute the observed data. In order to test hypotheses concerning the effects of age, changes in the demography of the group must be taken into account. In the present three-year study, the number of days each animal occupied a given age class was calculated, following the technique suggested by ALTMANN and ALTMANN (1977). Transitions from one age class to another were taken into account. Therefore, each animal's representation in an age class can be expressed as a proportion of the combined total number of individuals in that age class. An expected proportion of wounds can be derived from this information, based simply on presence in the group. For example, adult females were present on 19,290 days, or 49.5% of the 38,993 total animal days of the study period. Based on their representation in the group, adult females would be expected to receive 49.5% of the total wounds.

Similarly, expected values for body parts were calculated based on their proportion of total body surface area, following definitions and measurements of adult Japanese macaques (*Macaca fuscata*) (HORI, TOKURA & TADAKI, 1972) (see Fig. 1). Since the proportions of body surface were based on a small sample size, values were pooled and mean surface area proportions were used. There was no significant difference by sex in the surface area proportions of specific parts (t-test). The difficulties in extending these proportions to non-adult classes are recognized, but additional data are not available. Other difficulties are recognized in species differences; however, since proportional surface area was used, the overall margin of error is negligible.

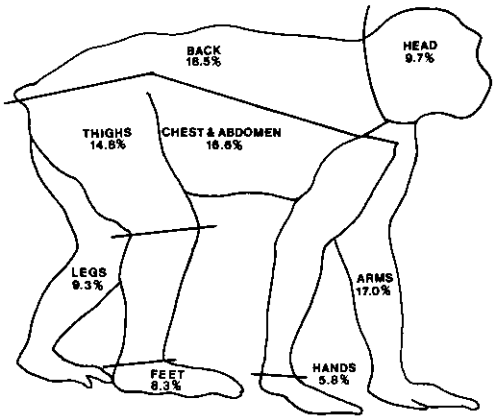

Fig. 1. Percentage of total body surface area by body part. Data are taken from HORI, TOKURA and TADAKI (1972) for Japanese macaques (*Macaca fuscata*).

Differences between observed and expected values were analyzed by chi-square goodness-of-fit tests. All tests having a $p<.05$ were considered significant.

RESULTS

A total of 1,262 wounds was received in the three-year period. Abrasions were significantly more common (74%) than lacerations (25%) and punctures (1%) ($\chi^2 = 1065.85$, $p<.05$). Males were wounded relatively more often than females. Gender was significantly associated with wound frequency ($\chi^2 = 10.461$, $p<.05$). Males received relatively more wounds than expected based on their total time in the group, but females received relatively fewer wounds than expected (Fig. 2).

These data indicate that males are wounded more frequently than females, but this gender difference may not have been equally true for all age classes. The effects of age on the observed gender differences were examined by dividing the study animals into adult males and females (including adults and subadults) and into immature males and females (including juveniles and infants). There was a significant association between age/sex class and total number of wounds ($\chi^2 = 352.599$, $p<.05$). Adult males received relatively more wounds, but

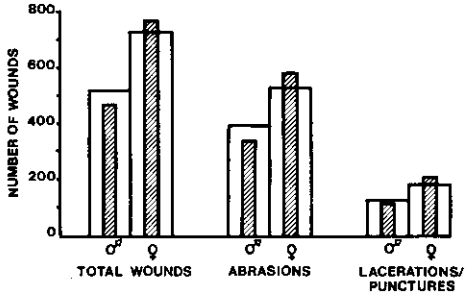

Fig. 2. Gender differences in observed wounds (open bars) and expected wounds (cross-hatched bars) for total wounds, non-serious wounds (abrasions) and serious wounds (lacerations/punctures).

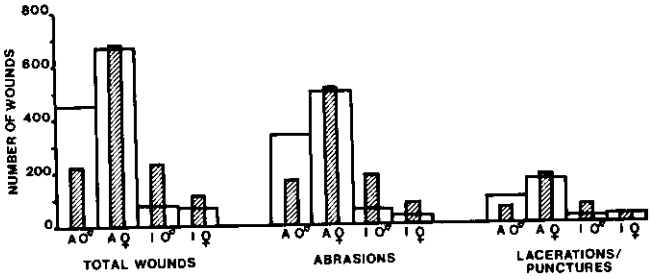

Fig. 3. Age/sex differences in observed vs. expected wounds for adults and immatures. Other details as in Figure 2.

other age/sex classes received relatively fewer wounds (Fig. 3). This sex difference was true for serious and for non-serious wounds. Adult males received relatively more serious and non-serious wounds than expected, adult females received approximately the number expected, and immature animals received relatively fewer wounds than expected. These data indicate that, based on their availability as recipients of wounds, (1) adult males are wounded more often than other age/sex classes and (2) adult males receive more serious wounds than other age/sex classes.

DOMINANCE RANK

Wounds received by adult animals were not distributed randomly relative to dominance rank. The rank of both adult males and adult females was significantly associated with the number of wounds received. High-ranking adults received fewer wounds than expected, but middle- and low-ranking adults received more wounds than expected (Table 1). Therefore, for both adult males and females, high-ranking individuals are wounded less often than other animals.

Table 1. Wounds and dominance rank.

Rank	No. of wounds	
	Observed	Expected
Adult males:		
High	65	148.19
Middle	171	143.64
Low	143	87.17
$\chi^2 = 87.67, p<.05$		
Adult females:		
High	66	204.34
Middle	105	184.73
Low	423	204.93
$\chi^2 = 360.12, p<.05$		

ADULT AGE

Wounds were also distributed non-randomly relative to adult age. Adult females were divided into old (≥ 10 years), middle-aged (5–10 years) and young (4–5 years). Adult males

Table 2. Wounds and adult age.

Age	No. of wounds	
	Observed	Expected
Adult males:		
Old	64	148.19
Middle/young	315	230.81
$\chi^2 = 78.54, p<.05$		
Adult females:		
Old	130	207.65
Middle	302	272.10
Young	180	132.25
$\chi^2 = 49.56, p<.05$		

were divided into old ($\geq$10 years) and middle-to-young (5–10 years). Among adults of both sexes, old animals received significantly fewer wounds than expected (Table 2); however, young adult females received significantly more wounds than expected based on their time in the group.

Location of Wound

Distribution of Wounds Within Age/Sex Classes

Wounds were also distributed non-randomly relative to body part ($\chi^2 = 738.366, p<.05$). Seventy-three percent of all wounds occurred on the head, back and feet. Wound location was significantly associated with gender ($\chi^2 = 963.726, p<.05$). Females received more wounds than expected on the head, back and feet, and fewer wounds than expected on the chest/abdomen, arms and thighs (Fig. 4). When wounds were divided into non-serious (abrasions) and serious (lacerations and punctures) wounds, there also were significant associations between gender and wound location (abrasions: $\chi^2 = 709.978, p<.05$; lacerations/punctures: $\chi^2 = 303.892, p<.05$). The distribution of non-serious wounds was the same as the distribution of total wounds. In the case of serious wounds, females received a disproportionate number of wounds on the back and feet, but males were wounded disproportionately on the head and back (Fig. 5).

The division of sex classes into adults and immatures revealed a similar pattern ($\chi^2 = 1456.408, p<.05$). Adult males received more wounds than expected on the head, back, arms and hands, adult females received more wounds than expected on the head and feet, and immature females received more wounds than expected on the feet. Immature males received the expected number of wounds per body part. These data indicate that the location of wounds is non-random within age/sex classes. Adult males were wounded most often on the forequarters, but adult and immature females were wounded most frequently on the hindquarters.

Age and Sex Class Differences in Wound Location

Differences among age/sex classes in the number of wounds per body part were examined. Areas receiving disproportionate numbers of wounds within age/sex classes were examined for gender and age differences. Males and females differed significantly in total number of wounds on the head ($\chi^2 = 73.537, p<.05$), arms ($\chi^2 = 9.609, p<.05$), hands ($\chi^2 = 6.873,$

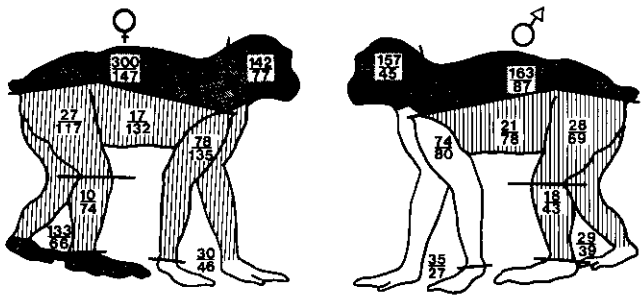

Fig. 4. Distribution of total wounds by gender and body part. Stippled areas indicate body parts which received significantly more wounds than expected, striped areas indicate body parts which received significantly fewer wounds than expected, and unshaded areas indicate body parts which received the expected number of wounds based on body surface area.

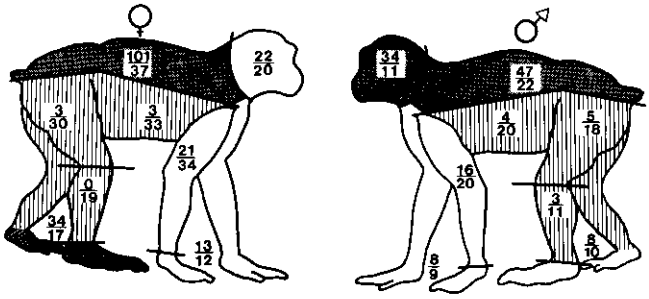

Fig. 5. Distribution of serious wounds by gender and body part. Other details as in Figure 4.

$p<.05$) and feet ($\chi^2 = 39.798$, $p<.05$). Males received relatively more wounds on the head and hands, but females received relatively more wounds on the feet. A similar gender difference was observed for non-serious wounds. For serious wounds, males received relatively more head wounds, but females received more wounds on the back and feet. Age/sex classes differed significantly in the number of wounds on the head ($\chi^2 = 260.805$, $p<.05$), arms ($\chi^2 = 204.155$, $p<.05$), hands ($\chi^2 = 55.020$, $p<.05$) and feet ($\chi^2 = 65.046$, $p<.05$). These data indicate that age/sex classes differ in the distribution of wounds. Adult males received more wounds on the head, arms and hands than other age/sex classes, but adult and immature females received more wounds on the feet.

RATES OF AGGRESSION

Rates of aggression for males in this study were much higher than rates for males in another study of stumptail macaques (BERNSTEIN, WILLIAMS & RAMSAY, 1983). Therefore, data on aggression for males were compared to a similar set of data collected for females (although data for males and females were collected in two different studies, behavioral categories overlapped sufficiently to justify comparison). Hourly rates of aggression were calculated for the following behaviors, which were observed in the two samples: contact aggression (hit, bite); non-contact aggression (stare, head bob threat, slap ground, ear flatten, pant threat, bared teeth threat, brow raise, open mouth threat, displace, chase); and submission (avoid, grimace, crouch, cringe, teeth chatter, hip present). This comparison suggests that in the

Table 3. Rates of agonistic behavior for adult males and females.*

Behavior	Initiates			Receives		
	Males	Females	*p*	Males	Females	*p*
Biting	0.27±0.24	0.18±0.30	ns	0.02±0.19	0.07±0.14	ns
Total contact aggression	0.62±0.24	0.40±0.49	ns	0.25±0.14	0.13±0.25	ns
Non-contact aggression	3.62±1.39	1.69±1.17	<.043 (t = 2.862)	0.77±0.50	1.23±0.87	ns
Submission	1.68±1.18	1.72±1.57	ns	8.44±8.74	0.50±0.59	ns
Total agonism	5.93±0.60	3.81±2.01	<.001 (t = 4.050)	9.46±8.37	1.86±0.84	ns

*Mean and standard error of hourly rates of aggressive behaviors for adult males and adult females; *p*-values are the probability of t' in COCHRAN's modified student's *t*-test (SNEDECOR & COCHRAN, 1967).

present study, adult males were more aggressive than adult females. Adult males initiated significantly more agonistic encounters than adult females (Table 3). Males initiated more contact and non-contact aggression than females, but only the difference in non-contact aggression was statistically significant.

Differences in wounding patterns among adults of different ages also suggest that adult age may affect rates of aggression. Therefore, adult females were divided into old (≥10 years), middle-aged (5–10 years) and young (4–5 years), and adult males were divided into old (≥10 years) and middle-to-young (5–10 years) animals. Rates of aggression were then calculated for each age class. Although there were minor differences in rates of aggression among age classes, none of these differences was statistically significant (COCHRAN's modified student's *t*-test) (Table 4) (SNEDECOR & COCHRAN, 1967).

Table 4. Adult age and rates of agonism.*

Behavior	Males		Females		
	Old	Middle/young	Old	Middle	Young
Initiated:					
Contact aggression	0.66±0.26	0.60±0.27	0.17±0.28	0.62±0.63	0.34±0.37
Non-contact aggression	4.36±0.86	3.13±1.61	1.72±1.32	1.85±1.19	1.44±1.17
Submission	1.16±0.23	2.03±1.52	1.06±0.49	2.13±1.40	1.83±2.35
Total agonism	6.18±0.37	5.76±0.74	2.94±1.58	4.61±2.00	3.61±2.30
Received:					
Contact aggression	0.12±0.05	0.33±0.10	0.22±0.40	0.08±0.15	0.11±0.17
Non-contact aggression	0.59±0.42	1.22±0.66	1.00±0.79	1.48±1.06	1.11±0.72
Submission	6.74±1.12	9.58±12.13	0.61±0.88	0.46±0.43	0.44±0.50
Total agonism	7.45±0.65	10.80±11.53	1.83±0.62	2.02±0.96	1.67±0.94

*Mean ± one standard error of the mean of hourly rates of aggressive behaviors for old (≥ 10 years), middle (5–10 years) and young (4–5 years) age classes for adult females, and old (≥ 10 years) and middle-to-young (5–10 years) age classes for adult males.

DISCUSSION

These data indicate that age, sex and dominance rank influence the total number of wounds received, the types of wounds and their location. Adult males are wounded more often than other age/sex classes. Adult males also receive more serious wounds than other age/sex classes. Low-ranking animals are wounded more often than high-ranking individuals. Moreover, the location of wounds within most age/sex classes is non-random. Adult males receive a disproportionate number of wounds on the forequarters, but adult and immature females are

wounded disproportionately on the hindquarters. Immature males are wounded in proportion to body surface area. Finally, age/sex classes differ in the number of wounds on individual body parts. Adult males receive more wounds on the head, arms and hands than other age/sex classes, and adult and immature females receive more wounds on the feet than other age/sex classes.

The higher frequency of wounds received by adult and subadult males is not unexpected, given the potential advantages of aggression to male reproductive success (TRIVERS, 1972). A single aggressive encounter can add one or more offspring to a male's lifetime reproductive success, but female reproductive success is not likely to be affected significantly unless competitive advantages are maintained over long periods of time (WHITTEN, 1984).

The higher rates of wounding observed for adult and subadult males in the present study appear to contradict behavioral data on aggression in captive stumptail macaques and in other species in which the rate of aggression was lower for adult males than for other age/sex classes (BERNSTEIN, WILLIAMS & RAMSAY, 1983). However, data presented here suggest that the adult males in the present study did engage more frequently in aggression than adult females. More frequent aggressive interactions may have increased the likelihood of injury to males. However, the only significant sex difference in rate of aggressive behavior was observed in the rate of initiation of non-contact aggression. Hourly rates of aggression were higher for the males in this study than for the males in the previous study. Since animals in both studies were housed under similar conditions, environmental factors are not the probable cause of these differences. The higher rates observed in the present study could be due either to differences in sampling design or to individual differences in the rates of aggression by males.

The observation that low-ranking adults were wounded more frequently is also not surprising. Since these animals are at the bottom of the social hierarchy, they may be more frequent recipients of aggression. The low rates of wounding noted in the older animals, however, are contrary to expectation. Given their low reproductive value, old animals would be expected to risk more than young animals in aggressive interactions. There are several possible explanations for the low rates of wounding noted in these subjects. First, the oldest animals in the present study may not have been significantly lower in reproductive value than other group members. The older females were more successful reproductively than young females and, in addition, the youngest adult males were not successful in mating. Dominance rank also may have been a confounding factor, since many old adults in the group were high- or middle-ranking. Finally, a comparison of the rates of aggression for adults of different ages suggests that age did not significantly affect rate of participation in agonistic encounters. Therefore, older animals did not appear to follow courses of action which would have either reduced or increased the probability of serious injury. They may simply have been more skillful in avoiding injury.

These considerations suggest that differences in wounding patterns may result, in part, from differences in fighting techniques. During introductions to captive groups of rhesus macaques, males used canines in aggressive encounters with other males, but used incisors in aggressive interactions with females (BERNSTEIN, GORDON & ROSE, 1974). The predominance of wounds on the head received by males and adult females may be a consequence of head-to-head fighting, but wounds on the feet may result from bites directed toward fleeing opponents or from the defensive use of limbs. During playfighting among juvenile rhesus macaques, animals in an on-bottom position frequently receive bites on the extremities if they use their limbs to push at the on-top opponent's face (SYMONS, 1978).

Wounding patterns can reveal much about the costs of competition for different individuals, but they cannot explain how those costs arise. Many reports have described age/sex differences in rates of aggressive behavior, but few studies have examined systematically the effects of age, rank and sex on patterns of aggressive behavior. Data presented here suggest that differences in patterns of aggression may have significant effects on the rate and severity of injury, and these data indicate that an examination of individual differences in the sequence of aggression may be productive.

CONCLUSIONS

The data from this study indicate that: (1) adult males are wounded more frequently than other age/sex classes; (2) adult males receive more serious wounds than other age/sex classes; (3) high-ranking individuals are wounded less frequently than other animals; (4) the location of wounds is non-random within age/sex classes (adult males are wounded most frequently on the forequarters; adult and immature females are wounded most frequently on the hindquarters); and (5) age/sex classes differ in the distribution of wounds (adult males receive more wounds on the head, arms and hands; adult and immature females receive more wounds on the feet).

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