REPRODUCTION AND POST-NATAL DEVELOPMENT OF SOUTH AFRICAN MUSTELINES (CARNIVORA: MUSTELIDAE)

D T ROWE-ROWE Natal Parks Board, Pietermaritzburg Accepted: June 1977

ABSTRACT

Ictonyx striatus and Poecilogale albinucha were bred in captivity. Data indicate a breeding season which extends from the beginning of spring to the end of summer. In both species copulation was prolonged. A gestation period of 36 days was recorded for *Ictonyx* and 32 days for *Poecilogale*. Litter size was one to three for both mustelines. After 20 weeks the young of both species were almost fullgrown. Eyes opened at c. 40 days (*Ictonyx*) and c. 52 days (*Poecilogale*). Both species started to eat solids prior to this event. Three juvenile vocalizations were recognized in blind young, but thereafter adult sounds were made. The first successful rodent kills were made at nine and 13 weeks by *Ictonyx* and *Poecilogale* respectively, in litters left with their mothers as well as in animals reared in isolation. Play was mainly of an aggressive nature, involving actions typical of adult fighting, prey capture and killing.

INTRODUCTION

Information on the reproduction of South African mustelines is limited to brief comments in general handbooks, mainly on litter size, and speculation on the breeding season (Shortridge 1934; Ansell 1960*a*; Maberly 1963; Smithers 1965; Dorst & Dandelot 1970). As part of a project to study the behaviour and ecology of the mustelids of Natal, striped polecats (*Ictonyx striatus*) and African weasels (*Poecilogale albinucha*) were kept in captivity. Both species bred, and it was possible to make observations on reproductive behaviour and post-natal development of the young, details of which are reported in this paper.

MATERIAL AND METHODS

The four polecats studied were a hand-reared pair and their two young (male and female). The weasels consisted of a hand-reared female, a wild-caught male and their two litters born in captivity. Animals were kept in wire-netting cages $3,7 \times 1,8 \times 1,5$ m and $3,7 \times 1,2 \times 1,2$ m with net floors covered with river-sand in the open at Pietermaritzburg ($29^{\circ}38 \text{ S}/30^{\circ}28 \text{ E}$). Each cage contained an asbestos-roofed shelter ($55 \times 45 \times 20 \text{ cm}$) covering the sleeping box. Both species were fed on a staple diet of day-old domestic chickens, rats and mice when available, and occasionally ox-heart. Polecats were also given canned pets' food on alternate days.

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The mass of immature animals was measured once a week on an Ohaus Triple Beam balance until their eyes opened; then they became too restless and had to be placed in a light basket suspended from a Salter spring balance, and measured to the nearest 10 g. It was not possible to obtain accurate linear measurements once the eyes had opened.

Adults were weighed once a month, and each male's scrotum was examined and subjectively assessed as small, medium, or large. "Small" meant that the testes were withdrawn or almost withdrawn into the body, "large" referred to a scrotum c. 10 mm across and protruding c. 5 mm (weasels), or 20-25 mm across and protruding c. 10 mm (polecats), and "medium" to scrotal testes of intermediate measurements.

No special methods of introducing the male polecat to the female were employed - the female was placed in the male's cage during winter (July) and the two mated during early spring (September). Before the first mating the weasels' cage was divided by a mesh partition to separate them but this proved unnecessary.

RESULTS

Reproduction

In both species the testes remained large from spring (September) to early autumn (April), and decreased in size during winter (May-August).

In *Ictonyx* scrotal testes were apparent between 16 and 20 weeks of age and one male bred at 22 months although he had had no mate the previous summer. In *Poecilogale* scrotal testes were apparent at 13 weeks and attained "medium size" by 20 weeks, but large scrotal testes were only observed after the first winter. One male mated successfully at 33 months, but an 11-month old male would not copulate.

The hand-reared female polecat, birth date approximately December 1972, had her first litter in October 1973, at an approximate age of 10 months, having been mated at nine months. The tame weasel, estimated to have been born late in the season (April 1972), had her first litter at the beginning of December 1973 when she was approximately 19 months old. Gestation periods, reckoned from the last recorded copulation onwards, were 36 days on three occasions for *Ictonyx*, and 31; 33; 31 and 32 days for *Poecelogale*. Maximum litter size was three for both species. Sex ratios at birth were 4 males : 4 females in four polecat litters; and 6 males : 4 females in four weasel litters. Two weasels in another litter were not sexed.

Young animals collected were aged, using growth curves (Figure 1) and other criteria of known-age mustelines, and approximate birth dates were determined. All polecats were born between September and December. The number of litters per month, including those born in captivity were: September (1), October (3), November (3) and December (1). Months in which weasel litters (including captive animals) were born were: September (1), October (3), November (2), December (3), February (1), March (1) and April (2). Although the data are few, they do suggest that both species have young mainly during spring and

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summer. Whether *Poecilogale* does have a longer breeding season than *Ictonyx* will only become apparent when more records have been collected.

During 1973 the litters born all survived and were left with their dams, which did not breed again until the following spring, when both females lost their young when only a few days old. They successfully remated shortly afterwards. The weasel's litter was removed when eight weeks old and she mated again, indicating that the species is polyoestrous in summer.

Both species have two pairs of mammary glands (one pair inguinal and one abdominal) which show no development until about the tenth day of pregnancy, when they begin to increase in size until the young are born.

All of the nine musteline parturitions took place during the hours of daylight, although both species are nocturnal. During the night following parturition the adult females ate very little of the food provided, having obviously fed on the placenta. Timing of parturition appears to have obvious advantages, as the adult female can then remain with the altricial young for about 30-36 hours before having to leave the den to hunt.

Courtship and mating

The adult female polecat was intolerant of the male, and although no fighting was observed, she often snapped at him and yapped when he came near her. When receptive, however, the female crouched in front of the male and allowed him to smell her vulva, and sometimes adopted a submissive posture with outstretched neck, head turned to one side, and open mouth. The male then grasped the female by the back of the neck and dragged her under cover. Copulation did not usually take place at once, as the male sometimes lost his grip and the process of crouching, vulva-smelling, neck-grasping and dragging was repeated. Throughout these exchanges the male made a quiet chirping noise. Eventually the male would mount the female, grasping the skin at the back of her neck in his mouth, and clasping her around the lumbar region with his forefeet. The female remained in a crouching position with the tail held to one side. The male did not grip the back of the neck all the time, but only occasionally. The rest of the time his neck was outstretched, with his throat along the back of her neck. Initially the male made rapid pelvic thrusts for about 10 seconds, then paused for about three seconds. After about 30 minutes the thrusts lasted about three to five seconds, with pauses of about six seconds. The female yapped occasionally during the initial stages of copulation, but later became very vociferous, yapping and shrieking loudly for five to 15 seconds at a time. Only one copulation was timed from onset to conclusion, and this had a duration of 106 minutes. Other copulations noted were also of a prolonged nature, being > 75; 60 and 25 minutes.

When male and female weasels encountered each other the male made a quiet chattering sound, which appeared to be a greeting call showing lack of aggression. If the female was receptive she crouched, allowed the male to nibble her cheek, smell her vulva and grasp her by the back of the neck. The female might also indicate receptiveness by dancing around the male. Eventually the male would grasp her by the back of the neck and drag her under cover where copulation took place. Throughout coitus the male grasped the female by the skin at the back of the neck, and clasped her around the pelvic region with the fore-feet. The female generally remained silent, but occasionally yapped. The male usually made three to five pelvic thrusts, then paused for six to eight seconds. Copulations timed from start to finish lasted 78 and 65 minutes; another was between 62 and 72 minutes, and two were > 30 and 27 minutes.

Physical development of young

The young of *Ictonyx* and *Poecilogale* were born in an altricial state, being pink and almost hairless, blind and deaf. The eyes were closed, but eye-slits were present. Although the ears were closed, the pinnae were free.

Newborn polecats had overall lengths of 110-115 mm (tail 25-30 mm) with a mass of c. 15 g. The skin was pink, but the pigmentation of the dark stripes was visible (Figure 2A). When 10 days old they were covered with white hair, 1-2 mm long. At this stage the dark stripes appeared grey. By the age of 19-21 days the hair was 3 mm long and distinct black and white stripes were apparent. The eyes began to open at 35 days and had opened completely by the time they were 42 days old. The lower canines erupted first at 32 days (i.e. three days before the eyes started to open). Neither the appearance nor the replacement of molars and premolars was determined. The permanent canines erupted and grew while the deciduous counterparts were still in place. The deciduous carines were shed by 13-14 weeks. Mass increases of the young polecats up to the age of 30 weeks are illustrated in Figure 1.

At birth weasels (two litters of three) had a mass of c. 4 g and an overall length of 70 mm (tail 15 mm). The skin was pink with only traces of white hair. A distinct mane of white hair grew from the skin covering the posterior portion of the head, and a hump 8 mm long extended from the base of the skull to the shoulders (Figure 2B). Dark skin pigment became visible when the young were seven days old, by which stage the mane had grown considerably. By 14 days the dark parts of the body were grey; and distinct black and white marking was visible at 28 days (Figure 2C). From the age of 14-21 days, while the rest of the body hair was growing, the mane altered in colour from white to tan. By the time the weasels were 42-49 days old, the mane had been shed and all that remained of the hump was a slight thickening of skin. The weasels' eyes opened between 51 and 54 days after birth. Upper and lower canines erupted at 35 days, and by the age of 49 days (before the eyes opened) incisors and premolars were also present. Permanent canines erupted during the eleventh week and grew while the deciduous ones were still in place. The deciduous canines were shed at 13 weeks. One of the females in the first litter died at the age of 12 weeks and a male in the second litter died when 39 days old. Mass increases of surviving weasels up to the age of 31 weeks are illustrated in Figure 1.

Growth curves for both species are sigmoidal. Computor-calculated von Bertalanffy equations (Hanks 1972) for growth in mass are:

 $W_t = 1303 \ (1 - e^{-0.1885 \ (t - 1.472)})^3 \ \text{kg (polecat male)}$ $W_t = 942 \ (1 - e^{-0.2032 \ (t - 1.232)})^3 \ \text{kg (polecat female)}$ $W_t = 396 \ (1 - e^{-0.1527 \ (t - 1.873)})^3 \ \text{kg (weasel male)}$ $W_t = 275 \ (1 - e^{-0.1623 \ (t - 1.324)})^3 \ \text{kg (weasel female)}$

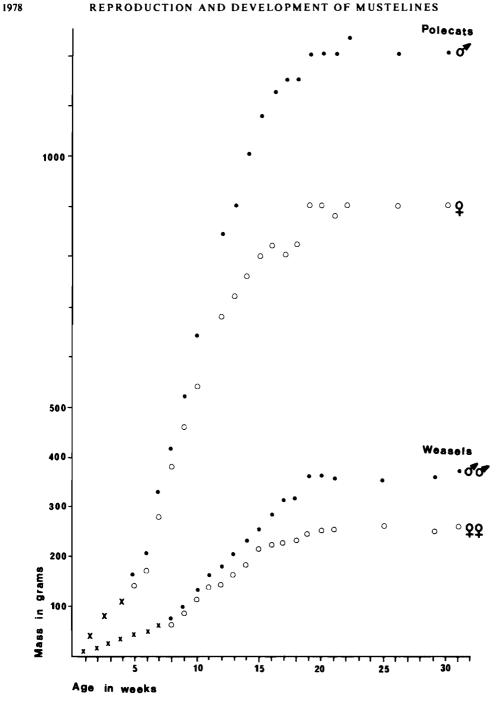


FIGURE 1

Mass increases of a male and female polecat, and average mass increases of two male and two female weasels. Initially males and females were approximately the same size (indicated by x).

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Transport of young

Newborn polecats were picked up by their mother by grasping them in her mouth across the shoulders (Figure 2A) or the middle of the body. When the young were three weeks old the mother picked them up by the skin at the back of the neck.

Each young weasel, up to the age of four weeks, possessed a large hump at the back of the neck and a mane of long hair immediately anterior to the hump. Observations on the transport of young indicated that the mother picked them up by the hump (Figure 2C). By seven weeks the mane and hump had disappeared and the mother grasped the young by the loose skin of the scruff of the neck.

Behavioural development

Posture and locomotion. During the first week after birth neither polecat nor weasel young were able to crawl. When the young were separated from the mother, they remained stationary, and with raised heads emitted continuous high-pitched squeaks. The young polecats moved their heads slowly from side to side. In weasels the head-up posture was more exaggerated (Figure 2B) and the head was jerkily moved up and down and from side to side while the animal emitted squeaks.

Crawling in both species was preceded by the ability to move the anterior part of the body around in a circle, pulling with the fore-legs. Polecats could do this at seven days and weasels at 10-14 days.

When 10 days old the young polecats could crawl a few centimetres. The young weasels started to crawl feebly at 19 days, and by 28 days could move no more efficiently than polecats of half their age. Proficiency of crawling improved in both species until their eyes opened.

Unsteady walking was observed in polecats at 39 days and in weasels at 56 days. Shortly after the polecats were seven weeks old locomotor proficiency had developed to the stage of the animals being able to trot and follow their mother. This stage was reached during the eleventh week in weasels, and during the twelfth week the characteristic "looping" running action, typical of adults, was first noted.

When the polecats were eight weeks old they were capable of curling their tails over their backs, and before they were nine weeks old they were capable of hunching the back, curling the tail over it, and reversing. The proficiency of this display improved until it resembled that of an adult at 12 weeks (Figure 2D). At 13 weeks both polecat young were first noted occasionally sitting on their haunches and raising the fore-quarters off the ground.

Vocalization. Only three calls made by the blind young were recognized: a contact call and two distress calls. The adult calls were first made after the eyes had opened. Sonographic analyses, and call development and context are dealt with by Channing & Rowe-Rowe (1977).

Feeding. Both species lived on mother's milk only until their canines had erupted (c. 32 and 35 days for polecats and weasels respectively), and then began to feed on the soft portions of prey which the adult female placed in the nest. The adult female usually ate the



FIGURE 4 A (top left) An adult female polecat with four-day-old-young, which are almost harress, e.g., dark stripes. Also illustrating the manner in which young are picked up. B (top right) Seven-day-old African weasels, showing lack of black stripes, and presence of mane and neck hump. C (bottom left) Four-week-old African weasels, covered with distinct black and white hair. Also illustrating the manner in which the young are picked up. D (bottom right) Threat display of the striped polecat.

head and shoulders of a mouse or chicken then placed the carcass beside the young. The young licked juices from the prey and ate viscera. The young polecats started to take "solids" about three days before their eyes opened. The weasels gradually ingested more solids, until by c. 52 days (when the eyes were opening) they were eating small bones (ribs of mouse) as well as meat.

The young of both species were suckled during the day and at night. After the young had started to take solid food they suckled less. The young polecats appeared to be weaned by eight weeks and the weasels by 11 weeks.

During the first two weeks of their life the young weasels were sometimes seen clinging to the mother's nipples if she left the nest suddenly. The young animals usually released their hold after the female had covered a distance of about 200 mm, but occasionally an individual would cling persistently and the mother would remove it by grasping it by its hump and pulling it off. Observations indicated that it was not possible to recognize teatselection by individuals. The young suckled during all hours (even when six to seven weeks old), and often slept attached to a nipple.

Prey capture. The young of both species were regularly presented with live prey after their eyes had opened. No live prey was killed by the young polecats until they were eight weeks old. At this stage they scratched crickets from under stones and held them down with their fore-feet while eating, but showed no interest in young rats. Pushing the snout into the soil and scratching with the fore-feet (as in adults looking for invertebrates) was also noted.

When nearly nine weeks old the young polecats each killed their first rat. The first kills were clumsy, but proficiency soon developed. Young 60 g rats (about 13 per cent of the mass of the polecats) were killed with some difficulty by a number of badly orientated bites, but within a week of the first kill, a 60 g rat was neatly killed by placing a foot (or both feet) on it and biting at the back of the neck, side of the neck, or throat.

The breeding pair of polecats were hand-reared animals, separated from their mothers before their eyes opened. When acquired they were estimated to be about 12 weeks old. Although they had no previous experience in dealing with live vertebrate prey, both polecats killed young rats (50-70 g) when offered them for the first time.

The ontogeny of prey capture and killing behaviour in the weasel was observed in two animals which remained with their mother, and two which were separated from the mother and hand-reared after their eyes had opened.

From the age of nine weeks onwards live mice (15-20 g) were placed in the cage with the female weasel and her young two or three times a week. At first she merely killed the mice and took them to the sleeping box. During the twelfth week (when the young were leaving the nest and following the mother) a change in killing behaviour was noted. The adult female would kill a mouse (sometimes not very thoroughly, leaving it kicking), then hurriedly return to the nest, touch the young with her snout and trot back to the mouse again, moving to and fro a number of times. At least one live mouse per day was placed in the cage after this behaviour was observed. The young weasels at first cautiously followed the mother to the mouse and smelt it and the spot at which it was killed. After a few days the

young would follow the female to the dead (or immobilized) mouse and bite at it, sometimes tugging and growling simultaneously. In their fourteenth week both of the young weasels made their first kill (a 15 g mouse each), and when placed in a separate cage with six mice of similar size on the following day, killed them all. All the elements of the adult killing pattern (Rowe-Rowe in press) were noted.

The hand-reared weasels showed no interest in live prey until they were in their twelfth week. They would then follow a mouse and make tentative nips at it, usually at the base of the tail, but did not succeed in making a kill. At this stage the permanent canines had erupted but were shorter than the deciduous ones which had not yet been shed. Sometimes the young weasels bit a mouse across the body, but apparently without determination, as the rodents were not injured. The lower milk canines were shed first, but as long as the upper ones were still in place no successful kills were made. By 13 weeks the upper deciduous canines were shed and within a few days 20 g mice were first killed.

Greeting and submission. Similar greeting ceremonies were observed between the mother and young of *Ictonyx* and *Poecilogale*. In both species greeting behaviour by the young was observed for the first time about two weeks after their eyes had opened. When the mother polecat returned to her young after an absence, a young animal would approach her, nuzzle her inguinal region, then roll over on to its side and cock a leg. The mother then smelt the young's inguinal region while it smelt hers.

The greeting ceremony in weasels was similar, but the actions were faster and the young did not lie down. The young making the greeting call, nuzzled the mother's inguinal region and she reciprocated. When more than one young approached the mother they tumbled over each other in their haste and excitement, all making greeting sounds.

Submissive behaviour was first observed in polecats at nine weeks and in weasels at 14 weeks when the young were allowed into adult males' cages. In both species the young animal lowered the front portion of its body, and turning the head sideways, laid it right against the ground. In the polecat the young opened its mouth, but this was not observed in the weasel. Greeting sounds were made by the adult male weasel, and the adult male polecat responded by "fleaing" the young (nibbling the fur with the incisors), smelling its genitals, or briefly licking inside its mouth.

Adult male weasels were never heard to make greeting sounds when they encountered each other, but when adult males encountered adult females they did (cf. "Courtship and mating"). The greeting chatter appears to be a sound which the adult male uses to indicate lack of aggression to juveniles.

Play. The young of *Ictonyx* and *Poecilogale* were first observed playing within a week of their eyes opening, i.e. during the seventh and ninth weeks respectively. At first the animals played quietly in the nest box but as locomotor efficiency improved, play in both species became more energetic. During the eighth week (polecats) and eleventh week (weasels) the young were first observed playing outside the nest boxes.

In the pair of polecats which was left with the mother, play continued as a major activity until about 15 weeks, then began to decrease in intensity and duration. The hand-reared polecats remained playful until 20-24 weeks old. Play in the weasel litter which was left with the mother was obvious until about 17 weeks, then decreased. The hand-reared weasels were very playful until about 20 weeks, and would indulge in a limited amount of play even as adults.

Play, in both species, was mainly of an aggressive nature. In young polecats the animals grasped each other by the skin of the cheeks or side of the neck, then wrestled, rolling and kicking. A chasing game was also observed in which the roles of pursuer and pursued alternated. These games did not usually last long and invariably ended in wrestling and biting.

Play in the hand-reared polecats included displays, running, rolling, and fighting. The games were played with humans or with house cats. Display games involved adopting the threatening attitude illustrated in Figure 2D. The animal would advance towards a person, stopping just short, then reverse rapidly. This would be repeated a number of times, often changing the angle of approach. The polecat sometimes went into a roll (either in the approach, or after reversing). The roll was executed very rapidly, with the animal going down on to the side of the head and shoulder first, then rolling over laterally to land on the feet again and display.

Play amongst young *Poecilogale* consisted mainly of fighting games. The young animals wrestled with one another, grasping the skin of the checks, rolling laterally, and kicking. They also gripped one another by the skin at the back of the neck or by that of the lumbar region. The young animals also indulged in running and display games - running in all directions in the cage, with tails erect and fluffed, bouncing on the fore-feet. Play of hand-reared weasels with humans took the same form as that observed in intra-specific games.

DISCUSSION

The main characteristics of the breeding cycles of South African mustelines are similar to those of the European and North American members of the subfamily which do not have delayed implantation, summarized by Ewer (1973) as having: one or two litters/year; a season confined to spring and summer; and short gestation periods.

Seasonal variation in testicular size in the present study is similar to that reported in European mustelines, *Mustela nivalis* (Hill 1939) and *M. putorius* (Poole 1970).

The physical and behavioural development of weasels was slower than that of polecats, probably because of the weasel's shorter gestation period and the fact that the young are born in a more altricial state. Both species, however, grew and developed rapidly.

The purpose of the mane on the back of the neck in young weasels is not clear, since they are not carried by it. It might serve to stimulate the mother when the long hairs touch her vibrissae, guiding her mouth towards the hump, and this would be of particular advantage in a dark burrow. Rowe-Rowe (1975) showed that African weasels live in burrows or other sheltered places. The hump has apparently evolved specifically for the purpose of providing a safe place to grasp the altricial young.

Behaviour analogous to "teaching" the young to kill has only been reported in one

species, viz. in Mustela nivalis by Heidt et al. (1968). On the other hand East & Lockie (1964, 1965) found that there was no difference in the age at which they killed nor in efficiency of killing, between young *M. nivalis* separated from their mother and those which remained with her. The significance of the teaching behaviour is therefore not altogether clear. Ewer (1969, 1973) referring to similar behaviour in domestic cats (*Felis catus*), cheetah (*Acinonyx jubatus*), tiger (*Panthera tigris*) and Canadian river otter (*Lutra canadensis*), in which the mothers introduced live prey to the young, concluded that this was not teaching behaviour. The mother was merely presenting the young with prey and preventing it from escaping, and "the natural responses of the young automatically lead to their learning how to improve their killing technique".

The killing pattern of young polecats in their ninth week was typical of the adult killing pattern described by Rowe-Rowe (in press).

Development of the killing technique by captive-bred weasels in their fourteenth week was similar to observations previously made on a wild-caught female and her young (Rowe-Rowe 1972). The exact ages of these young were not known, but estimates from the growth curves (Figure 1) indicate that they were 14-15 weeks old when they made their first kill (a 40 g rat).

Submissive behaviour does not appear to have been previously recorded in mustelids. The pattern observed in the two South African mustelines, viz. of presenting the neck and turning the mouth away, has however been recognized as a submissive posture in the Canidae. Van Lawick-Goodall & van Lawick (1970) described similar postures in wild dogs (Lycaon pictus) and golden jackals (Canis aureus) which they described as "one of the most common gestures of subordination". Lorenz (1954) similarly described neck-presentation in the domestic dog (C. familiaris) and European wolf (C. lupus), which he regarded as a submissive signal.

The submissive postures adopted by immature mustelines are obviously signals of subordination to adults. In the courtship behaviour of *Ictonyx*, submission by the female probably indicated the desire to make contact, as under normal circumstances the female was intolerant of the male and snapped at him when he approached.

Poole (1966) noted that of the 13 behaviour patterns present in adult aggression of *Mustela putorius*, nine were present in aggressive play. Similarly, in *Ictonyx* and *Poecilogale*, certain behaviour patterns were common to aggressive play and true aggression. In *Ictonyx* these included nipping the base of the tail, flight, rolling, and biting the cheeks or side of the neck. In *Poecilogale* they included bouncing on the fore-feet, flight, biting lumbar skin and cheeks, kicking and lateral rolling. Kicking and lateral rolling were also common to prey-killing. Sustained biting and screaming, observed in serious fights (Rowe-Rowe 1975), were absent from play.

Ewer (1973) stated that play in carnivores is made up of actions that are used in earnest, primarily those concerned with prey capture, fighting, and escape behaviour; and that play provided a means of doing all the things the central nervous system was prepared for, without the risks inherent in the real situation. This apparently applies to the play observed in the two South African mustelines.

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