

# An Ecological Study of *Caiman crocodilus crocodilus* Inhabiting Savanna Lagoons in the Venezuelan Guayana

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**Summary.** Mark and recapture studies were carried out for three and a half years on a population of *Caiman c. crocodilus* inhabiting a savanna lagoon system in the Venezuelan Guayana. Sub-adult and adult caimans migrated from permanent lagoon refuges to temporary lagoons during the wet season. A distinct homing response by artificially displaced caimans was observed.

The wet season was the most significant time of the year for both feeding and growth. It was estimated that caimans take 6 years to reach a size of 97 cm. Thereafter the growth rate was variable. During a dry year there was little growth, but during a wet year a large caiman could increase in length by up to 10 cm.

During the first 18 months of life, young caimans remained near the nest site. Older caimans dispersed and competed for territories which resulted in a high incidence of damage, particularly to the tails, as a result of intraspecific fighting.

## Introduction

This study was undertaken in order to put into perspective seasonal studies of the hematology and hemostatic mechanisms of *Caiman crocodilus*, being performed at the IVIC field laboratory in El Manteco, Estado Bolivar, Venezuela. Most of the work was completed between 1974 and 1976, with further observations in 1977.

## Methods

Caimans of less than 1.2 m total length were captured by hand, and larger specimens with a noose. Within 12 h after capture individuals were sexed, measured and weighed. Snout-vent lengths to the posterior edge of the cloaca and total lengths were recorded to the nearest 0.5 cm. Weights were to the nearest 1 gm for hatchlings, to the nearest 5 gm for medium sized caimans and to the nearest 100 gm for large specimens. Caimans were marked by clipping the ventral

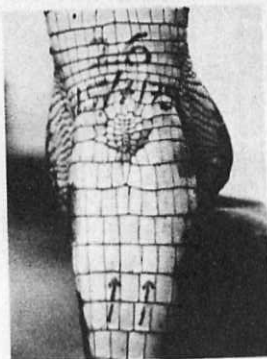


Fig. 1. Scars on ventral caudal scales of a caiman, 10 months after being marked

caudal scales. Figure 1 shows a caiman 10 months after having first been marked. Such marks persisted for at least 26 months, but generally were remade after a year. Scar tissue formed within a month, and there was never any evidence of infection.

Stomach contents were analysed of caimans captured in lagoons similar to those where the mark and recapture studies were being made.

Mapping of the Mapurite lagoon system was performed using a compass and a jeep. Subsequently in June 1975 aerial photographs of the area were taken.

Daily maximum and minimum air temperatures were recorded in gallery forest 10 km to the east of El Manteco. Daily rainfall was recorded in the town of El Manteco where the IVIC laboratory is situated. In order to follow the rate and the extent to which lagoons were filling up or drying out, an arbitrary zero datum was set in lagoon 'B' on the 26th May 1974. Changes in depth of this lagoon were periodically recorded.

### Study Site

To the north and the east of El Manteco is the Yuruari savanna. The Rio Yuruari drains into the Esequibo river in Guiana, and not into the Orinoco as do the other main rivers in the Bolivar State. Figure 2 shows the Mapurite lagoon system. The vegetation is closed savanna dominated by chaparro trees (*Curatella americana*) and Manteco trees (*Byrsonima crassifolia*). The land to the west of the perimeter fence of the ranch, 'Hato Melendri', belongs to the town and supports a few small homesteads. To the east of the fence there has been some clearing of chaparros and the vegetation is more open. Drainage is to the northeast. The lagoon system lies in a natural valley and for some 2 km in any direction no similar lagoon systems occur. It is thus considered a 'closed' system. In the area are four permanent lagoons. Lagoons 'B' and 'E' are natural, whereas lagoons 'G' and 'H' were artificially formed some 40 years ago by damming the eastern parts. There are nine temporary lagoons (A, C, D, F, I, J, K, L, and M), and a ditch (N). The horizontal lined areas indicate the extent to which the lagoons had dried out in June 1975. At this

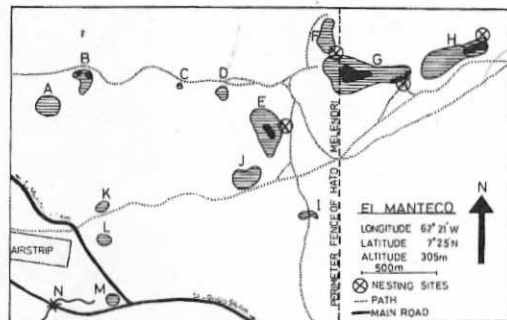


Fig. 2. The Mapurite lagoon system

time the total area of water in the four permanent lagoons was 2.28 ha. At the height of the rainy season the total area of all the lagoons was 23.32 ha. Full temporary lagoons had a maximum depth of about 1 m, and permanent lagoons were about 3 m deep at the deepest part. According to Ewell and Madriz (1968) the El Manteco area may be classified as dry tropical woodland (bosque seco tropical). The annual rainfall for this life-zone is between 1000 and 1800 mm. Between 1958 and 1972 the mean annual rain-fall was 1409 mm at El Manteco. During the 3 years of study, rainfall in El Manteco was much less being 630, 990, and 1200 mm for 1974, 1975, and 1976 respectively. All the permanent lagoons were extensively covered with cyperaceous vegetation which did not permit night-time censuses to be carried out.

### Results

#### Mark and Recapture Studies

Between May 1974 and September 1976 a total of 73 captures were made in temporary lagoons and 116 in permanent lagoons. Figure 3 shows the numbers of caimans captured monthly in permanent and temporary lagoons during this period, the weekly rainfall, the level of lagoon 'B', and the mean maximum and minimum air temperatures. There are two main seasons; a dry season from January to June and a wet season from July to December. Caimans were most frequently captured in temporary lagoons during the wet season months. The expected dry season did not occur in 1976 and the temporary lagoons remained full. During this period, however, very few caimans were encountered in temporary lagoons. During the wet season caimans were encountered at the edges of the lagoons, whereas during the dry season they were congregated in the centres of the permanent lagoons, hiding under the cyperaceous vegetation.

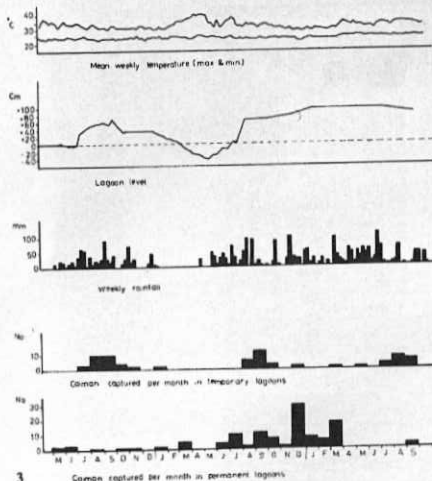


Fig. 3. The monthly rate of capture of caimans in permanent and temporary lagoons between May 1974 and September 1976

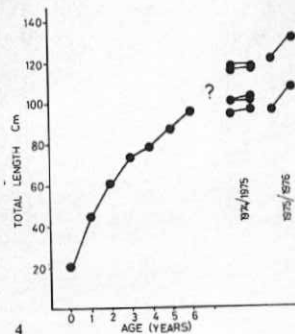


Fig. 4. Growth curve of *Caiman crocodilus*. Growth in caimans older than 6 years varies from year to year

Table 1. Numbers of first captures and recaptures (in parenthesis) in lagoons of the Mapurite system

Lagoon	Adults/sub-adults	Hatchlings
'A'	—	—
'B'	2	—
'C'	— (2)	—
'D'	6 (3)	—
'E'	9 (11)	11 (10)
'F'	15 (24)	—
'G'	24 (14)	32 (21)
'H'	3 (5)	2
'I'	4	—
'J'	13 (12)	—
'K'	5 (1)	—
'L'	—	—
'M'	4 (4)	—
'N'	3 (2)	—
Total	88 (78)	45 (31)

Table 2. Homing by fifteen displaced caimans

From	To	Number
'G'	'F'	5
'G'	'D'	1
'G'	'C'	1
'G'	'E'	1
'G'	'K'	1
'G'	'M'	1
'G'	'N'	1
'G'	'J'	3
'J'	'G'	1
Total		15

Table 3. Independent migrations by twenty caimans

From	To	Number
'G'	'F'	5
'F'	'G'	2
'G'	'D'	1
'G'	'E'	2
'G'	'J'	1
'G'	'H'	1
'E'	'J'	3
'J'	'E'	2
'J'	'D'	1
'J'	'C'	1
'J'	'M'	1
Total		20

Within the Mapurite system a total of 49 males, 39 females, and 45 hatchlings were caught. Table 1 summarizes the numbers of first captures and subsequent recaptures in each lagoon. No caiman were ever caught or even seen in lagoons 'A' and 'L'. Hatchlings were only found in permanent lagoons 'E', 'G', and 'H'. Hatchlings were always released at the site where they had been captured.

In order to study homing, some marked caimans were displaced to another lagoon. On three occasions caimans displaced from 'E' to 'G' were recaptured in 'G'. On fifteen occasions displaced caimans were recaptured in the lagoon in which they had originally been captured. Table 2 indicates the lagoons to which they had been displaced and the lagoon to which they had homed. There was homing on 83% of occasions. An example of such homing is provided by caiman '115'. This caiman was first captured on the 28th February 1976 in lagoon 'M'. It was released the following day in lagoon 'G'. On the 16th March 1976, which was the first rainy night since the caiman was first captured, '115' was caught in the savanna between lagoons 'G' and 'E'. It was released immediately. Ten days later it was recaptured in lagoon 'M'. Thus, caiman '115' had homed a total distance of 2.4 km.

On 31 occasions hatchlings, and on 40 occasions larger caimans were recaptured in the lagoon in which they had been captured and subsequently released into. On 20 occasions, however, larger caimans were found to have migrated to another lagoon. Table 3 summarizes these changes of lagoon. Such migrations were essentially short term migrations from a dry season refuge in a permanent lagoon to a rainy season territory in a temporary lagoon. General observations indicated that migrations to the larger and deeper temporary lagoons, such as 'F', 'J', 'K', and 'M' could last for the whole of the rainy season, whereas migrations to shallower lagoons such as 'C', 'D', and 'I' were accomplished within one night. Caimans migrated at night and invariably preferred cloudy rainy nights to moonlit dry nights. Caiman '26' provides an example of migration to a permanent refuge lagoon during the dry season. This caiman was captured on the 30th September 1974 in lagoon 'J' and released in lagoon

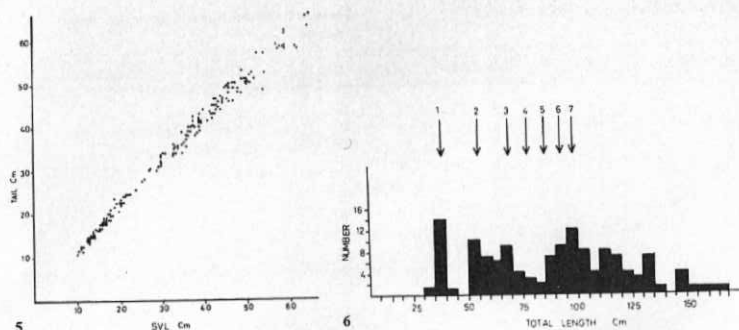


Fig. 5. Relationship between snout-vent length (trunk) and tail length. A regression line of  $Y = 2.77 + 0.96X$  was obtained

Fig. 6. Size frequency histogram of the Mapurite population

'G'. On the 30th November 1974 it was recaptured in lagoon 'J' and released in 'J'. On the 22nd January 1975 it was recaptured and released in 'J'. On the 15th July 1975 it was recaptured and released in lagoon 'E'. On the 1st September 1975 it was found to have returned to lagoon 'J'. Caiman '12' gives an example of foraging movements to small pools. It was first captured in 'C' on the 22nd October 1974, and released into 'G'. It was recaptured in 'D' on the 6th November 1974 and released into 'G'. On the 10th September 1975 it was recaptured in 'C' again.

### Growth

A growth curve was made from data on 36 recaptured specimens. From Figure 4 it can be seen that in the study area a caiman takes 6 years to reach a size of 97 cm. The growth curve is a composite for the first 6 years because there was no difference in growth rates within any one size class from one year to the next. In large caimans, however, in the 12 months between 1974 and 1975 there was little or no growth in the five individuals studied. Whereas in the twelve months between 1975 and 1976, a much wetter year, 2 large caimans increased their total lengths by more than 10 cm. Caimans less than 2 years old grew steadily during the whole year, but thereafter the growth rate slowed during the dry season.

26% of the specimens had damaged tails. In order to calculate the total length that such a caiman should have been if undamaged the snout vent lengths of undamaged caimans were plotted against the tail length (Fig. 5).

The growth curve was used to calculate the size that each caiman should have attained by June 1977. Figure 6 shows the size frequency histogram for

the Mapurite population. It can be seen that there are peaks for the year classes 1, 2, 3, and 6/7, but none for year classes 4 or 5. It is concluded that reproduction was not successful in the years 1972 and 1973. It should be noted that during these 2 years there was extensive hunting of the caimans for hides, until the Venezuelan government put a moratorium on all hunting of wildlife in 1974. The local people say that the Mapurite system was hunted, but not intensely. Possibly, breeding adults were shot out of the Mapurite system in these 2 years.

Unmarked caimans are still being captured, so the total population is not yet known. It is estimated to be about 200. The density of caimans would thus be about 1 caiman/100 m<sup>2</sup> of permanent lagoon, and 1 caiman/100 m<sup>2</sup> of temporary lagoon.

### Diet

Stomach contents were analysed from 21 caimans caught outside of the Mapurite lagoon system. Table 4 summarizes these data. It should be noted that these are primary food items, and that secondary items such as small insects ingested by frogs are not included in this table. These 21 samples may be put into 5 groups. The dry season group had a mean of 3 food items/caiman, whereas the wet season group had a mean of 29 food items/caiman. 66% of the food items during the wet season were frogs. Although 21 species of frog commonly breed in these lagoons only three species were of any significance in the diet of the caimans. These three species both call and breed in shallow water at the edges of lagoons. The aquatic frog, *Pseudis paradoxus*, which is common in these lagoons all year round was apparently never taken by caimans. Juvenile caimans had their stomachs packed with small insects, and were also observed taking *Bufo granulatus*. The three crab-eating caimans were caught in or near streams. It is significant that only in this group were high numbers of gastroliths in evidence. Although small fish and decapod shrimps were common in these lagoons, they were only found on one occasion. These five caiman were caught in a permanent lagoon which had almost dried out at the end of the 1977 drought. The water was only a few centimetres deep, and large numbers of fish and shrimps were packed into the remaining free water. The shrimps were 1 to 3 cm long, and the caimans must have fed in the manner of flamingos to extract them. It would appear that in this area caimans do not feed on actively swimming prey, but on floating semi-aquatic prey.

According to local people large caimans in this area catch small domestic pigs. However, since they are usually nocturnal this seems to be unusual.

On one occasion a 12 year old boy was caught by a large caiman while swimming in a lagoon. Figure 7 shows the wound which required 50 stitches. It can be seen that the teeth marks are very distinct indicating a snapping action by the caiman. Damage was in fact minimal and the patient only required stitches because the wounds were sub-cutaneous. It thus seems probable that this attack was territorial rather than to do with feeding.



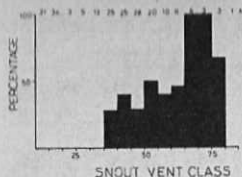


Fig. 8. Occurrence of tail damage in a sample of 206 caimans, sub-grouped into 5 cm class intervals

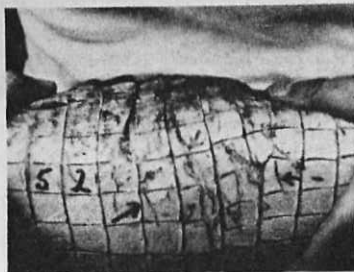


Fig. 9. Scars on the body of a caiman caused by intra-specific fighting

months of hunting in the Mapurite area that the caiman had quickly learned the sound of the arrival of our jeep. What effect this had on recaptures is difficult to gauge. Some released caiman were never recaptured, yet others were easily recaptured up to five times. Caimans often submerged when being approached. One caiman in a small pond remained submerged in the same position for 1 h. It was then poked with a stick and followed around the pond for a further 20 min. During this period it could not be induced to surface. SCUBA gear was used to observe caiman under water in the reservoir. Subadult caiman reacted to the diver by swimming away rapidly and burrowing in the lake bed, some 4 m below the surface. Hatchlings when handled under water played 'dead'; in contrast to their aggressive behaviour when on land.

It was stated earlier that 26% of the caimans had damaged tails. Caimans with whole tails have between 22 and 24 tail joints with a vertical fin. Tail damage occurred on 68% of occasions from the joints 9 to 16. Figure 8 shows the incidence of damaged tails according to size class. It can be seen that small caimans with a snout-vent length of less than 35 cm were undamaged. Thereafter, incidence of damage tended to increase with size. Of the 53 caimans with damaged tails 33 were males. Sufficient data were not obtained to calculate the regeneration rates and hence estimate if damage was seasonal. Regeneration rates varied between 7 mm and 69 mm per year.

In addition to damaged tails, 14 other instances included bite marks on the body and missing feet. Figure 9 shows scars on the body of a 6450 gm female caiman who total length was 125 cm. The scars were undoubtedly caused

by a bite from another caiman. It is thought that all these wounds were the results of intraspecific fighting.

### Breeding

In the Mapurite system five nests were produced during the study period. Figure 1 shows the nest sites. Two were in 1974 at the north ends of lagoons 'G' and 'H'. Two more in 1975 were at the south-east of 'G' and east of 'E'. In 1976 only one nest was produced, at the same site as the nest in 1974 at north 'G'. Hatching occurred between October and November. One nest outside of the Mapurite system was examined. It was 148 cm across and 51 cm high, and made out of leaves and twigs. The egg chamber contained 24 eggs and had an air temperature of 31.4°C prior to opening. Two eggs were removed from this nest. One went bad, and the other hatched on the 16th October at 1145 h. Hatching was accompanied by the hatchling calling four times. In contrast to newly hatched chicks the small caiman was highly aggressive and attempted to bite when picked up.

Young caimans remained together as a pod for about 18 months. The pod that hatched from the 1974 'G' nest was still together and near to the nest site in February 1976. They had split up by September 1976 when two of them were found in lagoon 'F'. The 1976 'G' pod numbered 18 in February 1977 and 14 in June 1977 indicating that mortality was not great.

Adult caimans generally reacted to the distress calls of young ones. This response usually consisted of one or two adults swimming to within 2 to 3 m of the vocalizing young one and displaying. Such displays included swimming broadside on and tail-flagging, porpoising, and tailslapping. Vocalizations were either a low keyed version of the young one's distress call or a noise that sounded like the snuffling of a horse. After displaying the adult would sometimes submerge then surface in another spot and repeat the display. On two occasions an adult caiman attacked the observer who was holding the small caiman. One of these instances occurred in September 1976 when a 61 cm, 490 gm male had been caught. The distress calls were answered by a large number of adult caiman in a moriche palm swamp about 30 m away. In all, 19 adult caimans swam towards the observer. One of these chased the observer out of the water and along the lagoon shore. It returned to the lagoon and was lassoed when it attacked a second time. It was a 128 cm, 8550 gm female. The fact that so many caiman responded indicates that adults which are not parents will defend young. If pods stay together for 18 months and are defended by the parents it may be that caimans breed on alternate years, which would explain the appearance of a nest at north 'G' in 1974 and 1976.

### Discussion

Caimans, inhabiting savanna lagoons systems in south-eastern Venezuela, migrate from dry season refuges in permanent lagoons to temporary lagoons

during the wet season. Such migrations also occur in the Llanos of Venezuela (Staton and Dixon, 1975). Mark and recapture studies showed that there is a marked homing response in sub-adult and adult caimans and implies territoriality.

Young caimans fed almost exclusively on insects. Similar findings have been reported by Donoso-Barros (1965), Alvarez del Toro (1974), and Staton and Dixon (1975). The diet of larger caimans seems more variable. The present study indicated that, apart from an instance of caimans preying upon fish and shrimps trapped in a drying out lagoon, there was little feeding during the dry season as compared to the wet season when the most important items were frogs. Donoso-Barros (1965) also reported anurans in the diet of Venezuelan *Caiman c. crocodilus*. Staton and Dixon (1975) recorded the armoured catfish as the main food item for this caiman in the Guarico State of the Llanos, whereas Castroviejo et al. (1976) reported that in the Apure State the aquatic snail, *Pomacea ursus*, and crabs to be the most frequent prey, although they also found fish. Alvarez del Toro (1974) states that in Mexico *Caiman c. chiapasius* feed mainly on crabs and fresh-water crayfish. It would appear that the diet of *Caiman crocodilus* is simply an expression of available food rather than being the result of specific feeding strategies.

Growth rate of caimans was slow, it taking 6 years to reach a size of 97 cm. Rivero Blanco (1974) reports that captive caiman, fed on a high protein diet of meat and fish, could reach a size of 1 m within 3 years. Since diet is variable it would seem probable that growth rates too vary between caimans in different areas.

The density of caimans in the Mapurite lagoon system was estimated at 1 caiman/100 m<sup>2</sup> during the dry season. In Llanos populations the figure during the dry season was 1 caiman/80 m<sup>2</sup> (Staton and Dixon, 1975). Alvarez del Toro stated that in Mexico prior to hide hunting, densities as high as 1 caiman/10 m<sup>2</sup> could be found. The results of the growth rate study permitted a size frequency analysis to be made of the Mapurite population. Year classes could be resolved for the first 7 years. Two year classes were absent and this correlated with a 2 year period of hide hunting. Staton and Dixon (1975) reported size class diversity for a sample of 247 Llanos caimans. Their analysis indicates a much higher mortality of hatchlings in the Llanos, with low annual recruitment. The maximum size that adult caiman attain in the Llanos is greater than in the Venezuelan Guayana. Males in the Llanos reach a total length of 2.34 m, whereas in the Bolivar State no caiman larger than 2 m were ever encountered.

In contrast to the Llanos, the caimans studied in this report were strictly nocturnal. Daytime basking by crocodylians is well documented and Lang (1976) has shown that in *Alligator mississippiensis* this behaviour is thermoregulatory and has a circadian rhythm. Staton and Dixon (1975) consider this behaviour to be thermoregulatory in *Caiman crocodilus*, and reported that basking behaviour reduced as the dry season progressed. Diefenbach (1975) states that the preferred body temperature of this species ranges between 28.5 to 31.5° C for small individuals and 32.0 to 36.2° C for large ones. Staton and Dixon (1975) reported a mean cloacal temperature of 30.0° C for Llanos caimans. The mean for Mapurite caimans was 27.27° C, which is rather low although these measurements were made at night when the caimans were cooling. Does

the apparent absence of basking behaviour indicate that Mapurite caimans do not thermoregulate? Diefenbach (1975) states that small caiman do not have to leave the water to thermoregulate and can raise their body temperature up to 4° C above that of the surrounding water. It could be that in the Bolivar State the caimans thermoregulate in the warm surface water of the extensive cyperaceous vegetation mats.

It was found that caimans could remain submerged in response to being approached for at least 1 h and 20 min. Lever (1975) recorded that small crocodiles can remain submerged for half an hour and large crocodiles for up to 2 h. Smith et al. (1974) state that in the alligator such submersion is accompanied by a pronounced bradycardia from 31 down to 2 bpm.

Tail damage was found to occur in caimans with a snout-vent length of greater than 35 cm. In contrast, Staton and Dixon (1975) found tail damage in smaller individuals. Rivero Blanco (1974) found nesting females as small as 100 cm long. Staton and Dixon (1976) consider the minimum size at reproduction to be greater, being approximately 130 cm. It is, therefore, improbable that the tail damage was caused during courtship. Caimans with a snout-vent length of greater than 35 cm are more than 2 years old. It was shown that pods of young caimans disperse when they are about a year and a half old. It would seem that tail damage is the result of intraspecific fighting for territory.

Breeding behaviour and nesting have been the subject of detailed reports by Alvarez del Toro (1974) and Staton and Dixon (1976). In the Llanos hatching occurs at the end of the wet season from late October through December. Although in the present study few data were obtained it is apparent that breeding strategies in the Venezuelan guayana are similar to those of the Llanos. Rivero Blanco (1974) recorded a density of 0.085 nests/ha. If their average 2 nests/year in the Mapurite system the density is 0.086 nests/ha of flooded lagoon/year. Only permanent lagoons were used for nesting and there was a maximum of only 1 nest/permanent lagoon/year. This suggests only 1 breeding pair of caimans/permanent lagoon. However, in the case of lagoon 'G' there may have been 2 breeding females nesting alternate years. The 1974 and 1976 nests at north 'G' were probably produced by the same female. If parental care lasted for 18 months until the 1974 pod dispersed, she would not have been available for breeding until the 1976 season.

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