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NESTING OF PARAGUAYAN CAIMAN *(CAIMAN YACARE)* IN BRAZIL

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ABSTRACT

In southwestern Brazil Caiman yacare *nest mainly during the rainy season between December and April. The hatching peak is in March. Nests are built near water and consist of mounds of vegetation with average dimensions of 134 cm long, 117 cm wide, and 40.5 cm high. The average number of eggs in 49 nests was 31(21-38). Eggs averaged 67.7 mm in length, 42.6 mm in width, and 75.3 g in weight. Hatchlings were 23-24 cm long and weighed 46-52 g. Predators, primarily coati and crab-eating fox, destroyed 77% of the nests and partially destroyed another 8.3%. Only 12.5% of the nests escaped predation.*

Few female caiman guard nests closely in daytime, most making sporadic visits only at night. Females excavate the nest when young hatch, and circumstantial evidence suggest that they assist hatchlings to emerge by cracking eggs with their teeth; afterwards they may remain with and protect their young. However, females vary greatly in their attentiveness to nests and young and this appears to be partly in response to human disturbance. Some females cease to guard nests in day-time after one or two visits by man.

INTRODUCTION

Observations on the nesting of various South American crocodilians have been published (Medem 1963, 1971; Staton and Dixon, 1977; Braun, 1973) but little information is available on the Paraguayan caiman, a species which in Brazil is confined to the Paraguay River system. Between January and April 1979 we studied nesting of *Caiman yacare* (Daudin, 1802) along 10 km of the Bento Gomes River (16°15'S, 56°30'W) just east of the town of Poconé in southwestern Mato Grosso State. Supplementary observations were made at Jofre, a ranch bordering the Transpantaneal Highway about 105 km south of Poconé. The Bento Gomes is a small river, no more than 30 m wide, bordered by a mosaic of gallery forests, thickets, pastures, and, on somewhat higher ground, by *cerrado*, a vegetation type which shows a physiognomic gradient from open woodland to dense forest (Goodland, 1971). Between December and March, when over half of the annual precipitation of about 1200 mm falls, the low-lying areas bordering the Bento Gomes River may become flooded to a depth of 1 m or more. Jofre, our other study area, consists of large, seasonally inundated pastures and marshes and sloughs broken by islands of forest, a habitat typical of the Pantanal, as this upper basin of the Paraguay River is called.

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METHODS

Nests were located by walking along river banks, through patches of forests and other likely locations. In addition, local residents were paid to report nest to us. During our first visit to a nest, measurements were made on nest and eggs; other such relevant data as clutch size and distance of nest from water were also collected. Temperature and relative humidity were recorded on the nest and within the egg chamber. One egg from each nest was opened and the embryo measured to provide information on its approximate age and probable hatching date. Most nests were checked at intervals for predation, hatching, or other changes, the frequency of visits depending on ease of access and proximity to hatching. A total of 21 nights were spent in a blind or in a tree near 5 different nests to observe activity of adults and young.

RESULTS

A total of 69 nests were found, 55 at Poconé and 14 at Jofre. Of these, 2 nests lacked eggs, the female having built a nest but failed to deposit a clutch, and 14 nests had already been destroyed by predators, leaving 53 nests which provided information on clutch size, hatching dates, and other reproductive information.

Nesting season

The eggs in 13 nests at Poconé hatched between March 3 and April 1, and the hatching dates of 30 other nests were calculated on the basis of embryo size. As Figure 1 shows, most hatching occurs during March, with a sharp peak between March 21-30. The incubation period of *C. yacare* is unknown, but that of the closely related *C. crocodilus* is said to be 70-73 days (Alvarez del Toro, 1974;

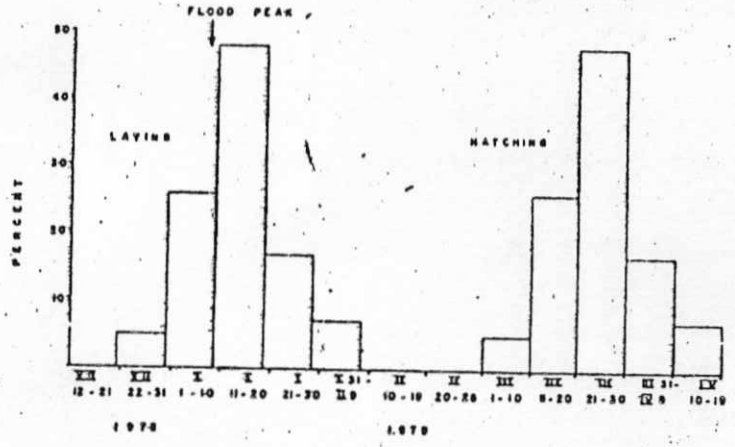

Fig. 1. Estimated laying dates and hatching dates of eggs in 43 *C. yacare* nests in Poconé.

Staton and Dixon, 1977), somewhat longer than the 63-65 days calculat for *Alligator mississippiensis* in the United States (Joanen, 1969). Assuming th *C. yacare* requires an incubation period of about 70 days, most egg layi occurred during January. Although Paraguayan caiman have a pronounc annual laying peak between late December and early February, some individu nest during other months as well, judging by the fact that we also observ hatchlings in Poconé and Jofre during October and December, and, in oth parts of the Pantanal, during June and September.

Peak laying and incubation coincide with the height of the rainy season. 1978 there were occasional rainy days in October and November, but heav prolonged rains began in mid-December and continued intermittently throug March. The highest flood level around Poconé was reached on about January and lesser peaks were around February 18 and March 23. As noted in Figure most caimans began to lay eggs after the peak of the flood, behavior which n doubt saved many nests from inundation.

Nesting during the rainy season is of apparent selective advantage to *yacare* for several reasons: 1) Flooding enables caiman to disperse widely fro the few remaining pools into which they may be crowded during the dry seaso and to nest in places where chances of egg predation are reduced. Late hatchlings find water so widespread that they can avoid competition with olde caimans during the first months of like. 2) Low humidity reduces hatching succe in crocodilian eggs (Staton and Dixon, 1977). By nesting during the rain season, Paraguayan caiman maintained a relative humidity exceeding 90% i the egg chamber. 3) The dry season in the Pantanal is also the cool time of yea when temperatures may drop below 10°C at night but climb to above 38°C i daytime. By contrast, temperatures during the rains vary little, fluctuatin generally between 23° and 3°C. This assures the embryo a relatively constan environment for development, especially since temperatures within the eg chamber are less variable than those outside. Webb *et al.* (1977) documente this well for *Crocodylus porosus* in Australia, and our data for *Caiman yacare* sho a similar trend. The mean of 71 temperatures on top of the nest was 26.7°C (21.5 32), and, at the same time, in the egg chamber 29.3°C (28.8-32).

Nest and eggs

One main requisite for a nest site is the presence of leaf litter, dead grass, o other vegetal material from which the female can construct a mound, anc another is the proximity of water. At Jofre, caiman nested in the forests border ing flooded pastures; at Poconé, they used various forest types: 14.6% were in gallery forest bordering the river, 41.8% were in secondary forest, the site o abandoned pastures, ranging from thickets mixed with bamboo to scrubby forest with a dense undergrowth, and 43.6% were in *cerrado*. Most *cerrado* nests were on tree-covered hillocks protruding above flooded terrain. Only 3 of 69 nests lacked shade. However, in other areas we saw from the air nests of grass built in open marshes, and we were told that on the upper Paraguay River some caiman nest on sandbars, indicating that availability of nest material rather than the presence of shade determines the site.

When first observed, 40% of the nests were within 5 m of water, 16% were within 6-10 m, 12% were within 11-20 m, 10% within 21-40 m, and 13% more than 41 m. However, as flood waters retreated, a few nests became isolated several hundred meters from water.

Two or three nests may be found together in a part of suitable habitat though none were closer than 20 m from each other.

Nests were mainly composed of vegetation which the female had fashioned

Table 1. Nest, egg, and young dimensions of *Caiman yacare* (this study) compared to those of *Caiman crocodilus crocodilus* (Staton and Dixon, 1977). Measurements are in cm.

	Caiman yacare			*Caiman crocodilus*		
	N	Mean	Range	N	Mean	Range
Nest						
Length	50	133.7	94-160	22	117.0	90-200
Width	50	116.9	65-150	22	104.5	80-150
Height	50	40.5	25-60	22	44.5	30-65
Egg chamber						
Length	38	28.1	23-45			
Width	37	23.9	15-32			
Height	30	10.5	7-17			
Depth from top	41	16.0	10-28			
Egg						
Length	190	67.7	55.8-75.5	323	63.8	56.5-72.8
Width	190	42.6	33.5-46.6	323	40.7	37.2-43.7
Weight, g	20	75.3	59-83	241	59.8	48.7-77.4
Clutch size	49	31.0	21-38	30	28.6	17-38
Hatchling*						
Snout-vent length	19	11.7	10.7-12.2	100	11.3	9.8-12.3
Tail length	19	12.3	11.8-13.1	100	-	9.3-11.5
Weight, g	19	49.2	46-51	100	41.5	31.0-51.2
Adult female from Jofre						
Snout-vent length	23	87.7	83-94			
Tail length**	23	70.9	-82			
Weight, kg	23	18.2	13.9-22.7			

* All young were from the same nest.

** Several females have part of the tail missing.

into a conical mound, using material available at the site. Nest material was transported for no more than 3.5 m, as measured from the center of the nest. Average nest size at the base was 134 cm long, 117 cm wide, and 40.5 cm high (Table 1). Thirty percent of the nests were built against the side of a tree or termite mound. Nest material consisted mainly of dead leaves mixed with twigs and earth (78% of the nests); several nests contained an appreciable amount of grass (9%), palm fronds (6%), bamboo (3%) or herbs (1%), and two nests (3%) were composed solely of humus.

The eggs are deposited into an egg chamber which measured an average of 28 cm in length, 24 cm in width, and 10 cm in height (Table 1). This chamber was located approximately in the center of the nest at an average depth of 16 cm from the top. Eggs typically lay on their sides and parallel to each other, and they were basically arranged in two layers; a few eggs sometimes formed the beginning of a third layer or stood on end at the edge of the chamber.

One nest contained only 6 eggs when discovered, having apparently been partially predated. The average number of eggs in 49 other nests was 31 (21-38). Eggs are white, elliptical and have a hard, rough shell which feels like sandpaper. Five eggs from each of 38 nests were measured, and these showed an average length of 67.7 mm (55.8-75.5) and width of 42.6 mm (33.5-46.6). Average egg size varied considerably from nest to nest: 28 eggs in one nest averaged 73.5 x 44.9 mm whereas 33 eggs in another averaged 58.4 x 37.9 mm, to mention only the extremes. Carvalho (1955) gave egg sizes of 72-78 x 42-45 mm. One female (snout-vent lenght 83 cm, weight 13 kg), among the smallest we measured in the Pantanal (see Table 1), had 29 large eggs with average measurements of 71.4 x 45.7 mm, showing that egg size cannot readily be correlated with female size. Eggs within a nest tended to be of about the same size, except in one instance when a nest contained 9 conspicuously small eggs most or all of which were infertile. Average egg weight, based on a sample of 20 eggs from 10 nests, was 75.3 g (59-83).

Nineteen hatchlings from one nest had a total length of 23-24 cm and weight of 46-51 g (Table 1). (Another egg from this nest contained full-term dead twins, joined at the abdomens, with a total weight of 53 g). Two young from another nest were also 23-24 cm long and weighed 55 and 62 g, respectively.

Nest destruction

We ascertained the fate of 48 nests with eggs at Poconé. Of these 37 (77%) were wholly destroyed, 36 of them by predators and one by a combination of predators and flooding. All eggs in one nest (2.1%) were infertile. Four nests (8.3%) were partially predated but some eggs hatched, and 6 nests (12.5%) remained intact, most or all eggs hatching successfully. At Jofre, 7 out of 13 nests (54%) had already been destroyed by predators in early March, nearly a month before most were due to hatch. A further two nests had been partially destroyed by flooding, 39% of the eggs being rotten.

The coati *(Nasua nasua)* was the principal predator. At Poconé it was seen at one nest, trapped at two others, and suspected of having eaten the eggs of at least 9 further nests. The second most important predator was the crab-eating fox *(Cerdocyon thous)*. One was trapped at a nest, and another was observed to eat 12 eggs at a nest which the female caiman had opened at hatching time but failed to guard after being disturbed by us. Local informants told us that tegu lizard *(Tupinambis)* and capuchin monkey *(Cebus apella)* also prey on nests. Other possible vertebrate predators in the area include dog, domestic pig, peccary *(Tayassu)*, six-banded armadillo *(Euphractus sexcinctus)*, white-eared opossum *(Didelphis albiventris)*, tayra *(Eira barbara)*, crab-eating raccoon

(Procyon cancrivorus), the larger cats *(Felis pardalis, F. concolor, Panthera onca)*, rat *(Thricomys)*, and possibly certain snakes. Large red ants invaded one nest at hatching time and ate 5 young before the female opened the nest and released the others. Ants also destroyed 4 hatchlings at a second nest, but since we removed the remaining eggs for weighing and measuring, this nest is excluded from our computations.

All eggs in a nest may be taken by a predator or predators during a single visit. However, some nests are robbed repeatedly, a few eggs at a time, untill all are gone. For example, one nest had 34 eggs on February 2. Six eggs had disappeared by February 28; on March 4 one more egg was missing and on March 7 still another egg. A day later a predator had eaten 4 more eggs and broken two. We set several traps and caught a female coati. On March 12 all remaining eggs were gone but a second female coati was in a trap. Another nest had 29 eggs on February 22. Fourteen of these eggs had disappeared by March 19, an unknown predator or predators having made 4 visits and taken 1 to 7 eggs each time; flooding destroyed the remaining eggs. Such partial predation has also been reported in American alligator (Joanen, 1969), Nile crocodile (Modha, 1967), and spectacled caiman (Staton and Dixon, 1977).

Occasional eggs were infertile and in some the embryo died during development. A total of 232 eggs from 8 nests were sampled to determine what percent of the eggs failed to hatch due to these causes. Four eggs were infertile or contained very small embryos, 3 contained large dead embryos, and one contained a live embryo which was so retarded in growth that its survival seemed unlikely, a total of 3.4% of the sample. When this percentage is extrapolated to a larger sample of 1089 eggs in 37 nests, including those destroyed by predators and it to this figure is added one nest in which all eggs were infertile, then a total of 69 eggs (6.3%) failed to hatch. Other causes of death in this sample included 783 eggs (71.9%) taken by predators, 16 eggs (1.5%) destroyed by floods, and 2 eggs (trace) broken inadvertently by the female caiman. Only 219 eggs (20.1%), or one in five, hatched.

Maternal care

Female caiman show maternal behavior during several stages of the reproductive cycle, first by guarding the nest, then by helping to release young from the egg chamber, and finally by protecting hatchlings. Male *Caiman crocodilus* (Alvarez del Toro, 1969) and *Crocodylus niloticus* (Pooley and Gans, 1976) in captivity may assist females at the nest, but male *Caiman yacare* were not seen near nests in the wild even though their large size (up to 58 kg) would make them useful protectors.

Nest guarding. Females were seldom encountered at nests in daytime. At Poconé, 8 (17%) of 47 nests with eggs were guarded by a female during our first visit. However, since most nests were located by someone else and reported to us, ours was actually the second instance of human disturbance at these nests. At Jofre, 3 (43%) of 7 nests were guarded by a female when we first found them. We do not know why some females guard nests closely and others do not. Possibly certain females have learned to avoid humans by remaining safely in deep water during daytime, being survivors from the 1960's when caiman were intensively hunted in the area. There is also evidence that even a single instance of nest disturbance may influence subsequent guarding behavior, although we never molested females except once to weigh and measure one. For example, a female was present at four nests during our first visit but not later. At another nest, the female was guarding on our first three visits, on February 3 and 9 and on March 4, but between March 7 and 28, when the nest was checked almost daily, she was present only once. By contrast, one female was always within 15 m of her nest in spite of the fact that we visited repeatedly and once spent 7 consecutive nights in a blind nearby.

The responses of female caiman to nest predators remain unknown. Joanen (1969) reported that an American alligator made no attempt to protect her eggs when a raccoon (*Procyon lotor*) ate them. However, judging by the behavior of female caiman toward human intruders at the nest, at least some would defend their eggs against coati, fox and other such predators. Some females fled at our approach or remained passive, lying quietly in the undergrowth a few meters from the nest. However, 3 females actively guarded the nest at our approach, two of them climbing up on the nest and lying there with mouth open hissing and growling, and one walking directly at us with growls until we retreated. Kushlan (1973) described similar behavior toward man by American alligator.

Although most females were rarely if ever at the nest in daytime, tracks revealed that they visited occasionally at night. For example, a predator opened and partially robbed a nest and the female afterward covered the remaining eggs. Another female opened then closed her nest about 3 weeks before hatching, in the process breaking two eggs, and two nights later she investigated the egg chamber again. Visits probably increase as the hatching date approaches: one female came to her nest during three consecutive nights before she opened it and released the young.

Behavior of female at hatching time. Females were so shy that it was difficult to observe behavior at nests. However, one female tolerated our blind near the nest, although her actions were probably affected by our presence. Starting on March 23 we observed the nest every night and for much of the day. Usually lying quietly on the forest floor, the female neither visited the nest nor the water 11 m away. But at noon on March 28 she climbed onto the nest and remained 25 minutes before descending. By 2100 hours she had climbed up on the nest 7 more times for periods of from 20 to 75 minutes. At 1845 the yippy barks of calling young could be heard within the nest, and at 1945 the female vocalized once, a single grunt. At 2115 she began to excavate the egg chamber, digging slowly by sweeping debris sideways and backwards with a front or hindleg and pushing it off the mound with the side of her snout. She remained sporadically active until shortly after midnight, by which time one side of the egg chamber was open. Between 0150 and 0310 she reclined on the nest again, digging only a little at intervals. Three young, judging by their calls, had by then left the nest and gone to water. The female made one more visit to the nest, for 15 minutes at 0935, and then entered the water, remaining there all day and the next night even though the calls of the young in the nest were clearly audible. Occasionally she emitted single, resonant grunts. Young continued to emerge and move to water without the female's assistance until on April 1, 4 days after the first young appeared, 20 of the 30 eggs had hatched and several of the remaining ones were pipped.

Hatching of young in this nest was poorly synchronized. Similarly, at another nest 5 young hatched over a period of 3 days, and, with the female absent, were killed by ants in the egg chamber. However, the female opened the nest on the fourth day and within a few hours the surviving young were out of their eggs and into the water. Joanen (1969) mentioned one American alligator nest from which several young emerged by themselves but hatching was not completed until the female opened the nest a week later. By contrast some clutches hatch quickly. We checked the eggs of 3 nests without noting evidence that hatching was imminent, yet the female opened the nest during the following night and by morning all except 2 young were out of their eggs. Another nest contained only eggs at 1005, yet 6 hours later the nest had been opened and all young had hatched and gone to water. One nest contained nearly full-terms eggs. We opened one egg at 1500 hours and released the young into the egg chamber.

and also added a hatchling from another nest, hoping to observe the responses of the female. She arrived at 2130 and reclined on or beside the nest without responding to the calls of the young. Since our presence seemed to affect her behavior we departed after an hour. By 0700 the female had opened the nest and all young had hatched even though they were probably several days premature.

Although the vocalizations of young and the occasional calls and movements of the female near the nest may serve to synchronize hatching to some extent, our observations show that hatching may either extend over several days or occur so rapidly that passive stimulation seems an improbable explanation. Pooley and Gans (1976) described how Nile crocodile induce young to hatch by gently cracking the eggs with their teeth, and, in a similar situation, Alvarez del Toro (1969) observed how a captive male spectacled caiman not only crushed eggs with his teeth but also with his legs and tail. It seems likely that Paraguayan caiman behave similarly. A piece of other circumstantial evidence supports this supposition. When young hatch slowly by themselves, they leave the shells intact, except for the holes through which they escape. But at nests in which young hatched together, shells are characteristically shattered, as if something had crushed them.

Our observations indicate that female caiman have two main functions at hatching: 1) Females open up the nests, allowing young to escape from the egg chamber. This function may not be essential if nest material is loose enough for young to push or dig their way out. However, many nests consist of such compacted mounds of leaves and earth, laced together with a network of growing rootlets, that young probably cannot escape unaided. Joanen (1969) found that half of the young in 2 American alligator nests died when the females failed to liberate them. *Crocodylus porosus* in Australia and Nile crocodile also excavate nests at hatching (Webb *et al.* 1977; Modha, 1967). 2) Females crack open eggs assuring a simultaneous hatch. A prolonged hatching period exposes to predation either the eggs or those young which have gone to water since the female cannot guard both at the same time. For example, 16 of the 28 eggs in a nest had hatched and female was in attendance when we arrived at 0845. She fled and failed to return to the nest, although she called from the swamp nearby, and that night a fox ate the remaining eggs.

Guarding hatchlings. Young move independently toward water soon after hatching and lie singly or together in the shallows. Two young emerged from eggs between 1100 and 1110 and reached the water's edge 1.7 m away at 1340. Scattered young call occasionally with the same yippy bark heard during hatching, and the female may grunt one or more times, the vocalizations probably serving to maintain contact. Some families leave the nest area within a day or two. For instance, one clutch hatched during the night. By the following afternoon 7 young were still near the nest mound and others were in the river nearby. The female visited the mound at 2110, but on perceiving us she dove into the water. By morning neither female nor young were in the vicinity. Another family remained in a flooded thicket near the nest for several days after the young hatched. The female ignored us until a young gave several rapid yips, a "distress" call to which she responded by rushing to within 3 m of us with mouth open, her tail churning the water. Defense behavior was also observed in a female which for at least 11 days remained in a small pool with her 23 hatchlings. When we approached to within 6 m of the hatchlings, they raised their tails perpendicularly from the water, the black, parallel bars on the tails being conspicuous visual signals. Several young called. The female had been submerged nearby and she first lunged with much splashing toward us, then sank slowly, blowing bubbles through her nose. Instances of *C. crocodilus* guarding young are described by Gorzula (1978).

We have no information for how long female Paraguayan caiman remain with their young. *Crocodylus porosus* and *Caiman crocodilus* females may guard hatchlings for at least 2 1/2 months (Webb *et al.*, 1977, Staton and Dixon, 1977). However, some newborn *C. yacare* young seem to have little or no contact with a female. For instance, about 30 recent hatchlings were without a female in a small pool over 1 km from a river.

DISCUSSION

Our preliminary results show that the nesting biology of *C. yacare* closely resembles that of *C. crocodilus* as described by Staton and Dixon (1977). Similarities include the dimensions of nests, eggs, and young (see Table 1), as well as such other details as clutch size, nest construction and location, and incubation during the rainy season. This similarity is not surprising, for there is, in fact, disagreement about the taxonomic status of *yacare*, some authors (Medem, 1960) listing it as a distinct species and others (Brazaitis, 1973) as a mere subspecies or *crocodilus*. Most of our data need no further comment, but two aspects need brief elaboration since they concern conservation of caiman in the Pantanal.

Females vary in their attentiveness to nests, a point also noted for American alligators by Joanen (1969). Some guard closely whereas others visit only occasionally; some flee from man whereas others attack; some help hatchlings from the eggs and later protect them whereas others abandon them. Some of this variation can no doubt be traced to basic individual differences in temperament. However, it was also our impression that females are so sensitive to being disturbed at the nest that even one contact may be enough to change patterns of guarding behavior. Several females ceased to protect nests in daytime after one visit by us. The response may have been fortuitous, but it did make eggs more vulnerable to coati and other diurnal predators. Certain females always left their nests unguarded, making only occasional visits at night. Perhaps such animals had adverse contacts with man in previous years. Whatever the explanation, we have little doubt that nesting females may modify their behavior in response to human disturbance, and if such disturbance inadvertently increases predation some populations may be unable to absorb this additional loss.

A total of 77% of the nests at Poconé were destroyed by predators, especially by the coati, which is the most abundant of the larger carnivores in the Pantanal area. For comparison, 32 nests of spectacled caiman in Venezuela showed a 50% predation rate, mainly by tegu lizard; a further 15.6% of the nests were raided by humans and 9.4% were trampled by cattle, a total loss of 75% (Staton and Dixon, 1977). Predators and floods destroyed only 18.6% of alligator nests in Louisiana (Joanen, 1969). The predation rate in our study area was extremely high, and in some years flooding might destroy more nests than it did in 1979, yet the caiman populations seemed to be expanding. However, hide hunters are still decimating or virtually eradicating caimans in large parts of the Pantanal. Coati nest depredation probably increases the rate of decline of such populations, and, in the event that poaching is reduced, it could slow the rate of recovery.

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