Instituto Nacional de Pesquisas da Amazônia

Programa de Pós-Graduação em Ecologia

Variação temporal na predação de ninhos de jacaré-açu (*Melanosuchus niger*, Alligatoridae) na Amazônia Central, Brasil

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Manaus – AM

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Orientador: Dr. William Ernest Magnusson

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requerimentos para obtenção do título de Mestre em Biologia (Ecologia)

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BANCA EXAMINADORA DA DEFESA ORAL PÚBLICA

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 08 dias do mês de março do ano de 2017, às 09h00min, no Auditório dos PPG'S ATU/CFT/ECO, Campus III, INPA/V8. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Igor Luis Kaefer,** da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). **George Henrique Rebêlo,** do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). **Ronis da Silveira,** da Universidade Federal do Amazonas - UFAM, tendo como suplentes o(a) Prof(a). Dr(a). Fabricio Beggiato Bacaro, da Universidade Federal do Anazonas - UFAM, e o(a) Prof(a). Dr(a). Albertina Pimentel Lima, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **KELLY CRISTHYNA TORRALVO,** intitulado: **"VARIAÇÃO TEMPORAL NA PREDAÇÃO DE NINHOS DE JACARÉ-AÇU (MELANOSUCHUS NIGER, ALLIGATORIDAE) NA VÁRZEA AMAZÔNICA",** orientado(a) pelo(a) Prof(a). Dr(a). William Ernest Magnusson do Instituto Nacional de Pesquisas da Amazônia - INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A) ☐ REPROVADO(A)

☒ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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SINOPSE

Este trabalho testou a relação de variáveis temporais com o ataque e predação de ninhos de jacaré-açu, na várzea da Amazônia Central. Foram utilizados vestígios deixados no local e registros fotográficos para identificação das espécies de predadores. As diferenças entre os métodos foram testadas. A presença da fêmea e a perturbação humana também foram testados em relação aos eventos de predação registrados.

Palavras-Chave: jacaré, predação de ninhos, *Melanosuchus niger*, várzea, Amazônia

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Ao Instituto de Desenvolvimento Sustentável Mamirauá pelo ideal e pela oportunidade oferecida e a CAPES pela bolsa de estudos concedida durante os dois anos de curso.

"... A idéia romântica de tratar a mulher como uma videira aderente e, assim, eliminar metade das energias da humanidade, está rapidamente desaparecendo e dando lugar à ideia de que os fortes são para os fortes - os intelectualmente fortes..."

Trecho traduzido do livro "Woman in Science" (H. J. Mozans, 1913)

RESUMO

Na várzea amazônica, o período de nidificação do jacaré-açu (*Melanosuchus niger)* ocorre na época da seca, quando áreas terrestres ficam disponíveis. O período de incubação pode durar até 90 dias. As principais ameaças ao sucesso da nidificação do jacaré-açu são a inundação e a predação dos ninhos. Os principais predadores de ninhos de jacaré-açu são a onça pintada (*Panthera onca*), o lagarto jacuraru (*Tupinambis teguixim*), o macaco prego (*Sapajus macrocephalus*) e o homem (*Homo sapiens*). Neste estudo, foi investigada a relação entre os ataques de predadores aos ninhos e o período de incubação e avaliou-se a influência da predação inicial na predação subsequente na Reserva de Desenvolvimento Sustentável de Mamirauá. Também foi avaliada a influência da presença de fêmeas perto dos ninhos e da manipulação de ninhos na ocorrência de ataques. Os resultados de dados obtidos com armadilhas de câmeras e de vestígios deixados por predadores foram comparados em estimativas de taxas de predação por diferentes predadores. A predação de ovos foi registrada em 32% dos 658 ninhos monitorados por dois anos. Os resultados sugerem que a probabilidade de predação em ovos de jacaré-açu é relativamente constante ao longo do período de incubação e que a predação nos ovos foi menor quando adultos, presumivelmente fêmeas, estavam presentes. A abertura dos ninhos e o manejo dos ovos não aumentaram o número de ataques aos ninhos. A abertura do ninho por um predador pareceu aumentar as possibilidades de um ataque subsequente, porque a maioria dos ataques aos ninhos ocorreu logo depois que um predador abriu primeiramente o ninho. No entanto, os ataques de outra espécie de predador não parecem ser necessários para

iniciar ataques de qualquer espécie de predador. Os resultados baseados em armadilhas fotográficas e vestígios foram semelhantes, porém os dados de vestígios subestimam o número de espécies que atacaram quando o ninho teve mais de um evento de predação. Isso torna o método ineficaz para os estudos que procuram informações sobre todas as espécies de predadores envolvidos.

ABSTRACT

Temporal Variation in Black Caiman (*Melanosuchus niger,* Alligatoridae) Nest Predation in Central Amazonian, Brazil

In the Amazon floodplain, the nesting period of the black caiman (*Melanosuchus niger*) occurs in the dry season, when land areas are available. The incubation period can extend up to 90 days. The main threats to the success of nesting of black caiman are flooding and predation of nests. The main predators of black caiman eggs are jaguars (*Panthera onca*), tegu lizards (*Tupinambis teguixim*), capuchin monkeys (*Sapajus macrocephalus*) and humans (*Homo sapiens*). In this study, we investigated the relationship between predator attacks on nests and incubation period, and evaluated the influence of initial predation on subsequent predation in the Mamirauá Sustainable Development Reserve. We also evaluated the influence of presence of females near the nests and manipulation of nests on the occurrence of attacks. We compared results from data obtained with camera traps and vestiges left by predators on estimates of rates of predation by different predators. Egg predation was recorded in 32% of the 658 black caiman nests monitored for two years. Our results suggest that the probability of predation on black caiman eggs is relatively constant throughout the incubation period and that predation on eggs was lower when adults, presumably females, were present. The opening of nests and handling of eggs did not increase the number of attacks on black caiman nests. Nest opening by a predator appeared to increase the chances of a subsequent attack because most of the attacks on nests occurred soon after a predator first opened the nest. However, attacks by another species of predator do not appear to

be necessary to initiate attacks by any of the species of predator. Results based on camera traps and vestiges were generally similar, but of vestiges underestimates the number of species that attacked the nest in more than one predation event. This making the method ineffective for studies that seek information on all species of predators involved.

SUMÁRIO

INTRODUÇÃO GERAL

A nidificação de diversas espécies que habitam sazonalmente áreas alagáveis está concentrada no período de seca, quando áreas terrestres estão disponíveis - por exemplo aves aquáticas (ZARZA *et al*., 2013), quelônios (FACHIN-TERAN e VON-MÜLHEN, 2003) e jacarés (VILLAMARIN *et al.*, 2011). Os ninhos são predados por animais que utilizam os ovos como recurso alimentar (FACHIN-TERAN e VON- MÜLHEN, 2003; DA SILVEIRA *et al*., 2010; VILLAMARIN *et al.*, 2011; BARÃO-NÓBREGA *et al*., 2014), o que pode representar um baixo recrutamento de novos indivíduos para as populações de presas.

O período de nidificação do jacaré-açu (*Melanosuchus niger)* ocorre na época da seca (setembro a janeiro) e pode durar até 90 dias, entre a postura dos ovos e o nascimento dos filhotes. As principais ameaças ao sucesso da nidificação da espécie são a inundação e a predação dos ninhos (VILLAMARIN e SUAREZ, 2007; VILLAMARIN *et al*., 2008).

Diferentes espécies de vertebrados já foram registradas como predadores de ninhos de crocodilianos (SOMAWEERA *et al*, 2011; CAMPOS E MOURÃO, 2014). Na várzea amazônica os principais predadores de ninhos de jacaré-açu são a onça pintada (*Panthera onca*), o lagarto jacuraru (*Tupinambis teguixim*), o macaco prego (*Sapajus macrocephalus*) e o homem (*Homo sapiens*) (VILLAMARIN *et al*., 2008; DA SILVEIRA *et al.*, 2010; BARÃO-NÓBREGA *et al.*, 2014).

Considerando as informações bases, no Capítulo I foi apresentada a relação entre os ataques de predadores aos ninhos de jacaré-açu e o período de incubação, em

ninhos monitorados na Reserva de Desenvolvimento Sustentável Mamirauá, região de várzea no Médio Solimões. Também foi avaliada a influência da predação inicial na predação subsequente, a influência da presença de fêmeas perto dos ninhos e a manipulação de ninhos na ocorrência de ataques. Em complemento, os resultados de dados obtidos com armadilhas fotográficas (*cameras trap*) e vestígios deixados por predadores foram comparados, em estimativas de taxas de predação por diferentes predadores.

Com o uso de armadilhas fotográficas foi possível uma identificação precisa dos predadores e a observação direta dos eventos de predação. Graças ao método foi registrado um possível uso de ferramenta por macaco-prego (*S. macrocephalus*) para a abertura de um ninho de jacaré-açu, durante um evento de predação na Reserva Mamirauá. O registro foi obtido oportunisticamente no período de monitoramento dos ninhos de jacarés foi interpretado segundo hipóteses do uso de ferramentas por primatas e é apresentado como apêndice da dissertação (Apêndice I).

OBJETIVOS

O objetivo geral nesse trabalho foi relacionar variáveis temporais com as taxas de predação e os tipos de predadores de ninhos de jacaré-açu, em ambientes de várzea. O trabalho foi organizado para responder especificamente às seguintes perguntas:

(1) A probabilidade de predação de ovos em ninhos de jacaré-açu varia ao longo do período de incubação?

(2) A proporção de tempo que as fêmeas atendem aos ninhos afeta a probabilidade de predação?

(3) A predação por uma espécie de predador influencia a predação por outras espécies?

(4) As proporções de ninhos atacados por diferentes predadores estimados a partir de registros de vestígios refletem as proporções de ninhos efetivamente atacados por esses predadores?

(5) A abertura e manipulação de ovos para fins de pesquisa tornam os ninhos mais vulneráveis à predação?

Capítulo I.

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Temporal Variation in Black Caiman Nest Predation in Central Amazonian *Várzea*.
Manuscrito em revisão – *Plos One*

RESEARCH ARTICLE

Temporal Variation in Black Caiman Nest Predation in Central Amazonian *Várzea*.

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Abstract

On the Amazon floodplain, the main predators of black caiman (*Melanosuchus niger*) eggs are jaguars (*Panthera onca*), tegu lizards (*Tupinambis teguixim*), capuchin monkeys (*Sapajus macrocephalus*) and humans (*Homo sapiens*). In this study, we investigated the relationship between predator attacks on nests and incubation period, and evaluated the influence of initial predation on subsequent predation in the Mamirauá Sustainable Development Reserve. We also evaluated the influence of presence of females near the nests and manipulation of nests on the occurrence of attacks. We compared results from data obtained with cameras traps and vestiges left by predators on estimates of rates of predation by different predators. Egg predation was recorded in 32% of the 658 black caiman nests monitored for two years. Our results suggest that the probability of predation on black caiman eggs is relatively constant throughout the incubation period and that predation on eggs was lower when adults, presumably females, were present. The opening of nests and handling of eggs did not increase the number of attacks on black caiman nests. Nest opening by a predator appeared to increase the chances of a subsequent attack because most of the attacks on nests occurred soon after a predator first opened the nest. However, attacks by another species of predator do not appear to be necessary to initiate attacks by any of the species of predator. Results based on camera traps and vestiges were generally similar, but of vestiges underestimates the number of species that attacked the nest in more than one predation event. This making the method ineffective for studies that seek information on all species of predators involved.

Introduction

Susceptibility of reptile and bird nests to attacks by predators may vary with incubation phase and parental behavior [1,2]. On the Amazon floodplain, the main predators of black caiman (*Melanosuchus niger*) eggs are jaguars (*Panthera onca*), tegu lizards (*Tupinambis teguixim*), capuchin monkeys (*Sapajus macrocephalus*) and humans (*Homo sapiens*) [3,4]. However, it is not known if the intensity of attacks by predators varies throughout the incubation period or whether some nests are more vulnerable than others.

Black caimans nest in the dry season (from September to January in central Amazonia) and the incubation period can extend up to 90 days [5,6]. The second most frequent cause of egg mortality after predation is nest flooding [3,7], which occurs at the end of the incubation period. Nests of black caiman are mostly located in flooded forests (*várzea*) around isolated water bodies where the water level rises later in the season [8].

The black caiman is widely distributed in the Amazon basin, but occurs most frequently in *várzea* in sympatry with spectacled caimans (*Caiman crocodilus*). Female spectacled caimans nest in the same period and same general area as black caimans [8]. The main predators of spectacled caiman eggs are also tegu lizards, capuchin monkeys, jaguars and humans [9]. Spectacled caimans often nest further away from water bodies than black caimans, and may attend the nest over the whole incubation period, far from water and often without feeding [10,11]. Unlike the spectacled caiman, black caiman females usually nest near water bodies and remain in the water most of the time

[4,7,12].

Black caimans produce up to 60 eggs per clutch [6,7] and several events of predation involving different species of predators can occur in a single nest. In other species, the behavioral response of the prey to reduce the action of a predator may facilitate the action of a second species [13,14]. In the case of nest predation, the action of the first predator can act as a facilitator to the foraging of a second predator by exposing the eggs.

Black caiman nests are mounds of earth, leaves and sticks. Predators attacking nests leave characteristic vestiges, such as holes, scattered shells and footprints. These have been used to identify egg predators of black and spectacled caimans [4,9]. However, it is unknown if these records allow the correct identification of predators. More precise data have been obtained using camera traps for nests of other species of crocodilians [15,16].

Predator attacks on caiman nests can also be influenced by research activities carried out during the incubation period. Studies have shown an increase of up to 70% in attacks on nests of other caiman species that were exposed to human disturbance, such as opening nests or capture of females [9,17,18].

In the present study, we investigated the following questions: (1) Does the probability of egg predation on black caiman nests vary throughout the incubation period? (2) Does the proportion of time that females attend nests affect the probability of predation? (3) Does predation by one species of predator influence predation by other species? (4) Do the proportions of nests attacked by different predators estimated

from records of vestiges reflect the proportions of nests effectively attacked by those predators? (5) Does opening nests and handling of eggs for research purposes make them more vulnerable to predation?

Material and methods

The study was conducted in the Mamirauá Sustainable Development Reserve (MSDR) located in central Amazonia between the Amazon (Solimões) and Japurá Rivers (Fig. 1). The reserve is covered by *várzea* habitats and subject to a large monomodal flood pulse of up to 10 m in amplitude [19].

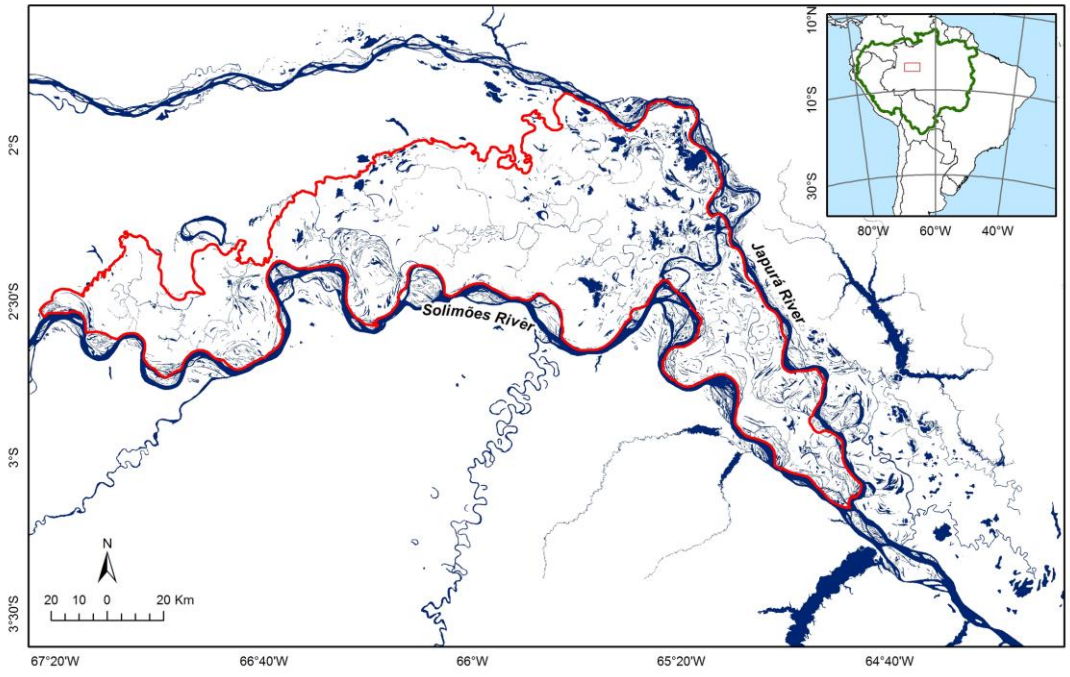

Figure 1. Location of the study area. Red lines show the limits of the Mamiraua Sustainable Development Reserve – MSDR. The green line on the inset indicates the limits of the Amazon basin. Map created by Jefferson Ferreira Ferreira.

Nests were monitored between October, November and December of 2013 and 2014. Nest searches were undertaken on foot or from small boats near 288 water bodies, mainly lakes, and the locations of nests were recorded with a GPS model Garmin 76CSx®. Identification of predators was based on vestiges for 595 nests and on records from camera traps in 63 nests.

Evidence of predation, such as holes in the nest, missing eggs, scattered shells and footprints near the nest, were used to identify predators that attacked nests monitored without camera traps. Camera traps, model PC800 Reconyx®, were attached to trees near 63 nests, positioned so that the entire nest was captured in the images, and photos were downloaded every 15 days. In most cases, the nests were monitored with camera traps shortly after they were built (estimated at less than 13 days from the date used here as the earliest nest construction) until the end of the nesting period. If all eggs in a nest had been removed by predators, the camera trap was installed on another nest without evidence of predation in the same lake.

Nests were visited from one to six times, and the presence or absence of a caiman, presumably the female, near the nest was recorded on all visits.

Of the 63 nests monitored by camera traps, 14 were opened for counting and measuring eggs. This procedure was part of other research activities and involved manual opening of the nest, removal, handling and replacement of eggs, and nest closure.

Entry permission to the Mamiraua Sustainable Development Reserve was granted by the Instituto de Desenvolvimento Sustentável Mamirauá. This is study is included in

the authorization for scientific activities n. 46635-2 of the Biodiversity Authorization and Information System - SISBIO.

Data analysis

It was not possible to know the exact time of egg incubation when nests were first found. The earliest record of nests found in this study was October 3rd. Therefore, we fixed 01 October as the starting date of the incubation period for estimating the age of nests used in analyses.

We calculated the probability of predation during the incubation period for 63 nests monitored with camera traps. The total incubation period (90 days) was divided into 7-day intervals for analysis. For these analyses, we used only the first predation event for each nest. Temporal clumping of attacks on nests by each kind of predator in the two years of sampling was analyzed using a serial randomness test [20].

To investigate the relationship between female presence and the probability of predation, we only used nests that received at least 3 visits between early October and late December (n = 30). A Fisher's exact test was used to analyze the contingency table.

To test whether some nests were more susceptible to predation than others, we tested whether the proportion of nests with eggs taken by zero, one, two or three species of predator differed from the expected ratios if attacks by each species of predator were independent, using a chi-square test of a contingency table.

To determine if attacks by a species of predator were dependent on the previous attacks by another species of predator, we compared the proportions of observed

predation with each species acting as the first, second or third predator with a chi-square test of a contingency table.

To test whether a predation event stimulated subsequent attacks regardless of the predator, we compared the mean time between predation events with the mean differences when the dates of predation were randomized 999 times.

To determine whether vestiges could be used to estimate the proportions of nests attacked by different species of predators, the total proportions of nests in both years in which predators were identified by vestiges (n = 595), was compared with the proportions of nests attacked by different species of predators for nests monitored with camera traps (n = 63), using a Fisher's exact test of a contingency table.

To test whether the opening of nests by researchers affected the probability of egg predation, the proportion of nests opened for counting and measuring eggs that were attacked by predators was compared with the proportion of nests that had not been opened that were attacked by predators, using a Fisher's exact test of a contingency table.

Results

Predation was recorded in 32% of the 658 black caiman nests monitored in MSDR. The camera traps recorded the species already known to be predators of black caiman eggs (*Panthera onca*, *Tupinambis teguixim*, *Sapajus macrocephalus*), and the common opossum (*Didelphis marsupialis*) was photographed taking eggs from one nest that had been opened 18 days before for research activity, but not previously attacked by other

predators.

There was no statistically significant relationship (serial randomness test: p> 0.25 in all cases) between the time since the beginning of incubation period and attacks by any of the predator species (Fig. 2). Despite the lack of a significant relationship (p=0.25), predation by capuchin monkeys was concentrated between the fourth and eighth week of incubation (Fig. 2b). Attacks on black caiman nests by jaguars were recorded only in one nest in the eighth week of incubation (20 to 26 November) in 2013 and in two nests attacked in the third week (15 to 21 October) in 2014. Data for jaguars were insufficient for statistical tests.

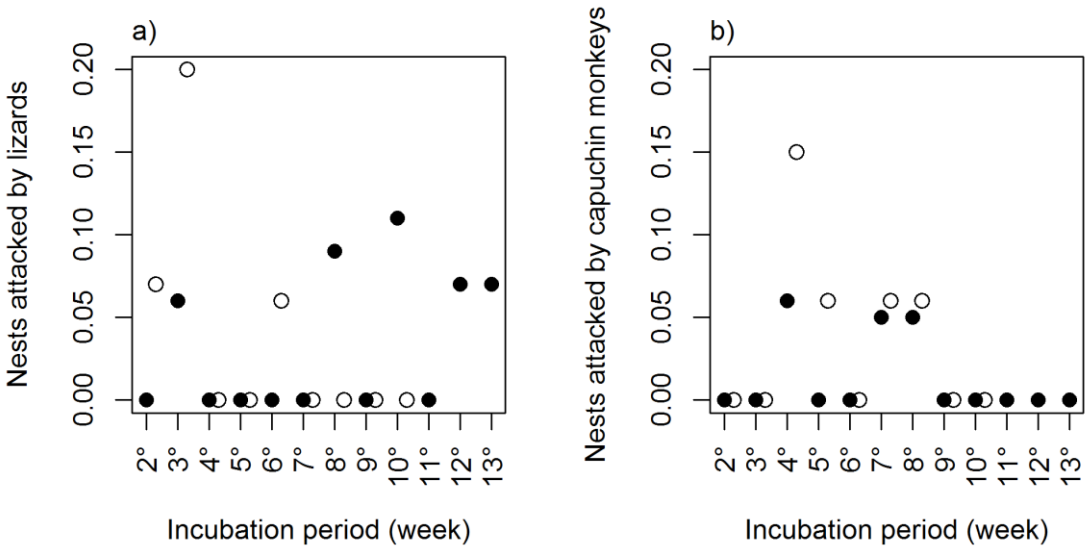

Figure 2. Relationships between the proportion of nests attacked by each species of predator and nest age for nests monitored in 2013 (○) and 2014 (●). The number of nests available in 2013 in the 2nd to 10th weeks of incubation were 15, 15, 13, 17, 18, 18, 17, 18 and 17, respectively. The number of nests available in 2014 in the 2nd to 13th weeks of incubation were 16, 17, 18, 22, 23, 22, 24, 19, 16, 15, 15, and 15, respectively.

The proportion of nests that were attacked by predators in which we recorded an adult, presumably the female, close to the nest (1 of 30) was significantly lower (Fisher's Exact Test: P = 0.02) than the proportion of nests at which adults were not recorded that were attacked (11 of 30), indicating a lower rate of attack on nests attended by adults.

The probability of a nest being attacked by more than one species of predator was higher than expected by chance if nests were equally likely to be attacked (chi-square test: P = 0.03), indicating that the probability of predation varied between nests.

Occurrence as initial or later predator did not vary between species (chi-square test: P> 0:31), indicating that predation by one species is not necessary for predation by any other species. However, the difference in the age of the nest between the first and second attacks (mean 3.84) was lower than the mean (22.25) expected if the time between the first and second attacks was no greater than expected by chance (P = 0.001), indicating that nest opening in the first predation event facilitated subsequent attacks by the same or other species of predators (Fig. 3).

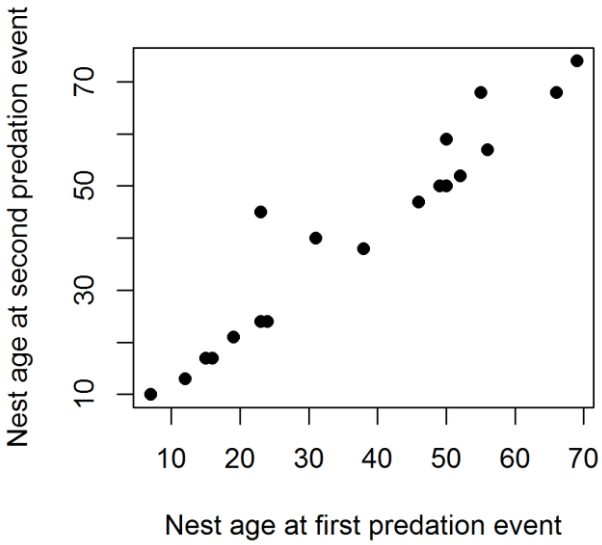

Figure 3. Relationship between the times to first and second predation events in black caiman nests monitored in the years 2013 and 2014.

The proportions of nests attacked by different predators estimated from vestiges were similar to the proportions of nests attacked identified by camera traps when the nest was attacked by only one species of predator (*Fisher's Exact Test:* P= 0.74). However, the proportions of nests estimated to be attacked by more than one species of predator differed between the two identification methods used (*Fisher's Exact Test*: P=0.01). The proportion of nests that were not attacked was similar between methods (0.71 monitored by vestiges and 0.62 monitored by cameras traps) and predators could not be identified for a small proportion (0.02) of nests monitored by vestiges (Table 1).

Table 1. Number and proportion of predators that attacked nests monitored by vestiges (N=595) and nests monitored by cameras (N=63) in the years 2013 and 2014.

	Vestiges	Cameras
No predation	421 (0.71)	39 (0.62)
1 predator	136 (0.23)	14 (0.22)
>1 predator	25 (0.04)	10 (0.16)
unknown	13 (0.02)	0

The proportion of nests attacked by predators did not differ statistically between nests that had been opened for research purposes (14 of 63) and nests that had not been opened (49 of 63) for nests monitored by cameras (*Fisher's Exact Test*: P≈1), indicating that there was little or no effect of research activity on the probability of nest attacks.

Discussion

The attack rate for predators on black caiman nests recorded (32%) is lower than those recorded in previous studies. In a study conducted in Mamirauá Sustainable Development Reserve (MSDR) between 1994 and 1996, eggs in 46% of nests suffered predation (n=50) [4]. Between 2007 and 2008, 70% of nests in MSDR (n = 148) were attacked by predators [3]. However, the kinds of predators identified were similar in all studies. We also recorded a common opossum attacking a black caiman nest that has never been register in other study previously.

We don't register human attacks, because locals already know the use of

cameras traps in nests monitoring to avoid been caught. However, through vestigies we registered that about 30% of attacks in caiman's nests was by humans.

There was no statistically significant relationship between nest age and attacks by any of the predator species. Predation on eggs in nests of other species has been related to visual and olfactory attractors that help predators find nests [18,21,22]. We expected more attacks at the beginning of incubation because newly built nests are higher and surrounded by bare ground, which could increase visual detection by predators. It is also likely that females release odors during oviposition, as has been suggested for some turtles [21] and water birds [22]. We also expected a higher rate of attacks on nests at the end of incubation because of the possibility that full term embryos were vocalizing in eggs [23,24], which may attract predators. However, our results suggest that the probability of predation on black caiman eggs is relatively constant throughout the incubation period.

Females of many species of crocodilians guard nests during the incubation period, presumably minimizing predator attacks [9,18,25]. Studies in western Ecuador [7] and in MSDR [4,12] reported aggressive behavior of females against humans when defending their nests. Even after a flood that killed all eggs in a nest, a black caiman (presumably the female) attended the nest for a further 15 days [7]. After predation events, female *Alligator mississippiensis* and *Caiman latirostris* reconstruct attacked nests and continue to defend them [26,27].

Our data showed that predation on eggs in nests in MSDR was lower when adults, presumably females, were present. However, even though camera traps

appeared to be effective for recording nest predators, they did not capture all the occasions on which females were close to nests. On some visits, females were seen on nests, but there was no register by the camera trap at that time. Therefore, we could use only data obtained during visits to record the presence of females. It would be interesting to follow the activities of black caiman females throughout incubation period, as has been done with Amazonian spectacled caimans [11]. The use of more sensitive photographic equipment that records the presence of females could indicate whether nest defense by females is equally effective against all species of predators. It is feasible that caimans are effective against tegu lizards, capuchin monkeys and opossums, as these are natural prey for the species. However, nest defense may be less effective against humans and jaguars, which regularly prey on adult black caimans [4].

Nest opening by a predator appeared to increase the chances of a subsequent attack because most repeat attacks on a nest occurred soon after the nest was first opened by a predator. However, an attack by another species does not appear to be necessary to facilitate attacks by other predator species as there was no statistically significant difference between species in the probability of being the first or a subsequent predator. We do not know whether repeated attacks on nests by the same species involved the same individuals, but it is likely that repeated attacks occurred because the predators involved were satiated during the first attack and returned after digesting the previous meal.

Use of vestiges to identify predators is a low-cost method that was adequate for identifying the principal predators on eggs in black caiman nests in this study. This

method could be replicated by local communities in caiman management areas [28]. However, it is likely that the use of vestiges underestimates the number of species that attacked the nest in more than one predation event, and this makes the method ineffective for studies that seek information on all species of predators involved.

All nests of *Caiman yacaré* in the Pantanal that were subjected to perturbations by researchers were attacked by predators, but only half of the undisturbed nests were attacked [17]. Increased predation on eggs after human interference has also been shown in experiments with *Caiman latirostris* nests in Argentina [18]. An increase of up to 40% was found in predation of eggs in nests of *Caiman crocodilus* that were subject to research activities, such as opening and handling eggs and capture of attending females [9]. In this study, opening nests and handling eggs did not increase the number of attacks on black caiman nests. However, great care was taken in opening the nests in this study and other methods of handling and types of disturbances may not be as benign.

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APÊNDICE I.

Torralvo, K.; Botero-Arias, R.; Magnusson, W.E.
Tool use by Amazonian capuchin monkeys during predation on caiman nests in a high-productivity forest
Manuscrito aceito em 09/03/2017– *Primates*
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NEWS AND PERSPECTIVES

Tool use by Amazonian capuchin monkeys during predation on caiman nests in a high-productivity forest

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ABSTRACT

Descriptions of new tool-use events are important for understanding how ecological context may drive the evolution of tool-use among primate traditions. Here, we report a possible case of the first record of tool use by wild Amazonian capuchin monkeys (*Sapajus macrocephalus*). The record was made by a camera trap, while we were monitoring caiman's nest predation at Mamirauá Reserve in Central Amazonia. An adult individual was registered in a bipedal posture, apparently using a branch as a shovel to dig eggs out of a nest. Caiman eggs are frequently depredated by opportunistic animals, such as the capuchins. As the Mamirauá Reserve is covered by a high-productivity forest and caiman eggs are a high-quality food resource seasonally available on the ground, we believe that tool use by capuchins is more likely to be opportunity-driven, rather than necessity-driven, in our study site.

Keywords: behavior, nest predation, opportunistic tool-use, primate culture, Sapajus.

INTRODUCTION

Tool use is defined as "the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool" (Shumaker et al. 2011). Feeding is the main context of tool-use by primates (Bentley-Condit and Smith 2010) and recent studies have focused on the role of ecological conditions in shaping foraging tool use (Koops et al. 2014). The necessity hypothesis posits that tools are used mainly when food resources are scarce (Moura and Lee 2004). The opportunity hypothesis posits that encounter rates with tool materials and tool-required food resources drive tool-use behavior (Spagnoletti et al. 2012; Koops et al. 2014).

Among the neotropical primates, capuchins have long been known for being the only species able to use tools in captivity and in the wild (Fragazy et al. 2004; Shumaker et al. 2011). The use of a tool to crack encased food items on a hard substrate has been observed only in some wild populations of the capuchin belonging to the genus Sapajus. Most of the observations concern capuchins inhabiting dry savanna-like environments (Ottoni and Izar 2008), rarely a dry forest (Souto et al. 2011), and never the Amazon rain forest.

Capuchin monkeys are widely distributed across the Amazon (Alfaro et al. 2012) and are known for their generalist and opportunistic feeding behavior (Fragaszy et al. 2004; Visalberghi and Fragazy 2013). The large-headed capuchin (Sapajus macrocephalus) is identified as one of the top predators of caiman eggs in a long-term caiman nest monitoring, in a floodplain forest in Central Amazonia (K. Torralvo, *in prep*.). During the low water season, caiman females build their mound nests with leaves, sticks and soil (Villamarín et al. 2011). Caiman eggs are frequently depredated by opportunist animals, such as jaguars (*Panthera onca*), tegu lizards (*Tupinambis teguixim*), humans (*Homo sapiens*) and capuchins, which are among the main predators of caiman eggs (Da Silveira et al. 2010; Barão-Nóbrega et al. 2014).

Descriptions of novel tool-use events, even based on few records, help in understanding the factors favoring the emergence of tool use among primates. Here, we report a egg predation event in which we believe may be the first record of tool use by wild Amazonian capuchin monkeys (*Sapajus macrocephalus*) in a high-productivity flooded forest. The record was made by a camera trap, while we were monitoring black caiman, Melanoshucus niger, nest predation at Mamirauá Reserve - a large protected area of high-productivity forests in Central Amazonia.

METHODS

The Mamirauá Sustainable Development Reserve is a protected area located between Japurá, Solimões and Auati-Paraná Rivers, in the Central Amazon, Brazil. The reserve contains a várzea, a type of floodplain forest, which is entirely and seasonally

flooded by nutrient-rich white-water rivers, which increase substantially the primary productivity of these forests in comparison with the upland terra firme forests (Prance, 1979; IDSM, 2010).

The study was conducted during the low-water seasons (October-December) of 2013 and 2014 years, while we were monitoring caiman-nest predation in 63 nests. Nests were monitored with camera traps Reconyx PC800, programmed to take pictures at 10-seconds intervals, as long as the camera sensor identified movements. The overall sampling effort was of 6923 camera-trap*days. The tool-use episode reported here was opportunistically recorded at one of the nests (2°48'29"S, 65°4'49"W), which was monitored for 20 days (approximately 470 hours).

RESULTS

We recorded a total of 117 predation events in 25 caiman nests. Capuchins were responsible for 39% (N = 46) of the predation events. Nests were raided by single individuals or groups of 2-4, which usually approached the nest, took the eggs and carried them away to another place on the ground or a nearby tree (fig. 1f).

We registered a single episode, that we interpreted as a tool use by *Sapajus macrocephalus*, during a predation event on a caiman nest. This episode was registered approximately 366 hours after the monitoring of the nest has started. On this occasion, two capuchin monkeys started the nest predation event at 14:34h and finished at 15:18h, after 34 minutes. The tool use occurred at 15:01h, 18 minutes after the monkeys started removing eggs (fig. 1). At 15:01:28h, one of the individuals, apparently

an adult male, was registered over the nest looking for the eggs (fig. 1a). At 15:01:38h, this individual was photographed in a bipedal posture, holding a long stick of wood (about 25 cm) with his two hands, apparently using it as a shovel to dig into the nest and remove the upper layers of the nest to access the eggs in the nest mound (fig. 1b). Ten seconds later, a second individual appeared in the scene, positioning behind the first one, which was manipulating nest interior (fig. 1c). At 15:01:58h, the first individual left the scene carrying an egg (fig. 1d), while the second one kept manipulating something in the nest (fig. 1e).

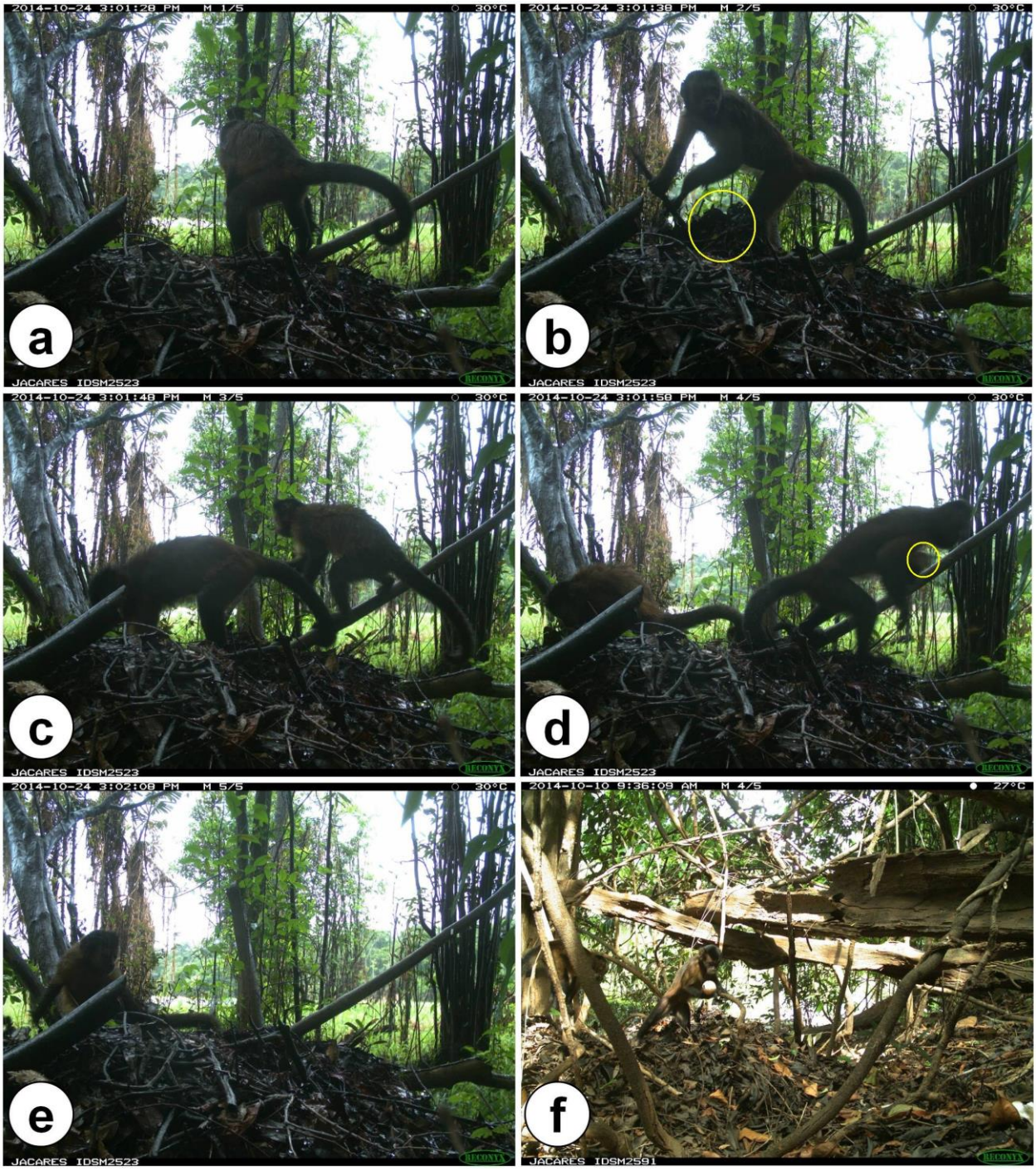

Figure 1. Tool use record by *S. macrocephalus* at Mamirauá Reserve, Central Amazon. (a) Individual above a black caiman nest. (b) Individual using a stick as a shovel to remove the litter vegetation - note the litter content being dislocated near the hind

limbs of the monkey (yellow circle). (c) A second individual reaches the monitored scene, while the first one is reaching into the nest interior. (d) Individual leaving the nest holding one egg (yellow circle), while the second one kept reaching into the nest (e). (f) Capuchin in a bipedal posture carrying an egg away.

DISCUSSION

We believe that the episode reported here may represent a possible case of tool use behavior and, if so, this is the first record of tool use by a capuchin species in the Amazon forests. Although we recognize the possibility that the monkey was only removing a stick from the nest because it could be an obstacle to its hand search for the eggs, we believe that it is more likely to be a tool-use episode based on (i) the posture of the individual, which was holding the stick with his two hands in opposite positions (left hand supinated and right hand pronated), in the same way we would hold a shovel, and (ii) the litter content being moved between the stick and the hind limbs of the monkey (see yellow circle in Fig. 1b). Our interpretation of using the stick as a shovel to dig into the nest and remove the litter vegetation, we consider that the episode described here, fits appropriately in the tool-use definition (sensu Shumaker et al. 2011).

We also believe that the use of tools can be advantageous in caiman egg predation. In a predation event, opening the nest is the first step to reach the internal chamber. This is probably hindered by compressed rotting vegetation and by the common presence palm-leaves thorns of Bactris sp. (Torralvo, pers. observ.), an this could encourage the use of a stick instead of the hands by the capuchins. But if this type

of tool-use behavior is advantageous in this population, why didn't we recorded more events in the other monitored nests? In fact, if this behavior is common, there is a fair chance that we did not registered other tool use events because of the design of our study, in which was designed to look for the predator species of caiman eggs. We highlight that only direct observations or videos would provide appropriate evidence of tool-use behaviour in this population.

Most reports of tool use by wild capuchins has been reported for species inhabiting arid environments, such as *caatinga* and cerrado in Brazil (Ottoni and Izar 2008), which led a few researchers to propose the food-scarcity explanation for feeding tool use (Moura and Lee 2004). However, systematic observations of tool use have been carried out on two wild groups of bearded capuchins living in Fazenda Boa Vista (Piauí State, Brazil) to test whether tool use was related to food scarcity or to the opportunities to perform it. Spagnoletti et al. (2012) found that the rate of stone tool use by capuchins was correlated with palm nuts availability and not with monthly availability of fruits and invertebrates; moreover, the rate of tool use did not differ between the group that received little additional food (provisioned) and the one that did not.

The Amazonian várzea forests are more productive than terra firme forests due to their seasonal flooding by nutrient-rich white-water rivers, which fertilize the soil (Prance 1979). This is why primates tend to have higher abundances in várzea forests (Peres 1997). Therefore, it seems unlikely that food scarcity would account for tool use in the Mamirauá's population.

It has been shown that capuchin monkeys use tools opportunistically when they encounter food items that require this behavior (Spagnoletti et al. 2012; Koops et al. 2014). At the Mamirauá's forests, as the water level decreases after 4-6 months of flood (Ramalho et al. 2009), the environment offers new resources to be exploited on the ground. This is when caiman females built their nests, piling leaves and branches and placing the eggs under a mound of vegetation (Rueda-Almonacid et al. 2007; Villamarín et al. 2008). Even though nests are commonly guarded by the females (Lang 1987), caiman eggs are frequently taken by animals with opportunistic habits, such as the capuchins (Da Silveira et al. 2010; Barão-Nóbrega et al. 2014). Since this tool-use episode occurred in a forest with high primary productivity, and the caiman eggs are a high-energy food resource seasonally available on the ground, we add evidence that opportunity, rather than necessity, may be the main factor promoting tool use invention and transmission among primate cultures.

Although we interpreted this event to be a case of tool use, we acknowledge that this interpretation is debatable. It is worth noting that this possible single tool-use event presented here was registered opportunistically. The intervals at which the camera traps took pictures (10 seconds) were not appropriated to look carefully at the manipulative ability of capuchin monkeys. Therefore, we believe that a long-term study designed specifically to look at the capuchin's behavior, with direct observations or videos instead of pictures, would be more appropriate to describe the capuchin predation behavior, manipulative abilities of nest materials, and perhaps reveal other tool-use events.

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SÍNTESE

Cerca de 32% dos ninhos de jacaré açu-açu monitorados na Reserva Mamirauá foram predados durante os anos de monitoramento. Os predadores como a onça pintada (*Panthera onca*), o lagarto jacuraru (*Tupinambis teguixim*), o macaco prego (*Sapajus macrocephalus*) e o homem (*Homo sapiens*) atacam os ninhos em busca dos ovos que se tornam um recurso alimentar adicional na época da seca em regiões de várzea, na Amazônia.

Nesse trabalho a identidade dos predadores de ninho de jacaré-açu foi corroborada com outros estudos. O gambá-comum (*Didelphis marsupialis*) também foi registrado atacando um ninho de jacaré-açu. Resultados sugeriram que a probabilidade de predação nos ninhos é constante durante o período de incubação. Foi apresentado taxas menores de predação quando adultos, presumivelmente fêmeas, estiveram presentes. A abertura dos ninhos e o manejo dos ovos por pesquisadores não aumentaram o número de ataques registrados. Os dados também mostraram que ataques de outra espécie de predador não são necessários para iniciar ataques de qualquer outra espécie de predador.

O registro oportunístico de um possível uso de ferramenta por macaco-prego (S*apajus macrocephalus*) durante a predação de ninho de jacaré-açu, foi apresentado como apêndice dessa dissertação. O registro foi interpretado baseado na hipótese de oportunidade que diz que as taxas de encontro com materiais potenciais para serem ferramentas e recursos alimentares que requerem o uso de ferramentas, direcionam o comportamento (Spagnoletti et al. 2012; Koops et al. 2014). Ao considerar que a

Reserva Mamirauá é composta por florestas de alta produtividade, a hipotese de necessidade (Moura and Lee 2004) foi descartada.

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