Population structure of the broad-snouted caiman (*Caiman latirostris*) in natural and man-made water bodies associated with a silvicultural landscape

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Abstract. The broad-snouted caiman (*Caiman latirostris*) is a South American crocodilian with a wide geographical distribution. Water bodies originally occupied by the species have suffered extreme anthropogenic pressure; however, the broad-snouted caiman has a high adaptive capacity to colonize man-made habitats such as decanting pounds and artificial reservoirs for agriculture or livestock. In this context, the present study aimed at identifying the population structure of the broad-snouted caiman in a silvicultural landscape in southeastern Brazil. Fifty-two caimans of various classes were captured with baited traps and steel cable snares at night. The estimated population size was 51 individuals excluding class I individuals. The population density was estimated to be 2.6 individuals/ha with a linear density of 11.3 individuals/km. The intermediate values of linear density estimates herein are similar to other areas, suggesting that silvicultural landscapes can be relevant for broad-snouted caiman conservation. Therefore, the role of silvicultural landscapes in crocodilian conservation should be taken into consideration for environmental certification processes related to forestry in the Neotropics.

Key words. Crocodilians, population density, sex ratio, anthropogenic environments, biomass, conservation, distribution, linear density, forestry plantations, sexual dimorphism.

Introduction

The broad-snouted caiman (*Caiman latirostris*) is a medium-sized crocodilian, with individuals rarely growing longer than two meters in nature (VERDADE 1998). This species exhibits a wide latitudinal distribution ($5-34^{\circ}$ S) in South America, including Argentina, Bolivia, Brazil, Paraguay and Uruguay (VERDADE & PIÑA 2006, VERDADE et al. 2010). This wide geographical distribution of the species may be a result of its ability to use various habitat types, such as rivers, lakes, wetlands and floodplains (MEDEM 1983, VERDADE & PIÑA 2007).

This crocodilian species has been facing complex conservation issues (VERDADE et al. 2010). Water bodies originally occupied by the broad-snouted caiman have suffered extreme pressure as a result of anthropogenic pollution from urban sewage, industrial waste and agrochemicals (SCOTT et al. 1990, MECHE et al. 2009, PIÑA et al. 2009). For this reason, the species was considered endangered in the past (BERNARDES et al. 1990). However, currently, the broad-snouted caiman is no longer regarded as threatened (MACHADO et al. 2008, IUCN 2014), in part due to its high adaptive capacity to colonize man-made habitats such as decanting pounds and artificial reservoirs for agriculture or livestock (VERDADE & LAVORENTI 1990, BORTEIRO et al. 2001, 2006, 2008, FREITAS-FILHO 2007, MARQUES et al. 2013a, b). Apparently, these anthropogenic environments provide a stable water supply throughout the year, lessening the effect of a lack of precipitation on reproduction (SI-MONCINI et al. 2011).

Forestry plantations have been expanding in the last four decades in Brazil for economic reasons, predominantly over low-productivity pasture (VIANNA et al. 2007, ABRAF 2012, SBS 2013). In 2012, there were seven million hectares of *Eucalyptus* and *Pinus* plantations in Brazil, covering approximately 18% of the state of São Paulo (ABRAF 2013). Forestry plantations generally contain artificial reservoirs (e.g., small weirs) that supply water in the case of

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forest fires. The broad-snouted caiman is able to colonize such environments, which render them potentially useful for the species' conservation, especially in the state of São Paulo, which acts as a connecting region between the southern (i.e., Paraná River basin) and northern (i.e., São Francisco River basin) populations of this species (VILLE-LA et al. 2008).

The present study aims at identifying the population structure of the broad-snouted caiman in a silvicultural landscape of São Paulo state, southeastern Brazil. The specific objectives of this study were to assess the species' distribution, population density, biomass, linear density, and sex ratio in this environment. Such information might be useful for the decision-making process concerning the conservation of this species.

Material and methods Study area

This study was carried out on two silvicultural farms, Três Lagoas (23°20'41"–23°22'0" S, 48°27'57"–48°28'0" W) and Arca (23°18'51"–23°20'0" S, 48°27'30"–48°28'20" W), located in the municipality of Angatuba, south-central São Paulo state, southeastern Brazil (Fig. 1). The local climate is subtropical (Cwa) according to the Köppen system, with dry winters (temperatures below 18°C) and wet summers (temperatures above 22°C). The average monthly precipitation during the study period was 116 mm, ranging from 1.6 mm in August 2010 to 369.9 mm in January 2011 (data provided by the Estação Experimental de Ciências Florestais de Itatinga, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo).

The Três Lagoas and Arca farms have total areas of 3,242 and 1,122 ha, respectively. The local landscape is a mosaic of Eucalyptus plantations, abandoned pastures, fragments of native vegetation, and water bodies. The study area is located in a transition zone between the Atlantic Forest and the Cerrado biomes. Historically, the area has experienced at least two major cycles of deforestation and revegetation since 1870 (LISBOA 2008). The current landscape matrix consists primarily of plantations of Eucalyptus grandis, E. urophila and their hybrid E. "urograndis". The native vegetation fragments are composed of Cerrado sensu stricto, Cerradão, Semideciduous Forest, and Riparian Forests at various stages of regeneration (ATHAYDE 2012). The abandoned pastures are composed of exotic pastures dominated by Brachyarya (syn. Urochloa).

These farms include three lagoons (Lagoão, Lagoa Suja, Três Lagoas) with average diameters ranging from 267 to 557 m and 46 weirs with average diameters of 10 to 100 m that are currently maintained as part of the fire-control programme (Fig. 1). Anecdotal records of local fishermen suggest the occurrence of at least one relatively abundant species of fish (*Hoplias malabaricus*) and one species of freshwater turtle (*Mesoclemmys vanderhaegei*) that can serve as prey to crocodilians in these water bodies.

Sampling methodology

Field campaigns were conducted during three days/nights each month from February through June of 2010 and from October of 2010 through April of 2011. The first day/night sampling session was dedicated to searching all water bodies for the presence or absence of individuals in order to assess the species' local distribution. Capture sessions were carried out during the other two days/nights in five water bodies (lagoons: Lagoão, Lagoa Suja, Três Lagoas; weirs: Açude Vermelho, Açude do Casemiro) preselected based on information from local human residents. The sampling and capture efforts were similar across all water bodies selected.

Caimans were captured from a boat with the aid of steel cable snares and sealed-beam headlights (HUTTON et al. 1987). In small water bodies, the animals were attracted by an observer imitating hatchling vocalizations and captured near the shore (WALSH 1987). In addition, baited traps (three iron hoops, 1 metre in diameter with a 6-cm meshwidth; bait: bovine kidney) were placed near the shores of the water bodies.

The captured animals were individually marked with microchips (Destron, TX1414B) and notching (by cutting away single and double external tail scutes using previously established numerical combinations; adapted from BOLTON 1994). Sexing was based on the visual examination of genital morphology with a speculum of proper size (CHABRECK 1963, ALLSTEAD & LANG 1995). Biometric measurements (total length and snout-vent length – TL and SVL, respectively) were taken with a measuring tape, and body mass (BM) was recorded with a dynamometer (VERDADE 2000, 2003).

Analytical methodology

The size classes proposed by LARRIERA et al. (2006) were adapted to the range of snout–vent length measurements found according to the regression equations established for the species by VERDADE (2000) as follows: class I (hatch-lings) < 25 cm; class II (juveniles) 25–67.9 cm; class III (adults) 68–101 cm; and class IV (large males) > 102 cm.

The population size was estimated from the capture-recapture data obtained over the multiple sampling periods used during this study (COOCH & WHITE 2010). A binary capture history was constructed for each individual, with the values o and 1 indicating the absence or presence, respectively, of that individual on each occasion. A capture history of "0011", for example, indicates a history of four sampling occasions during which the individual was captured only on the third and fourth occasions.

The population was assumed closed during the study period, satisfying the assumptions of the CloseTest program (STANLEY & BURNHAM 1999; $\chi^2 = 12.0$, p = 0.442). The sampling sites were located in the spring areas of the catchments, possibly limiting the dispersion of the local individuals. Under such conditions, the dispersion rate of the species per generation is usually low (VERDADE et al. 2002). Local residents who helped with locating crocodilians were intimately familiar with the population and often able to identify individuals that had moved from one water body to another. During the study period, these residents did not detect any evidence of the arrival of new individuals or the disappearance of resident adults. Closed population models have previously been used to estimate population size (OTIS et al. 1978). They describe two processes that affect the patterns of detection and non-detection associated with capture on multiple occasions: the single-capture probability (p) and the recapture probability (c). Possible sources of variability in the p and

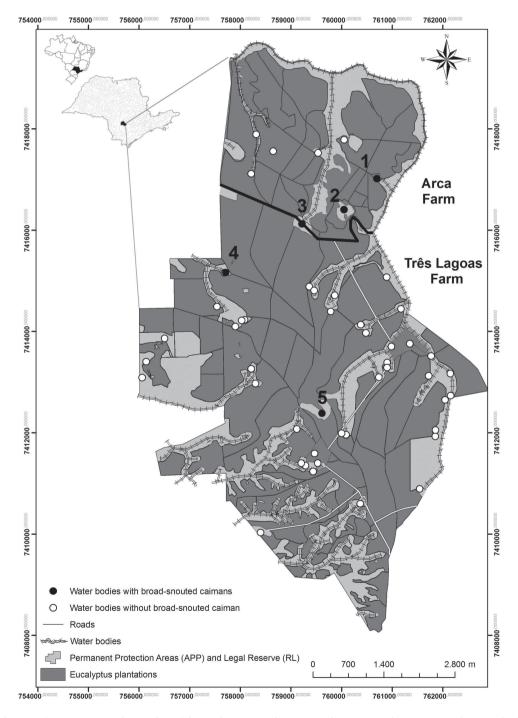


Figure 1. Study Area (Três Lagoas and Arca farms) located in Angatuba, São Paulo state, southeastern Brazil. Water bodies in which the broad-snouted caiman (*Caiman latirostris*) was captured (1 – Açude Vermelho; 2 – Lagoão; 3 – Lagoa Suja; 4 – Açude do Casemiro; 5 – Três Lagoas).

c parameters were described by the inclusion of individual and environmental covariates in the models. Hatchlings (class I) were not included in the analysis due to the low survival rate of individuals in this size class.

The capture probability was modelled in terms of individual capture probabilities that can vary according to sex and size (WOODWARD & MARION 1978, WOOD et al. 1985, LANG 1987a, SARKIS-GONÇALVES et al. 2004). The minimum air temperature and capture methodology were also considered in the analysis because they can affect an individual's capture probability. The models were selected using the AICc (Akaike Information Criterion, corrected), and models with Δ AICc \leq 2 were considered equally plausible (BURNHAM & ANDERSON 2002). If more than one model was considered better and equally plausible, the estimates were derived from the average of these models (model average estimate). The analyses were performed using the MARK software (WHITE & BURNHAM 1999).

The population density and biomass were expressed in units of NI/ha (NI = number of individuals) and kg/ha, respectively. The biomass calculation was based on the mean body mass of juveniles and adults and on the proportion of juveniles to adults as identified from capture results in the study area. Linear density (NI/km) was calculated based on the estimated population size and the total perimeter of the water bodies (VERDADE 2001) because the broad-snouted caiman primarily uses the margins of water bodies (VER-DADE et al. 2006). The total area and perimeter of the water bodies (19.5 ha and 4.51 km, respectively) were measured from aerial images of the study area using ArcGIS 9 (ESRI, Redlands, California, USA).

A Chi-square test (ZAR 1996) was applied to investigate whether the sex ratio differed from 1:1. A t-test (ZAR 1996) was used to assess sex-based differences relative to snout– vent length and body mass in juveniles (class II) and adults (classes III and IV). Data normality and homoscedasticity were confirmed prior to the analyses. All statistical tests were performed with Minitab 16 software. Measurements are expressed as mean \pm standard deviation (SD) and range.

Results

We captured a total of 52 broad-snouted caiman (*Caiman latirostris*) individuals in the study area. Of these, 16 belonged to class I (30.8%), 28 to class II (53.8%; \bigcirc : 7; \bigcirc : 21), and 8 to class III (15.4%; \bigcirc : 4; \bigcirc : 4). No class-IV individuals were captured. The broad-snouted caiman was present in three (100%) lagoons, but only in two (4.3%) weirs. The number of individuals captured varied markedly between the water bodies: 27 individuals (51.9%) in Lagoa Suja, 22 (42.4%) in Lagoão, 1 (1.9%) in Três Lagoas, 1 (1.9%) in Açude Vermelho, and 1 (1.9%) in Açude do Cazemiro (Fig. 2).

The models related to capture method and animal size were considered better suited and equally plausible (Tab. 1) for which reason the population size estimates were derived from their average (model average estimate; Tab. 2). The estimated population size for the study area was 51 individuals (95% CI: 36–70 individuals), with class I (hatchlings) excluded from the analyses. According to this estimate, the capture of juveniles and adults of the sampled population was highly successful (70.5%). The estimated density was 2.6 individuals/ha (95% CI: 1.8–3.5 ind/ha) with a linear density of 11.3 individuals/km (95% CI: 7.9–15.5 ind/km), and a biomass of 13.3 kg/ha (95% CI: 9.2–17.9 kg/ha). The sex ratio was 1:1 ($\vec{\sigma}$: \mathbb{Q}) for adults and 1:0.33 for juveniles, significantly differing from the 1:1-ratio for the later ($\chi^2 = 7$, df = 1, p = 0.008).

The snout-vent length and body mass of juvenile females (class II) were greater than those of juvenile males

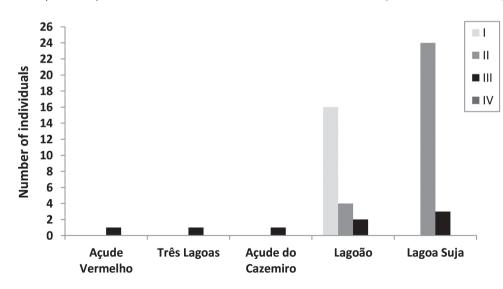


Figure 2. Number of broad-snouted caimans (*Caiman latirostris*; N = 52) captured, by size-class and water body (I – hatchlings: < 25.0 cm; II – juveniles: 25.0–67.9 cm; III – adults: 68.0–101.0 cm; and IV – large males: > 102.0 cm snout–vent length). Natural lagoons: Três Lagoas (N = 1), Lagoão (N = 622), and Lagoa Suja (N = 27). Weirs – Açude Vermelho (N = 1) and Açude do Casemiro (N = 1).

Table 1. Model selection by MARK software for broad-snouted caiman (*Caiman latirostris*) capture-recapture data, using AICc, Δ AICc, AICc Weight, Model Likelihood, and number of parameters (k). p – single-capture probability; c – recapture probability; svl – snout-vent length of individuals; met – capture method; temp – minimum air temperature; AICc – Akaike Information Criterion corrected. The parameter for the effect of temperature is not significant (95% CI including zero) for which reason we excluded this model from the model-averaged estimate.

Model	AICc	Δ AICc	AICc weight	Model likelihood	k
${p(svl) = c}$	331.8292	0.0000	0.38291	1.0000	2
${p(met) = c}$	332.2697	0.4405	0.30722	0.8023	2
${p(temp) = c}$	332.6706	0.8414	0.25142	0.6566	2
${p(sex) = c}$	335.5885	3.7593	0.05845	0.1526	2

(SVL: $t_{1,27} = 4.7$, p < 0.001; BM: $t_{1,27} = 3.5$, p < 0.001. However, no such difference has was found in adults (SVL: $t_{1,7} = -2$, p = 0.108; BM: $t_{1,7} = -2$, p = 0.105; Tab. 3 and Fig. 3).

Discussion

The current distribution of the broad-snouted caiman in the study area may result from a combination of two factors: the history of human occupation and the social hierarchy among individuals. The largest number of animals were caught in Lagoa Suja and Lagoão, which are environments with calm and shallow water, dense aquatic vegetation, and relatively low human presence (like those described for the species by MEDEM 1983, WALLER & MICUC-CI 1993, APARICIO & RIOS 2008, FUSCO-COSTA et al. 2008).

Table 2. Population size estimates (N) and confidence intervals (95% CI) for models with Δ AICc \leq 2 and the model-averaged estimate for the broad-snouted caiman (*Caiman latirostris*) on two farms in the municipality of Angatuba, south-central São Paulo state, southeastern Brazil. p: single-capture probability; c – recapture probability; svl – snout-vent length of individuals; met – capture method.

Model	Ν	95% CI
${p(svl) = c}$	54	41-92
${p(met) = c}$	47	40-63
Model-averaged estimate	51	36-70

On the other hand, Três Lagoas, a similar environment with a greater degree of human activity (e.g., fishing) held fewer individuals.

The effects of social hierarchy can also affect the distribution and density of animals. Generally, crocodilians are social animals that compete for limited resources displaying aggressive behaviours during mating, basking, foraging, and nesting (LANG 1987a, GOULD & GOULD 1989, VERDADE 1992). In this context, young individuals are frequently antagonized by adults (MAGNUSSON 1984) and their mortality rate tends to be higher. These conditions could explain, at least partially, the occurrence of solitary individuals in the other water bodies studied (Açude Vermelho, Açude do Casemiro and Três Lagoas). Future studies should therefore prioritise the possible relationship between resource availability and social hierarchy in anthropogenic environments.

The population structure found in this study is similar to that described for the species from other localities,

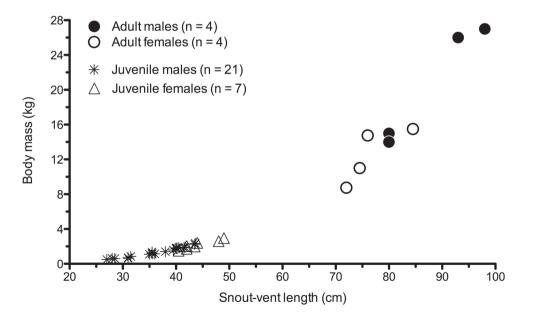


Figure 3. Sex-dependent variation in snout-vent length and body mass in juvenile and adult broad-snouted caimans (*Caiman latirostris*) (N = 52).

	Ν	Snout-vent length (cm)		Body Mass (kg)	
		Mean±SD	Min-Max	Mean±SD	Min-Max
Class I	16	10.9±0.3	10.2-11.4	0.03±0.01	0.02-0.04
Class II	28	38.2±5.8	27.0-49.0	1.57±0.65	0.49-2.95
Class III	8	82.2±9.1	72.0-98.0	16.50 ± 6.58	8.75-27.00
Class II – Female	7	44.1±3.2	40.5-49.0	2.17±0.50	1.50 – 2.95
Class II – Male	21	36.3±5.1	27.0-43.6	1.35±0.56	0.49-2.35
Class III – Female	4	76.7±5.4	72.0-84.5	12.50 ± 3.18	8.75-15.50
Class III – Male	4	87.7±9.1	80.0-98.0	20.50±6.95	14.00-27.00

Table 3. Descriptive data of size classes and sexes of the broad-snouted caiman (*Caiman latirostris*) on two farms in the municipality of Angatuba, south-central São Paulo state, southeastern Brazil.

with most individuals being of class II (juveniles), but with individuals of class IV (large males; MICUCCI & WALLER 1995, PACHECO & LLOBET-QUEREJAZU 1998, VERDADE 2001; APARICIO & RIOS 2008, BORTEIRO et al. 2008) being rare or absent. Historical selective hunting of larger individuals may have generated such pattern (e.g., VELASCO & AYARZAGUENA 1995). Human hunting pressure markedly affects the distribution, demography and social behaviour of vertebrates including crocodilians (VERDADE 1996). The broad-snouted caiman is a common target of fishermen because the species feeds on fish caught in fishing nets and hunters are interested in its meat and skin (FILOGONIO et al. 2010). Information about hunting is difficult to obtain in Brazil due to the existing restrictive legislation (VERDADE & SEIXAS 2013).

Crocodilians present a great variation in growth rates due to seasonality, food availability, temperature and hatching season (CHABRECK & JOANEN 1979, MAGNUSSON & TAYLOR 1981, MESSEL & VORLICEK 1984, ABERCROMBIE & VERDADE 2002, PIÑA & LARRIERA 2002). However, the interaction between temperature and food supply is possibly the most relevant determinant in crocodilian growth rates (LANG 1987b) and may have influenced the present results.

Linear density estimates of the broad-snouted caiman tend to vary greatly across the species' distribution range. MOURÃO & CAMPOS (1995) found low densities in the Paraná River (0.07-0.28 ind/km) and attributed their result to the cautious nocturnal behaviour of the species in response to the observers' spotlight. FUSCO-COSTA et al. (2008) also found low values of linear density in the northwestern area of Santa Catarina Island (0.25 ind/km), as did CARVALHO & BATISTA (2013) in the Grande Sertão Veredas National Park (< 1 ind/km). Studies conducted at other localities have shown intermediate densities (VERDADE 2001: 6-8 ind/km in northeastern Brazil; BORTEIRO et al. 2008: 2.1-4.4 ind/km in altered landscapes in northwestern Uruguay). The highest linear densities reported for the species are for the Pilcomayo River basin in Bolivia (PACHECO & LLOBET-QUEREJAZU 1998: 3-58 ind/km). The intermediate values of linear density estimates herein suggest that silvicultural landscapes can be relevant for broad-snouted caiman conservation because the use of anthropogenic environments by the species may help connecting populations across its geographical distribution and consequently their gene flow.

In this study, the apparent occurrence of a greater number of males than females in class II (juveniles) may have been caused by several factors. Crocodilians are subject to temperature-dependent sex determination (TSD, see, e.g., LANG & ANDREWS 1994, PIÑA et al. 2003, DEEM-ING 2004) during a relatively short incubation period (for temperature-sensitive period, TSP, see, e.g., LANG & AN-DREWS 1994, LANCE 2008). The TSP of the broad-snouted caiman is the late first and early second third of embryonic development (PIÑA et al. 2007b). Therefore, the incubation temperature inside the nest in this period will determine the sexes of subsequent hatchlings and thus affect the sex ratio of the population. The temperature inside the nest, on the other hand, is a function of, for example, air temperature, exposure to rainfall, and level of insolation at the exact location of the nest (MAGNUSSON 1979, LANG et al. 1989, CAMPOS 1993). LARRIERA (1995) and MONTINI et al. (2006) have reported that female broad-snouted caiman are able to nest in savannas (sites with a gentle slope that may become inundated during periods of heavy rain), amongst floating vegetation (vegetation that floats when the water level increases), and forests. In the study area, the nesting habitats (e.g., savannah and forest) vary as a function of silvicultural management practices. Hypothetically, variation in the availability of nesting habitats can affect the sex ratio of the species over time.

There are marked differences in snout-vent length and body mass between the sexes of individuals in class II (juveniles) in this study (females > males). This pattern could possibly be a result of a clutch effect (VERDADE 1997). Same-sex litters of crocodilians due to TSD remain together during the early stages of ontogenetic development. Possibly, the sampled juvenile males and females originated from different clutches. The capture of males in Lagoa Suja and most of the females in Lagoão and the low variance between biometric measurements between individuals of each sex corroborates such hypothesis. Future studies using the molecular markers isolated for the species (ZUCOLOTO et al. 2002, 2006, 2009) might help to identify the parentage of individuals in wild populations of the species. The sink-source metapopulation pattern predicts that patches of habitat with better resources (source) tend to export individuals; however, sub-optimal patches (sink) tend to import individuals (PULLIAM 1988, HANSKI 1998). Maybe the broad-snouted caiman population in the study area is part of a dynamic metapopulation, thus populations might be increasing locally, and animals are colonising sub-optimal environments that may be affecting the overall population structure (e.g., absence of large-sized individuals). This sink-source metapopulation pattern of the species has been noted in other regions of São Paulo state, too (VERDADE et al. 2002).

The present results suggest that the broad-snouted caiman may adapt relatively well to silvicultural landscapes in southeastern Brazil, which can be relevant to the maintenance of gene flow between the northern and southern populations of the species. However, land use and management practices in agricultural/silvicultural environments vary in response to socio-economic factors (VERDADE et al. 2014). These changes can quite likely affect the conservation of this species by, for example, an increased use of agrochemicals that can cause genotoxicity in the species (POLETTA et al. 2009). For this reason, environmental certification (e.g., Forest Stewardship Council - FSC) should take into consideration the role of silvicultural landscapes for this crocodilian's conservation in the Neotropics as the local largest aquatic predator. In addition, long-term diversity monitoring programmes in these areas should include crocodilians (e.g., monitoring nesting activities, see LAR-RIERA 1993) and investigate the effect of spatial-temporal heterogeneity in the adaptive process of the species in relation to its diet (e.g., by using stable isotopes; MARQUES et al. 2014) and space use (e.g., by employing radiotelemetry and molecular markers) throughout the silvicultural production cycle.

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