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Evaluating Behavior and Enclosure Use of Zoo-housed Broad-snouted Caiman (*Caiman latirostris*): A Case Study in the Zoo of Córdoba (Argentina)

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***Abstract*.—Zoo environments represent a useful opportunity for animal research, particularly for species that are difficult to observe in the wild. Moreover, studying the behavior of zoo-housed populations provides important information about the welfare state of animals. We described the behaviors of a zoo-housed population of seven Broad-snouted Caimans (*Caiman latirostris*) composed of males and females of different ages. We evaluated the associations of behavior frequencies with attributes of individuals (sex and age class) and with environmental variables (season, time of the day, and daily mean temperature). We calculated the Spread of Participation Index to estimate the use of space in relation to attributes of individuals and environmental variables. Additionally, we evaluated the suitability of the enclosure and management measures by assessing the Five Freedoms. The results showed higher frequencies of aquatic behaviors in adults than in subadults, which may reflect an ontogenetic shift in behavior or, conversely, may be a consequence of a dominance hierarchy. There were almost no differences in behavior frequencies between sexes. Aquatic behaviors were associated with lower temperatures, which could be attributed to thermoregulation. The results also showed daily movements from water in the morning to land at midday and in the afternoon. A high rate of agonistic behaviors was recorded, and possible causes and implications are discussed. Enclosure use was low, with some zones being poorly used or not used at all, and with marked variability among individuals. Finally, 53% of the husbandry recommendations for this species were met in the study population*.

Key Words.—captivity; crocodiles; ethogram; Five Freedoms; Spread of Participation Index

Resumen.*—Los zoológicos son ambientes que permiten avanzar en la investigación de diversas especies, particularmente aquellas difíciles de observar en vida silvestre. Los estudios de comportamiento en estos ambientes proveen información importante acerca del estado de bienestar de los animales. Aquí describimos los comportamientos de una población de siete Yacarés Overos (*Caiman latirostris*) compuesta por machos y hembras de distintas edades. Evaluamos la asociación de las frecuencias de comportamientos con atributos individuales (sexo y clase etaria) y con variables ambientales (temporada, hora del día y temperatura ambiente media). Calculamos el Índice de Dispersión de la Participación para estimar el uso del espacio en relación a atributos individuales y variables ambientales. Adicionalmente, evaluamos la adecuación del habitáculo y medidas de manejo mediante el análisis de las Cinco Libertades. Los resultados mostraron mayor frecuencia de comportamientos acuáticos en adultos que en subadultos, lo cual podría reflejar un cambio ontogenético comportamental o bien ser una consecuencia de la jerarquía de dominancia. Hubo pocas diferencias comportamentales entre sexos. Los comportamientos acuáticos estuvieron asociados a temperaturas bajas, pudiendo atribuirse al comportamiento de termorregulación. Los resultados también mostraron un movimiento diario desde el agua a la mañana hacia la tierra al mediodía y tarde. Registramos una alta tasa de comportamientos agonistas y se discutieron las posibles causas e implicancias. El uso del espacio fue reducido, con zonas escasamente utilizadas o no utilizadas, y marcada variabilidad entre individuos. Finalmente, un 53% de las recomendaciones de manejo para esta especie se cumplieron en la población en estudio.

Palabras clave.—cautiverio; cocodrilos; etograma; Cinco Libertades; Índice de Dispersion de la Participación

Figure 1. Adult Broad-snouted Caiman (*Caiman latirostris*) at Córdoba Zoo, Argentina. (Photographed by Lilen Prystupczuk).

Introduction

In captive animal husbandry, knowing the suitability of the facilities and management measures is crucial to provide good standards of animal welfare (Broom 1991; Mellor 2016). In zoo-housed populations, the artificially created environment plays an important role in determining the diversity of behaviors that animals can display (Clark et al. 2012; Rose and Roffe 2013). Enclosures that are suitable for a species stimulate the occurrence of appetitive behaviors (Duncan 1998), are enriching to the animals, and render a better quality experience for the visitors (Fabregas et al. 2012). Thus, animal behavior, as well as the way animals use the available space, provides important information about the suitability of the enclosure of zoo-housed populations (Ross et al. 2011; Rose and Robert 2013). In recent years, an increasing number of studies on species of conservation and/or sustainable use interest have been conducted in zoos (Anderson et al. 2008; Fernandez and Timberlake 2008; Labaque et al. 2010, 2013; Loh et al. 2018). Zoo environments are particularly useful for the study of species whose behaviors are difficult to observe in the wild.

Crocodilians have a wide repertoire of behaviors, including elaborate social and reproductive ones (Garrick and Lang 1977; Lang 1987; Senter 2008; Brien et al. 2013a). Given the close association between climate and behavior demonstrated for reptiles (Brandt and Mazzotti 1990; Seebacher 1999; Simoncini et al. 2013), behaviors are expected to show daily and seasonal variations, as well as variations associated with sex and individual ontogenetic development (Hunt 1977; Morpurgo et al. 1993). The Broad-snouted Caiman (*Caiman latirostris*; Fig. 1) is a South American crocodilian species occurring in Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Verdade et al. 2010). The species has been threatened historically by hunting and habitat loss (Rueda-Almonacid et al. 2007). Several projects of sustainable use involving the ranching technique have been developed in Argentina, to contribute to the recovery of natural populations (Larriera and Imhof 2006). Broad-snouted Caimans that are illegally traded are confiscated and relocated to zoos, which function as reception centers (Aprile and Bertonatti 1996; Bertonatti 2017). Thus, in Argentina, captive populations of Broad-snouted Caiman are housed both in breeding farms and in zoos. The literature indicates that wild Broad-snouted Caimans limit their activities to basking and diving in winter, and that feeding, territorial fights, and copulation occur in spring and summer (Larriera and Imhof 2006). In captivity, studies have focused on thermoregulatory (Verdade et al. 1994; Bassetti et al. 2014;), agonistic (Verdade 1992, 1999), and reproductive behaviors (Verdade 1995; Piffer and Verdade 2002).

The Córdoba Zoo, in Córdoba, Argentina (31°25'S; 64°10'W), houses a population of Broad-snouted Caimans of unknown life history that arrived at the zoo after separate confiscations from illegal traffic. The goal of this study was to obtain a first estimation of general indicators of the welfare of the population and to provide the institution with guidelines for its improvement. Thus, we aimed to describe the behavior and use of space of the Broad-snouted Caiman population housed in the Córdoba Zoo, considering its associations with individual attributes (size and sex) and environmental variables (season, time of the day, and temperature). We also assessed the adequacy of the enclosure, husbandry, and management measures in this population according to the Five Freedoms (Appendix Table), an internationally accepted guideline for animal welfare (Farm Animal Welfare Council 1993).

Materials and Methods

Animals and enclosure.—Our study involved seven Broad-snouted Caimans (three adult males, one adult female, and three subadult females, according to the age classes proposed by Larriera et al. 2006) housed in Córdoba Zoo. Their snout-vent length (SVL) and weight varied from 37–89 cm and 1.6–31.6 kg, respectively (Table 1). The enclosure consisted of a 130-m^2 concrete pool and a 90-m^2 central island (Fig. 2). There were also 72 Hilaire's Side-necked Turtles (*Phrynops hilarii*) in the enclosure, which we considered only in terms of the interspecific interaction with Broad-snouted Caiman. Feeding consisted of chicken or beef, and live chicks offered at the same time every day in spring and summer. In fall and winter, feeding was interrupted, following the species physiology (Hutton 1987; Lance 2003).

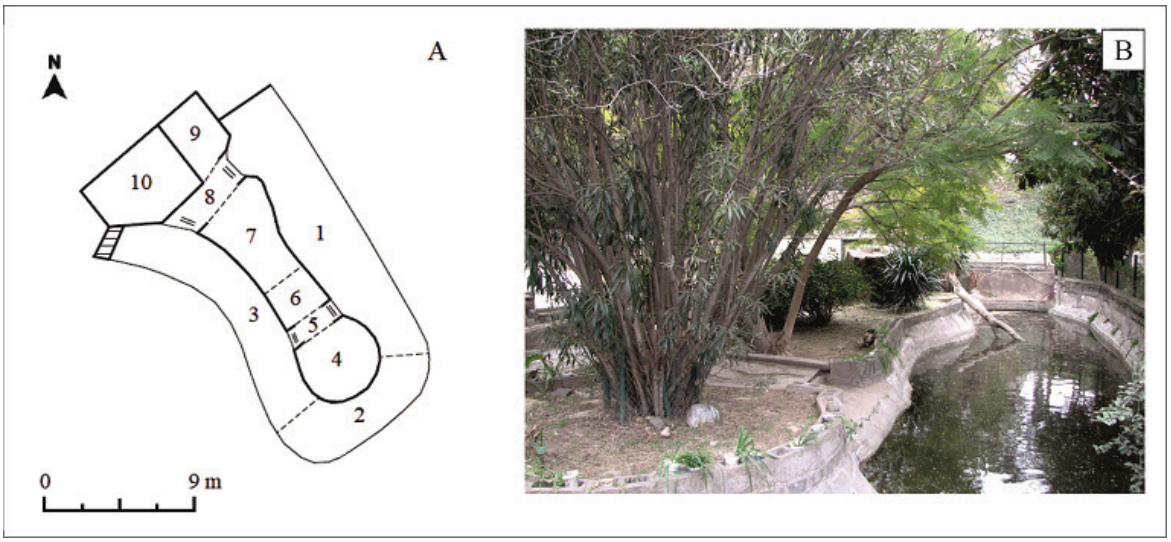

Figure 2. Enclosure of the Broad-snouted Caiman (*Caiman latirostris*) population in Córdoba Zoo, Argentina. (A) Zones considered for the Use of Space analyses. Zone 1 to 3 is a pool, zone 4 to 10 is land. Areas of each zone are as follows: 1 is 68 m^2, 2 is 22 m^2, 3 is 40 m^2, 4 is 14 m^2, 5 is 4 m^2, 6 is 9 m^2, 7 is 20 m^2, 8 is 8 m^2, 9 is 11 m^2, and 10 is 24 m^2. (B) Photograph of the enclosure from a south-east view (close-up of zones 1 and 4). (Photographed by Lilen Prystupczuk).

Behavioral observations and use of space.—We conducted behavioral observations between December 2015 and June 2016, including the reproductive and post-reproductive periods. In December, we made preliminary observations to define a schedule for further behavioral observation. We described but did not include in the analysis of quantitative data, behaviors observed in December. The zoo was open to the public during the observations and visitors flow was normal around the enclosure (mean of 314 visitors around the enclosure per day). We applied the ad libitum sampling technique, following the protocol of Altmann (1974). Observations were made by the same observer throughout the study, from one fixed location partially hidden from view of the animals and after a 15-min period for habituation to the observer. Observations took place during three 2-h periods between 0900 and 1800 on two consecutive days for three weeks per month. We recorded behaviors as events every time they occurred, and we identified the individuals displaying them by tail notches and individual features (Verdade et al. 2006). In case that two behaviors occurred at the same time, we recorded both behaviors. Simultaneously to ad libitum observations, we performed instantaneous scan samples every 30 min (15 per day) to record the location of individuals. We classified behavior and location data by sex and age class of individuals and by environmental variables: (1) season; reproductive (January-March) or post-reproductive (May and June); (2) time of the day; morning (0900–1159), midday (1200–1459), or afternoon (1500–1759); and (3) mean daily temperature (http://magya.omixom.com); cold (6.5–13.6° C), warm (13.7–22.6° C), or hot (22.7–29.4° C) recorded at the moment of the observations.

We recognized and described the behaviors based on literature of Broad-snouted Caiman (Verdade 1999; Piffer and Verdade 2002; Bassetti et al. 2014), related species such as American Alligator (*Alligator mississippiensis;* Garrick and Lang 1977; Spotila et al. 1977; Palis 1989; Vliet 1989), Freshwater Crocodile (*Crocodylus johnstoni;* Seebacher 1999), Morelet's Crocodile (*Crocodylus moreletii;* Platt et al. 2006), Nile Crocodile (*Crocodylus niloticus;* Downs et al. 2008) and Saltwater Crocodile (*Crocodylus porosus;* Brien et al. 2013b), or crocodilians in general (Brattstrom 1974; Lang 1987; Senter 2008; Brien et al. 2013a; Brandt and Mazotti 1990). We summarized recorded behaviors in an ethogram. We obtained the relative frequency of each behavior and evaluated the association between frequencies and attributes of individuals and environmental variables.

We evaluated agonistic interactions in the population. We defined agonism as any interaction in which aggression and intolerance appeared to be signaled by postures or actions by one or both individuals;

Table 1. Snout-vent length (SVL) and weight of the Broad-snouted Caimans (*Caiman latirostris*) in Córdoba Zoo, Argentina, obtained on April 2016. Abbreviations of individuals are amA = adult male A, amB = adult male B, amC = adult male C, af = adult female, sfA = subadult female A, sfB = subadult female B, and sfC = subadult female C.

Individual	SVL (cm)	Weight (kg)
amA	89	31.6
amB	88	25.0
amC	67	14.2
af	75	11.6
sfA	56	6.3
sfB	49	3.5
sfC	37	1.6

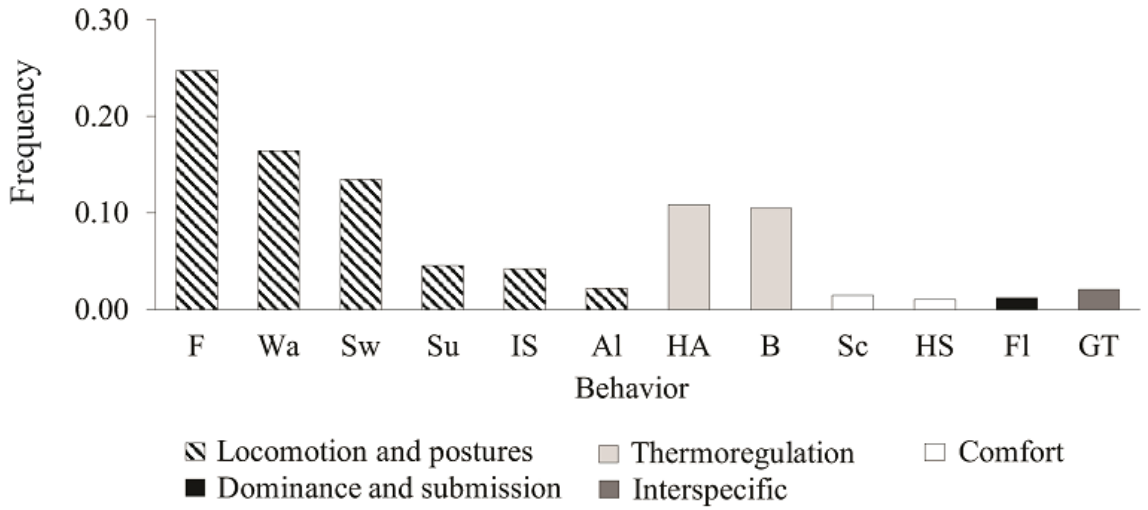

Figure 3. Frequencies of behaviors recorded in the Broad-snouted Caiman (*Caiman latirostris*) population in Córdoba Zoo, Argentina, from January to June 2016. The most frequent behaviors (events of the particular behavior/total events > 0.010) are shown. Subcategories of behavior are indicated with different bar fill patterns: F = floating, Wa = walking, Sw = swimming, Su = submerged, IS = immersed swimming, Al = alert, HA = heat avoidance, B = basking, Sc = scratching, HS = head shake, Fl = flight, and GT = gregarism with turtle.

an aggressor as an individual that made deliberate advances toward or physical contact with another individual (Brien et al. 2013a, b); and an aggressed as an animal that is subject to an agonistic behavior from an aggressor. We evaluated the association between the frequency of agonistic interactions and sex, size ratio, and weight ratio of the involved individuals. When (aggressor SVL)/(aggressed SVL) and (aggressor weight)/(aggressed weight) ranged between 0.8 and 1.2, we considered that individuals were of equal size and weight, respectively (Verdade 1992).

We estimated the use of space by calculating a modified Spread of Participation Index (SPI; Dickens 1955; Plowman 2003) using the data of the location of individuals in the enclosure. This index ranges between 0 (equal use of all the zones) and 1 (use of only one zone). We virtually divided the enclosure into 10 zones and obtained the area of each zone using Google Earth Pro (V 7.3.2.5776; Google LLC, Mountain View, California, USA). We evaluated differences in SPI values associated with attributes of individuals and environmental variables.

Assessment of enclosure, husbandry, and management measures.—We determined a set of criteria regarding each one of the Five Freedoms (Farm Animal Welfare Council 1993, see Appendix Table) based on literature on husbandry of Broad-snouted Caiman and related species. We assessed the fulfilment of these criteria on the study population based on our observations and information provided by the institution.

Statistical analyses.—We evaluated the association of frequencies of behaviors with attributes of individuals and with environmental variables using Chi-square Contingency Tables. We evaluated differences between SPI values among attributes of individuals and environmental variables. We tested all data for normality and homogeneity of variances using Shapiro-Wilk and Levene's tests, respectively. We performed one-way ANOVA when assumptions were met, Kruskal-Wallis test when data were not normally distributed, and Wilcoxon test when homogeneity of variance was not met. We evaluated the association between the frequency of agonistic interactions and sex, size ratio, and weight ratio of the involved individuals using a Kruskal-Wallis test because data were not normally distributed. We ran statistical analyses using INFOSTAT 1.0 (http://www.infostat.com.ar) with an $\alpha = 0.05$ (Balzarini et al. 2008).

Results

Behavioral observation and use of space.—We described 31 behaviors (Table 2), including courtship and copulation, which we recorded only during preliminary observations (27.5 h from a total of 204.5 h of observations). Categories and subcategories of behaviors are following Lang (1987). We compared frequencies of the 12 overall most frequent behaviors (frequency > 0.010; Fig. 3) in terms of attributes of individuals and environmental variables.

Swimming, floating, and submerged behaviors had significantly higher frequencies during the post-reproductive than the reproductive season, in the morning than at midday and in the afternoon, and on cold than on warm or hot days. In contrast, walking, alert, and heat avoidance behaviors were more frequent during the reproductive season than during the post-reproductive

Table 2. Ethogram showing behaviors recorded on a mixed-sex and mixed-age population of Broad-snouted Caiman (*Caiman latirostris*) in Córdoba Zoo, Argentina, from December 2015 to June 2016. Behavior codes are Wa = walking, Sw = swimming, IS = immersed swimming, F = floating, Su = submerged, Al = alert, Fo = foraging, I = ingestion, B = basking, HA = heat avoidance, G = gaping, Sc = scratching, HS = head shake, Y = yawning, V = vocalization, TW = tail wagging, GP = gular pulsation, JC = jaw clap, HB = head bob, TA = tail arched, Ad = advance, Ch = chase, St = strike, Bi = bite, Fl = flight, Im = immersion, CT = competition with turtle, AT = agonism with turtle, GT = gregarism with turtle, Cs = courtship, Co = copulation. Behaviors described in: Lang 1987 (1); Brien et al. 2013a (2); Brien et al. 2013b (3); Seebacher 1999 (4); Palis 1989 (5); Platt et al. 2006 (6); Brandt and Mazotti 1990 (7); Downs et al. 2008 (8); Bassetti et al. 2014 (9); Spotila et al. 1977 (10); Vliet 1989 (11); Piffer and Verdade 2002 (12); Senter 2008 (13); Garrick and Lang 1977 (14); Brattstrom 1974 (15); Verdade 1999 (16).

Behavior		Description
Maintenance		
Locomotion and postures	Wa	Locomotion on land (1)
	Sw	Locomotion in water with the head and top of the back out of the water (1)
	IS	Locomotion in water completely submerged (1)
	F	Immobile on the water surface (2,3)
	Su	Immobile, deep in water for more than one min (1,4)
	Al	Still posture, upright head, looking at one particular direction (1)
Feeding	Fo	Exploration on land or in water in search of food (5,6)
	I	Manipulating and consuming food items
Thermoregulation	B	Immobile on land, exposing more than 50% of the body to direct sunlight (or a percentage that, according to sunlight availability, suggests heat-seeking) (1,4,7,8,9)
	HA	Immobile on land, with more than 50% of the body in the shade (or a percentage that, according to shade availability, suggests heat avoidance) (1,8)
	G	Mouth held open for more than one min; simultaneous to basking or heat avoidance (1,8,10)
Comfort	Sc	Rubbing posterior claws on the head or the back
	HS	Rapid side to side head movement
	Y	Wide and slow mouth opening and closing while basking or during heat avoidance
Social interactions		
Communication	V	Growling, bellowing, hissing or producing other vocal sounds (1,3,11,12,13)
	TW	Repeated side to side movement of the tail or its distal portion (1,2,3,11,13,14)
	GP	Pulsated movements on the gular zone in an alert posture (10)
	JC	Partial opening and rapid closing of jaws on the water surface (2,3)
	HB	Repeated up and down head movements in an alert posture (15)
Dominance and submission	TA	On the water, head and distal portion of the tail arched above the water surface (1,2,11,12,13,14,16)
	Ad	Walking or swimming towards another individual, initiating an agonistic interaction (2,3)
	Ch	Running after an aggressed individual until it is out of reach (2,14)
	St	Lifting the head and chest and leaping on an aggressed individual
	Bi	Jaws closed on an aggressed individual (1,2,3)
	Fl	Moving away from an aggressor (1,2,3)
	Im	Diving in response to the approach of a dominant individual, submerging until the latter moves away (1)
Interspecific	CT	Competition for food or sites with one or more *P. hilarii* turtle
	AT	Any posture or action that signals aggression and/or intolerance to one or more *P. hilarii* turtles
	GT	Physical contact without any sign of aggression or intolerance with one or more *P. hilarii* turtles
Reproduction		
	Cs	Growling. On the water, male lies his head on the neck of the female (1,12,13,14)
	Co	Male mounts female, placing over and slightly behind her, and making ventral contact every couple of min. Male raises his nostrils out of the water. Female stays submerged. Copulation lasts approximately 15 min (1,14)

season and on hot than on warm and cold days, except for alert behavior, which was equally frequent on warm and hot days (Fig. 3). Basking behavior was more frequent in subadults than in adults, at midday than in the morning and afternoon, and on cold days than on hot days. Immersed swimming behavior was recorded more frequently during the reproductive season than during the post-reproductive season, and was less frequent at midday than in the morning and afternoon (Fig. 3). Flight behavior was more frequent in subadults than in adults, in males than in females, during the reproductive season than during the post-reproductive season, on warm and hot days than on cold days, and in the afternoon than in the morning. The remaining behavior

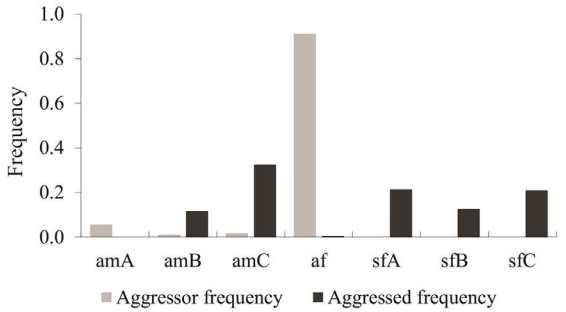

Figure 4. Frequencies of agonistic interactions recorded in individuals of the Broad-snouted Caiman (*Caiman latirostris*) population housed in Córdoba Zoo, Argentina, from January to June 2016. Abbreviations are amA = adult male A, amB = adult male B, amC = adult male C, af = adult female, sfA = subadult female A, sfB = subadult female B, and sfC = subadult female C.

frequencies did not show clear patterns of variation according to the recorded variables, although some of them were significantly different (Tables 3 and 4).

We recorded 172 agonistic interactions in which the involved individuals were clearly identified (of a total of 185 interactions). Encounters were initiated mostly (91% of the times) by the adult female and never by subadult individuals. All three subadult female and two out of the three adult males received aggressions from conespecifics (Fig. 4). The frequency of agonistic interactions was not associated with sex ($H = 7.55$, df = 1, $P = 0.948$), size ratio ($H = 2.35$, df = 2, $P = 0.188$), or weight ratio ($H = 2.07$, df = 2, $P = 0.230$) of the involved individuals.

Spread of Participation Indexes ranged between 0.42 (in subadult female C) and 0.79 (in adult male B; Fig. 5). Indexes did not show significant differences associated to age class (adult SPI = 0.56 ± [SD] 0.16, S: subadult SPI = 0.47 ± 0.05; $W = 10.00$, $P = 0.628$), sex (female SPI = 0.46 ± 0.04, male SPI = 0.60 ± 0.17; $W = 16.00$, $P = 0.229$), season (reproductive SPI = 0.52 ± 0.14, post-reproductive SPI = 0.65 ± 0.17; $F_{1,12} = 2.30$, $P = 0.155$), time of the day (morning SPI = 0.48 ± 0.16, midday SPI = 0.60 ± 0.11, afternoon SPI = 0.58 ± 0.10; $H = 5.19$, df = 2, $P = 0.075$), nor mean daily temperature (cold SPI = 0.65 ± 0.16, warm SPI = 0.54 ± 0.12, hot SPI = 0.54 ± 0.14; $F_{2,18} = 1.39$, $P = 0.275$).

Assessment of enclosure, husbandry and management measures.— We defined 34 criteria for the assessment of the Five Freedoms (Appendix Table). Overall, 53% of the criteria were evaluated as optimum. Optimum criteria for freedom to express natural behavior, freedom from hunger and thirst, freedom from pain, injury or disease, freedom from discomfort and freedom from fear and distress, corresponded to percentages of 88, 67, 40, 38, and 29, respectively.

Discussion

Behavioral observation and use of space.—In this study, we described behaviors previously recorded for the Broad-snouted Caiman and related species, as well as behaviors that we did not find in the literature survey. Maintenance behaviors were the most frequent, which is consistent with previous studies reporting that this species, like other crocodilians both in captivity and in the wild, spend most of their time practically immobile, engaged in thermoregulatory behaviors, with short periods of activity (Lang 1987; Larriera and Imhof 2006). According to Seebacher (1999), crocodilians shift between an array of postures intermediate from basking to diving, with different heat exposure that allows them to achieve their preferred body temperature. Therefore, we considered it important to record heat avoidance behavior, which consists of an individual choosing to stay on land and avoiding direct sunlight. Gaping behavior was included in the thermoregulation

Table 3. Comparison of the most frequent behaviors (frequency > 0.010) by individual attributes recorded on a mixed-sex and mixed-age population of Broad-snouted Caiman (*Caiman latirostris*) in Córdoba Zoo, Argentina, from January to June 2016. Frequencies expressed as percentages. For age class, A = adults, S = subadult, and for sex, M = males and F = females. We used Chi-square to test for differences between age classes and between sexes.

	Attributes of Individuals					
	Age class			Sex		
Behavior	A	S	*P*-value	M	F	*P*-value
Walking	13.1	21.1	< 0.001	15.9	18.3	0.036
Swimming	18	7.1	< 0.001	14.5	9.6	< 0.001
Immersed swimming	4.5	3.8	0.165	4.1	4.6	0.425
Floating	28.6	19.4	< 0.001	25	23.9	0.412
Submerged	3.2	6.4	< 0.001	4.5	4.5	0.960
Alert	1.6	2.9	< 0.001	2.1	2.5	0.361
Basking	8.3	13.6	< 0.001	10.4	10.7	0.813
Heat avoidance	8.8	133.7	< 0.001	10.2	13.3	< 0.001
Scratching	1.3	1.8	0.072	1.6	1.1	0.202
Head shake	0.9	1.2	0.295	1.1	0.8	0.417
Flight	0.8	1.7	< 0.001	1.0	2.0	< 0.001
Gregarism with turtle	2.8	1.1	< 0.001	2.5	0.5	< 0.001

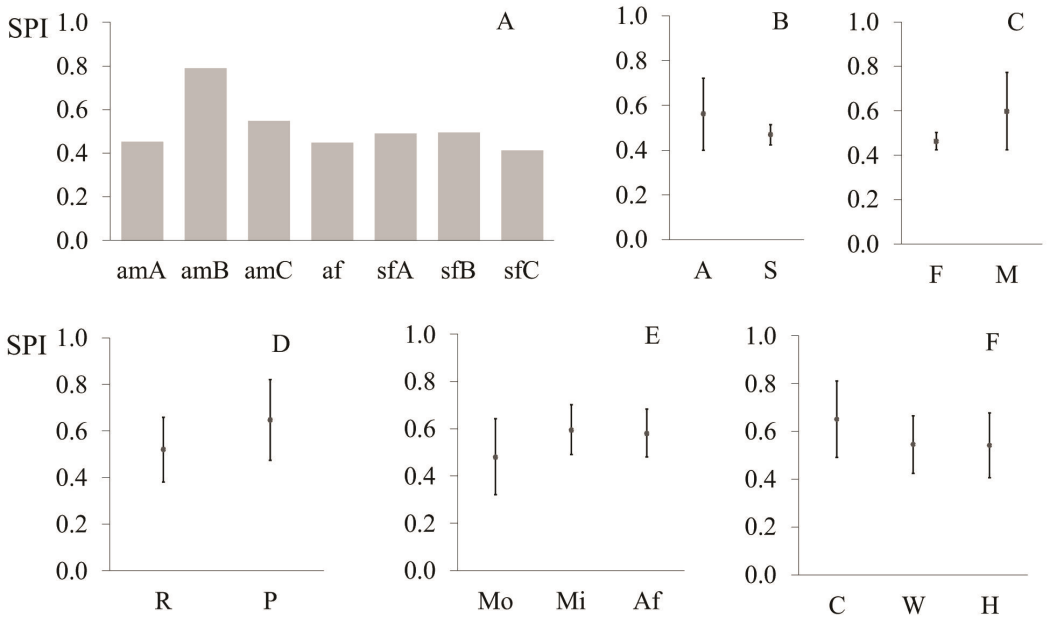

Figure 5. Spread of Participation Index (SPI) values obtained from the Broad-snouted Caiman (*Caiman latirostris*) population housed in Córdoba Zoo, Argentina, from January to June 2016. No significant differences were found. Error bars represent one Standard Deviation. (A) SPI values by individual, amA = adult male A, amB = adult male B, amC = adult male C, af = adult female, sfA = subadult female A, sfB = subadult female B, and sfC = subadult female C. (B) SPI values by age class, A = adult and S = subadult. (C) SPI values by sex, F = female and M = male. (D) SPI values by season, R = reproductive and P = post-reproductive. (E) SPI values by time of the day, Mo = morning, Mi = midday, and Af = afternoon. (F) SPI values by mean daily temperature, C = cold, W = warm, and H = hot.

subcategory because it was found to allow reduction of the heating rate of the head (Spotila et al. 1977); however, other authors suggest that this behavior may have other roles, probably a social one (Lang 1987; Downs et al. 2008). Similarly, gular pulsation behavior was observed in thermoregulation contexts associated with gaping, but more frequently in social interaction contexts and an alert posture; for this reason, it was included in social communication behaviors. We recorded head bob behavior in five of the seven individuals and, although it was not described for crocodilians, it is considered a social communication behavior in other reptiles (Labra et al. 2007; Cox et al. 2009; Hellmuth et al. 2012).

Despite the occurrence of copulation between the adult female and adult male A, we did not record territorial defense, nesting, or breeding in the study period nor was there evidence of these behaviors in the zoo records. The absence of nesting material (i.e., vegetation, dry grass) and nesting shelters, and the mixed composition of the population in terms of sex and age are unsuitable characteristics for reproduction, according to recommendations of Brien et al. (2007) and compared with successfully breeding populations of Broad-snouted Caimans (Larriera 1991; Yanosky and Mercolli 1993; Verdade and Sarkis 1998; Verdade et al. 2006). These results may be taken into account for the management of this population in the future because they may be useful for the design or modifications of the enclosure or of the composition of the population.

Interactions with Hilaire's Side-necked Turtle consisted mostly (72%) of aggregation of individuals of both species basking or floating (e.g., turtles were regularly seen resting on the backs of larger caimans). The remaining events consisted of interspecific competition for food or basking sites (15%), and interspecific agonism (13%), which was equally frequent in adult and subadult Broad-snouted Caimans. There were no instances of the caimans trying to prey on turtles, although freshwater turtles are cited as an item consumed by Broad-snouted Caimans in the wild (Rueda-Almonacid et al. 2007). Furthermore, this population was observed since 2012 by zoo staff and volunteers, and this behavior was not recorded before (unpubl. data). These results suggest that sharing the enclosure with Hilaire´s Side-necked turtles would not compromise the welfare of the Broad-snouted Caiman as long as enough resources are provided, which minimizes competition.

The association found between aquatic behaviors (floating and swimming) and adult age class as well as between land-related ones (walking, heat avoidance, and basking) and subadult age class may be explained by an ontogenetic shift in behavior or, conversely, by the preference for pool areas from which smaller, and therefore low-ranking individuals, are excluded. The associations between sex and behavior frequencies did not evidence a clear pattern and may be confounding with the effects of variation in behavior among individuals, age class, or dominance hierarchy. Because

Table 4. Comparison of the most frequent behaviors (frequency > 0.010) by environmental variables (season, time of day, temperature) recorded on a mixed-sex and mixed-age population of Broad-snouted Caiman (*Caiman latirostris*) in Córdoba Zoo, Argentina, from January to June 2016. Frequencies expressed as percentages. Abbreviations are R = reproductive, P = post-reproductive, Mo = morning, Mi = midday, Af = afternoon, C = cold, W = warm, H = hot. We used Chi-square to make statistical comparisons.

	Season			Time of day				Temperature			
	R	P	*P*-value	Mo	Mi	Af	*P*-value	C	W	H	*P*-value
Walking	18.0	12.2	< 0.001	9.7	24.3	-	< 0.001	13.0	14.9	-	0.088
				9.7	-	16.4	< 0.001	13.0	-	19.9	< 0.001
				-	24.3	16.4	< 0.001	-	14.9	19.9	< 0.001
Swimming	12.4	16.5	< 0.001	19.4	10.3	-	< 0.001	16.7	13.0	-	0.001
				19.4	-	9.1	< 0.001	16.7	-	12.1	< 0.001
				-	10.3	9.1	0.231	-	13.0	12.1	0.317
Immersed swimming	5.4	1.1	< 0.001	5.3	1.9	-	< 0.001	0.8	5.6	-	< 0.001
				5.3	-	5.6	0.650	0.8	-	4.9	< 0.001
				-	1.9	5.6	< 0.001	-	5.6	4.9	0.245
Floating	21.1	34.7	< 0.001	34.6	17.6	-	< 0.001	33.6	24.4	-	< 0.001
				34.6	-	19.7	< 0.001	33.6	-	19.9	< 0.001
				-	17.6	19.7	0.088	-	24.4	19.9	< 0.001
Submerged	2.6	9.8	< 0.001	6.5	1.9	-	< 0.001	9.0	5.0	-	< 0.001
				6.5	-	4.9	0.024	9.0	-	1.4	< 0.001
				-	1.9	4.9	< 0.001	-	5.0	1.4	< 0.001
Alert	2.5	1.3	0.003	0.7	2.2	-	< 0.001	1.3	2.5	-	0.010
				0.7	-	4.1	< 0.001	1.3	-	2.4	0.018
				-	2.2	4.1	< 0.001	-	2.5	2.4	0.780
Basking	10.2	11.2	0.257	5.8	16.3	-	< 0.001	12.0	9.4	-	0.008
				5.8	-	10.0	< 0.001	12.0	-	10.6	0.152
				-	16.3	10.0	< 0.001	-	9.4	10.6	0.169
Heat avoidance	12.5	6.3	< 0.001	5.9	12.6	-	< 0.001	6.8	9.5	-	0.003
				5.9	-	15.7	< 0.001	6.8	-	14.5	< 0.001
				-	12.6	15.7	0.004	-	9.5	14.5	< 0.001
Scratching	1.5	1.6	0.792	1.7	1.3	-	0.189	1.2	1.8	-	0.194
				1.7	-	1.5	0.535	1.2	-	1.4	0.675
				-	1.3	1.5	0.541	-	1.8	1.4	0.293
Head shake	1.2	0.5	0.008	0.8	1.4	-	0.029	0.5	1.0	-	0.080
				0.8	-	0.9	0.592	0.5	-	1.4	0.011
				-	1.4	0.9	0.144	-	1.0	1.4	0.304
Flight	1.6	0.0	< 0.001	0.9	1.1	-	0.533	0.0	1.8	-	< 0.001
				0.9	-	1.7	0.012	0.0	-	1.3	< 0.001
				-	1.1	1.7	0.066	-	1.8	1.3	0.162
Gregarism with turtle	2.1	2.1	0.978	2.7	1.6	-	0.008	1.8	3.2	-	0.010
				2.7	-	1.8	0.055	1.8	-	1.2	0.081
				-	1.6	1.8	0.557	-	3.2	1.2	< 0.001

of the small sample size and the absence of subadult males on our study, we are not able to evaluate which one of these factors (or their combination) affects the most to the aforementioned pattern.

Many of the associations found between behavior and the environmental variables could be explained by means of thermoregulation. As there was no artificial control of temperature in the enclosure, water and air temperature fluctuated naturally. As a consequence of their heat capacity, water temperature is more stable than air temperature (Halliday et al. 2013), so it is expected that Broad-snouted Caimans stay in water at low ambient temperatures, as crocodilians commonly do (Brandt and Mazzotti 1990). Accordingly, frequencies of aquatic behaviors were greater at low temperatures (cold daily mean temperature, in the morning, and the post-reproductive season), and frequencies of land-related behaviors were greater at high temperatures (hot daily mean temperature, at midday, and in the reproductive season). Regarding daily activity patterns, we observed individuals in water (swimming, immersed swimming, floating, submerged) during the morning, and then they moved onto land (walking, alert, basking, heat avoidance) at midday and in the afternoon, consistently with findings described by Bassetti et al. (2014) for Broad-snouted Caiman, by Seebacher and Grigg (1997) for Freshwater Crocodile, and by Downs et al. (2008) for Nile Crocodile. Greater frequencies of alert and flight

behaviors were expressed in the reproductive season, corresponding with higher levels of social activity in this period (Larriera and Imhof 2006). Immersed swimming behavior, which was more frequent in the reproductive season (unlike the remaining aquatic behaviors), may be a preferred mode of locomotion in the context of frequent agonistic interactions in this season, as it allows Broad-snouted Caimans to move without being spotted by other individuals.

In Broad-snouted Caiman populations, agonistic behaviors are common for the establishment of dominance hierarchies; however, these behaviors may turn more frequent in captivity, when densities are higher than in the wild. Agonistic behaviors were reported to cause 15% of the global mortality of a captive Broad-snouted Caiman population (Verdade 1992); therefore, they are of great importance for the welfare of individuals, and their minimal occurrence is desirable. In the study population, agonistic encounters represented 2.6% of the total behavior events. These levels were higher than those recorded by Brien et al. (2013a) in juvenile crocodilians of seven species (0.004 agonistic interactions per individual per hour in Brien et al. 2013a versus 0.139 agonistic interactions per individual per hour in the Córdoba Zoo). Given the low number of studied individuals, our results cannot be extrapolated to species level; nevertheless, they allow us to characterize the dominance relationships of this particular population and to compare them to other mixed-sex and mixed-age captive populations to identify management measures that improve their welfare state under controlled breeding conditions. The high percentage of interactions initiated by the adult female suggests that she is a dominant individual, whereas all of the subadults plus the male adult B and male adult C, frequently aggressed by the adult female, could be considered subordinates to her. As reported by Verdade (1992) for this species, neither sex nor size affected the occurrence of agonistic interactions. In contrast to his results, however, agonistic encounters in the Córdoba Zoo were equally frequent between individuals of different weight than between individuals of the same weight. All of the agonistic encounters occurred in the reproductive season, both in water and on land, and were not associated with feeding.

Individual SPIs indicated that Broad-snouted Caimans made a variable use of the enclosure, with some of them making a very limited use (adult male B, SPI = 0.79) and others making an intermediate use (subadult female C, SPI = 0.42). The SPI for the entire population (SPI = 0.35), showed that, independently of individual use and preferences, some zones of the enclosure were poorly used or not used at all. This situation could be improved through enrichment and development of a more complex environment so that individuals disperse across the entire enclosure, instead of aggregating in the preferred sectors. According to ideal despotic distribution (Fretwell 1972), high-rank individuals tend to occupy the best habitats, excluding the subordinates, which can be translated into a more restricted use of space by dominant individuals. This was apparent in the post-reproductive season, when dominant individuals, adult male A and the adult female, were regularly seen in a pool area near a warm water source, while the remaining individuals were distributed in the remaining areas. Differential space use related to social hierarchy has been documented in captive (Hedeen 1983; Robitaille and Prescott 1993; Leighty et al. 2010) and wild (Boydston et al. 2003; Murray et al. 2007) populations of different species.

We characterized some important behavior and husbandry aspects of Broad-snouted Caimans at the Córdoba Zoo. The absence of reproduction, the association between frequencies of particular behaviors and attributes of individuals, the high rate of agonistic encounters, and the limited use of space are all factors that might be related to the welfare of caiman in this population. Our results highlight the importance of zoos as venues for conducting studies that contribute to the general knowledge of the species, while providing significant information about the study population, potentially leading to its improved welfare. Based on our observations, we suggest the Córdoba Zoo modify their inadequate management criteria to fulfill the Five Freedoms for Broad-snouted Caimans in their care.

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Appendix Table. Evaluation of the suitability of the enclosure and management measures of a mixed-sex and mixed-age population of Broad-snouted Caiman (*Caiman latirostris*) in Córdoba Zoo, through an analysis of the Five Freedoms from January to June 2016. Criteria adapted from: Lang 1987; Verdade and Santiago 1990; Ladds 1993; Verdade et al. 1994; Pinheiro and Lavorenti 2001; Sarkis-Goncalves et al. 2001; Piña and Larriera 2002; Larriera et al. 2006; Bassett and Buchanan-Smith 2007; Brien et al. 2007; Koza et al. 2011; Zayas et al. 2011; Draper and Harris 2012; Hellmuth et al. 2012; Burghardt 2013; Australian Ministers responsible for Primary Industries 2014. Australian Animal Welfare Standards and Guidelines. Exhibited animals – Crocodilian. Available at https://www.dpi.nsw.gov.au/__data/assets/pdf_file/0015/510081/guide-exhibited-animals-crocodilian.pdf (Accessed 11 December 2018); Bassetti et al. 2014; Mellor 2016.

Freedom	Criterion	Recommendation	Evaluation
Freedom from hunger and thirst	Food quantity	25% of Broad-snouted Caiman weight, six days a week, in the reproductive season	Optimum
	Food composition	A mixture of beef, chicken, and/or fish. Include fur, feathers, bones and/or entrails	Optimum
	Dietary supplements	Vitamins and mineral supplements	Inadequate
	Variety on the food presented	Include live prey and vary items and feeding schedule	Optimum
	Food access	Access to food for the whole population	Optimum
	Water	Access to fresh drinking water	Inadequate
Freedom from discomfort	Enclosure size	19 m^2 to > 350 m^2	Optimum
	Air temperature	17–36° C	Optimum
	Basking and shade areas	Present	Optimum
	Water salinity	Freshwater	Inadequate
	Type of substrate	Non-abrasive	Inadequate
	Pool margins	Steps or ramps of 10–20° slope	Inadequate
	Nesting shelters	Present	Inadequate
	Enclosure cleaning	Periodically	Inadequate
Freedom from pain, injury or disease	General external appearance	Apparent good state, good skin condition, absence of injury	Inadequate
	Prevention and treatment of injury and disease	Periodic veterinary care	Inadequate
	UV radiation	Access to UV radiation	Optimum
	Social hierarchy effects	Mitigation for low-ranking animals	Inadequate
	Isolation, treatment and recovery facilities	Present	Optimum
Freedom to express natural behavior	Repertory of behavior	Wide repertory including previously described behaviors	Optimum
	Stereotyped behavior	Absent	Optimum
	Self-directed behavior	Absent	Optimum
	Agonistic behavior	Absent or infrequent	Inadequate
	Exploratory behavior	Present	Optimum
	Reproductive behavior	Present	Optimum
	Natural feeding behavior	Present	Optimum
	Chances of non-negative interspecific interactions	Present	Optimum
Freedom from fear and distress	Shelters	Physical and visual barriers	Inadequate
	Apparent negative effects of visitors	Absent	Optimum
	Chances of moving away from visitors	Present	Optimum
	Interaction with keeper and management routine	Minimum associated distress	Inadequate
	Interaction with conspecifics	No caiman housed with other > 1.2 times his or her weight	Inadequate
	Retention and capture installations	Present	Inadequate
	Training program	Present	Inadequate