



## Short report

## Flexibility in the social behavior of captive female capybaras (Mammalia, Rodentia)



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## ABSTRACT

Capybara (*Hydrochoerus hydrochaeris*) lives in stable groups composed of adult males and females with their young. The species shows flexibility in social organization in response to short-term environmental changes, but apparently does not show flexibility in social behavior. To gain insights into mechanisms underlying changes in social relationships, we analyzed the social dominance hierarchy of five captive capybara groups, composed of four to 13 adult females kept in outdoor paddocks ranging from 400 to 4500 m<sup>2</sup>. In addition, we evaluated the effects of group size and space allowance on two complementary properties of social structure: linearity and steepness. Captive female capybaras exhibit a linear social dominance hierarchy. There was also more predictability in the dominance success–hierarchical steepness – in the dominance hierarchy with a decrease in the space per individual. This variability in response to changing circumstances shows flexibility in capybara's social behavior.

## 1. Introduction

The social organization (the composition of groups), the mating system, and the social structure (describing who interacts with whom) concurrently characterize the social system of a species (Kappeler and van Schaik, 2002). The basic unit of capybara (*Hydrochoerus hydrochaeris*) social organization is the family unit, which consists of a dominant male, several possibly related adult females with their young, and one or more subordinate males (Herrera, 2013). The most common mating system of capybaras is polygynous in which one male is responsible for most of the copulation after pre-copulation competitions (Herrera and Macdonald, 1993). A strictly linear dominance hierarchy characterizes the social structure of capybara males (Herrera and Macdonald, 1993). However, the free-range capybara females do not appear to have a particular social structure among them (Herrera, 2013). In captivity, Ferraz et al. (2013) observed a monopolization of feeding resources by only one female that won conflicts against all other females – characteristic of a despotic dominance hierarchy.

Capybara groups appear to be relatively stable and range from four to 16 adults in the seasonally flooded savannahs of Venezuela (Herrera and Macdonald, 1987). Moreover, the species shows flexibility in social organization – reversible changes in the social organization at a population level in response to short-term changes of the environment (Schradin, 2013). During dry seasons, several groups come together to the dwindling pools, which results in associations of more than 100

capybaras (Ojasti, 1973). In the following rainy season, however, they divide up into their original groups (Herrera and Macdonald, 1987). However, apparently capybara does not show flexibility in social behavior. Flexible social behavior refers to individual variability in response to changing circumstances (Barrett et al., 2013). The increase in capybara group size did not result in an increase in cooperative behavior; on the contrary. (1985) studied the effect of the size of breeding groups (5, 10 or 15 adults) and the space allowance (enclosures with 32 m<sup>2</sup> and 120 m<sup>2</sup>) upon the social dominance hierarchy, agonistic interactions rate, and reproduction. The authors recorded increases in rates of aggression and mortality, as well as a decrease in reproduction rate with the group size. However, there was no relationship between these parameter and space allowance (Ojasti and Sosa Burgos, 1985). Furthermore, Ojasti and Sosa Burgos (1985) verified that low-ranking individuals were the ones that lose weight and died during the study.

The lack of social dominance among free-ranging capybara females (Herrera, 2013) is probably explained because there is no need to compete for grass, the capybara's main food resource (Ojasti, 1973; Macdonald, 1981), which is dispersed in its range. In contrast, farmed capybaras usually compete for food due to the spatial concentration of this resource. In captivity it is possible to manipulate ecological factors in ways to gain insights into mechanisms underlying changes in social relationships (Calhoun, 1950). Therefore, we aimed to describe the social dominance hierarchy of captive female capybaras and to evaluate

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**Table 1**  
Description of the agonistic behavioral patterns observed among capybaras.

| BEHAVIORAL PATTERN          | DESCRIPTION                                                                                                                                                       |
|-----------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Aggressive behaviors</b> |                                                                                                                                                                   |
| Threat                      | An individual interrupts the feeding activity and turns its head sideways towards a co-specific, with or without physical contact with the muzzle.                |
| Push                        | An individual presses its muzzle into different parts of an opponent's body (muzzle, genitals, and side of the body or hip), pushing and displacing the opponent. |
| Chase                       | The animal runs after an opponent that has fled; when finished, the attacker gives up or the opponent is displaced.                                               |
| Bite threat                 | An individual tries to bite the opponent, after a chase or a threat, giving the appearance of a warning to maintain distance.                                     |
| <b>Submissive behaviors</b> |                                                                                                                                                                   |
| Avoid                       | An individual interrupts the feeding activity and start walking away from approaching individual well before it is within one body length.                        |
| Flee                        | Run away at least one body length upon approach of other individual within one body length.                                                                       |
| Retreat                     | During this pattern, the head is usually held low and the movement increases an individual's distance from an approaching individual.                             |

Adapted from Azcárate-Bang (1980) and Ferraz et al. (2013).

the relationship between rank and body mass. We also intended to evaluate the effects of group size and space allowance on two complementary properties of social structure: linearity and steepness. The linearity is the main structural characteristic of a dominance hierarchy that ranges from zero (non-linear hierarchy) to 1.0 (perfect linear hierarchy) (Whitehead, 2009). The hierarchical steepness, a core aspect of social structure, is a continuous measure of dominance gradients measuring predictability of the dominance success (deVries et al., 2006). Adopting a different arrangement of the feeders, to avoid monopolization of feeding resources as occurred in Ferraz et al. (2013), we hypothesized that capybara females organize themselves in linear hierarchy dominance. Following previous results showed by Ojasti and Sosa Burgos (1985), we expected a correlation between rank and body mass independently of the group size and space allowance. We also expected an increase in agonistic rate with the increase of group size independently of the space allowance, as described by Ojasti and Sosa Burgos (1985). Moreover, we predicted decreases in both the hierarchical linearity and steepness along with the increase in group size and decreases in space allowance due to the increase in competition.

## 2. Methods

### 2.1. Ethical statement

The protocol of this experiment was carried out in accordance with the 'Guidelines for the use of animals in research' as published in Animal Behaviour (1991, 41, 183–186).

### 2.2. Study site and animals

The study was carried out with five capybara groups belonging to the Applied Ethology Laboratory, Universidade Estadual de Santa Cruz (UESC), Ilhéus, Brazil. Capybara groups were kept in outdoor paddocks ranging from 450 to 4500 m<sup>2</sup>, surrounded by a chain-link fence, with earth underfoot, low bushes, an artificial tank made of brickwork, and one water trough. Spread inside the paddocks, there were one to four feeders (1.5 m long × 0.3 m wide × 0.3 m high, each one), allowing at least a linear space of 0.30 m between individuals.

The studied groups ranged from four to 13 adult females, varying in age from 2 to 7 years old. Four of the groups were composed of one adult male varying in age from 4 to 6 years old. However, the largest one had two adult males, both aged two years. The females of each group had lived together since weaning, to avoid infanticide and/or lethal fights, in accordance with Nogueira and Nogueira-Filho (2012). The composition and space allowance of each group were: Group A – 13 females and two males, 300 m<sup>2</sup> per individual; Group B – nine females and one male, 450 m<sup>2</sup> per individual; Group C – six females and one male, 64.3 m<sup>2</sup> per individual; Group D – five females and one male, 75 m<sup>2</sup> per individual; Group E – four females and one male, 90 m<sup>2</sup> per individual. The groups had lived together since weaning and

in the composition and space allowance described here since two years before the study started. Following Eibl-Eibesfeldt (1970) and Wilson (1975), this time is sufficient to allow the establishment of a hierarchy in the groups.

Capybaras were fed once a day at 16:00 h with a combination of 5.0 kg of Napier grass (*Pennisetum purpureum*), and 0.5 kg of concentrate feed per animal, as recommended by Mendes and Nogueira-Filho (2013). The Napier grass was offered in suspended bundles, one for each capybara, while the concentrate feed was furnished in the feeders. We hung these bundles in the paddock fences and at least 5.0 m from one another to decrease the occurrence of feeding competition, following Nogueira and Nogueira-Filho (2012). Water was available *ad libitum*.

### 2.3. Social dominance data collection

We weighed and marked the animals prior to the data collection period, by cutting the animals' fur. Over the next 25 days, the capybaras were exposed to the observers for an adaptation period. During the habituation period three observers, using the *ad libitum* method (Altmann, 1974), selected the agonistic patterns used in the study: threat, push, chase, bite threat, avoid, flee, and retreat (Table 1). The inter-observer agreement was high (Kappa = 0.85).

Animals were observed from a distance of 5.0 m outside the paddock fences, between 16:00 and 18:00 h – the period of greatest activity of the capybaras (Macdonald, 1981). Each individual was observed during 15mins of continuous-recording focal animal sampling sessions (Altmann, 1974), totaling 10 focals per animal and 73.5 h of data collection on non-consecutive days over four months. Previous to observation sections, we randomly selected groups, individuals and the order in which they were observed per day. Observers continuously recorded the occurrence time, duration, initiator and receiver of aggressive and submissive behaviors. Then animals were ranked based upon their dominance over other individuals using the de Vries' et al. (2006) dominance score.

### 2.4. Statistical methods

To describe the capybara females' social structure we excluded male and female interactions for all following data analyses. To test for linearity of hierarchy, we calculated the Landau corrected linearity index *h'* (de Vries, 1995). This index ranges from zero (non-linear hierarchy) to 1.0 (perfect linear hierarchy), and the statistical significance of *h'* is provided by a re-sampling procedure using 1000 randomizations (Whitehead, 2009). In the sequence, we applied the I & SI method proposed by deVries (1998) to show the dominance order most consistent with a linear hierarchy for each matrix. In the linear rank order, the top individual is assigned rank 1 and the lowest-ranking individual rank *n*. Following that, we determined the steepness of females' hierarchy and tested whether it is significantly greater than

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