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Analyzing the hierarchical relationships for a group of *Sciurus granatensis* (Mammalia: Rodentia: Humboldt, 1811) in Caracas, Venezuela

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ABSTRACT

Social relationships within mammalian groups involve the development of hierarchical relationships among their members to avoid conflict. This hierarchy is established through aggressive dyadic encounters. Therefore, one way to determine if a hierarchy exists is to quantify the aggression-submission interactions and the movements between pairs of individuals. Here, we studied the social interactions in a group of *Sciurus granatensis* located within an urban forest patch in the city of Caracas, Venezuela, in order to determine the existence of a dominance hierarchy during their visits to the available artificial feeder. Also, we propose a non-invasive identification method to the identification of individuals based on morphological characters. The individuals were filmed for 19 consecutive days, from their resting areas to the trough. Interactions were analyzed using focal observation and exploration methods, which were subsequently described on an ethogram and classified into displacement (intimidation and withdrawal) and aggression (attack and attack with persecution). Overall, 19 individuals were identified within the group and 156 (with a daily average of 8.2 ± 4.3) interactions were recorded for 11 of them. The most common form of interaction was intimidation. Moreover, it was found that there were residents and occasional visitors in the group. The existence of dominance was determined with a Landau linearity index (h = 0.636). Two individuals shared the highest hierarchical rank. We observed a significant inverse correlation between tail thickness and the social rank. We concluded, based on the non-invasive identification system proposed, that there is a linear hierarchy in the group.

KEYWORDS

Agonistic interactions, animal behavior, dominance, non-invasive identification, Red-tailed Squirrel, urban fauna.

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INTRODUCTION

Aggressive behaviors result in the establishment of hierarchical relationships in individuals within a group, a product of the dominance/subordination relationship that is created as a result, of dyadic encounters (Krebs & Davies, 1997; Meng *et al.*, 2012). This hierarchy can be linear, despotic, triangular, or by coalition (Krebs & Davies, 1997). Aggressive interactions occur mainly as a consequence of competition in the acquisition of a resource, which can be food, partner, shelter, among others (Orians, 1969; Tanaka, 1996; Emlen, 2008). Studies have been carried out on hierarchical relationships in various groups of mammals, such as goats and primates (Alvarez, 1975; Barroso *et al.*, 2000; Klass & Cords, 2015), and specifically in sciurids of the genus *Xerus* (O'Shea, 1976; Waterman, 1995, 2002), *Callosciurus* (Tamura *et al.*, 1988), *Heliosciurus* (French & Smith, 2005), and *Sciurus* (Tamura *et al.*, 1988; Bordignon & Monteiro-Filho, 2000; Waisman & Jacobs, 2008).

The Red-tailed Squirrel, *Sciurus granatensis* Humboldt, 1811, is found in Central and South America (Cabrera, 1917; Handley Jr, 1978). It is typical of primary or intervened forests with semi-deciduous, riparian, evergreen, submontane and montane biomes (Linares, 1998), in dry or humid territories and, it is common in urban or semi-urban sectors (Méndez, 1993). Their diet consists mainly of hard-shelled nuts (being the main dispersers of the same) (Heaney & Thorington, 1978; Bonaccorso *et al.*, 1980; Leigh *et al.*, 1982) but they can be considered opportunistic, since consuming a wide variety of fruits and vegetables (Skutch, 1980). Despite that a linear and structured hierarchy has been reported specifically several squirrels of *Sciurus* genera, such as *S. carolinensis* (Koprowski *et al.*, 2016; Cerri *et al.*, 2020), there are no previous studies for these topics of hierarchical relationships in Red-tailed Squirrel across Neotropics.

Today, there are not studies that propose non-invasive identification systems (i.e., based on the natural differences among individuals and/or frequencies of appearance; see Stonehouse, 1978) to analyze the hierarchical relationships between sciurids populations. In fact, as far as we have knowledge, this approach has been used only in *S. carolinensis* groups based on their coloration patterns (Bohls & Koehnle, 2017). In contrast to large number of invasive identification systems, such as capture and marking (Stonehouse, 1978) or blood or tissue samples (Zemanova, 2020), the non-invasive methods are reliable and likely the most appropriate approach to the ethological wildlife studies. The invasive identification methods may intervene extensively in the behavior and generate stress into individual (Stonehouse, 1978; Zemanova, 2020; Bohls & Koehnle, 2017).

To address this, here we studied the social interactions in a group of *S. granatensis* located within an urban forest patch in the city of Caracas, Venezuela, in order to determine the existence of a dominance hierarchy during their visits to the available artificial feeder. This latter based on the hypothesis that whether there is a hierarchy in the group, it will be related to some morphological or temporal characteristic in the individuals. Also, we propose a non-invasive identification method to the identification of individuals based on morphological characters, which will be used to future ecological-social studies of this and other taxonomic groups.

METHODS

Sample period and study site.- We performed the study during nine months (from April to December 2015) in a little fragment of urban forest at the *"Jardín Ecológico de la Concha Acustica"* (10º28'48.5" N – 66º52'51.4" W), located in Colinas de Bello Monte, Caracas-Venezuela (Fig. 1). This area has approximately 6 ha of deciduous premontane dry forest, with an altitude of ca. 1,100 m a.s.l. and a two-seasonal climate: dry (December to April) and wet (May to November) seasons. Besides, annual rainfall varies from 550-1,100 mm, while the average temperature range between 18–24 ºC (Castillo & Levin, 2013).

Species focus.- The Red-tailed Squirrel is characterized by an ocher coloration on the back with variants of yellow, black, and bright orange with white hues in ventral area; its tail has very characteristic ocher colors with internal black shadows and with/without the black tip, in addition to an almost invariant ocher-colored eye ring (Boher, 1981). It has two reproductive periods per year, one at the end of December and the other between May and June, with a gestation period fewer than two months; the testicles of males remain visible all year round (Heaney & Thorington, 1978). They have diurnal habits, with

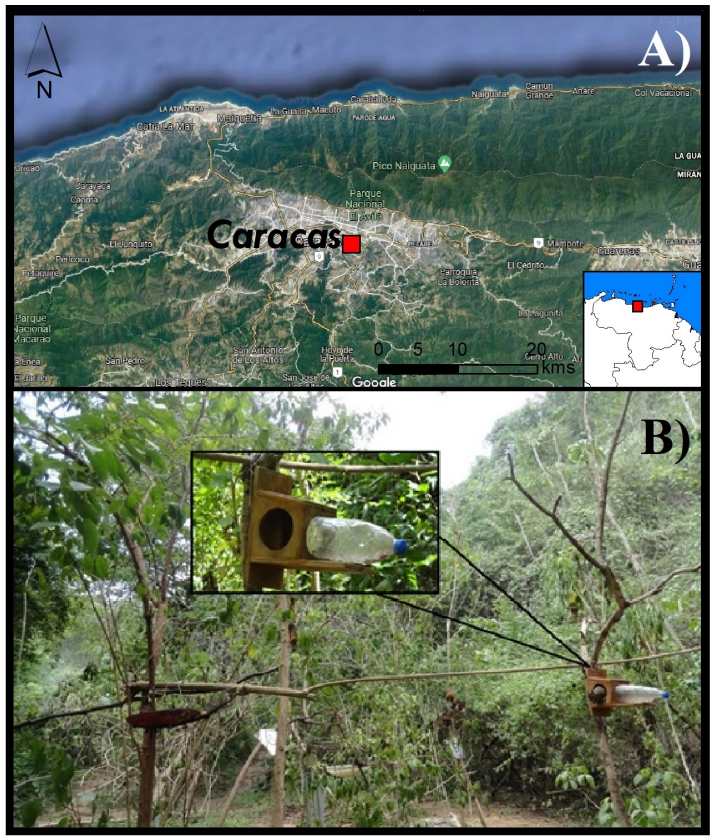

FIGURA 1 Study area and artificial feeder designed for this research. **(A)** Geographical localization of the "*Jardín Ecológico de la Concha Acustica*", Caracas-Venezuela; **(B)** General description of the food dispenser used to analyze the hierarchical relationships for a group of Red-tailed Squirrel (*Sciurus granatensis*) in a little fragment of urban forest.

a range of feeding activity from dawn until 11:00 h and then remain inactive until 15:30 h, when they feed again (Bonaccorso *et al.*, 1980).

Artificial feeder design and identification of individuals.- All observations were carried out in a single-entry feeder (Fig. 1), which allowed dispensing (one time by each individual) up to 30 units of peanuts without human intervention. This feeder was placed on a bamboo structure with access from three sides, which allowed the interaction of individuals. To familiarize individuals with this feeding system, a conditioning period was carried out (two months: April 26th to June 26th 2015) following the approach by previous studies of hierarchical relationships (Koprowski *et al.*, 2016; Cerri *et al.*, 2020).

For the non-invasive identification of individuals, we implemented a protocol based on morphological characters that did not vary over time. In this sense, during sessions of 3 h/day (8:30-11:30 h) and by three months (from July 5th to October 04th 2015), we observed and photographed the recorded individuals. Based on this evidence, we documented the morphological characters (color of the fur, tail, muzzle contour, eye contour, belly, and characters such as genitalia, breasts, body size, and scars) for each one of them (Table 1). The reliability of the proposed non-invasive identification system was evaluated through the criteria described by (Pennycuick & Rudnai, 1970), following the formula: $I = Log_2(1/F)$; where "I" is the amount of information relevant for the identification of an individual in bits (i.e., unit of the binary numbering for the absen-

TABLA 1 Morphological characters used for the identification of individuals of Red-tailed Squirrel (*Sciurus granatensis*) based on the proposed method of non-invasive differentiation. Characters with black-asterisk correspond to rare feature.

Symbol	Character	Description	Value	Value description	Information
G	Genitals	Male	1	Presence	Gender and Age
		Female	0	Absence	
T	Size	Scrawny	1	Little/Skinny	Age and Size
		Robust	2	Big/Fat	
C	Body Color	Coloring pattern	1	Grayish	Body
			2	Brown	
Cp	Chest spots	White spot coloring pattern	1	0 spot	Chest and belly
			2	1-6 spots	
Co	Eye Ring	Eye contour coloring pattern	1	Brown	Face
			2	White	
Cb	Beard	Grayish pattern around the mouth to the neck	1	Presence	Face
			0	Absence	
L	Tail thickness	Amount of fur	1	Little thick	Tail
			2	Very thick	
P	Coloring of the Tail	Coloring pattern	1	Spotted	Tail
			2	Feather tail	
Pp	Tip of the Tail	Black tip coloring pattern	1	Presence	Tail
			0	Absence	
Pb	Tail base	Coloring pattern	1	Black base	Tail
			2	Gray base	
M*	Bite	On the left ear	1	Presence	Oddity
			0	Absence	
B*	Spot on the tail	White on the lower dorsal part of the tail	1	Presence	Oddity
			0	Absence	
R*	Reflections in fur	White reflections in all the fur of the body	1	Presence	Oddity
			0	Absence	
J*	Juvenile	No visible genitalia and small size	1	Presence	Oddity
			0	Absence	

TABLA 2 General description of the behaviors observed for individuals of Red-tailed Squirrel (*Sciurus granatensis*) during this study.

Ethogram		
Classification	**Behavior**	**Description**
Aggression	Bite	Opening the muzzle and bite with incisors.
	Attack	Jump of one individual over another, keeping the limbs extended and exposing the nails.
	Persecution	Rapid movement of one individual after another.
	Intimidation	Stare from one individual to another. The head is kept in the direction of the opponent.
	Defense	Fixed gaze of an individual towards another, made before the resource to protect.
Submission	Escape	Rapid movement in the opposite direction to that of the rival. Occurs after aggressive interaction.
	Evasion	The individual moves with small steps, circling the area in which another individual is at close range.
	Guard	Rapid movement in the opposite direction to that of another nearby individual. Occurs without the need for prior aggressive interaction.
	Immobile	Immobility of the individual in the face of intimidation.
Feeding	Exploration	Movement with small steps, sniffing and rummaging among nearby objects. Frequent on the ground.
	Food intake	Sniffing food and taking with incisors.
	Food handling	Holds the food with the forelimbs positioned on two legs.
	Feeding by taking food	In the selected place, it takes the food with the forelimbs and positioned on two legs with the tail glued to the back.
	Feeding without taking food	The individual approaches the snout to the food without taking it with the forelimbs (these remain supported on the ground).
Others	Vocalization	Emission of high-pitched and consecutive sounds.
	Jump	Impulse by which the individual moves from one place to another.
	Relaxation	Immobility of the individual on a fixed surface. Drop the weight of the body on all four legs and place the tail on the back, keeping the tip on the head.

ce/presence of each character) and "F" is the frequency of their repetition.

Hierarchical relationships analyses.- *Ad libitum* and sweeping observations were made which were recorded on video with a digital camera brand Sony Cyber-shot model DSC-H70. These recordings began from the moment the food was placed in the feeder until the last unit of food (peanuts) was taken. All these observations were described in an ethogram (Table 2). The agonistic behaviors of each dyadic encounter that occurred at the feeder were recorded. The recordings were made from 9:00 h, for 19 continuous days (from November 16th to December 4th 2015). We determined the degree of linearity of the domain hierarchy using the linearity index of (Landau, 1951), while the dominance index (DI) was calculated to establish the ranks of each one individual within the domain hierarchy. To do this latter, we estimated the quotient between the numbers of interactions done by an individual and the number of total interactions (Hemelrijk *et al.*, 2005).

We performed a linear regression test assessing the relation between the dominance index and the age within the group (seniority). Besides, Spearman coefficient test and a one-way ANOVA were performed to analyze the effect of tail thickness and body size (defined qualitatively based on observations) into the dominance index observed. All these analyzes were performed using the RStudio v.1.1.456 program (R-Core Team, 2021).

RESULTS

Identification of individuals.- We identified, based on 10 morphological characters and four rare features (Table 1), a total of 19 individuals, of which 11 subsequently interacted with each other (see Appendix S1). The average accumulated bits for the group was of 10.0 ± 2.1. However, the bits accumulated for individuals in the group with rare features and low frequency characteristic were the highest (Fig. 2A). In fact, we observed that frequency of appearance of morphological characters and rare features is inversely proportional ($r = -0.642$; $P < 0.05$) to the number of bits they contribute for identification (Table 3).

Hierarchical relationships.- We recorded a total of 156 agonistic interactions (mean of 8.2 ± 4.3 interactions/days), which were classified into two types: displacement (subdivided into distancing and intimidation) and aggression (subdivided into attack and attack with persecution). The intimidation was the most common interaction observed, while the attack was the less frequent. Besides, we recorded a total of 25 reversals. It is important to note that we considered a total of eight individuals as "residents" because they appeared on the majority of the recording days; while three individuals (individuals' number 5, 6, and 8) were considered as "visitors" due to their low frequency of appearance. In fact, the individual number 5 was not observed again after its identification; therefore, it was excluded from the subsequent hierarchical analysis.

Overall, we obtained a Landau linearity index of $h = 0.636$. According to the dominance index, visiting individuals 8 and 6 were the lowest ranked, while among residents the lowest ranking was number 10 (Fig. 2b). In addition, two pairs were found that shared the first (individuals' number 3 and 11) and the fifth place (individuals 2 and 7) within the hierarchical range (Fig. 2b). Although the highest-ranking individuals obtained the same dominance index, individual number 3 only had one reversal while number 11 had fourteen. However, the regression model between the DI and seniority within group was not statistically significant ($R^2 = 0.0254$; $P > 0.05$) with a non-linear dispersion pattern. On the other hand, the Spearman tests shows not significant correlations between the ID and body size ($r = -0.245$; $P = 0.2876$), while ID and thickness of the tail showed significant negative correlation levels ($r = -0.572$; $P = 0.045$).

DISCUSSION

For a hierarchy to be perfectly linear, all dyads should be asymmetric, however, this is unlikely within nature, since reversals subtract asymmetry in dyadic interactions (Martin *et al.*, 1993). This latter could explain why the Landau index obtained in this study is not equal to 1. Likewise, the existence of a hierarchy that occurred by observing random interactions can be ruled out since the minimum group size required to avoid this error is five individuals (Appleby, 1983) and six or more to obtain statistically significant results in hierarchical analyzes (Martin *et al.*, 1993). In this sense, this index shows the existence of a hierarchy with a certain degree of linearity in the studied group of squirrels of the genus *Sciurus*, which concur with what was reported for others of the genus *Callosciurus* also associated with food sources (Tamura *et al.*, 1988).

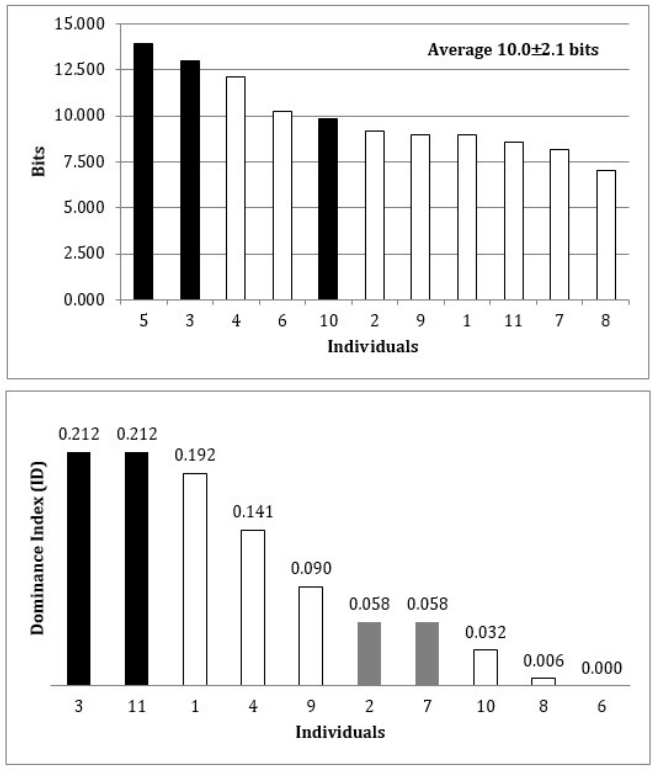

FIGURA 2 General description of bits and hierarchical rank observed for the individuals of Red-tailed Squirrel (*Sciurus granatensis*) during this study. **(Above)** Cumulate number of bits for individuals based on their attributes (black individuals have rare features; see Table 1); **(Below)** Hierarchical rank of individuals within the group, according to their dominance index (DI). Black bars represent individuals that share the first place and gray bars represent those who share the fifth place in the hierarchy. Individual number 5 was not observed.

It has been recorded that in certain groups of primates some individuals have similar status (Sapolsky & Ray, 1989; Bergman *et al.*, 2003). This coincides with the results of this work, where two pairs of individuals were found to share the first and fifth places within the hierarchical rank. Regarding the pair of individuals with the highest dominance index, number 11 had more reversals, which suggests that it is more prone to losing encounters than individual 3, as well as participating in dyads. There are reports for other species of individuals that share the highest rank within their social system, as is the case of the House Rat (*Rattus rattus*) (Macdonald *et al.*, 1995), male Olive-green Baboons (*Papio anubis*) (Sapolsky & Ray, 1989) or baboons (*P. ursinus*) (Bergman *et al.*, 2003). This shows that, under certain conditions, more than one individual can share the same hierarchical rank with another, either for a transitory period, such as access to food, or much longer, such as pair control. This issue remains poorly studied, but our intuitive hypothesis does not seem totally wrong. Therefore, more research is needed on these ideas.

On the other hand, most of the interactions were distancing. This could be explained due to both to the fact that this species is described as solitary (Nitikman, 1985) and with the low population densities when they are not found in optimal environments (Garcés-Restrepo & Saavedra-Rodríguez, 2013). In fact, the individuals of Red-tailed Squirrel rarely approach each other without being aggressive (Heaney & Thorington,

TABLA 3 Frequencies, probabilities, and bits values observed to the morphological characteristics selected for the identification of individuals of Red-tailed Squirrel (*Sciurus granatensis*) during this study. The acronyms in symbols correspond to same nomenclature used in Table 1. Black-asterisk in symbols represent characters referred to as "oddities".

Symbol	Value	Frequency	Probability	Bits
G	1	0.500	0.994	1.000
	0	0.500	0.994	1.000
T	1	0.455	0.987	1.138
	2	0.545	0.998	0.874
C	1	0.636	1.000	0.652
	2	0.364	0.950	1.459
Cp	1	0.727	1.000	0.459
	2	0.273	0.846	1.874
Co	1	0.545	0.998	0.874
	2	0.455	0.987	1.138
Cb	1	0.545	0.998	0.874
	0	0.455	0.987	1.138
L	1	0.455	0.987	1.138
	2	0.545	0.998	0.874
P	1	0.182	0.621	2.459
	2	0.818	1.000	0.290
Pp	1	1.000	1.000	0.000
	0	0.000	0.000	-
Pb	1	0.182	0.621	2.459
	2	0.818	1.000	0.290
M*	1	0.091	0.264	3.459
	0	0.909	1.000	0.138
B*	1	0.091	0.264	3.459
	0	0.909	1.000	0.138
R*	1	0.091	0.264	3.459
	0	0.909	1.000	0.138
J*	1	0.091	0.264	3.459
	0	0.909	1.000	0.138

1978). Therefore, aggressive behaviors in which closeness and physical contact are necessary are less likely to occur and, due to their solitary habits, they tend to avoid frequent relationships and with less likelihood of encounters if the population density is low. These behaviors and interactions coincide with the behaviors reported for the species in Colombia, in captive studies (Espinel, 2007).

The negative correlation between tail thickness and hierarchical rank had not been previously described for tree squirrels. For this reason, it is recommended to extend the analysis of this correlation with a larger sample, so that the scope of these results can be extended to larger groups. This is a novel outcome. A sparse tail is likely to give individuals adaptive advantages that allow them to win dyadic encounters or move more quickly to escape rivals or access food, as well as better imitation. It has been reported that the amount and color of fur varies with age in other sciurids such as *S. carolinensis*, adults generally having more hair than juveniles (Sharp, 1958), with which it could be assumed that in a group of *S. granatensis* studied, individuals of higher rank do not fully reach adulthood. Likewise, the inverse pattern that was observed, where the dominant is smaller, has been described in some rodents (Clarke & Faulkes, 1997), as well as those males are smaller than females (Heaney & Thorington, 1978), which explains why most males have the highest dominance index. However, the common thing is the opposite, that is, the largest individuals are those that tend to reach high hierarchical ranks, both in rodents (Herrera & Macdonald, 1993; Macdonald *et al.*, 1995; Gabathuler *et al.*, 1996) and in other groups of mammals (Barroso *et al.*, 2000; Knowles *et al.*, 2004; French & Smith, 2005).

In addition, the correlation between seniority within the group and the hierarchical rank was not significant. Furthermore, the value of the determination index R^2 indicates that only 2% of the variation of the seniority parameter, as measured, can explain or influencing the variability of the social status parameter. This could be due, in the first place, to the way the parameter is measured, since the accumulated days of sighting do not necessarily reflect the length of time within the group. This is probably because although most of the higher-ranking individuals had more time within the group, the lower-ranking individuals were evenly distributed throughout the days. It has been reported that factors such as coat color serve as an indicator of social status (Tamura *et al.*, 1988; Wauters *et al.*, 1990). However, the coloring factor of both the body and the tail established in this study did not show any apparent pattern when correlated with the dominance index. But it is important to note that individuals with a higher rank have also gray coloration in the tail, which coincides with that reported for *S. carolinensis*, where individuals with dark gray tails were related to more aggressive behaviors (Bohls & Koehnle, 2017).

The average of accumulated bits for the 11 individuals is a highly reliable quantity. In fact, the minimum required to greatly reduce the probability of duplication of the characters in a sample of 50 individuals onwards (Pennycuick, 1978). Similar average values were reported for species such as lions (*Panthera leo*) (Pennycuick & Rudnai, 1970), Tundra swans (*Cygnus columbianus bewickii*) (Scott, 1978), Sri Lankan leopards (*Panthera pardus kotiya*) (Miththapala *et al.*, 1989), Australian sea lions (*Neophoca cinerea*) (Osterrieder *et al.*, 2015), and Polar bears (*Ursus maritimus*) (Anderson *et al.*, 2007), where the samples were greater than 20 individuals. Besides, because the individuals with the highest number of bits were those with rare features or infrequent characters, they were attributed greater reliability in their identification according to the reliability criterion (Pennycuick & Rudnai, 1970). Although the proposed identification system presented characters and patterns with high repetition probabilities, the contribution of bits of each one is within the minimum reported (1 bit) for a sample of 12.5 individuals (Pennycuick & Rudnai, 1970). Due to this, it is suggested to take into consideration additional characters that complement the identification system to give robustness to the amount of information and reduce the chances of duplication (Miththapala *et al.*, 1989). The rare features used in this study are optimal as complementary characters, likewise, characters such as scars, sex, and the shape and size of the body complement and enrich the identification system since they are invariable over time (Anderson *et al.*, 2007).

In conclusion, the results of this study constitute a contribution to the knowledge of the behavior of *S. granatensis*, indicating the existence of a linear domain hierarchy in a group when they are associated with a food source. Another outstanding result was the existence of an inverse correlation between this hierarchical system and the thickening of the tail, which had not been described before for this species. It is worth

noting that the non-invasive identification system proposed in this study constitutes a reliable alternative to differentiate individuals without any type of disturbance by the researcher (which could affect their behavior) and is easily applicable in their natural habitat. Finally, to continue deepening into the knowledge of *S. granatensis*, it is proposed to carry out future studies with methods similar to those used in the present work but increasing the observation time and the size of the study group, which will allow validating the scope of these findings in larger groups.

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CONFLICTS OF INTEREST

The author declare no conflicts of interest.

SUPPLEMENTARY MATERIAL

Appendix S1. General description for the 11 individuals of Red-tailed Squirrel (*Sciurus granatensis*) identified here based on morphological characters described in Table 1. Information could be directly downloaded at: http://erevistas.saber.ula.ve/index.php/ecotropicos/article/view/E0019

RESUMEN

Análisis de las relaciones jerárquicas en un grupo de *Sciurus granatensis* (Mammalia: Rodentia: Humboldt, 1811) en Caracas, Venezuela. Las relaciones sociales dentro de los grupos de mamíferos implican el desarrollo de relaciones jerárquicas entre sus miembros para evitar conflictos. Esta jerarquía se establece mediante encuentros diádicos agresivos. Por ello, una forma de determinar si existe una jerarquía es cuantificar las interacciones agresión-sumisión y los desplazamientos entre pares de individuos. En este trabajo se estudiaron las interacciones sociales en un grupo de *Sciurus granatensis* dentro de un parche de bosque urbano en la ciudad de Caracas, Venezuela, para determinar la existencia de una jerarquía de dominancia durante sus visitas a un alimentador artificial. Además, se propone el uso de un método de identificación no invasivo con base a los caracteres morfológicos de los individuos. Los individuos fueron filmados durante 19 días consecutivos, desde sus áreas de descanso hasta el comedero. Las interacciones se analizaron utilizando métodos de observación focal y de barrido; posteriormente fueron descritas en un etograma y se clasificaron en desplazamiento (intimidación *vs*. retirada) y agresión (ataque *vs*. ataque con persecución). Se identificaron 19 individuos dentro del grupo y un total de 156 (con un promedio diario de 8,2 ± 4,3) interacciones para 11 de ellos. La forma más común de interacción fue la intimidación. Se encontró que había individuos residentes y visitantes ocasionales en el grupo. La existencia de dominancia se determinó con un índice de linealidad de Landau (h = 0,636), y se observó que dos de los individuos compartían el rango jerárquico más alto. Se observó una correlación negativa significativa entre el grosor de la cola y el rango social de los individuos. Se concluyó, con base a este método de identificación no invasivo, que existe una jerarquía lineal en el grupo.

Palabras clave: Interacciones agonísticas, comportamiento animal, dominancia, identificación no invasiva, ardilla de cola roja, fauna urbana.

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