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RESEARCH ARTICLE

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Individual behavioral differences and health of golden-headed lion tamarins (*Leontopithecus chrysomelas*)

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Abstract

Individual behavioral differences may influence how animals cope with altered environments. Depending on their behavioral traits, individuals may thus vary in how their health is affected by environmental conditions. We investigated the relationship between individual behavior of free-living golden-headed lion tamarins (*Leontopithecus chrysomelas*) responding to a novel object (to assess exploration-avoidance), and their habitat use and health status (endoparasitism; clinical measures: biometric data, heart rate, respiratory frequency, and temperature; fecal glucocorticoid metabolites). As parasite transmission can be affected by individual variation in social contact and social grooming, we also evaluated whether more sociable individuals show higher endoparasite loads compared with less sociable animals. Four groups living in landscapes with different levels of human disturbance were investigated: two in degraded forest fragments in an agricultural matrix (DFAM—higher disturbance), and two in a cocoa agroforestry system (*cabruca*—lower disturbance) in the Atlantic forest of South Bahia, Brazil. Using a subjective ratings approach, highly correlated adjective descriptors were combined to produce *z*-score ratings of one derived variable ("confidence"), which was selected to characterize the tamarins' exploration/avoidance responses during a novel object test. The higher the confidence score, the longer female tamarins spent foraging for prey independent of landscape, and the greater their body mass independent of sex and landscape. Only DFAM individuals showed intestinal parasite infection. Endoparasite loads were positively correlated with the number of grooming partners, suggesting an association between social grooming and transmission (more groomers = more endoparasites). Individual behavior, including in a test situation, may thus have some predictive value for behavior in a free-living context, and for its health consequences.

KEYWORDS

conservation medicine, coping styles, parasites, primates, temperament

1 | INTRODUCTION

The Brazilian Atlantic forest is ranked among the top biodiversity hotspots in the world because of its species richness and extremely high levels of endemism (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). This biome, however, is also one of the most threatened due to habitat destruction and fragmentation (Colombo & Joly, 2010). There is relatively little information on how wild animals cope in fragmented habitats such as those of the Atlantic forest, and how this impacts individual health and welfare (Acevedo-Whitehouse & Duffus, 2009; Delarue, Kerr, & Rymer, 2015; Zinsstag, Schelling, Waltner-Toews, & Tanner, 2011).

Human-induced rapid environmental change (Sih, 2013) has imperiled many animal populations due to habitat fragmentation, climate change, and environmental contamination (Deem, Karesh, & Weisman, 2001), which may lead to reduced food availability and impaired nutritional status (Amato et al., 2013). Animals that live in fragmented and degraded habitats usually face increased threats and challenges and also may show higher fecal glucocorticoid metabolite levels than those living in more preserved areas (Balestri et al., 2014; Martinez-Mota, Valdespino, Sanchez-Ramos, & Serio-Silva, 2007). Prolonged elevation of glucocorticoid levels may negatively affect an animal's health (Acevedo-Whitehouse & Duffus, 2009; Breuner, Patterson, & Hahn, 2008; Cavigelli, 2005; Kumaresan, Palanisamy, Pasupuleti, & Arockiaraj, 2017).

Together with physiological stress, the effects of anthropogenic disturbance on welfare and health of free-living animals may also be investigated using clinical measures including changes in biometric data, heart rate, respiratory frequency, immune function, and temperature (Junge, Barret, & Yoder, 2011). Such changes may reveal stress and immunosuppression in individuals, indicating potential poor health in a population (Lafferty & Gerber, 2002). Some studies have shown an association between behavioral responses and health of populations living in unprotected areas altered by human activities compared with populations living in relatively protected habitats (e.g., Gabriel, 2013; Homan et al., 2003; Sauther et al., 2006). In addition, a relationship between temperament traits and fitness traits (e.g., survival or reproductive success) has been observed (McDougall, Réale, Sol, & Reader, 2006; Réale & Festa-Bianchet, 2003; Sih, Bell, & Johnson, 2004). However, to the best of our knowledge, whether individual behavioral characteristics are associated with health (Capitanio, 2011) and survival in human-altered environmental conditions has not been studied.

Temperament describes the phenomenon of individual behavioral differences showing consistency over time and/or across situations (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Temperament traits can be divided into five categories or dimensions (shyness/boldness, exploration/avoidance, general activity, aggressiveness, and sociability; Réale et al., 2007). Positive correlations between boldness and reproductive success have been found (Smith & Blumstein, 2008). However, individuals that are more exploratory may expose themselves to higher risk of predation (e.g., Martin & Réale, 2008) and may also host higher parasite loads if they have greater home range or explore a greater diversity of habitats in comparison with less exploratory individuals (e.g., Barber, Mora, Payne, Weinersmith, & Sih, 2017; Bohn et al., 2017; Garcia-Longoria, Garamszegi, & Møller, 2014; Horváth et al., 2016; Patterson & Schulte-Hostedde, 2011). In contrast, shyer individuals expose themselves less to risky situations by limiting their foraging activity in comparison with bolder individuals (Réale et al., 2007) and this may adversely affect their nutritional status (Barber et al., 2017). Exploration/avoidance traits have been assessed by testing an individual's reaction to a novel environment, object or food (Réale et al., 2007). These tests may provide an indication of how individuals forage, disperse, and find shelter (Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

Individual differences in sociality can influence the general health of animals, including primates (Capitanio, 2011). Nonhuman primates involved in more social interactions have more health benefits than less social individuals (baboons, *Papio cynoceph alus*, Silk, Alberts, & Altmann, 2003; golden snub-nosed monkeys, *Rhinopithecus roxellana*, Jin, Su, Tao, Guo, & Yu, 2013; rhesus macaques, *Macaca mulatta*, Robinson et al., 2018). However, social interactions may also negatively influence health (Rushmore, Bisanzio, & Gillespie, 2017). For instance, a study on endoparasite transmission in Japanese macaques (*Macaca fuscata yakui*) showed a clear bias in nematode prevalence toward high-ranking individuals that occupy more central positions in both outward and inward directed grooming networks (MacIntosh et al., 2012). Therefore, highly social individuals may be more susceptible to acquiring endoparasites from other group members (Barber & Dingemanse, 2010; Godfrey, Bull, James, & Murray, 2009).

Additionally, animals can vary in their neuroendocrine and behavioral responses to acute stressors (Baugh et al., 2012; Koolhaas, Boer, Coppens, & Buwalda, 2010). Individual differences in behavior, sociality, and physiology may be associated with wild population survival (McDougall et al., 2006; Smith & Blumstein, 2008). A body of work on coping strategies indicates that aggressive individuals tend to be so-called “proactive copers,” showing active responses to challenge, low sensitivity to changes in their surroundings and a propensity to develop routine-like inflexible behavior. Conversely, nonaggressive individuals are “reactive copers” being more likely to attend carefully to changes in their surroundings and respond in a more measured and flexible way to challenge (Koolhaas, 2008). These two behavioral styles also appear to be linked to physiological differences with proactive copers being more likely to exhibit high sympathetic reactivity to challenge, and high testosterone and low hypothalamic–pituitary–adrenal (HPA) activity, while reactive copers show high HPA reactivity in response to challenge and low sympathetic and testosterone activity. Such variation in stress physiology may also affect individual immune responses (Besedovsky & Del Rey, 2007; Koolhaas, 2008; Malarkey & Mills, 2007; Steimer & Driscoll, 2005), which in turn may influence animals health, reproductive success, and survival (Breuner et al., 2008; Cavigelli, 2005; Romero, 2004).

Studies of links between individual behavioral differences and health are of particular importance in endemic and threatened species, such as the golden-headed lion tamarin (*Leontopithecus chrysomelas*). The golden-headed lion tamarin is a small primate species of southern Bahia State in the Brazilian Atlantic forest (Pinto & Rylands, 1997). The species is classified as endangered due to forest loss resulting in degradation and fragmentation (Kierulff, Rylands, Mendes, & Oliveira, 2008). The animals live in social groups ranging from three to 15 individuals (Oliveira, Neves, Raboy, & Dietz, 2011), usually composed of one dominant breeding pair, and a diverse number of offspring of various ages: adults, subadults, juveniles, and infants (Rylands, 1993). Groups defend their territory against other lion tamarin groups using aggressive vocalizations such as *long-calls*, *short staccato whistles* and *chatter* that can be also followed by agonistic interactions (Peres, 1989).

Most populations of golden-headed lion tamarin live in unprotected areas altered by human activities, such as degraded forest fragments embedded in an agricultural matrix and *cabruca*—a shaded cocoa (*Theobroma cacao*) agroforestry system (Oliveira et al., 2011; Raboy, Christman, & Dietz, 2004). Both of these environments (*agricultural matrix* and *cabruca*) present specific challenges to groups of tamarins, such as lower resource availability, higher exposure to predators, and higher hunting levels and human contact in comparison with groups living in more preserved areas (De Vleeschouwer & Oliveira, 2017; Oliveira & Dietz, 2011; Raboy et al., 2004). These challenges may result in increased stress levels and may negatively affect the health of the animals. Agricultural matrix composition and lack of connectivity may also influence dispersal and persistence of primates (Anderson, Rowcliffe, & Cowlishaw, 2007). This environment, in general, seems to result in higher levels of disturbance and risks to animals because nonforested patches of cultivated land, interspersed with roads, dirt paths and with frequent human presence typically characterize the agricultural matrix area (Anderson et al., 2007). In contrast, *cabruca* is considered a valuable landscape because it connects forest patches, making populations less vulnerable to negative genetic effects of habitat fragmentation (Estrada, Raboy, & Oliveira, 2012). Furthermore, in contrast to other degraded landscapes, *cabruca* seems to provide important resources such as sleeping sites and bromeliads for foraging tamarins (Oliveira et al., 2011; Raboy et al., 2004). However, as far as we know, no data concerning the links between tamarin individual behavioral characteristics and health are available from either landscape.

In this study, we evaluated the relationship between individual behavioral responses of tamarins in one context—exploration/avoidance of a novel object representing a potential threat (Réale et al., 2007)—and individual health status in two different landscapes. We compared individuals from groups living in degraded forest fragments in an agricultural matrix (DFAM), and in *cabruca* systems to determine whether the tamarins' behavioral responses varied according to their environments (Wolf & Weissing, 2012). Furthermore, we also hypothesized that clinical measures (biometric data, heart rate, respiratory frequency, and temperature) would differ between these two landscapes and that measures of fecal glucocorticoid metabolite concentrations (FGCMs; see Romero, 2004) as an indicator of physiological stress would be elevated in the groups living in agricultural matrix. In addition, as adult female tamarins spend more time searching for food and feeding than males, which is positively related to the birth and survival of twin offspring (Bicca-Marques, 2003; Box, 1997), we hypothesized differences in foraging and feeding behavior between adult female and male golden-headed lion tamarins that may result in differences between female and male tamarins in some clinical measures. Finally, if exploratory behavior and social interactions through grooming influence endoparasite transmission (Barber & Dingemanse, 2010; MacIntosh et al., 2012; Wren, Remis, Camp, & Gillespie, 2016), we hypothesized that more exploratory and more sociable individuals performing more grooming contact would show higher endoparasite loads compared with less exploratory individuals and those less involved in grooming.

2 | METHODS

2.1 | Ethical note

The research adhered to the American Society of Primatologists principles for the ethical treatment of nonhuman primates and the Brazilian laws applicable to where the present study was conducted. This study was approved by the Committee on Animal Research and Ethics of the Universidade Estadual de Santa Cruz, under protocol #018/2015. The permission to capture, mark animals, and collect biological materials was approved by the Brazilian Environmental Agency (ICMBio/SISBIO), under #23457-6 and #471783.

2.2 | Animals and study areas

From August 2016 to April 2017 we studied 27 individuals (25 adults and two subadults (120DF and 121DF; Table 1) belonging to four groups of golden-headed lion tamarins. Group composition changed over the study period, mainly due to births, predation, natural deaths or disappearances, and migration. Therefore, it was not possible to collect all types of data from all individuals (direct behavioral observation $N = 24$; novel object test $N = 20$; sociality assessment $N = 27$; fecal sampling for glucocorticoid metabolites analysis $N = 27$; clinical measures $N = 20$; and endoparasite load $N = 27$). The information we collected for each individual in the four social groups is indicated in Table 1, and the number of individuals used was indicated in each analysis.

The tamarin groups lived in two landscapes of the Brazilian Atlantic forest in South Bahia state. These two landscapes are part of the Atlantic forest biome, characterized by high temperature and high relative humidity. In this region, temperature ranges from 19°C to 28°C, with an annual rainfall of over 2,100 mm (Coimbra-Filho & Mittermeier, 1973; Mori, Boom, Carvalho, & Santos, 1983). Two of the tamarin groups (Ribeiro [RIB] and Manoel Rosa [MRO]) lived in the rural area of the Municipality of Una (15°15′52″S, 39°8′46″W). This landscape is characterized by disturbed secondary forest patches in an agricultural matrix of pastures, rubber-trees, cassava, and cocoa crops, unpaved roads and intense human presence.

TABLE 1 Characterization of golden-headed lion tamarin individuals of each group and description of data collected

Individual	Group	Landscape	Sex	Evaluation[a]	Observation
14CM	ALM	CAB	M	1, 2, 3, 4, 5, 6	
15CF	ALM	CAB	F	1, 2, 3, 4, 5, 6	
17CM	ALM	CAB	M	1, 2, 3, 4, 5, 6	
18CF	ALM	CAB	F	1, 2, 3, 4, 5, 6	Breed. Fem.
19CF	ALM	CAB	F	1, 2, 3, 4, 5, 6	
13CF	ALM	CAB	F	3	Breed. Fem.
21CM	ALM	CAB	M	3	
23CM	ALM	CAB	M	3	Breed. Male
5CM	BOM	CAB	M	1, 2, 3, 4, 5, 6	
6CF	BOM	CAB	F	1,2,3,4,5,6	
7CF	BOM	CAB	F	1,2,3,4,5,6	
8CM	BOM	CAB	M	1,2,3, 4,5,6	
9CF	BOM	CAB	F	1,2,3,4,5,6	
12CM	BOM	CAB	M	3	
20CF	BOM	CAB	F	1, 2, 3, 4, 5, 6	Breed. Fem.
82DM	RIB	DFAM	M	1, 2, 3, 4, 5, 6	Breed. Male
92DF	RIB	DFAM	F	1, 2, 3, 4, 5, 6	Breed. Fem.
93DF	RIB	DFAM	F	1, 2, 3, 4, 5, 6	Breed. Fem.
118DM	RIB	DFAM	M	1, 2, 3, 4, 5, 6	
119DF	RIB	DFAM	F	1, 2, 3, 4, 5, 6	
126DM	RIB	DFAM	M	3	
102DM	MRO	DFAM	M	1, 2, 3, 4, 5, 6	Breed. Male
115DM	MRO	DFAM	M	1, 2, 3, 4, 5, 6	
120DF	MRO	DFAM	F	3, 4	Subadult
121DF	MRO	DFAM	F	3, 4	Subadult
125DF	MRO	DFAM	F	1, 2, 3, 4, 5, 6	
1DF	MRO	DFAM	F	1, 2, 3, 4, 5, 6	Breed. Fem.

Note: Symbols code: Individual: number followed by landscape (C: cabruca and D: DFAM) and sex (F: female and M: male); Group: ALM: Almada; BOM: Bomfim; RIB: Ribeiro; MRO: Manoel Rosa; Landscapes: CAB: cabruca; DFAM: degraded forest fragments in an agricultural matrix; Sex: M: male; F: female; Evaluations: 1 = novel object test; 2 = behavioral direct observation; 3 = sociality assessment; 4 = parasitological analysis; 5 = fecal glucocorticoid metabolite concentrations; 6 = clinical measures parameters. Breed. Fem.: breeding female; Breed. Male: breeding male.
[a]The test or measure in which each individual participated.

We classified this area as "DFAM" (Figure 1). The other two groups (ALM and BOM) lived at Almada and Bomfim private farms in the rural zone of Ilhéus, Bahia (14°39′S, 39°11′W), in a landscape characterized by the cocoa (*T. cacao*) agroforestry system—*cabruca* (Figure 1). *Cabruca* is a system of shade cropping in which the middle and understory trees of intact forests are removed and replaced with cocoa trees but with preservation of the tall trees (Raboy et al., 2004). The golden-headed lion tamarin groups from both landscapes, DFAM and *cabruca*, have been monitored and habituated to the presence of researchers since 2007 and 2014, respectively. Groups are monitored in the forest by using radio telemetry and twice per year individuals are captured using banana bait and tomahawk traps (48.3 cm length × 15.2 cm width × 15.2 cm height), following procedures described in Dietz, De Sousa, and Billerbeck (1996). In the present study, after capture, we took the animals to a field laboratory (about 500 m from the capture site), where they waited approximately 4 hr before being anesthetized (intramuscular 10 mg/kg ketamine and 0.3 mg/kg midazolam, following Catenacci, De Vleeschouwer, Pessoa, & Nogueira-Filho, 2016). The waiting time between capture and anesthesia was necessary to guarantee that the animals had fasted.

Anesthesia was applied by the first author, a veterinarian who collected the individuals' general clinical measurement data (heart rate [bpm], respiratory frequency [mpm], and temperature [°C]) for up to 4 min following immobilization after anesthetic injection. The potential effect of physical restriction and/or ketamine administration may have affected such measures. However we followed the same procedures for all individuals in both landscapes (DFAM and *cabruca*). Thereafter, we determined the tamarins' sex and collected biometric data (body mass [kg], total and tail length [cm]), and estimated their age. The individuals received a unique tattoo number made on the interior part of their right thigh for permanent identification, and a dye mark (Nyanzol Dye®) on the tail and arm for identification during observations in the field. One or two individuals in each group were equipped with a radio collar (model RI-2D; Holohil Ltd., Ontario, Canada) to facilitate later monitoring and observation in the field using radio telemetry. In general, for this purpose, we chose the heaviest animals and always excluded pregnant females. All handling procedures took around 20 min after

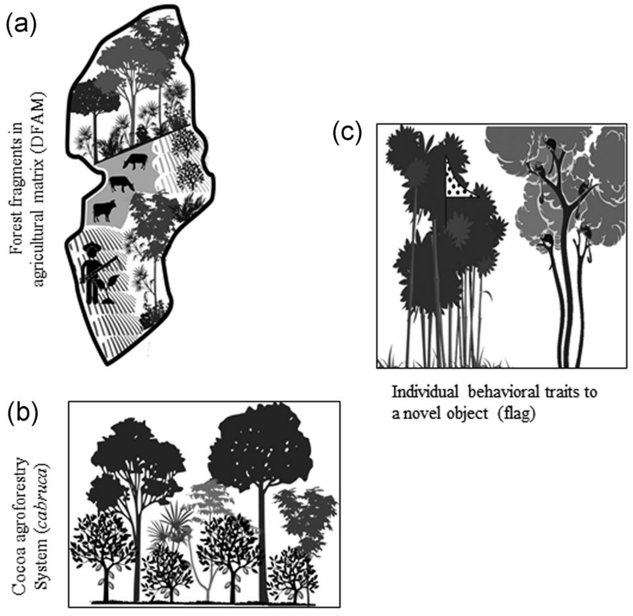

FIGURE 1 The schematic representation of studied landscapes (a: DFAM; b: *cabruca*) and the novel object test

immobilization for each animal. Later, we calculated the body mass index (BMI), which was determined by the relationship between body mass and size (the body weight in grams divided by the square of the head and body length in cm [excluding the tail], following Soto-Calderón, Acevedo-Garcés, Álvarez-Cardona, Hernández-Castro, & García-Montoya, 2016). We kept the subjects in the laboratory overnight to ensure full recovery from anesthesia and, after feeding them banana (~45 g/animal), we released them early in the morning of the next day at the site where they were captured. This procedure has been used and adapted to ensure animal safety over the course of the past 25 years, resulting in a very safe process with no detrimental effects on the animals if performed adequately (L. S. Catenacci, personal observation). Following release, we took at least 5 days to restart data collection (behavioral and feces for glucocorticoid metabolites analysis). This period of time was necessary to make sure that fecal glucocorticoid metabolites did not reflect stress of capture and time in captivity.

2.3 | Behavioral data collection

For 8 months (August 2016 to January 2017; March to April 2017), we followed each group for 2 days per month, resulting in a total of 506 hr of data collection. We used signals from the radio transmitter collars to locate each group before the animals woke up and observed them from the moment they left the sleeping site (tree hollow) in the morning until they entered the same or a different sleeping site in the evening. Each group was followed for about 22 hr a month. Individual dye marks disappeared in early January 2017 and forced us to suspend observations until the animals were captured again in March 2017, after which observations were resumed.

The golden-headed lion tamarins were observed using continuous focal animal sampling (Altmann, 1974); each focal observation lasted 10 min/animal. We randomized the order in which animals were observed, and when the last animal was observed, we restarted a new random order. When an animal disappeared from sight, the observation was interrupted and resumed once the animal was plainly visible again. Moreover, when it was not possible to distinguish the exact behavioral pattern displayed by the focal individual, we also interrupted the observation and resumed when the animal was plainly visible again. The observations were voice-recorded (digital voice recorder RR-US450; Panasonic, Ontario, Canada). Then, weekly in the lab, we calculated the proportions of observation time that each individual spent in social grooming and in the behavioral categories related to exploration (eating, foraging for fruits and flowers or animal prey, and traveling). Behavioral state descriptions are provided in Table 2.

2.4 | Individual behavioral differences

Differences in the individual behavior of tamarins were assessed using a test of exploration/avoidance of a novel object (Réale et al., 2007). Because gaining access to the individuals for testing was difficult, and hence it was not possible to measure individual behavioral consistency over time in response to different types of challenge (Gosling, 2001; Sih et al., 2004), we evaluated individual tamarin behavior in this context alone and once only (Réale et al., 2007).

One week before the start of behavioral data collection, we presented animals with a homemade flag (0.60 m length x 0.45 m height) of white fabric with five black dots (ø: 5.0 cm) on both sides of the flag (Figure 1). We set up the flag the day before the test and after animals had entered a tree hollow to sleep. The flag was set up in front of the entrance to the hollow, at a distance of 2.0 m on average from the sleeping site.

During the novel object test, we video-recorded individual responses to the novel object when each one left the sleeping site and saw the flag for the first time, using a camcorder (DCR-SR45; Sony, Tokyo, Japan) for later video analysis. We just considered the data obtained when each individual left the tree hollow separately, to avoid an individual being affected by the reaction of other individuals. We assessed individual behavioral characteristics using a subjective rating approach (Feaver, Mendl, & Bateson, 1986; Wemelsfelder, Hunter, Mendl, & Lawrence, 2001). The subjective rating has been validated for several other species (e.g., cat: Feaver et al., 1986; cattle: Sant'Anna & Paranhos da Costa, 2013; collared peccary [*Pecari tajacu*]; Nogueira, Macedo, Sant'Anna, Nogueira-Filho, & Paranhos da Costa, 2015) and adapted for golden-headed lion tamarins.

TABLE 2 Behavioral states recorded by direct observation of golden-headed lion tamarins

Behavior	Definition
Social grooming[a]	The individual gives or receives grooming behavior—manipulation of the fur of another conspecific with hands or mouth
Eating[b]	The individual manipulates or puts inside its mouth fruits, flowers, nectar, gum, or animal prey
Foraging for fruits and flowers[b]	The individual appears to be visually searching for fruits and flowers
Foraging for prey[b]	The individual uses manipulative foraging to locate animal prey concealed in sites such as dried leaves and tree bark
Traveling[b]	The individual is moving from one place to another, covering a certain distance

[a] Adapted from Muroyama (1991).

[b] Adapted from Raboy and Dietz (2004).

For subjective rating analysis, video clips (30 s) with each lion tamarin's reaction to the novel object were shown to three experts with experience in animal behavior observations who had not participated in data collection (SSCN, SLGNF, and ASF). The judges were instructed to evaluate the animal's behavior during the flag test in terms of 14 adjectives providing descriptors of tamarin behavioral style: “relaxed,” “apathetic,” “calm,” “agitated,” “fearful,” “curious,” “stressed,” “alert,” “tense,” “active,” “shy,” “smart,” “bold,” and “cautious.” The definition used for each adjective is presented in Table S1. Following the above authors’ references, for each adjective (which was accompanied by a written definition; see Rouff, Sussman, & Strube, 2005), each judge placed a mark on a visual analogue scale represented by a line of 125 mm with a minimum value (0) at the left end of the line representing absence of the behavioral characteristic and the maximum value (125) representing the most intense manifestation. The scores were obtained by measuring (using a small ruler of 125 mm) the distance in millimeters from the left end of the line to the judges’ marks. The adjectives were previously chosen by primatologist researchers (B. R. and D. S. F.—who had not participated in data collection) based on studies of personality in nonhuman primates (lion-tailed macaques, *Macaca silenus*, Rouff et al., 2005; Sulawesi black crested macaques, *Macaca nigra*; Barbary macaques, *Macaca sylvanus*; common squirrel monkeys, *Saimiri sciureus*; Baker, Lea, & Melfi, 2015), and on the tamarin behavioral repertoire.

2.5 | Fecal sample collection and endoparasite analysis

While following groups for behavioral data collection, we gathered fresh feces noninvasively from identified individuals immediately after defecation to determine both parasite load and FGCMs. Feces were collected only during the morning until midday to minimize confounding effects of circadian rhythms on hormone levels. After collection, fecal samples were homogenized and weighed. Fecal sample weight ranged from 1.0 to 3.0 g. After weighing, half of each sample (0.5–1.5 g of feces) was immediately preserved in 4% buffered formalin solution for later parasitological analysis (Monteiro et al., 2007). Parasite identification and parasite load (EPG: number of eggs/g feces) were determined following a modified Ritchie's technique adopted by Monteiro, Jansen, and Pinto (2003) and Monteiro et al. (2007) for golden lion tamarins (*Leontopithecus rosalia*). Nevertheless, due to the small amount of feces collected per individual, we could not test for fecal flotation (Willis method; Gillespie, 2006). A 1.0 ml aliquot of each formalized fecal sample was sent to Universidade Federal de Minas Gerais, Brazil for parasitological identification.

2.6 | FGCM analysis

The other half of each fecal sample collected (0.5–1.5 g of feces) was used to assess the individual's glucocorticoid metabolite concentration. These samples were individually stored in Eppendorf plastic tubes labeled with individual identity, date, and hour and kept inside Styrofoam at a mean temperature of 7°C until return to the field station in the evening after behavioral data collection. Fecal samples were subsequently refrigerated (−20°C) at the field laboratory. On the following day, we took the fecal samples to Universidade Estadual de Santa Cruz where they were thawed to prepare for freeze-drying (FreeZone® Plus 4.5L Cascade Benchtop; LABCONCO) following Wasser et al. (2000).

The freeze-dried samples were sent to the Laboratory of Hormonal Measurements at the Federal University of Rio Grande do Norte, Brazil. In this laboratory an ELISA immunoassay for glucocorticoid metabolites, in which cortisol is the main hormone (around 60%), was performed in line with methods described by Sousa and Ziegler (1998). Accordingly, 0.1 g of feces was weighed, and steroids were extracted into 5 ml of ethanol at 50%. A 500 μl aliquot was reserved for solvolysis (Ziegler et al., 1996) and after this procedure samples were resuspended in 500 μl of ethanol and stored at 5°C until assay quantification.

The polyclonal anticortisol R4866 was used at dilution of 1:16,000 and the enzyme horseradish peroxidase conjugated to the antigen used at dilutions of 1:75,000. Both were obtained from University of California (Davis, CA). The standard curves ranged from 3.16 to 1,000 pg/ml. For assay precision assessment, intra-assay and interassay coefficients of variation (CV) were calculated. For intra-assay CV, the measured concentrations were used from samples run in duplicates in each assay, while interassay CV was estimated from concentrations of a high (30% of binding) and low control (70% of binding) run in each assay. Intra-assay and interassay CVs were 2.5 ± 1.3% and 8.7 ± 3.0%, respectively. For subsequent analysis, we used the glucocorticoid metabolite concentration mean obtained from each animal for which we had at least three samples collected in 3 different months over the study period.

2.7 | Analysis of individual sociality

We used grooming interactions to assess the sociality of each individual in the tamarin groups. Through the observations, we identified the givers and receivers of grooming interactions and, using the software package SOCPROG 2.8 (Whitehead, 2009) we obtained the eigenvector centrality of each tamarin in the grooming interactions. The eigenvector centrality measures the importance of a node (i.e., an individual) in a network. Individuals with high eigenvector centralities are connected to many other individuals that are, in turn, connected to many individuals (Whitehead, 2009). We also used the sociogram software version 1.0 (Lewejohann, 2005) to obtain the network diagrams of social grooming for each group. From such network diagrams, we obtained the number of grooming partners of each individual allowing us to test the correlation of this parameter with the parasite load following Wren et al. (2016).

2.8 | Data analyses and statistics

To assess individual behavioral characteristics during the novel object test (flag) we did not use principal component analysis (PCA), usually applied in subjective rating analysis (e.g., Nogueira et al., 2015; Sant'Anna & Paranhos da Costa, 2013) due to the sample size ($N = 20$). PCA requires a larger sample size ($N > 150$) to obtain an accurate solution (Guadagnoli & Velicer, 1988). Therefore, we followed the recommendations highlighted by Feaver et al. (1986) and used nonparametric analysis to assess individual behavioral characteristics. In this analysis, seven golden-headed lion tamarins listed in Table 1 (13CF, 21CM, 23CM, 12CM, 120DF, 121DF, and 126DM) were not included because they were not present in the groups at the time of the novel object test or we were unable to identify them during the test.

From the 14 adjectives used during subjective ratings (cited above), we used only those with Kendall's coefficients of concordance (W) > 0.70 among the three judges. Thus, the between-judge agreement for these retained adjective descriptors accounted for over half of the variance, as recommended by Feaver et al. (1986). Six of 14 adjectives (calm, agitated, fearful, stressed, shy, and bold) showed $W > 0.70$ interjudge concordance and were used to assess responses in the novel object test. The complete information on interjudge Kendall's coefficients of concordance is presented in Table S2.

For each one of these six adjectives we calculated the mean value of the observers' ratings for each individual. Thereafter, to reduce the influence of distributional effects, the ratings of the three judges were converted to a z score [(individual score−mean)/SD]. These mean z scores were then checked for between-adjective correlations using Spearman rank correlation tests. Following that, highly correlated adjective descriptors were combined to produce z-score ratings, providing an indication of dimensions of behavioral distinctiveness in exploration/avoidance of golden-headed lion tamarins. One derived variable ("confidence") was selected to characterize responses in the novel object test. We used t-tests to compare the "confidence" z scores between sexes (female vs. male) and landscapes (*cabruca* vs. DFAM).

To verify the relationship between individual behavioral characteristics and their foraging and feeding behavior, and to test our hypotheses that tamarins' foraging and feeding behavior are different between the two landscapes and sex we used a general linear model (GLM) to compare the proportion of time tamarins were observed foraging for animal prey, eating, traveling, and foraging for fruits and flowers. The model included the fixed factors of landscape (*cabruca* vs. DFAM) and sex (female vs. male), and the "confidence" z score as a covariable, and all their potential interactions. We used the same statistical model to compare the proportion of time tamarins were observed in social grooming.

Subsequently, we used the same statistical model to verify the relationship between individual behavioral characteristics and health status, and to test our hypothesis that tamarins living in the agricultural matrix landscape and *cabruca* would differ in clinical measures and physiological stress. For this analysis we compared clinical measures (biometric data [body mass, kg] and body index; heart rate [bpm]; respiratory frequency [mpm]; body temperature [°C]; recorded during sedation), and FGCM (ng/g dry feces). For all GLM analyses we used only data from adult golden-headed lion tamarins for whom we had determined a "confidence" z score ($N = 20$). Model fit was evaluated graphically by exploring residual patterns. Some callitrichine females show elevated FGCMs during pregnancy (e.g., *Callithrix jacchus*, Ziegler & Sousa, 2002; *L. rosalia*, Bales, French, Hostetler, & Dietz, 2005). Thus, we excluded the data from the female 1DF of the MRO (DFAM) group for the GLM analysis of the FGCM, as this female was pregnant during fecal sample collection.

As endoparasites were only recorded in fecal samples from golden-headed tamarins living in DFAM, we compared how parasite load of tamarins (EPG: eggs/g) varied according to individual behavioral characteristics using a Pearson correlation test. We used a Spearman rank correlation test to assess the association between the number of grooming partners an individual had and its endoparasite load (EPG) for individuals living in DFAM ($N = 11$), and separately for individuals living in each group of DFAM (MRO: $N = 6$ and RIB: $N = 5$). As the number of grooming partners did not fulfill assumptions of normality of residuals and homogeneity of variance even after transformation, we analyzed how the number of grooming partners was affected by sex (female vs. male) and landscape (*cabruca* vs. DFAM) using nonparametric Mann–Whitney tests. The Minitab v. 19.1 software (Minitab Inc., State College, PA) was used for all statistical analyses, considering a $p < .05$ significance level. Values are provided as means ± standard errors (SE).

3 | RESULTS

3.1 | Individual behavioral differences in the novel object test

Of the six most reliable adjective descriptors of tamarin behavior, the adjectives "calm," "bold," "stressed," and "fearful" were highly positively or negatively correlated ($r_s > .70$ or $r_s < -.70$) with each other as shown in Table 3, suggesting potential underlying variables which we named "Explorer," "Unperturbed," and "Equable" based on the associations between adjectives shown below (see Table 3). To meaningfully combine z scores we used the opposite z scores of the following adjective descriptors: z scores of "not-fearful" = $(-1) \times z$ scores of "fearful"; z scores of "not-stressed" = $(-1) \times z$ scores of "stressed."

$$\text{Explorer} = (\text{bold} + \text{not-fearful})/2 \tag{1}$$

$$\text{Equable} = (\text{calm} + \text{bold})/2 \tag{2}$$

$$\text{Unperturbed} = (\text{calm} + \text{not-stressed})/2 \tag{3}$$

There were correlations between "explorer" and "equable" z scores ($r_s = -.92$; $p < .0001$), "explorer" and "unperturbed" z scores ($r_s = .69$; $p < .001$), and "equable" and "unperturbed" rating z scores ($r_s = .81$; $p < .0001$), indicating strong similarity between these derived variables and likely reflecting just one underlying behavioral

TABLE 3 Spearman correlations coefficients of mean ratings of descriptor adjectives

	Calm	Agitated	Fearful	Stressed	Alert	Bold
Calm	—					
Agitated	.36	—				
Fearful	−.58	−.13	—			
Stressed	**−.71**	−.22	.51	—		
Alert	−.45	−.57	.41	.11	—	
Bold	**.71**	−.01	**−.72**	−.56	−.19	—

Note: Bold values represent $r_s > .70$ or $r_s < -.70$ used to combine the behavioral descriptors.

dimension which we named "confidence" and which was used in further analyses. To obtain the "confidence" *z* score for each individual, *z* scores of adjectives were combined in the following way:

$$\text{Confidence} = (\text{bold} + \text{calm} + \text{not-fearful} + \text{not-stressed})/4 \tag{4}$$

The "confidence" *z* scores ranged from −1.3 to 1.7 in DFAM (Figure 2a) and from −1.2 to 1.3 in the *cabruca* (Figure 2b). There were no differences in "confidence" mean *z* scores between tamarins living in DFAM and *cabruca* (DFAM: 0.13 ± 0.33, $N = 9$, *cabruca*: −0.11 ± 0.22, $N = 11$, *t* value = −0.63, $p = .54$), or between female and male tamarins (female: 0.01 ± 0.24, $N = 11$; male: −0.01 ± 0.31, $N = 9$, *t* value = −0.06, $p = .95$).

3.2 | Effects of landscape, sex, and "confidence" score on foraging behavior, clinical measures, and endoparasite load

Golden-headed lion tamarins living in *cabruca* spent more time foraging for prey than tamarins living in DFAM (*cabruca*: 0.19 ± 0.02, $N = 11$; DFAM: 0.15 ± 0.02, $N = 9$; $F_{1,12} = 10.57$, $p = .007$). Moreover, an interaction effect was detected between landscape, sex, and "confidence" ($F_{1,12} = 5.87$, $R^2 = .83$, $p = .03$, $N = 20$) on the proportion of time tamarins spent foraging. In DFAM, the higher the "confidence" *z* scores, the longer both females and males spent foraging for prey (females: proportion of time foraging for prey = 0.13 + 0.07 "confidence" *z* score, $N = 5$; $F_{1,3} = 28.53$, $R^2 = .90$, $p = .01$; males: proportion of time foraging for prey = 0.14 + 0.05 "confidence" *z* score, $N = 4$; $F_{1,2} = 19.78$, $R^2 = .91$, $p = .047$, Figure 3). In *cabruca*, however, females and males differed. The higher the "confidence" *z* scores, the longer only females spent foraging for prey (proportion of time foraging for prey = 0.21 + 0.09 "confidence" *z* score, $F_{1,5} = 17.49$, $R^2 = .78$, $p = .009$, $N = 7$, Figure 3), while there was no relationship between "confidence" z scores and the time males spent foraging for prey ($F_{1,2} = 0.64$, $R^2 = .24$, $p = .51$, $N = 4$, Figure 3).

Tamarins living in *cabruca* tended to spend less time eating than tamarins living in DFAM (*cabruca*: 0.06 ± 0.03, $N = 11$; DFAM: 0.14 ± 0.03, $F_{1,12} = 4.16$, $p = .06$, $N = 9$). Additionally, an interaction effect was detected between sex and "confidence" *z* score ($F_{1,12} = 11.44$, $R^2 = .64$, $p = .005$, $N = 20$) for the proportion of time tamarins spent eating. In both landscapes, male tamarins tended to spend less time eating as their "confidence" scores increased ($F_{1,4} = 5.38$, $R^2 = .57$, $p = .08$, $N = 6$). In contrast, there was no relationship between the "confidence" *z* scores and the time females spent eating ($F_{1,12} = 0.97$, $R^2 = .07$, $p = .34$, $N = 14$). Moreover, there were no effects of landscape, sex, "confidence" *z* score, or their interactions on the proportion of time that tamarins spent traveling and foraging for fruits and flowers (Table 4).

Body mass affected the "confidence" *z* score of golden-headed lion tamarins (body mass = 638.48 g + 8.23 "confidence" *z* score, $F_{1,12} = 6.22$, $R^2 = .37$, $p = .03$, $N = 20$, Figure 4), independent of the landscape ($F_{1,12} = 0.59$, $p = .46$, $N = 20$) and sex ($F_{1,12} = 0.01$, $p = .93$, $N = 20$). The statistical model also showed a near significant effect of the "confidence" *z* score on respiratory frequency ($F_{1,12} = 4.02$, $R^2 = .48$, $p = .07$, $N = 20$). There were, however, no effects of the landscape, sex, and "confidence" on BMI and other clinical measures

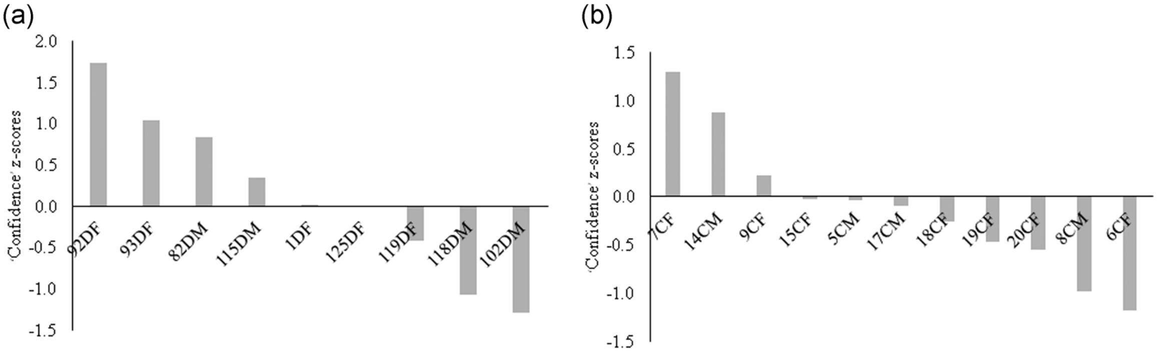

FIGURE 2 Behavioral ratings of tamarins from DFAM (a) and *cabruca* (b) on the "confidence" behavioral dimension. The scores for the "confidence" dimension were obtained from the four adjective *z* scores that were highly correlated (bold + calm + not-fearful + not-stressed)/4 and selected to characterize responses in the novel object test. The numbers identify the individual tamarin, the letters D and C the landscapes (D: DFAM, C: *cabruca*) and M and F correspond to animal's sex (M: male, F: female)

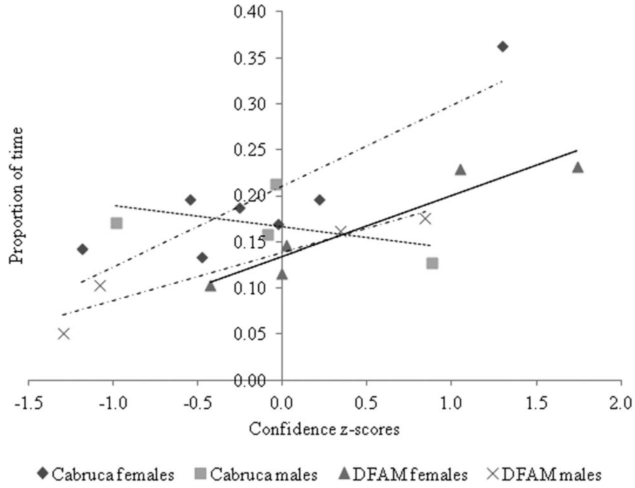

FIGURE 3 Proportion of time golden-headed lion tamarins spent foraging for prey according their "confidence" z scores, landscapes (DFAM: degraded forest fragments in an agricultural matrix; *cabruca*: cocoa agroforestry) and sexes following the equations according sexes and landscapes: females living in DFAM: Proportion of time foraging for prey = 0.13 + 0.07 "confidence" z score ($F_{1,3} = 28.53$, $R^2 = .90$, $p = .01$, $N = 5$); males living in DFAM: Proportion of time foraging for prey = 0.14 + 0.05 "confidence" z score ($F_{1,2} = 19.78$, $R^2 = .91$, $p = .047$, $N = 4$); females living in *cabruca*: Proportion of time of time foraging for prey = 0.21 + 0.09 "confidence" z score ($F_{1,5} = 17.49$, $R^2 = .78$, $p = .009$, $N = 7$); males living in *cabruca*: Proportion of time on foraging for prey = 0.17−0.02 "confidence" z score ($F_{1,2} = 0.64$, $R^2 = .24$, $p = .51$, $N = 4$)

(Table 5). Complete information on each individual is presented in Table S3.

There were no parasite eggs in fecal samples collected from golden-headed lion tamarins living in *cabruca*. In contrast, tamarins living in the DFAM were infected with four types of endoparasites: *Prosthenorchis* sp., *Trypanoxyuris* sp., *Primasubulura* sp., and Spiruridae. All endoparasites detected except *Prosthenorchis* sp., are nematodes. *Prosthenorchis* sp. is an acanthocephalan. In DFAM the endoparasite load (EPG: eggs/g) ranged from 0 to 70.4 eggs/g of feces (Table S3), with a mean of 29.8 eggs/g ($SE = 8.8$). There was no correlation between tamarins' "confidence" score and endoparasite load ($r_P = -.28$, $p = .47$, $N = 9$).

3.3 | Sociality and endoparasite load

There were no effects of landscape ($F_{1,12} = 0.24$, $p = .63$), sex ($F_{1,12} = 1.73$, $p = .21$), "confidence" ($F_{1,12} = 0.37$, $p = .55$), and their interactions (Table 4) on the proportion of time tamarins spent on social grooming. Social grooming was distributed unevenly among golden-headed lion tamarins. In general, male and female breeding individuals were involved in higher grooming interaction rates (Figure 5) and showed higher eigenvector centrality indexes (Table S3). The breeding females 1DF, 92DF, 93DF were more involved in social grooming with the breeding males 102DM, 82DM, and 23CM of the groups MRO, RIB, ALM, respectively, than with other individuals in each group, and showed lower eigenvector centrality in grooming interactions (Figure 5a–c). In the BOM group, the breeding female 20CF was most involved in grooming interactions with the female 7CF and with the male 8CM (Figure 5d). It was not possible to confirm if male 8CM was the breeding male in this group because we did not record sexual interactions with the breeding female. The other two males of this group, however, showed lower eigenvector centrality in grooming interactions than the male 8CM (Table S3). These results suggested that the male 8CM was the breeding male of the BOM group.

Overall, golden-headed lion tamarins had an average of 2.6 ± 0.3 grooming partners (Figure 5). Females had similar numbers (mean ± *SE*s) of grooming partners (2.6 ± 0.4, $N = 14$) as males (2.6 ± 0.3, $N = 13$, $Z = 0.44$, $p = .89$). Moreover, tamarins living in *cabruca* had similar numbers of grooming partners (2.4 ± 0.3, $N = 15$) to those living in DFAM (2.8 ± 0.4, $N = 12$, $Z = 0.73$, $p = .46$). In DFAM, there was a correlation between the number of grooming partners that an individual had and its endoparasite load ($r_s = .87$, $p = .001$, $N = 11$). There were also significant and near significant correlations when analyzed separately for each group of DFAM (MRO: $r_s = .95$, $p = .01$,

TABLE 4 Statistical model of associations ($F_{1,12}$ and p values) between landscape (*cabruca* vs. DFAM), sex (female vs. male), and "confidence" z score on the proportion of time spent foraging for prey, eating, traveling, foraging for fruits and flowers, and social grooming by golden-headed lion tamarins (*Leontopithecus chrysomelas*) living in *cabruca* (cocoa agroforestry, $N = 11$) and degraded forest fragments in an agricultural matrix (DFAM, $N = 9$) landscapes

Behavioral categories	Landscape	Sex	Confidence z score	L × S[a]	L × C[b]	S × C[c]	L ×S × C[d]
Foraging for prey	9.98 ($p = .29$)	3.18 ($p = .10$)	20.04 ($p = .001$)	0.67 ($p = .43$)	1.54 ($p = .24$)	7.24 ($p = .02$)	8.01 ($p = .02$)
Eating	4.16 ($p = .06$)	1.76 ($p = .21$)	7.34 ($p = .02$)	0.10 ($p = .76$)	0.07 ($p = .79$)	9.46 ($p = .01$)	0.20 ($p = .67$)
Traveling	4.16 ($p = .06$)	0.01 ($p = .91$)	0.79 ($p = .39$)	2.55 ($p = .14$)	2.72 ($p = .13$)	0.89 ($p = .36$)	0.42 ($p = .53$)
Foraging for fruits and flowers	0.42 ($p = .53$)	3.18 ($p = .10$)	0.95 ($p = .35$)	0.02 ($p = .90$)	0.00 ($p = .98$)	1.99 ($p = .18$)	0.19 ($p = .67$)
Social grooming	0.24 ($p = .63$)	1.73 ($p = .21$)	0.37 ($p = .55$)	1.87 ($p = .20$)	0.02 ($p = .90$)	0.04 ($p = .85$)	1.30 ($p = .28$)

[a] L × S: interaction between landscape versus sex.
[b] L × C: interaction between landscape versus "confidence" z score.
[c] S x C: interaction between sex versus "confidence" z score.
[d] L × S × C: interaction between landscape versus sex versus "confidence" z score.

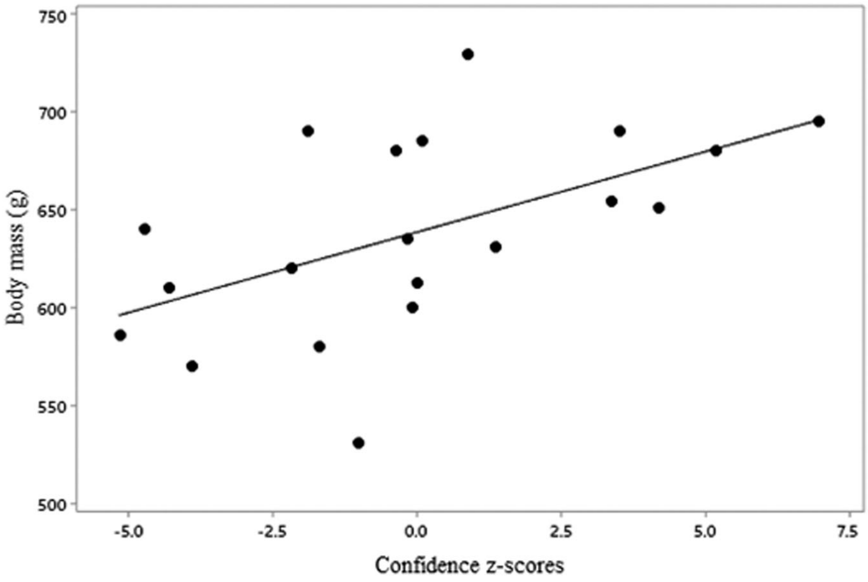

FIGURE 4 Relationship between body mass (g) of golden-headed lion tamarins and their "confidence" *z* scores following the equation: body mass (g) = 638.48 g + 8.23 "confidence" *z* score ($F_{1,12} = 6.22$, $R^2 = .37$, $p = .03$, $N = 20$)

$N = 6$; RIB: $r_s = .77$, $p = .07$, $N = 5$), indicating a consistent pattern across groups.

4 | DISCUSSION

Golden-headed lion tamarins showed individual differences in their reaction to a novel object test, and we observed effects of individual scores of "confidence" in the test, an individual's sex, and the landscape in which they lived on their foraging and feeding behavior. We also observed that more confident individuals had greater body mass. However, we did not find differences between female and male tamarins in clinical measures as hypothesized. Additionally, the hypothesis that FGCMs would differ between animals from different landscapes was not supported by our findings. Furthermore, we could confirm only partially the hypothesis that more exploratory and more sociable individuals show higher endoparasite loads because we only observed endoparasites in fecal samples collected from tamarins living in DFAM, while no endoparasites were found in the feces of those living in *cabruca*.

Responses to novelty in tests may indicate an individual's propensity to explore or avoid a potential threat (Liebl & Martin, 2012; Réale et al., 2007). Additionally, Réale et al. (2007) reported that bolder individuals spend more time foraging than shyer ones. The same was true in our study for golden-headed lion tamarins living in DFAM: the higher the "confidence" score (more "bold" and "calm," while less "fearful" and "stressed") the longer both females and males spent foraging for prey. For tamarins living in *cabruca*, however, only confident females spent more time foraging for prey. Moreover, in both landscapes there was a trend indicating an inverse relation

TABLE 5 Statistical model of associations ($F_{1,12}$ and *p* values) between landscape (*cabruca* vs. DFAM), sex (female vs. male), and "confidence" *z* score on biometric data (body mass and body index; heart rate; respiratory frequency; body temperature; recorded during sedation), and FGCM[a] of golden-headed lion tamarins (*Leontopithecus chrysomelas*) living in *cabruca* (cocoa agroforestry, $N = 11$) and degraded forest fragments in an agricultural matrix (DFAM, $N = 9$) landscapes

Behavioral categories	Landscape	Sex	Confidence *z* score	L × S[b]	L × C[c]	S × C[d]	L × S × C[e]
Body mass	0.59 ($p = .46$)	0.01 ($p = .93$)	6.22 ($p = .03$)	0.00 ($p = .99$)	0.14 ($p = .71$)	0.18 ($p = .68$)	0.68 ($p = .42$)
Body index	0.26 ($p = .62$)	1.17 ($p = .30$)	1.72 ($p = .21$)	0.01 ($p = .92$)	0.99 ($p = .34$)	0.75 ($p = .41$)	1.65 ($p = .22$)
Heart rate (bpm)	1.01 ($p = .34$)	0.25 ($p = .73$)	0.01 ($p = .94$)	1.81 ($p = .20$)	0.02 ($p = .90$)	0.05 ($p = .83$)	0.00 ($p = .99$)
Respiratory frequency (mpm)	0.02 ($p = .90$)	1.18 ($p = .30$)	0.37 ($p = .56$)	0.05 ($p = .83$)	0.20 ($p = .66$)	2.12 ($p = .17$)	0.28 ($p = .60$)
Body temperature (°C)	3.19 ($p = .10$)	1.94 ($p = .19$)	0.08 ($p = .79$)	0.57 ($p = .46$)	1.08 ($p = .32$)	0.00 ($p = .99$)	0.00 ($p = .97$)
FGCM (ng/g dry feces)	0.02 ($p = .61$)	0.44 ($p = .52$)	0.28 ($p = .61$)	0.09 ($p = .77$)	0.08 ($p = .78$)	1.51 ($p = .24$)	0.10 ($p = .75$)

Abbreviation: FGCM, fecal glucocorticoid metabolite concentration.

[a] For the FGCM analysis we excluded the data of the female 1DF, which was pregnant during fecal sample collection.

[b] L × S: interaction between landscape versus sex.

[c] L × C: interaction between landscape versus "confidence" *z* score.

[d] S x C: interaction between sex versus "confidence" *z* score.

[e] L × S × C: interaction between landscape versus sex versus "confidence" *z* score.

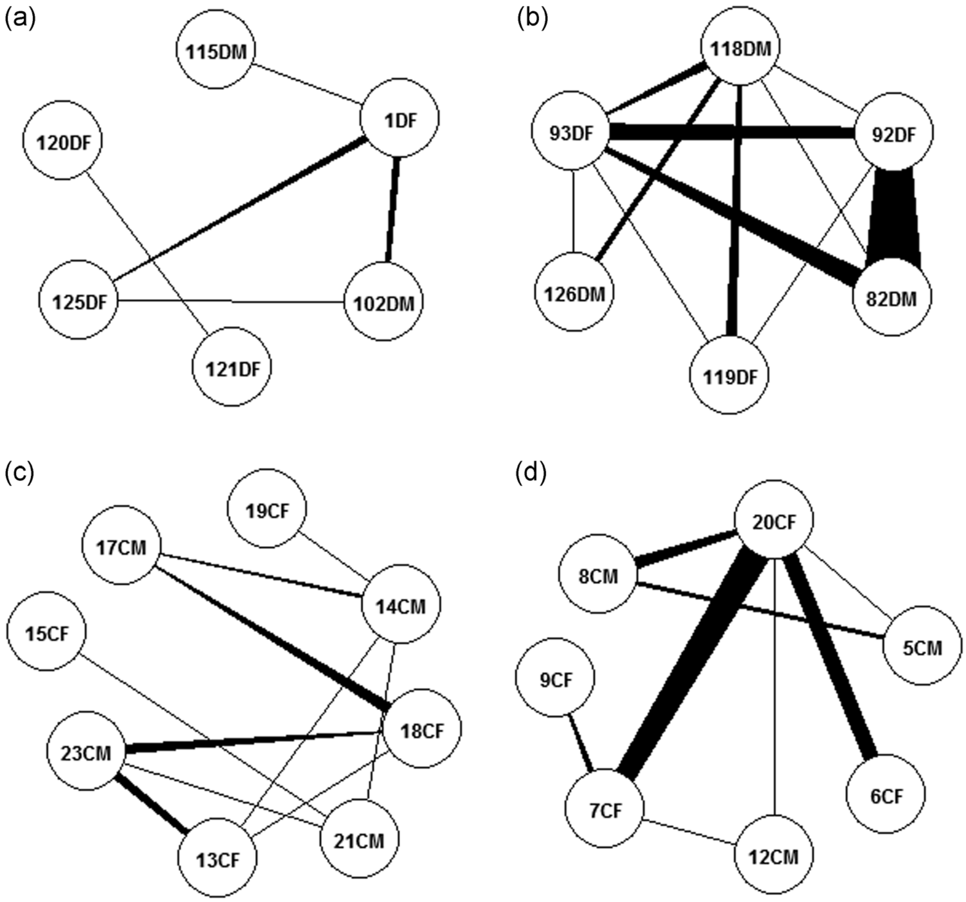

FIGURE 5 Network diagrams of the grooming interactions among golden-headed lion tamarins' groups (a: Manoel Rosa, b: Ribeiro, c: Almada, d: Bomfim). The alphanumeric code inside the boxes identified the individuals: their number, landscape (C: *cabruca* or D: DFAM), and sex (M: male or F: female). Lines represent the presence of an interaction between a pair of individuals with line thickness increasing with the frequency of interaction

between time eating and "confidence" scores in male golden-headed lion tamarins.

Usually, female tamarins spend more time foraging and feeding, which is positively related to the birth and survival of twin offspring (Bicca-Marques, 2003; Box, 1997). In turn, adult male tamarins play a major role in predator vigilance in their groups, which constrains their foraging and feeding investment (Bicca-Marques, 2003). Golden-headed lion tamarins are exposed to high levels of natural predation risk in *cabruca* (Oliveira & Dietz, 2011). Therefore, the role of male golden-headed lion tamarins in predator vigilance and differences in predation between landscapes may explain our results. It is reasonable to hypothesize that the higher their "confidence," the less time males living in *cabruca* spend foraging for prey due to the time they dedicate to vigilance. Unfortunately, we could not confirm this hypothesis because it was not always possible to distinguish whether individuals were resting or in predator vigilance.

Differences in the proportion of time golden-headed lion tamarins living in *cabruca* and DFAM spent on foraging for prey and eating may be explained by the use of pesticides in the *cabruca* system, which may disturb insect populations (Delabie, 1990). The use of pesticides in DFAM is rare or nonexistent (T. S. O. C., personal observation) because most of these areas are occupied by disturbed secondary forest patches in an agricultural matrix used for subsistence agriculture by low-income farmers, whereas *cabruca* is characterized by commercial cocoa production, which regularly uses pesticides.

Additionally, golden-headed lion tamarins select food according to the protein and fiber content of available fruit species (Catenacci et al., 2016). Such food selection may result in the intake of fruits with similar nutritional contents in both landscapes. Therefore, differences in vegetation composition between both landscapes probably did not affect tamarins' nutritional status, explaining the lack of differences in biometric data between DFAM and *cabruca*. In turn, the lack of effects of individuals' "confidence" scores, sex and landscape on other behavioral responses (foraging for fruits and flowers; traveling) could be explained by the high dietary diversity of golden-headed lion tamarins. The species is continuously searching for one of the 242 species of plants they use as source of food (Catenacci, De Vleeschouwer, & Nogueira-Filho, 2009; Catenacci et al., 2016; Oliveira, Hankerson, Dietz, & Raboy, 2010). Dietary diversity may also explain the relationship between "confidence" scores and body mass, independent of the sex and landscape. It is possible that "confident" tamarins are more successful in finding and eating food, which may explain their higher body mass, but this needs to be confirmed with further study.

BMI is usually considered a better indicator of body condition due to variation within populations and between age classes (Soto-Calderón et al., 2016). Surprisingly, there were no effects of individual "confidence," landscape or sex on BMI. Thus, further investigations must determine whether body mass or BMI is the better indicator of health status in free-living golden-headed lion tamarins. There is little information on health parameters of tamarins and because of this, the health and physiological data collected here were compared with reports for the genus *Leontopithecus*. Comparisons indicated that the respiratory frequency, heart rate, and body temperature of tamarins recorded in both landscapes were within normal range for the genus (Verona & Pissinatti, 2014). Even though the effect of physical and chemical restraint can cause changes in these parameters, the ketamine in combination with midazolam used in this study, provides good muscle relaxation as previously described in callitrichines (Furtado, Nunes, Intelizano, Teixeira, & Cortopassi, 2010). Thus, in this study such a combination minimized possible excitatory effects of the dissociative agents and promoted greater muscle relaxation in tamarins.

Overall, these clinical measures suggest that tamarins were within acceptable health parameters despite the endoparasite infections found in DFAM. The relatively high dietary diversity of golden-headed lion tamarins (Catenacci et al., 2009, 2016; Oliveira et al., 2010) may explain these results, allowing the animals to sustain themselves effectively in different environments and even when infected with parasites.

Our hypothesis that tamarins living in DFAM have health concerns was supported by our finding that they were infected with endoparasites while those living in *cabruca* had no endoparasites in collected feces. A human-disturbed environment tends to have lower biodiversity (Al-Shorbaji, Roche, Gozlan, Britton, & Andreou, 2016) and this could affect and increase the pressure of parasites in species with small populations such as the golden-headed lion tamarin. Monteiro, Dietz, and Jansen (2010) reported an intestinal helminth egg prevalence of 49% for *Prosthenorchis* sp. in golden-headed lion tamarins living at Una Biological Reserve (7,059 ha; ca. 15°10′S, 39°5′W). The Una Reserve is located near to the DFAM study site, in which we determined an intestinal helminth egg prevalence of 100% for the same helminth. Additionally, Monteiro et al. (2010) also stated that *Prosthenorchis* sp. infection results in a significant reduction in tamarins' health, which can potentially led to their death. However, the lack of other health concerns of individuals living in DFAM, suggests that animals may have developed resilience to the endoparasite.

Prosthenorchis sp. has a complex life cycle, having invertebrates as intermediate hosts, and vertebrates as final hosts (Machado-Filho, 1950). Transmission between tamarins possibly occurs by sharing contaminated food (invertebrates), a behavior commonly observed for this species (Moura, Nunes, & Langguth, 2010), or sites of food found in bromeliads, increasing chances of infection among more sociable individuals. This parasite infection raises questions on how tamarins will cope with altered environments and how this infection will affect individual long-term health parameters, reproduction, and ultimately species survival. Therefore, more investigation is needed to assess the long-term consequences on tamarins in DFAM of high prevalence of *Prosthenorchis* sp.

The intriguing absence of *Prosthenorchis* sp. in *cabruca* may be explained by the use of pesticides in this plantation system that may disturb insect populations (Delabie, 1990) which are the intermediate hosts of *Prosthenorchis* sp. (e.g., Blattodea and Coleoptera; Stunkard, 1965) and part of the tamarins' diet (Catenacci et al., 2016). This hypothesis needs to be confirmed with further study.

Basal FGCM did not differ between the landscapes. Moreover, the FGCM levels were within normal ranges seen in the genus *Leontopithecus* sp. (Wark et al., 2016). This result is unexpected, because DFAM landscape supposedly presents a more challenging environment for the animals due to anthropogenic impacts such as deforestation for agricultural proposes and opening of roads, compared with *cabruca*. On the other hand, tamarins are exposed to high levels of natural predation risk in *cabruca* (Oliveira & Dietz, 2011), which represents another ecological challenge. Usually, animals facing environmental stressors such as high levels of predation, food scarcity, or anthropogenic disturbance as we observed in both landscapes have higher glucocorticoid levels (Busch & Hayward, 2009; Rangel-Negrín, Alfaro, Valdez, Romano, & Serio-Silva, 2009). In a study of howler monkeys (*Alouatta pigra*) living in fragmented forest, glucocorticoid levels were higher compared with animals living in continuous forest (Martinez-Mota et al., 2007). In general, food scarcity is an important factor responsible for poor welfare and increase of glucocorticoids in the wild (sifakas [*Propithecus diadema*], Irwin, 2007; wild black capuchins [*Sapajus nigritus*], Moreira, Santos, Sousa, & Izar, 2016). However, food availability seemed not to be a greater challenge for tamarins in one environment relative to the other, as the proportion of time spent in foraging and eating fruits was similar in both landscapes. This might be because this species can eat several fruit species available in fragmented forest (Catenacci et al., 2016).

Stress hormone levels may reflect current levels of disturbance (Beehner & Bergman, 2017) but their links with long-term fitness are much less clear (Busch & Hayward, 2009). Fecal glucocorticoid metabolite data should thus be interpreted carefully (Dawkins, Edmond, Lord, Solomon, & Bain, 2004; Nogueira, Calazans, Costa, Peregrino, & Nogueira-Filho, 2011) and alongside other indicators of animal welfare such as the behavioral and health indicators measured here.

It has been suggested that high levels of sociality are usually associated with good animal health (Capitanio, 2011; Jin et al., 2013; Robinson et al., 2018). Social grooming, for instance, is important for removal of ectoparasites, maintenance of social bonds, and/or to reduce social tension in groups of nonhuman primates (Dunbar, 1991; Lehmann, Korstjens, & Dunbar, 2007). Social grooming, however, can increase the risk of transmission of parasites due to direct contact with infected individuals and ingestion of ectoparasites and endoparasites (Drewe, 2010; Gillespie, 2006; MacIntosh et al., 2012). In agreement with this, we found a positive association between the number of grooming partners and parasite load for animals living in DFAM. The groomer may ingest some larvae during grooming, as suggested for wild vervet monkeys (*Chlorocebus aethiops*), a species in which a positive correlation between the number of grooming partners and intestinal parasites infection was also observed (Wren et al., 2016). The same was recorded for Japanese macaques, with individuals who occupied more central positions in grooming networks exhibiting more infection by nematodes (MacIntosh et al., 2012). Our study, together with other findings (MacIntosh et al., 2012; Wren et al., 2016) shows the importance of investigating social bonds among individuals to provide information about the direction of endoparasite transmission. Parasite contamination of tamarin group members might also occur during sharing of the sleeping site (tree hollow). However, we might have then expected a more even distribution of parasites, but we observed more social animals to have a greater parasite infection. Thus, although it is possible that endoparasite contamination occurred in sleeping sites, social grooming may have been an important transmission mechanism for the golden-headed lion tamarin.

Overall our results point to associations between individual differences in behavior in the tested situation (novel object test), and behavior under free-living conditions, and between social grooming and endoparasite transmission. While the precise reasons for these associations, and their causal direction, cannot be determined from the current data, further research may indicate both whether they support that social behavior (grooming interactions) plays an important role for endoparasite transmission and if forest restoration aiming to regain ecological integrity may enhance tamarin's welfare by mitigating endoparasites in a challenging environment—the Brazilian Atlantic forest. Nevertheless, as our study has a small sample size and limited inference power for some of the clinical parameter values evaluated, we must consider our results as preliminary.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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