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Journal of Threatened Taxa

10.11609/jott.2026.18.1.28151-28262
www.threatenedtaxa.org

26 January 2026 (Online & Print)
18(1): 28151–28262
ISSN 0974-7907 (Online)
ISSN 0974-7893 (Print)

Open Access

40 Years
zooreach
Zoo Outreach Organisation

ISSN 0974-7907 (Online); ISSN 0974-7893 (Print)

Publisher
Wildlife Information Liaison Development Society
www.wild.zooreach.org

Host
Zoo Outreach Organization
www.zooreach.org

Srivari Illam, No. 61, Karthik Nagar, 10th Street, Saravanampatti, Coimbatore, Tamil Nadu 641035, India
Registered Office: 3A2 Varadarajulu Nagar, FCI Road, Ganapathy, Coimbatore, Tamil Nadu 641006, India
Ph: +91 9385339863 | www.threatenedtaxa.org
Email: sanjay@threatenedtaxa.org

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Cover: Golden-headed Lion Tamarin *Leontopithecus chrysomelas*. Watercolor and acrylics by P. Kritika.

Journal of Threatened Taxa | www.threatenedtaxa.org | 26 January 2026 | 18(1): 28151–28166

ISSN 0974-7907 (Online) | ISSN 0974-7893 (Print)

https://doi.org/10.11609/jott.9725.18.1.28151-28166

#9725 | Received 28 February 2025 | Final received 31 October 2025 | Finally accepted 31 December 2025

ARTICLE

Biological validation of fecal glucocorticoid and triiodothyronine measures in free-ranging Golden-headed Lion Tamarins (Kühl, 1820), (Mammalia: Primates: Callitrichidae: *Leontopithecus chrysomelas*): effects of the stress of capture and body condition

Roberto Fiorini-Torrico [1], Leonardo de Carvalho Oliveira [2], Damián Escribano [3], José Joaquín Cerón [4] & Kristel Myriam de Vleeschouwer [5]

[1,2] Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade, Applied Ecology and Conservation Lab,
Universidade Estadual de Santa Cruz, Rod. Jorge Amado km. 16, 45662-900 Ilhéus, BA, Brazil.
[1,5] Centre for Research and Conservation, Royal Zoological Society of Antwerp, Koningin Astridplein 26, B-2018 Antwerp, Belgium.
[2] Departamento de Ciências, Faculdade de Formação de Professores, Universidade do Estado do Rio de Janeiro,
R. Francisco Portela 1470, 24435-005 São Gonçalo, RJ, Brazil.
[2] Bicho do Mato Instituto de Pesquisa, Av. Cônsul Antônio Cadar 600, 30360-082 Belo Horizonte, MG, Brazil.
[3,4] Interdisciplinary Laboratory of Clinical Analysis of the University of Murcia (Interlab-UMU), Regional, Campus of International Excellence 'Campus Mare Nostrum', University of Murcia, Campus de Espinardo s/n, 30100 Murcia, Spain.
[1] beto.torrini@gmail.com (corresponding author), [2] leonardoco@gmail.com, [3] det20165@um.es, [4] jjceron@um.es,
[5] kristel.devleeschouwer@kmda.org

Abstract: Glucocorticoids (GCs) and thyroid hormones (THs), along with other physiological mediators, modulate the responses that allow lifelong adaptation to predictable and unpredictable environmental challenges. This has sparked the interest of primatologists who, with the advent of non-invasive sampling techniques, have been able to investigate changes in GCs and, more recently, THs under field conditions. These techniques need a validation process to ensure that the measurements are biologically meaningful for the species and the matrix being studied. Here, we aimed to validate the measurement of GC and triiodothyronine (T3) metabolites (fGCs and fT3, respectively) in the feces of wild Golden-headed Lion Tamarins (GHLTs; *Leontopithecus chrysomelas*), inhabiting highly disturbed forest patches in southern Bahia, Brazil. We assessed the effects of capture, body condition (weight and score), sex, dominance status, and group identity on the levels of fGCs and fT3 in samples collected during capture events and regular group-monitoring days. We found that capture and handling had a significant impact on both fGCs and fT3, whereas body condition score was relevant only to the variation in fT3 levels. These findings confirm the notion that the procedure of capture is a suitable acute stressor to validate non-invasive hormone measures and that fT3 is a promising marker for studying the fluctuations in energetic condition. Overall, our results demonstrate that a simple biological approach is sufficient to verify the applicability of non-invasive GC and TH determinations in fecal samples of wild GHLTs.

Keywords: Cortisol, hormones, Lion Tamarins, metabolites, non-invasive, thyroid hormones, wild.

Editor: Aniruddha Belsare, Auburn University, Albama, USA.

Date of publication: 26 January 2026 (online & print)

Citation: Fiorini-Torrico, R., L. de C. Oliveira, D. Escribano, J.J. Cerón & K.M. de Vleeschouwer (2026). Biological validation of fecal glucocorticoid and triiodothyronine measures in free-ranging Golden-headed Lion Tamarins (Kühl, 1820), (Mammalia: Primates: Callitrichidae: *Leontopithecus chrysomelas*): effects of the stress of capture and body condition. *Journal of Threatened Taxa* 18(1): 28151–28166. https://doi.org/10.11609/jott.9725.18.1.28151-28166

Funding: This study received financial support from the Centre for Research and Conservation of the Royal Zoological Society of Antwerp through the Flemish Ministry of Economy, Science and Innovation (R. Fiorini-Torrico's doctoral scholarship and logistic field support), and from the Rufford Foundation (Rufford Small Grant No. 29410-1).

Competing interests: The authors declare no competing interests.

Author details, Author contributions & Acknowledgments: See end of this article.

INTRODUCTION

Hormones are chemical messengers that regulate a wide range of bodily functions to maintain homeostasis in the face of environmental change (McEwen & Wingfield 2003; Nelson & Kriegsfeld 2017). They coordinate a series of physiological and behavioral adjustments through which animals appropriately respond to environmental and social cues, resulting in certain fitness outcomes (Higham 2016). Given their central role, hormones have been the focus of research across various fields (Palme 2005; Schwarzenberger 2007), including primatology. With the development of non-invasive and field-based techniques, researchers can now measure endocrine markers in matrices like feces or urine from wild primates, without altering their behavior or hormonal status (Schwarzenberger 2007). Moreover, these advances allow field observations to be combined with non-invasive endocrine monitoring, providing valuable insights into the adaptive aspects of hormone secretion and behavior (Cooke et al. 2014; Fiorini-Torrico et al. 2024) as well as impacts of human activities on the physiology of wild primates (Hodges & Heistermann 2011).

Glucocorticoids (GCs) are widely used in conservation research due to their mediation of the physiological stress response (Busch & Hayward 2009). This process initiates with the activation of the vertebrate hypothalamic-pituitary-adrenal (HPA) axis triggered by predictable or unpredictable environmental perturbations, ultimately leading to the secretion of GCs (Dantzer et al. 2014). These GC elevations then modulate energy allocation to cope with a variety of physical, metabolic, and psychological stressors (Emery-Thompson 2017). If GC increases are short-term, they enhance survival by promoting escape from noxious stimuli (Wingfield et al. 1998). Chronic elevations entail reductions in individual health and longevity (Sheriff et al. 2011; Beehner & Bergman 2017).

Thyroid hormones (THs) are also involved in vertebrate energy balance, but their non-invasive study in wildlife is more recent (Wasser et al. 2010). The synthesis of the two major forms of THs, thyroxine (T4) and triiodothyronine (T3), is controlled by the hypothalamic-pituitary-thyroid (HPT) axis. While the latter form is biologically more active, the former serves as a peripheral reservoir for T3 production via conversion (Behringer et al. 2018; Deschner et al. 2020). Given THs' particular sensitivity to nutritional deficits, which results in a lower metabolic rate (Eales 1988), it has been suggested that measuring both GCs and THs can help differentiate energetic from psychological influences (Emery-Thompson 2017), as well as distinct strategies to maintain energy balance (Wasser et al. 2010; Dias et al. 2017; Touitou et al. 2021).

To ensure the reliability of hormone measurements, it is essential to validate the hormonal assay for the species and matrix being investigated (Sheriff et al. 2011). Once GCs and THs are released into the bloodstream, they are metabolized by the liver and subsequently excreted into urine or the gut via the kidneys and bile ducts, respectively (Palme 2005; Behringer & Deschner 2017; Visser et al. 2017). Metabolites that reach the intestine are further broken down; as a result, most of the substances found in feces are conjugated forms of native GCs and THs (Touma & Palme 2005; Palme 2019). Consequently, all immunoassays, typically chosen to measure fecal metabolites, must be analytically validated for precision, accuracy, sensitivity, and specificity (Higham 2016). This not only guarantees that potential effects of storage, extraction, and laboratory protocols are accounted for, but also ensures that antibodies cross-react with target metabolites without major interference from other substances in the sample matrix (Hodges & Heistermann 2011).

In addition to analytical validation, studies should determine whether assays show biologically meaningful variations in the species physiology (Touma & Palme 2005). This can be done either through a physiological or a biological approach (Touma & Palme 2005). Physiological validation normally involves inducing changes in circulating hormone levels by administering a specific drug to later evaluate whether such changes are reflected in the excreted metabolites (Behringer & Deschner 2017). Furthermore, if repeated sample collection is possible, this type of experiment provides an opportunity to explore the lag-time between the stimulation of hormone secretion and its excretion in feces or urine (Hodges & Heistermann 2011; Behringer & Deschner 2017). Physiological validation can be very invasive, which is a concern when studying threatened species or wild individuals. In that case, biological validation may be more appropriate (Behringer & Deschner 2017). This alternative examines the levels of non-invasive markers in relation to a state or event known to alter the secretion of target hormones (Touma & Palme 2005). For GC metabolites, specifically, biological validation can be performed through procedures like capture, confinement, translocation, new housing conditions, disturbances by human presence or natural diurnal fluctuations in excreted GCs (reviewed by Touma & Palme 2005 and Higham 2016). For TH metabolites,

Image 1. Golden-headed Lion Tamarin *Leontopithecus chrysomelas* in the study area of Project BioBrasil at Colônia de Una, Bahia.

this has been achieved by assessing the influence of caloric restriction or low body mass (reviewed by Behringer et al. 2018), as well as the impact of infectious diseases (Dias et al. 2017).

In this study, we explore the effect of a series of intrinsic and stress-related factors on the levels of fecal GC and T3 metabolites, hereafter referred to as fGCs and fT3. We do so to validate the quantification of these markers in wild Golden-headed Lion Tamarins (*Leontopithecus chrysomelas;* GHLTs; Image 1), an endangered primate species restricted to the Southern Bahian Atlantic Forest in Brazil. More specifically, we evaluate the stress response of GHLTs to temporary capture and handling, predicting that fGC levels in samples collected during capture events will be higher than fGC levels during group monitoring days. We further examine the impact of body condition, predicting that higher body mass and better nutritional status (reflected by a qualitative body score) will both correspond with higher fT3 levels. We also assess the differences in fGCs and fT3 in relation to GHLTs' group identity, sex, and dominance status. Currently, there is no published study on the levels of T3 in Lion Tamarins, and only a few studies have used GCs in wild and captive populations of Lion Tamarins to address different hypotheses (e.g., Bales et al. 2002, 2005, 2006; Henry et al. 2013; Costa et al. 2020; Kaisin et al. 2023), including those that focused exclusively on the validation of the techniques (Wark et al. 2016; Bertoli et al. 2019). Therefore, this study adds to the literature showing the potential of non-invasive hormone analyses to understand the physiological responses of wild primates and may serve to better inform conservation actions for this and other threatened species.

MATERIALS AND METHODS

Study subjects

We studied 32 individuals belonging to four habituated groups of GHLTs (named ELI, MRO, OZA and RIB), all of which are monitored with radiotelemetry and captured routinely as part of the ongoing long-term research project BioBrasil (De Vleeschouwer & Oliveira 2017). The GHLT groups move freely in an area that comprises various privately owned farms located in the municipality of Una in South Bahia (see map in Image 2, geographic coordinates of field base: -15.285° S, -39.134° W). The study area is a mosaic of disturbed forest fragments of various sizes and an agricultural matrix that includes crop plantations (mainly cocoa, rubber, coffee, banana, and cassava), pastures, open fields, and unpaved roads (De Vleeschouwer & Oliveira 2017). The predominant natural vegetation in this region is classified as the Southern Bahian Moist Forest (Gouvêa et al. 1976) and the climate is characterized by an annual average temperature of 24 °C and precipitation of 2,500 mm, with no marked seasonality (Mori et al. 1983).

Following Miller et al. (2003), we categorized age of individuals into infants (<3 months), juveniles (3–12 months), subadults (12–18 months) and adults (>18 months). Dominance hierarchy and age of adult and subadult GHLTs were assessed based on historical group composition data from Project BioBrasil, behavioral observations, and information provided by BioBrasil's field assistants, who were able to recount the breeding history and relatedness of GHLTs over a longer period. Studies on Golden Lion Tamarins *Leontopithecus rosalia* (GLTs) show that dominant and subordinate breeders (males or females), within the same group, rarely display aggressive interactions and, instead, frequently engage in mutual affiliation, which is something typical of cooperative-breeding social structures (Baker et al. 1993, 2002). Despite that, dominance relationships of both males and females can be classified by examining a set of behaviors that indicate their status and roles within their social context (Baker et al. 2002). Therefore, to determine the dominance of adults and subadults, we considered their involvement in chases during intergroup encounters and intragroup aggression, their access to mates when females were expected to be fertile, their participation in carrying and nursing infants, as well as the frequency of mounts, copulations and arch-walks (Baker et al. 2002; Bales et al. 2005, 2006).

All activities described here involving captures, sample collection and monitoring were ethically approved by the International Committee for the Conservation and Management of the Lion Tamarins and the Brazilian Environmental Agency (ICMBio/SISBIO permit no. 23457-6).

Capture procedure

Study groups are captured twice a year by a multidisciplinary and trained team of biologists, veterinarians, and field assistants to replace radio-collars (model RI-2D, Holohil Systems Ltd., Ontario) on one or two adult individuals per group and to provide all individuals with a tattoo number and a unique dye mark (Nyanzol Dye). In this way, captures not only allow for the use of radiotelemetry to locate groups in the field but also facilitate identifying individuals during subsequent behavioral observations and sample collections.

Before capturing the GHLTs, platforms baited with banana were assembled in an area regularly used by the group (see Image 2), and Tomahawk traps were set up on these platforms gradually. The traps were activated once there was evidence the groups frequently visited the platform (De Vleeschouwer & Oliveira 2017; Catenacci et al. 2022). During capture days, traps were opened at 0500 h and monitored at regular intervals (0800, 1000, 1200, 1400, & 1630) to verify whether animals had been caught. Trapped GHLTs were taken to a nearby field laboratory and, following a fasting period of two to three hours, anesthetized with a combination of ketamine hydrochloride (dose 8–10 mg/kg) and midazolam (dose 0.25–0.5 mg/kg) to perform examinations (Catenacci et al. 2016; Costa et al. 2022). No infant GHLT was anesthetized or kept separate from its mother or caregiver (Catenacci et al. 2022). Due to the COVID-19 pandemic, which coincided with the present study, and the risk of spreading this disease to the animals (Fedigan 2010), we reinforced biosafety measures for all team members and shortened the handling time by limiting the collection of biometric data. Nonetheless, key variables such as body mass, measured with a one-gram digital scale after containment, and body condition score (see Table 1), determined based on Clingerman & Summers (2005), were still collected. All recovered animals were released either the same day before sunset or the following morning at the location where they were caught (Costa et al. 2020). For a more comprehensive description of the methods used during captures and examinations of GHLTs consult Catenacci et al. (2022).

Sample collection and preservation

Fresh, uncontaminated fecal samples were collected under two different circumstances: 1) during two capture

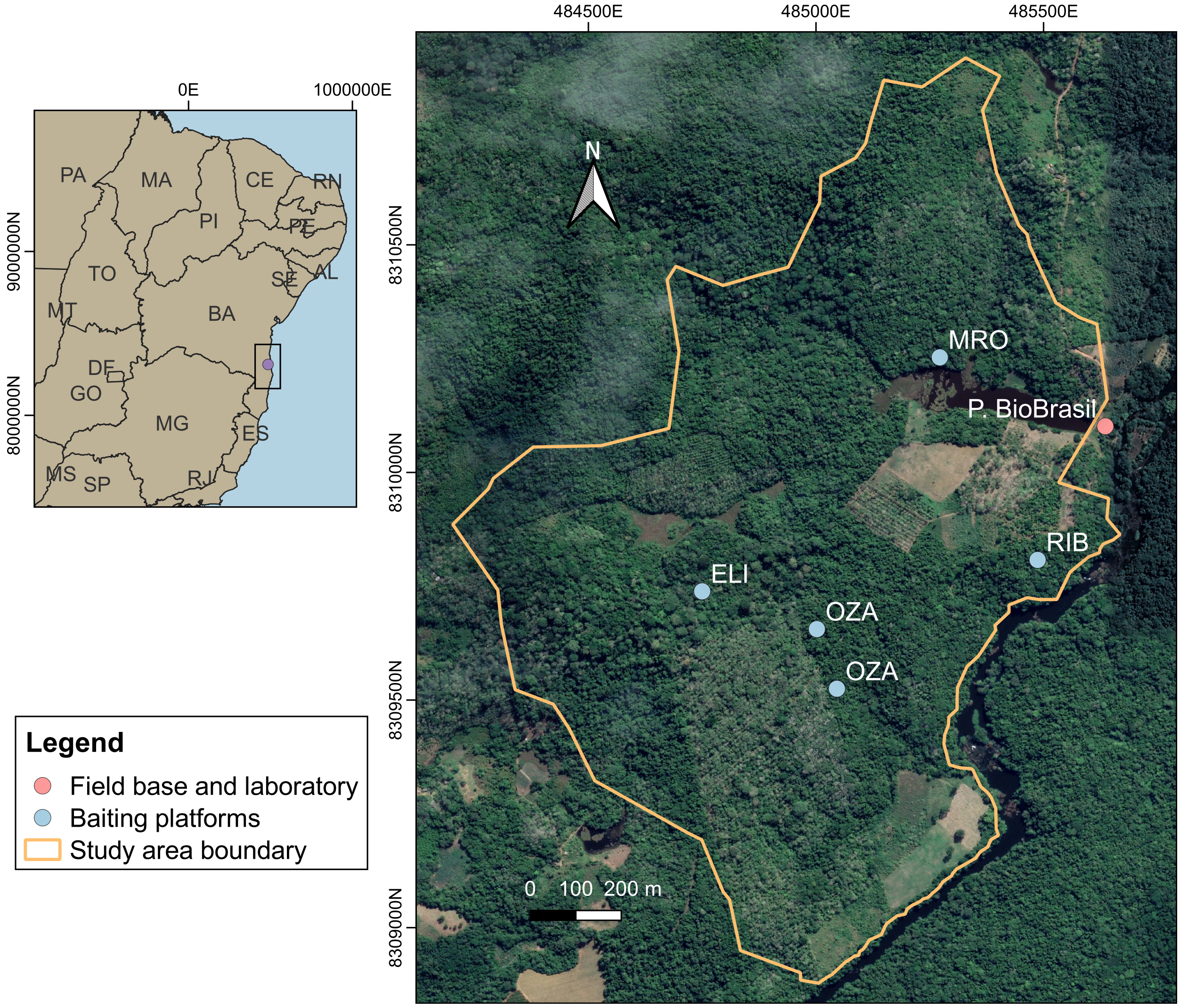

Image 2. Map of the study area and locations of the baiting platforms used during captures in 2021. The study area boundary was obtained based on GPS coordinates recorded every 20 min during whole-day follows of four habituated Golden-headed Lion Tamarins groups (geographic data provided by Project BioBrasil). Satellite image from July 2021 obtained from Google Earth (© Maxar Technologies, © CNES/Airbus).

events, one in April and the other in November 2021, including all four GHLT groups – capture samples; and 2) over 11 months of full-day field observations between December 2020 and October 2021, involving only MRO, OZA and RIB – monitoring samples. In both cases, we focused our sampling effort on adult and subadult individuals (see Table 2), as GC production increases and GC negative feedback becomes less responsive with age (Sapolsky & Altmann 1991; Gust et al. 2000). Samples were incidentally taken from juvenile and infant GHLTs, which represented 6.25% of capture and 4.67% of monitoring samples. During group monitoring days, feces were collected any time we observed an individual defecate. During captures, samples were taken opportunistically at the field lab following the fasting period. All samples were labelled with the date, the time of collection, and the individual's identity.

The time from when an individual was found in a trap (between 0800 and 1630) until it defecated and feces were collected was, on average, 4.80 ± 2.78 h. Importantly, before TH and GC metabolites are excreted in feces, their circulating forms are metabolized and pass through the intestinal tract (Behringer et al. 2018; Palme 2019). This introduces a delay time in the appearance of the hormonal signals in feces which more or less corresponds to the species' gut transit time (Palme et al. 1996, 2005; Palme 2005; Touma & Palme 2005). For some callitrichids, including GLTs, gut transit times range from 2.65–6.30 h (Power & Oftedal 1996; reviewed by Lambert 1998). This interval nearly coincides with the time elapsed before fecal samples were taken from trapped individuals (as mentioned above), increasing the likelihood of detecting hormonal changes caused by capture-related procedures.

Samples were stored inside 15 ml polypropylene screw-cap tubes prefilled with 4 ml of 80% ethanol (Hodges & Heistermann 2011), which is the preferred field preservation technique to prevent microbial degradation when immediate freezing is not available (Schwarzenberger 2007). Care was taken to ensure that stored samples were completely submerged in ethanol before tightly closing the lid (Hunt & Wasser 2003) and then transferred the tubes the same day of collection to a freezer at -20°C, where samples remained for 30–149 days until oven dried (Khan et al. 2002). To dry samples, we first let the alcohol evaporate overnight for about 12 hours (Terio et al. 2002) and then placed samples inside a laboratory oven at 50°C for 4 h (Gholib et al. 2018), at which point feces became crumbly suggesting complete water loss. Finally, samples were transferred to small, labelled plastic bags containing oxygen absorbers, sealed them, and took them back to a freezer at -20 °C until all samples were shipped to the lab for further processing.

Hormone extraction and assay

Extraction of fecal metabolites and quantification of fGCs and fT3 were conducted in the Interdisciplinary Laboratory of Clinical Analyses at Murcia University (Interlab-UMU), Spain, between April and June 2022. To extract the metabolites, we followed a method similar to that described in Wasser et al. (2000). First, large seeds, insect parts and plant debris from crushed dried feces were removed (Foerster & Monfort 2010), and weighed an aliquot of approximately 0.06 g (95.7% of the aliquots had an average weight of 0.0599 g ± SD 0.0023). All aliquots were pulverized and shaken for 15 h in 1 ml of analytical-grade methanol (Gómez-Espinosa et al. 2014; Rangel-Negrín et al. 2015). Extracts were then centrifuged at 3,500 rpm for 5 min, and 0.6 ml of supernatant was transferred to a separate tube. Supernatants were then evaporated inside a vacuum concentrator for 2 h, reconstituted with 0.15 ml of a PBS buffer, vortexed, and stored at -80 °C until analysis.

Commercial enzyme immunoassays (EIA) kits from IBL International GmbH for the determination of cortisol (RE52061) and total triiodothyronine (RE55251) to respectively measure fGCs and fT3 in our sample extracts. While the chosen T3 kit has already been validated for T3 metabolites excreted in feces and urine of non-human primates (Behringer et al. 2014; Cristóbal-Azkarate et al. 2016; Deschner et al. 2020; Sadoughi et al. 2021; Touitou et al. 2021), the cortisol kit has thus far been tested in teleosts (e.g., Nilsson et al. 2012; Cerqueira et al. 2017; Mazzoni et al. 2020) and some mammals (e.g., Brain et al. 2015; Almoosavi et al. 2021; Kaiser et al. 2023) but not in non-human primates. To prevent alterations in the assays, manufacturer's instructions of use were strictly followed. The standard curves for calibration of all 10 plates tested (5 for fGCs & 5 for fT3) exhibited an accuracy of $R^2 = 0.98–1$. Besides the coefficients of variation (CV) for repeatability already provided by the manufacturer (cortisol: intra-assay CV = 2.5–3.5 % and inter-assay CV = 2.1–5.2 %; total T3: intra-assay CV = 3.59–6.61 % and inter-assay CV = 5.23–6.73 %), we performed, prior to the analysis of main samples, an analytical validation on a small set of fecal samples collected from captive GHLTs from Terra Natura in Benidorm (Spain), following the same sample processing previously described. For both the fGCs and fT3 quantification, it was found that intra and inter-assay CVs were less than 15% and displacement curves obtained from serial dilutions of fecal samples ran parallel to the standard hormone curves with a R^2 close to 1.

Data analysis

The levels of fGCs and fT3 were compared between groups of the predictor variables by applying ANOVA to multiple mixed-effect models fitted with the 'lmer' function from the R package lme4 (Bates et al. 2015). Because data contained repeated measures for the same individual within and, in some cases, between groups, we consistently defined the individual identity as a random factor throughout this analysis. Both fGC and fT3 levels were transformed to logarithm with base 10 to conform with assumptions of normality of residuals and homogeneity of variance, verified each time data was reorganized. When dealing with fT3 levels measured in monitoring samples, ANOVAs were used with aligned rank transformed data from package ARTool (Wobbrock et al. 2011). If a significant effect was detected for a certain variable, a post-hoc analysis was performed by least-square means from package emmeans (Searle et al. 1980) or a contrast test provided by ARTool. We began evaluating the effect of the stress of capture on both metabolites considering the total number of samples (n = 289). We then split up the dataset between capture and monitoring collections and removed data from juveniles and infants to test the influence of sex, dominance, and dominance in interaction with sex (dominance*sex) on fGCs and fT3 levels. Body condition score and body weight were assessed only with capture samples, for the latter variable we excluded

Table 1. Description of the body condition scores used during two capture events to categorize nutritional status (body fat and muscle) of captured Golden-headed Lion Tamarins.

Body condition score	Definition
1	**Emaciated**: very prominent and easily palpable bones (hips, ribs, and spinal processes), very low to no palpable muscle mass over the ilium or ischium, subcutaneous fat layer is absent, very angular body, sunken anus between ischial callosities, and protruding facial bones.
2	**Thin**: prominent and palpable bones, low muscle mass over the hips and back, low fat reserves and subcutaneous fat layer, and angular body.
3	**Optimum**: bones are generally not visible but palpable to soft pressure, both muscle mass and fat layer are well-developed giving the spine and hips a firm but smooth touch.
4	**Overweight**: bones are not visible and only palpable to firm pressure, abundant subcutaneous fat layer, and smooth and less defined body contour.
5	**Obese:** bones are not visible at all and difficult to palpate, abundant fat deposits (abdominal, axillary, and inguinal region), difficult abdominal palpation due to large amount of mesenteric fat, and body contour without definition.

Adapted from Clingerman & Summers (2005).

Table 2. Number of fecal samples per sex and dominance status collected during capture events and regular monitoring days.

Collection type	Number of groups	Number of individuals	Number of fecal samples						
			♀ D	♀ S	♂ D	♂ S	J & I	♂ U	Total
Capture	4	22	10	10	3	5	2	2	32
Monitoring	3	25	39	54	68	83	12	1	257

Where adults and subadult Golden-headed Lion Tamarins are differentiated in dominant females (♀ D) and males (♂ D), subordinate females (♀ S) and males (♂ S) or males with undetermined dominance status (♂ U). Juveniles and infants are represented by "J & I".

juveniles from the dataset as body weight would not be comparable. To explore the differences in group identity, we solely considered samples from regular monitoring including all age categories. All statistical tests were run in R version 4.3.2. (R Core Team 2023) and considered significant at $p < 0.05$.

Since diurnal variation in hormone secretion may potentially confound the excretion of GCs and T3 metabolites (Sousa & Ziegler 1998; Foerster & Monfort 2010; Pizzutto et al. 2015; Behringer et al. 2023), especially in species with rapid gut transit time (Touma & Palme 2005; Rimbach et al. 2013) like GHLTs, we examined the effect of collection time on the fGC and fT3 levels within the complete dataset (all samples), as well as the separate datasets: monitoring and capture samples. To conduct this preliminary analysis, we used linear mixed-effect models ('lmer') for fGCs and generalized linear mixed-effect models ('glmer') for fT3, with individual identity as random term and time of collection as predictor. If collection time had a significant effect, we incorporated it as an additional random factor in the formula of our main analysis to account for the natural circadian fluctuations in the response variables.

RESULTS

We found that diurnal variation of metabolite excretion affected the levels of fT3 in the complete dataset ($p = 0.022$), and fGCs in the monitoring ($p = 0.009$) and capture ($p = 0.048$) datasets. Therefore, in addition to individual identity, we defined collection time as a random factor when using these datasets with the respective fecal metabolite. As this was beyond the scope of our main research questions, we do not discuss further how fGCs and fT3 reflect the GHLT's circadian rhythms.

Effects of the stress of capture and body condition

Concentrations of fGCs in capture samples were significantly higher than in monitoring samples ($F_{1,\ 267.92} = 36.81$, $p < 0.001$) with mean levels of 6462.14 ± SEM 921.76 ng/g and 2712.3 ± SEM 197.88 ng/g, respectively, for each collection type. Although the range of fGC levels observed in monitoring samples (181.81–22065.65 ng/g) was wider than that in capture samples (1020.81–21712.85 ng/g), the range of variation of both collection types nearly overlapped (Figure 1A). On the contrary, fT3 values measured in capture samples were significantly lower than in monitoring samples ($F_{1,\ 263.18} = 12.27$, $p < 0.001$) with mean levels of 29.7 ± SEM 2.73 ng/g and

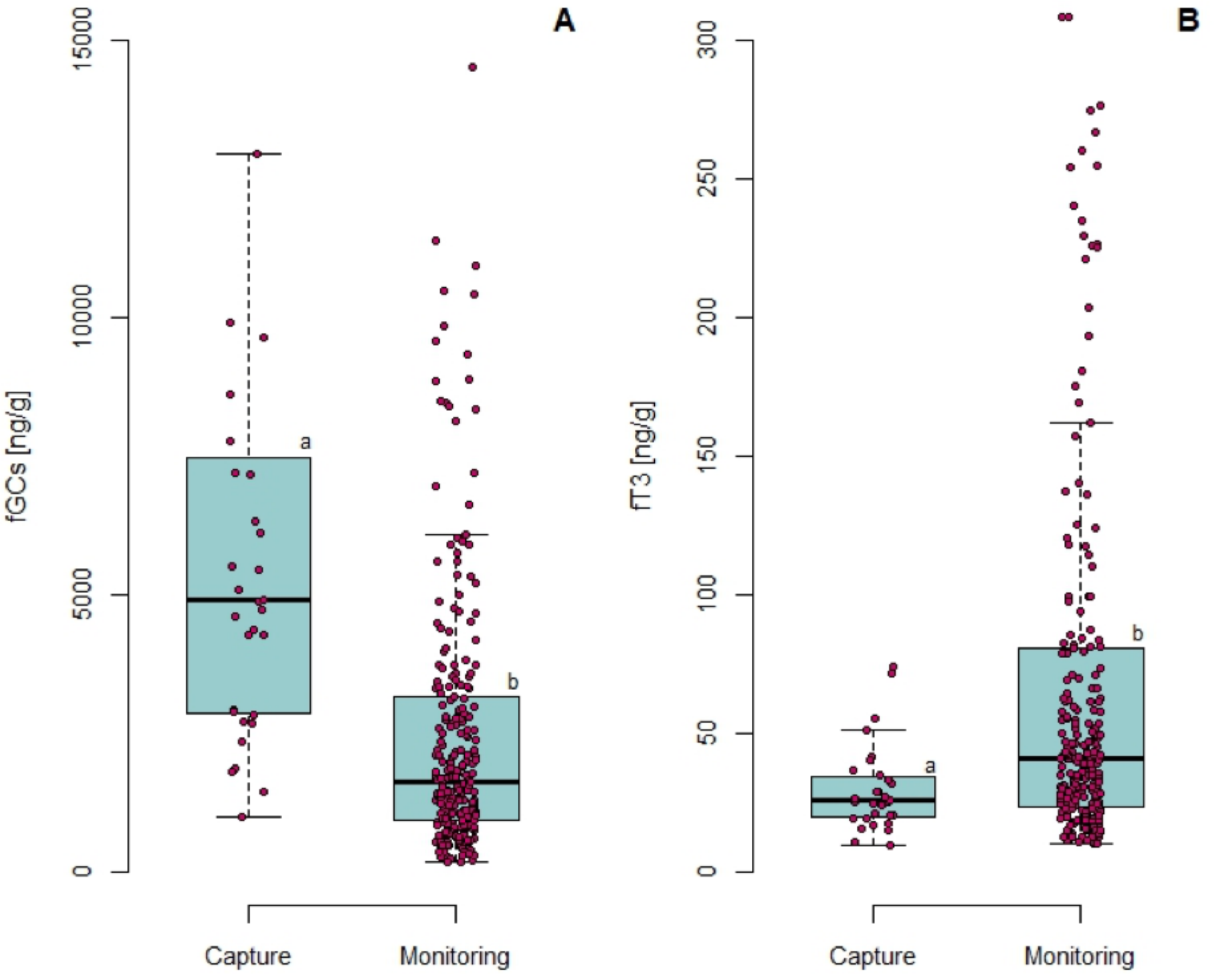

Figure 1. Levels of fecal metabolites of: A—glucocorticoids – fGCs | B—triiodothyronine – fT3 measured in samples collected in capture events and group-monitoring days. Data points are plotted as dots. Boxplots display the median at the center line, the 75th and 25th percentiles at the box limits, and 1.5 times the interquartile range from the 25th and 75th percentiles at the whiskers. Different lowercase letters indicate significant differences among groups.

89.55 ± SEM 7.98 ng/g, respectively. Also, in contrast to fGCs, the range of fT3 levels was much narrower in capture (9.86–74.44 ng/g) than in monitoring samplings (10.76–848.61 ng/g), as shown in Figure 1B. We found no significant effect of body weight on either metabolite. Body condition score of captured individuals was significantly associated with variation in fT3 levels ($F_{1, 27} = 5.54$, $p = 0.026$), this association linked higher fT3 concentrations to individuals with a better nutritional state (optimum versus thin), see Figure 2A.

The effect of sex, dominance, and group identity

Neither sex nor dominance was associated with significant differences in the levels of fGCs or fT3 for any collection type. Similarly, the interaction between sex and dominance was not significant for any of the metabolites measured in the monitoring samples (see Figure 3). There was a marginally significant effect of this interaction on the fGCs levels in capture samples ($F_{1, 17.28} = 3.58$, $p = 0.075$). Regarding only monitoring samples, group identity had a marginally significant effect on fGC values ($F_{2, 30} = 3.08$, $p = 0.061$), whereas for fT3 this effect was significant ($F_{2, 26.6} = 6.22$, $p = 0.006$) with fT3 levels in MRO being higher than in OZA and RIB (Figure 4). Given that the variation in fT3 among GHLT groups could potentially bias the previous results regarding stress of capture, we ran an additional test for fT3 and type of collection with individual identity nested within group membership as a random factor in the model configuration. This test confirmed that the procedure of capture has a significant effect on fT3 levels ($F_{1, 120} = 9.81$, $p = 0.002$) regardless of group identity.

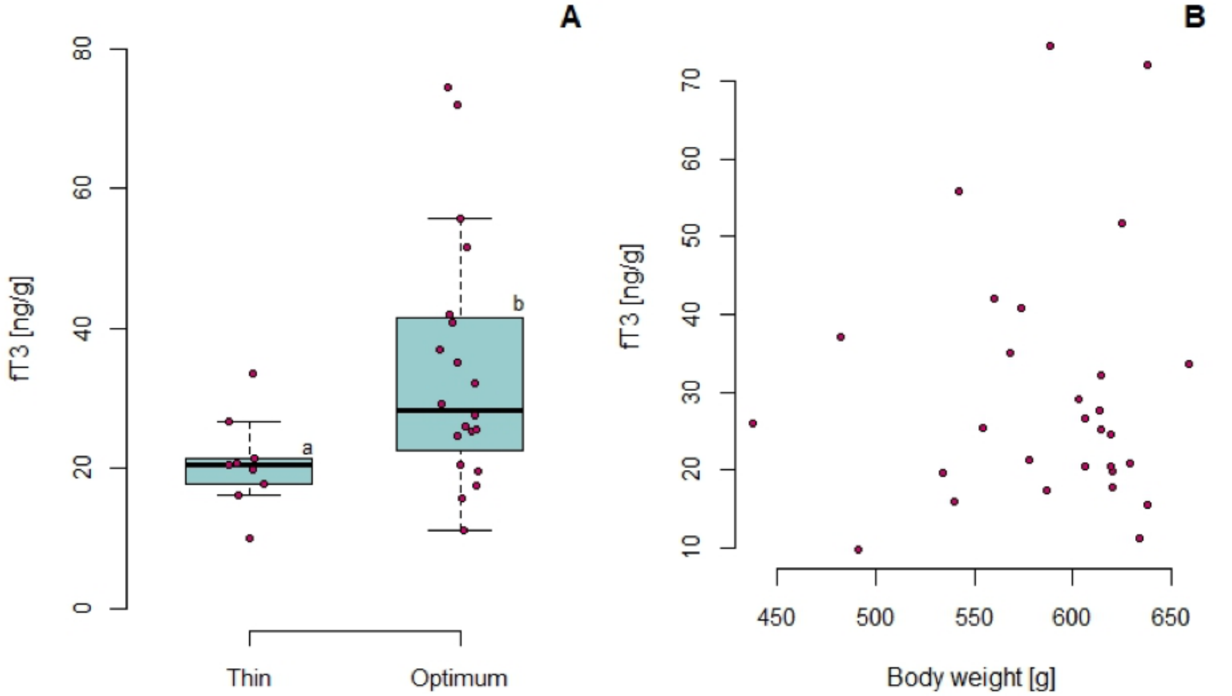

Figure 2. Levels of fecal triiodothyronine metabolites (fT3) measured in capture samples as a function of A—body condition score and | B—weight in grams. Data points are plotted as dots. Boxplots displaying the median at the center line, the 75th and 25th percentiles at the box limits, and 1.5 times the interquartile range from the 25th and 75th percentiles at the whiskers. Different lowercase letters indicate significant differences among groups.

DISCUSSION

Here we demonstrated, through a simple biological approach, that fGCs and fT3 can be reliably quantified in dried feces of wild GHLTs using commercially available cortisol and total triiodothyronine EIA kits. To do so, we evaluated the physiological response of individuals to the stress of capture and compared it to a natural situation. Additionally, we assessed the relationship between body condition and the metabolites of interest. Importantly, the present study offers a different validation approach from methodologies such as physiological validations, which normally allow consecutive sampling of tested subjects after induced stress and are intended to measure peak metabolite levels.

As expected, GC excretion in individuals during capture and handling procedures was, on average, higher than levels measured during the GHLT's daily activity throughout 11 months of sampling. This finding confirms the notion that the activation of the HPA axis during procedures such as physical restraints, captures, and transportation allow detecting GC alterations that show the capacity of individuals to mount their stress response (Touma & Palme 2005; Wikelski & Cooke 2006). Typically, fGC measurements in non-human primates are validated by obtaining multiple samples from captive individuals before and after a short-term stressor (e.g., capture, isolation, veterinary exam, anaesthesia) or a procedure to pharmacologically stimulate the HPA-axis, such as the adrenocorticotropic hormone (ACTH) challenge test (e.g., Heistermann et al. 2006; Rangel-Negrín et al. 2009; Rimbach et al. 2013). With this, researchers can delineate the fGC excretion profiles for each individual and identify the peak values, defined as the fGC concentrations exceeding two standard deviations above baseline (Gómez-Espinosa et al. 2014; Pizzutto et al. 2015; Wark et al. 2016). The latter value can correspond to the mean pre-capture concentration (Gómez-Espinosa et al. 2014), or the mean concentration calculated by iteratively excluding values greater than 2 SDs from the mean (Pizzutto et al. 2015; Wark et al. 2016). Studies using this approach have reported a lag time of 22.3–49.3 h in GLTs (n = 7; Wark et al. 2016) and 20–25 h in Black Lion Tamarins *Leontopithecus chrysopygus*(BLTs) (n = 6; Bertoli et al. 2019) between the stressful event or the ACTH injection and the first observed peak. Given such lag times, we presume that the timeframe considered in this study (4.80 ± SD 2.78 h) is not long enough to detect a peak in fGC excretion. The results simply indicate how the stress response of GHLTs,

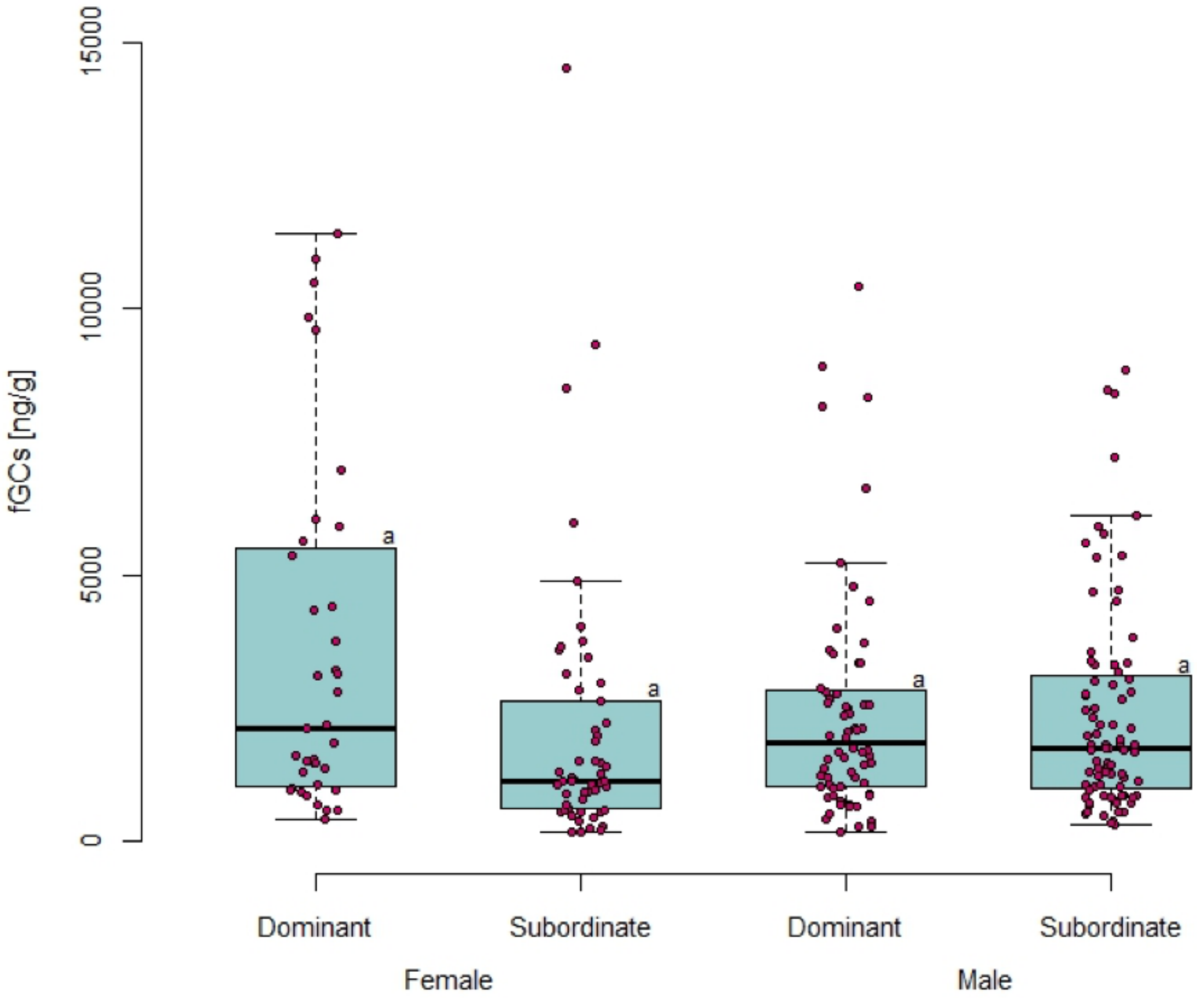

Figure 3. Levels of fecal glucocorticoid metabolites (fGCs) were measured in monitoring samples across different sex and dominance status of adult and subadult Golden-headed Lion Tamarins. Data points are plotted as dots. Boxplots displaying the median at the center line, the 75th and 25th percentiles at the box limits, and 1.5 times the interquartile range from the 25th and 75th percentiles at the whiskers. Different lowercase letters indicate significant differences among groups.

as measured by fGCs, differs between capture events and regular monitoring days, when habituated individuals move freely and interact with their environment. It is possible that lag time before fGC peaks appear in GHLTs will be similar to those found in congeneric species. To verify that, a different experimental design needs to be used which would likely require captive populations or free-ranging individuals to be retained in captivity to ensure repeated fecal sampling for at least three days following an induced stressor (Gómez-Espinosa et al. 2014; Wark et al. 2016; Bertoli et al. 2019).

Notably, the amplitude of fGC response to capture was similar to the one detected during monitoring days, especially regarding upper fGC concentrations. This may indicate that GHLTs in our study area face environmental stressors that trigger a stress response as intense as the one induced by capture and containment (Johnstone et al. 2012). The study groups occupy fragments of disturbed forest interspersed with agricultural areas (De Vleeschouwer & Oliveira 2017), a landscape that probably presents particular environmental challenges, such as high predation risk (Oliveira & Dietz 2011) or low opportunities to find food and shelter (Kalbitzer & Chapman 2018), which could stimulate or even sustain a GC elevation in the long term (Kaisin et al. 2021). It would be interesting to compare our results with those from GHLTs in different landscapes and explore the possible health consequences linked to an over-stimulation of the stress responses (Romero et al. 2009) in GHLTs occupying disturbed forests.

Contrary to our expectations, fT3 levels were affected by the stress of capture, but exhibited a response pattern opposite to that of fGCs. This significant effect suggests that, similarly to fGCs, the lag time for the appearance

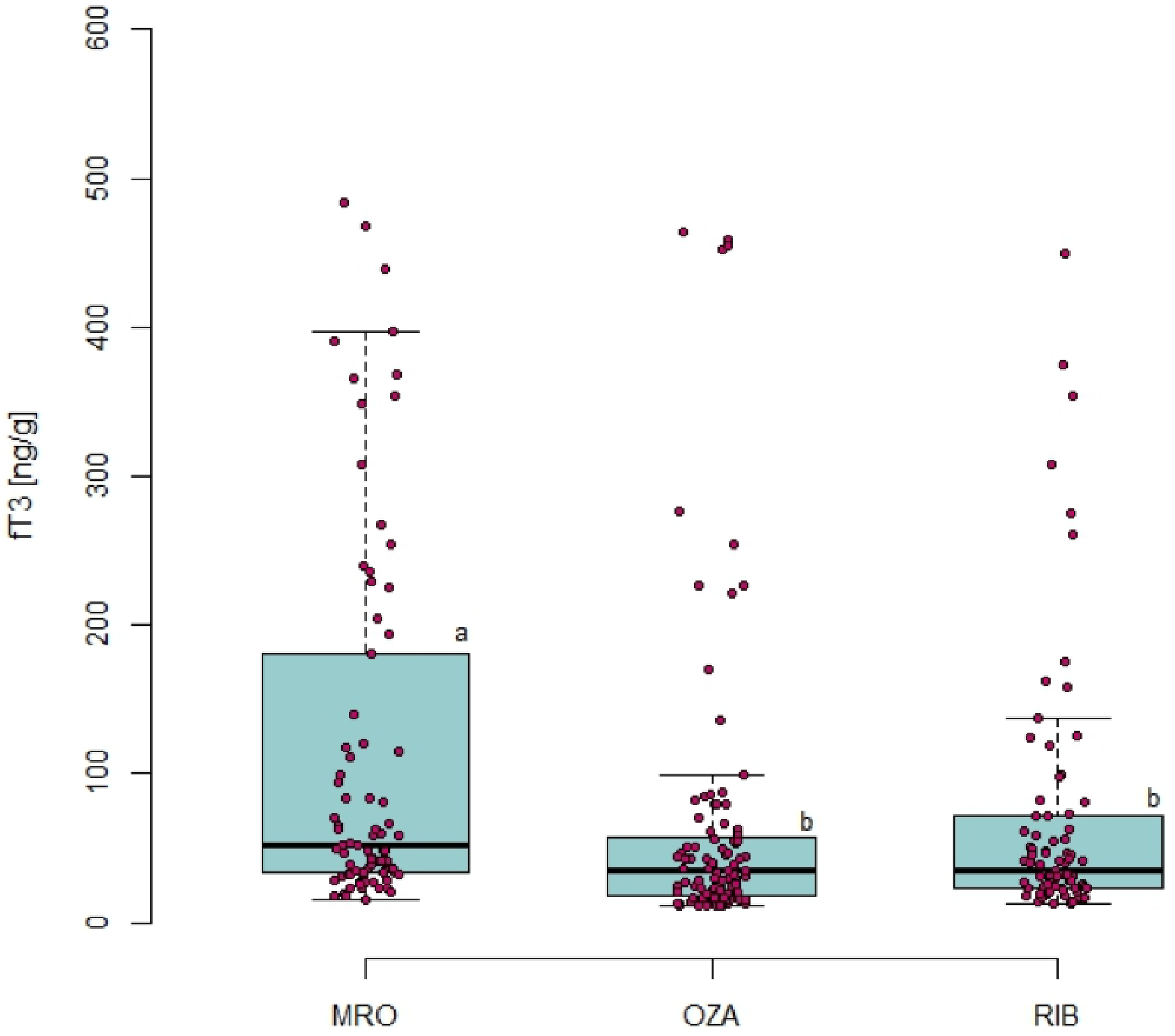

Figure 4. Levels of fecal triiodothyronine metabolites (fT3) as a function of group identity were evaluated for monitoring samples. Data points are plotted as dots. Boxplots display the median at the center line, the 75th and 25th percentiles at the box limits, and 1.5 times the interquartile range from the 25th and 75th percentiles at the whiskers. Different lowercase letters indicate significant differences among groups.

of T3 metabolites in feces is comparable to the species' gut passage time (Schaebs et al. 2016; Behringer & Deschner 2017). Furthermore, the lower fT3 but higher fGC levels in capture compared to monitoring samples raises the possibility of a cross-talk or interaction between the HPA- and HPT-axis (Behringer et al. 2018; Touitou et al. 2021), although levels of fGCs and fT3 in capture samples were not correlated, probably due to small sample size. It is frequently suggested that TH levels are downregulated by the release of GCs, associated with stressful situations (Burr et al. 1976; Behringer et al. 2018). Physiological pathways leading to this TH suppression include the inhibition of the thyroid stimulating hormone and the reduced conversion of T4 to T3 (Charmandari et al. 2005). For instance, Helmreich et al. (2005) found in male Sprague-Dawley rats that mild-electric foot-shocks led to significantly lower levels of serum T3 and, although corticosterone levels were not altered by this experiment, certain HPA-axis components may participate in TH regulation. This relationship may not be so straightforward, even when an acute stressor is involved, as demonstrated for Guadalupe fur seals by DeRango et al. (2019), who associated a capture event to a simultaneous reduction in T3 and an integrated stress response comprising cortisol and corticosterone levels. Furthermore, the potential cross-talk between T3 and GCs may have been confounded by food restriction, performed in order to anesthetize trapped individuals. In fact, various studies have successfully validated the measurement of T3 in primates by linking reduced food intake to lower levels of T3 in urine and feces (Wasser et al. 2010; Schaebs et al. 2016; Sadoughi et al. 2021). Regardless of the possible explanations, our results for the stress of capture indicate that under fearful situations, GC levels in GHLTs increase in order to promote alertness and a freezing response (Charmandari et al. 2005; Korte et al. 2005) while T3 decreases as a mechanism to modulate the metabolic rate and save energy (Behringer & Deschner 2017; Gesquiere et al. 2018). Both changes likely occur in preparation to future demands or additional stressors (Sapolsky et al. 2000).

Another aspect that links THs' secretion to metabolic activity in relation to energy balance is their response to weight gain or loss (Chatzitomaris et al. 2017). Specifically, when high food quantity and quality is accompanied by high T4 and T3 levels, bodyweight will normally increase (Behringer et al. 2018). In this study, no association was found between adults and subadults' body mass and fT3 levels, which could be attributed to the fact that weight values were not scaled to specific body length of each individual (DeRango et al. 2019). We measured this value (knee-to-heel distance) in some but not all sampled individuals because of the limitation in handling time during capture imposed by pandemic restrictions. Nonetheless, by using a semiquantitative body condition score, a tendency of lower fT3 levels was identified to be related with individuals presenting a bonier structure and a lesser amount of palpable muscle and fat (Clingerman & Summers 2005). This is in line with evidence that THs play a direct role in regulating the metabolism of brown adipose tissues and skeletal muscles (López et al. 2013).

Primate males and females normally differ in their strategies to achieve and maintain social dominance which, as reviewed by Cavigelli & Caruso (2015), results in dominant males having elevated metabolic demands due to the costs of competition over access to mates, especially during periods of social instability, whereas exclusion of quality food sources entails reduced energy intake, particularly for subordinate females. Accordingly, one may predict that dominant males and subordinate females will probably exhibit high GC but low T3 levels. Fecal glucocorticoid and fT3 concentrations across sex and dominance status in adult and subadult GHLTs were statistically indistinguishable. Such an absence of a dominance status effect is consistent with studies on free-ranging male and female GLTs, at least with respect to fGC metabolites (Bales et al. 2005, 2006). Furthermore, the pattern for fGCs coincides with a hierarchy system, commonly attributed to cooperatively breeding species, where subordinates are not subjected to high rates of aggression and usually rely on close kin support (Abbott et al. 2003). On the other hand, although not investigated here, it is likely that differences in fGCs in relation to female reproductive status may be present in wild GHLTs, as observed in several other primate species (e.g., Bales et al. 2005; Rimbach et al. 2013; Dias et al. 2017). To address such question and more accurately define reproductive condition in females, GC measures should be accompanied with the determination of estrogen conjugates and pregnanediol glucuronide (De Vleeschouwer et al. 2000; French et al. 2003).

During group monitoring, it was observed that the MRO group was going through various changes in composition which initiated with the death of the eldest dominant male, then the emigration of females and finally, the disintegration of the group with a single subordinate male using the original home range and attempting to enter a neighboring group. Considering such a dramatic and likely stressful group dynamic, one may presume higher fGC levels in MRO than in the other two groups. This was not the case for fGCs, but it was for fT3 levels. The significantly higher level of fT3 in MRO may point to the potential influence of ecological factors, such as the availability of space and associated access to food and shelter. Previous studies on GHLTs have reported differences in home range and feeding behavior among groups using distinct habitats (Oliveira et al. 2011; Costa et al. 2020), as may be generally expected. Coutinho (2018) who worked with three of our study groups during an earlier period, showed that groups have a substantial proportion of overlapping home range and differ in the time devoted to feeding on plants and animals. This requires additional investigation into the extrinsic factors that may potentially lead to constraints in energy intake and explain this variation in metabolic rate between groups.

CONCLUSION

This study validates the measurement of GC and T3 metabolites in wild GHLTs' fecal samples, employing two commercial EIA kits. It also provides further evidence that biological validation of hormonal measurements in wild individuals is an effective alternative to traditional pharmacological challenges, provided the tested factors are carefully considered. Taken together, the results show that fGCs respond to the stress of capture and possibly, under acute stressors, downregulate fT3 levels. While fT3 responded to changes in body condition and therefore may have a more direct connection to energetic challenges.

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Author details: R. Fiorini-Torrico was a PhD student in the Postgraduate Program in Ecology and Conservation Biology (PPGECB) at the State University of Santa Cruz. He is currently a postdoctoral researcher at the same institution and the research coordinator of Project BioBrasil. L.C. Oliveira is an adjunct professor in the Science Department at the State University of Rio de Janeiro and an associate professor in PPGECB. D. Escribano is a postdoctoral researcher in the Animal Production Department and the Interdisciplinary Laboratory of Clinical Analysis (Interlab-UMU) at Murcia University. J.J. Cerón is a full professor in the Animal Medicine and Surgery Department at Murcia University and the leader of Interlab-UMU. K.M. De Vleeschouwer is a senior research coordinator at the Antwerp ZOO Centre for Research and Conservation (CRC) and the director of Project BioBrasil.

Author contributions: R. Fiorini-Torrico conceptualized the research goals, collected the samples and data, conducted the formal analysis, and wrote and edited the manuscript. L.C. Oliveira supervised the project execution and provided critical reviews and commentary. D. Escribano contributed to lab analysis, supervised sample collection and lab techniques, and reviewed and commented on the manuscript. J.J. Cerón supervised lab work, provided essential lab resources, and offered critical reviews and suggestions. K.M. De Vleeschouwer supervised research activities, provided necessary field resources, and reviewed and commented on the manuscript.

Acknowledgments: The authors thank Dr. Laurence Culot and Dr. Marina Salas for their valuable input on earlier drafts of this manuscript. They also thank Project BioBrasil and the involved private owners, Interlab-UMU, the Applied Ecology and Conservation Lab (LEAC), and the Bicho do Mato Research Institute for supporting this project. Finally, they thank Igor Inforzato, Sofia Bernal and Camila Andrade for their crucial help with sample and data collection during captures.

Mr. Jatishwor Singh Irungbam, Biology Centre CAS, Branišovská, Czech Republic.
Dr. Ian J. Kitching, Natural History Museum, Cromwell Road, UK
Dr. George Mathew, Kerala Forest Research Institute, Peechi, India
Dr. John Noyes, Natural History Museum, London, UK
Dr. Albert G. Orr, Griffith University, Nathan, Australia
Dr. Sameer Padhye, Katholieke Universiteit Leuven, Belgium
Dr. Nancy van der Poorten, Toronto, Canada
Dr. Kareen Schnabel, NIWA, Wellington, New Zealand
Dr. R.M. Sharma, (Retd.) Scientist, Zoological Survey of India, Pune, India
Dr. Manju Siliwal, WILD, Coimbatore, Tamil Nadu, India
Dr. G.P. Sinha, Botanical Survey of India, Allahabad, India
Dr. K.A. Subramanian, Zoological Survey of India, New Alipore, Kolkata, India
Dr. P.M. Sureshan, Zoological Survey of India, Kozhikode, Kerala, India
Dr. R. Varatharajan, Manipur University, Imphal, Manipur, India
Dr. Eduard Vives, Museu de Ciències Naturals de Barcelona, Terrassa, Spain
Dr. James Young, Hong Kong Lepidopterists' Society, Hong Kong
Dr. R. Sundararaj, Institute of Wood Science & Technology, Bengaluru, India
Dr. M. Nithyanandan, Environmental Department, La Ala Al Kuwait Real Estate. Co. K.S.C., Kuwait
Dr. Himender Bharti, Punjabi University, Punjab, India
Mr. Purnendu Roy, London, UK
Mr. Saito Motoki, The Butterfly Society of Japan, Tokyo, Japan
Dr. Sanjay Sondhi, TITLI TRUST, Kalpavriksh, Dehradun, India
Dr. Nguyen Thi Phuong Lien, Vietnam Academy of Science and Technology, Hanoi, Vietnam
Dr. Nitin Kulkarni, Tropical Research Institute, Jabalpur, India
Dr. Robin Wen Jiang Ngiam, National Parks Board, Singapore
Dr. Lional Monod, Natural History Museum of Geneva, Genève, Switzerland.
Dr. Asheesh Shivam, Nehru Gram Bharti University, Allahabad, India
Dr. Rosana Moreira da Rocha, Universidade Federal do Paraná, Curitiba, Brasil
Dr. Kurt R. Arnold, North Dakota State University, Saxony, Germany
Dr. James M. Carpenter, American Museum of Natural History, New York, USA
Dr. David M. Claborn, Missouri State University, Springfield, USA
Dr. Kareen Schnabel, Marine Biologist, Wellington, New Zealand
Dr. Amazonas Chagas Júnior, Universidade Federal de Mato Grosso, Cuiabá, Brasil
Mr. Monsoon Jyoti Gogoi, Assam University, Silchar, Assam, India
Dr. Heo Chong Chin, Universiti Teknologi MARA (UiTM), Selangor, Malaysia
Dr. R.J. Shiel, University of Adelaide, SA 5005, Australia
Dr. Siddharth Kulkarni, The George Washington University, Washington, USA
Dr. Priyadarsanan Dharma Rajan, ATREE, Bengaluru, India
Dr. Phil Alderslade, CSIRO Marine And Atmospheric Research, Hobart, Australia
Dr. John E.N. Veron, Coral Reef Research, Townsville, Australia
Dr. Daniel Whitmore, State Museum of Natural History Stuttgart, Rosenstein, Germany.
Dr. Yu-Feng Hsu, National Taiwan Normal University, Taipei City, Taiwan
Dr. Keith V. Wolfe, Antioch, California, USA
Dr. Siddharth Kulkarni, The Hormiga Lab, The George Washington University, Washington, D.C., USA
Dr. Tomas Ditrich, Faculty of Education, University of South Bohemia in Ceske Budejovice, Czech Republic
Dr. Mihaly Foldvari, Natural History Museum, University of Oslo, Norway
Dr. V.P. Uniyal, Wildlife Institute of India, Dehradun, Uttarakhand 248001, India
Dr. John T.D. Caleb, Zoological Survey of India, Kolkata, West Bengal, India
Dr. Priyadarsanan Dharma Rajan, Ashoka Trust for Research in Ecology and the Environment (ATREE), Royal Enclave, Bangalore, Karnataka, India

Fishes

Dr. Topiltzin Contreras MacBeath, Universidad Autónoma del estado de Morelos, México
Dr. Heok Hee Ng, National University of Singapore, Science Drive, Singapore
Dr. Rajeev Raghavan, St. Albert's College, Kochi, Kerala, India
Dr. Robert D. Sluka, Chiltern Gateway Project, A Rocha UK, Southall, Middlesex, UK
Dr. E. Vivekanandan, Central Marine Fisheries Research Institute, Chennai, India
Dr. Davor Zanella, University of Zagreb, Zagreb, Croatia
Dr. A. Biju Kumar, University of Kerala, Thiruvananthapuram, Kerala, India
Dr. Akhilesh K.V., ICAR-Central Marine Fisheries Research Institute, Mumbai Research Centre, Mumbai, Maharashtra, India
Dr. J.A. Johnson, Wildlife Institute of India, Dehradun, Uttarakhand, India
Dr. R. Ravinesh, Gujarat Institute of Desert Ecology, Gujarat, India

Amphibians

Dr. Sushil K. Dutta, Indian Institute of Science, Bengaluru, Karnataka, India
Dr. Annemarie Ohler, Muséum national d'Histoire naturelle, Paris, France

Reptiles

Dr. Gernot Vogel, Heidelberg, Germany
Dr. Raju Vyas, Vadodara, Gujarat, India
Dr. Pritpal S. Soorae, Environment Agency, Abu Dubai, UAE.
Prof. Dr. Wayne J. Fuller, Near East University, Mersin, Turkey
Prof. Chandrashekher U. Rivonker, Goa University, Taleigao Plateau, Goa. India
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Dr. Susan Cheyne, Borneo Nature Foundation International, Palangkaraja, Indonesia
Dr. Hemanta Kafley, Wildlife Sciences, Tarleton State University, Texas, USA

Other Disciplines

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Dr. Mandar S. Paingankar, University of Pune, Pune, Maharashtra, India (Molecular)
Dr. Jack Tordoff, Critical Ecosystem Partnership Fund, Arlington, USA (Communities)
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Journal of Threatened Taxa is indexed/abstracted in Bibliography of Systematic Mycology, Biological Abstracts, BIOSIS Previews, CAB Abstracts, EBSCO, Google Scholar, Index Copernicus, Index Fungorum, JournalSeek, National Academy of Agricultural Sciences, NewJour, OCLC WorldCat, SCOPUS, Stanford University Libraries, Virtual Library of Biology, Zoological Records.

NAAS rating (India) 5.64

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Print copies of the Journal are available at cost. Write to:
The Managing Editor, JoTT,
c/o Wildlife Information Liaison Development Society,
3A2 Varadarajulu Nagar, FCI Road, Ganapathy, Coimbatore,
Tamil Nadu 641006, India
ravi@threatenedtaxa.org & ravi@zooreach.org

Journal of Threatened Taxa
www.threatenedtaxa.org

ISSN 0974-7907 (Online) | ISSN 0974-7893 (Print)

January 2026 | Vol. 18 | No. 1 | Pages: 28151–28262
Date of Publication: 26 January 2026 (Online & Print)
DOI: 10.11609/jott.2026.18.1.28151-28262

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