

# RESSALVA

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**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E  
BIODIVERSIDADE**

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**ECOLOGICAL, SOCIAL AND NUTRITIONAL DRIVERS OF PRIMATES'  
MOVEMENT**

**FELIPE SOARES BUFALO**

**Rio Claro – SP  
2026**



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MOVEMENT**

**Felipe Soares Bufalo**

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia, Evolução e Biodiversidade.

Orientador: Dra. Laurence Marianne Vincianne Culot

Coorientador: Dr. Luca Börger

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## RESUMO

Investigar os fatores que orientam o movimento animal é essencial para compreender processos ecológicos, mas os mecanismos de tomada de decisão envolvidos nesses deslocamentos são complexos e influenciados por múltiplos elementos. Primatas, devido à sua diversidade ecológica, capacidades cognitivas, e sistemas sociais elaborados, constituem excelentes modelos para examinar como animais integram informações bióticas e abióticas ao se deslocarem através do ambiente. Embora decisões de forrageio relacionadas à disponibilidade, qualidade e distribuição de recursos tenham sido centrais nas pesquisas sobre movimento, outras dimensões — como a estrutura do habitat, restrições energéticas, dinâmicas sociais e percepção de risco — também desempenham papéis fundamentais na determinação dos padrões de deslocamento diário. Apesar de avanços importantes na ecologia nutricional de primatas, ainda são poucos os estudos que investigam, de forma conjunta, como fatores ecológicos e sociais moldam os processos de tomada de decisão associados ao movimento. Nesta tese de doutorado, desenvolvemos uma perspectiva integrada sobre como recursos alimentares, junto a contextos ambientais, energéticos e sociais, moldam rotas diárias e o uso do espaço por primatas neotropicais. No primeiro capítulo, examinamos 14 espécies da América Central e do Sul para avaliar como diferentes tipos de recursos influenciam o planejamento de rotas. Mostramos que essas rotas emergem da interação entre ecologia alimentar e variabilidade espacial e temporal dos recursos, destacando a flexibilidade da cognição espacial em primatas. A partir desse panorama comparativo, no segundo capítulo, buscamos compreender melhor os fatores que influenciam e moldam rotas diárias, focando em uma espécie frugívora-faunívora ameaçada, o mico-leão-preto (BLT, *Leontopithecus chrysopygus*). Investigando os padrões de orientação de trajetos diários ao longo da distribuição da espécie, mostramos que BLTs ajustam suas rotas para alcançar árvores de alimentação de forma eficiente em diferentes contextos ambientais. No terceiro capítulo investigamos como a distribuição e o valor nutricional dos frutos influenciam estratégias de forrageio de BLTs em florestas fragmentadas, revelando preferências por recursos mais energéticos e padrões diários e sazonais claros no consumo de frutos e presas animais. Por fim, no quarto capítulo exploramos como fatores ambientais, energéticos e sociais interagem no planejamento de rotas, mostrando que

BLTs combinam memória espacial com informações sobre habitat, disponibilidade de recursos, demandas energéticas e contexto social para navegar por fragmentos florestais complexos. De forma geral, nossos achados avançam significativamente a compreensão de como fatores ecológicos, sociais e nutricionais orientam de forma conjunta os processos de tomada de decisão que orientam o movimento e o uso do espaço em primatas neotropicais.

Palavras-chave: Ecologia de movimento, primatas não humanos, planejamento de rotas, processos de tomada de decisão, nutrição

## ABSTRACT

Disentangling the drivers of animal movements is crucial for a better understanding of ecological processes, but the underlying decision-making processes are complex and affected by many different drivers. Primates, with their ecological diversity and cognitively sophisticated social systems, provide valuable models for examining how animals integrate biotic and abiotic information during movement. Although foraging decisions linked to resource availability, quality, and distribution have been central to primate movement research, other dimensions—such as habitat structure, energetic constraints, social dynamics, and risk perception—are equally important determinants of daily travel. Despite substantial advances in primate nutritional ecology, fewer studies have addressed how these ecological and social factors jointly influence movement decisions. In this PhD thesis, we develop an integrated view of how food resources, together with environmental, energetic, and social contexts, shape the decision-making processes underlying daily routes and space use in Neotropical primates. In the first chapter, we assess at a broad comparative scale whether and how different resource types influence route planning across 14 primate species from Central and South America. Our results show that route planning arises from the interplay between feeding ecology and the spatial and temporal variability of resources, highlighting that primate spatial cognition is a flexible strategy attuned to ecological context. Building on this comparative perspective, the second chapter focuses on the endangered frugivorous-faunivorous black lion tamarin (BLT, *Leontopithecus chrysopygus*) to investigate how environmental conditions influence route planning within a species' distribution range. We show that BLTs adjust their daily routes to efficiently reach feeding sites under varying ecological contexts. In the third chapter we examine how the spatial distribution and nutritional characteristics of fruits shape BLT foraging strategies in fragmented forests, revealing preferences for energy-rich resources and clear seasonal and daily shifts in fruit and prey consumption. Finally, in the fourth chapter of this thesis, we explore how environmental, energetic, and social factors interact to shape route planning in detail. Through this integrated approach, we show that BLTs flexibly combine spatial memory with cues on habitat structure, resource availability, energetic demands, and the social landscape when navigating complex forest fragments. Overall, our results considerably advance our understanding

of how ecological, social, and nutritional factors jointly influence decision-making processes underlying movement decisions in Neotropical primates.

Keywords: Movement ecology, primates, route planning process, decision making processes, nutrition

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## **1. GENERAL INTRODUCTION**

Understanding the drivers and patterns of animal movement is a central focus of ecological research (Gable et al., 2023; Morales et al., 2010; Schmitz et al., 2023), and research in the past decades has markedly increased thanks to technological and analytical advances that have enabled increasingly precise tracking and behavioral analyses (Harrison & van de Waal, 2022; Joo et al., 2022). A key unifying approach to organismal movements is the movement ecology framework (Nathan et al., 2008), which conceptualizes observed movement paths as an outcome of the interactions between the internal state of individuals and the external environment (biotic and abiotic), conditional on their movement and navigational capacities.

A considerable number of studies have focused on primates, because their ecological diversity, complex social structures, varied diets, and advanced cognitive abilities provide valuable models for studying movement processes in natural environments (Abreu et al., 2021; Johnson et al., 2015; Strandburg-Peshkin et al., 2017; Trapanese et al., 2018). Although primate movement is strongly driven by the search for feeding resources, and resource nutritional properties, distribution, and availability often shape their spatial strategies (Boyer et al., 2006; Byrne et al., 2009; Garber & Porter, 2014; Porter & Garber, 2013; Reyna-Hurtado et al., 2018; Trapanese et al., 2019), movement decisions also emerge from the interplay of social dynamics, habitat structure, energetic constraints, and risk perception (Cordes et al., 2025; Fürtbauer et al., 2024). Increasing evidence shows that individuals adjust habitat use and associated movement in relation not only to where and when food can be found (Asensio et al., 2011; Ban et al., 2016; Davis et al., 2022; Salmi et al., 2020) but also to the distribution of conspecific groups (Sobral et al., 2023), canopy architecture (Davies et al., 2017; Harel et al., 2022), habitat disturbance (Hariharan et al., 2025), and risk perception (Suscke et al., 2021). However, the cognitive mechanisms that allow primates to integrate these diverse sources of information remain insufficiently explored (Janmaat et al., 2021). In this thesis, we investigate how ecological, social, and nutritional factors jointly influence the decision-making processes underlying route planning and spatial use in Central and South American primates.

Primates exhibit flexible diets that vary with environmental conditions, particularly in response to changes in resource availability and quality (Bicca-Marques et al., 2020; Izar et al., 2022; Tutin, 1999). Regardless of context, they must meet daily energetic and nutritional requirements by balancing macronutrient intake according to individual needs and resource patterns, achieving what has been termed the “intake target” (Felton et al., 2009; Simpson et al., 2004; Uwimbabazi et al., 2021). Understanding how species acquire and balance nutrients is fundamental to assessing the foraging effort required for daily maintenance (Davis et al., 2022). Moreover, investigating movement provides insights not only into spatial requirements but also into the cognitive processes guiding route planning and habitat use.

Considering that fruits, leaves, and animal prey differ markedly in their distribution and temporal availability in tropical environments (Leigh & Windsor, 1996; Morellato et al., 1989), and that primates vary in their reliance on these resources, in the first chapter of this thesis, we examine how different food types influence the decision making processes on route-planning across Central and South American primates from different feeding guilds. Specifically, we tested whether various resource types contribute equally to decision-making processes underlying daily movement patterns among species with different dietary strategies.

In addition to species differences, considerable intra-specific variation in the decision-making processes can also be observed. Across the range of a primate species, the decision-making processes can vary according to the environmental contexts to which individuals are exposed. Depending on the environment, we can expect some variation regarding the 1) nutritional content of the resources available, 2) availability and the distribution of such resources, 3) structure of the forest and the energetic demands for moving through it, and 4) density of individuals and inter-group social interactions. Therefore, in chapters 2, 3, and 4 of this thesis, we focused on an Endangered and arboreal frugivorous-faunivorous primate, the black lion tamarin (BLT, *Leontopithecus chrysopygus*), to investigate the influence of different environmental contexts on group decision-making processes. In chapter 2, we investigated what aspects of the environment and the social life of BLTs are responsible for directing their daily routes in four different areas, characterized by contrasting environmental contexts (i.e., an area of

continuous forest; a 370 hectares forest fragment, one 100-ha forest fragment, and an area of 615-ha of riparian forest).

In Chapter 3, we examined how the nutritional characteristics, spatial distribution, and seasonal availability of fruits influence the foraging strategies of BLTs in a 100-ha Atlantic Forest fragment. To address this objective, we combined detailed behavioral observations of a habituated BLT group with assessments of fruiting phenology, invertebrate biomass, and the nutritional composition of consumed fruits over two field campaigns conducted between 2022 and 2023. This integrative approach allowed us to evaluate how BLTs adjust their fruit consumption and prey foraging patterns across daily and seasonal contexts, providing insights into the nutritional and environmental factors shaping their feeding decisions in a fragmented and seasonally variable habitat.

Finally, in chapter 4, we used the new energy-based step selection modelling approach (Klappstein et al., 2022; Potts & Borger, 2022) to combine the nutritional aspects of the fruits consumed by a group of BLTs with other environmental (i.e., distance from forest edge, resource availability, canopy structure, perception of predation risk) and social factors (i.e., probability of presence of conspecifics, inter-group vocal activity) across seasons in a forest fragment, allowing a more complete and precise understanding of the decision-making processes in route planning and the consequent space used by BLTs.

Together, the chapters of this thesis provide a multiscale and integrative examination of the drivers of primate movement, linking broad comparative patterns to fine-grained ecological, social, and energetic processes within a threatened South American primate. By combining behavioral observations, nutritional and phenological assessments, spatially explicit models, and high-resolution tracking data, this research advances our understanding of how primates flexibly integrate information about social, environmental, and energetic factors when making daily movement decisions. In this manner, we aim to shed light on how interactions among feeding guild, environmental context, social dynamics, ecological constraints, and nutritional factors converge to shape route planning and space use in wild primates. Ultimately, this work contributes to a deeper mechanistic understanding of primate movement ecology and provides insights relevant to the conservation of biodiversity in increasingly fragmented and dynamic tropical landscapes.

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## **GENERAL CONCLUSIONS**

Understanding the mechanisms that govern animal movement is central to ecology and primates—widely studied for their cognition, sociality, and feeding ecology—offer exceptional opportunities to investigate these processes (Janmaat et al., 2021; Joo et al., 2022; Trapanese et al., 2018). Yet, despite extensive research, integrative assessments of how ecological, nutritional, and social factors interact to shape primate decision-making and route planning remain limited (Trapanese et al., 2018). In this thesis, we address this gap by examining movement processes across multiple scales. We begin with a broad, multispecies analysis of Central and South American primates to evaluate how feeding strategies and resource predictability influence movement patterns. Building on this comparative foundation and acknowledging species-specific and context-dependent variation in foraging decisions, we then focus on the Endangered frugivorous–faunivorous black lion tamarin (BLT, *Leontopithecus chrysopygus*) to investigate, across its geographic range, the factors influencing route-planning decisions. By combining cross-species comparisons with detailed field studies, nutritional assessments, and integrated movement modelling, we show that primate movement decisions emerge from the interplay between spatial memory and environmental knowledge, resource availability and distribution, habitat structure, risk perception, and social dynamics.

In the comparative analysis presented in the first chapter of this thesis, covering Central and South American primates with contrasting dietary strategies, we show that route planning is strongly linked to feeding ecology and the spatial predictability of resources. We found that species that explored patchy and temporally variable foods exhibited more directed daily routes and clearer signs of spatial optimization, whereas species exploiting more evenly distributed resources followed less structured trajectories. Together, these findings suggest that movement strategies are not rigid, species-specific traits; rather, they arise from an adaptive alignment between cognitive capacities, dietary demands, and the spatial heterogeneity of the environment.

By focusing on BLTs across ecological contexts that differ in resource availability, habitat structure, and social dynamics, the subsequent chapters of this thesis deepen this

understanding at a finer scale. When examining the factors guiding daily routes across environments ranging from continuous forest to narrow riparian habitat and small forest fragments, we found a consistent pattern: route planning was strongly shaped by the need to reach fixed feeding trees—fruits and gum feeding sites. We also found that BLTs relied on landmarks to varying degrees depending on habitat configuration. This use of recurrent route intersections for reorientation appears to support navigation toward important feeding sites while potentially reducing the cognitive costs of tracking numerous resource locations across large areas or emerging from spatial constraints or canopy discontinuity imposed by fragmented landscapes (Davies et al., 2017; McLean et al., 2016). Importantly, these results provide the first evidence of a landmark-based route network system in BLTs, showing that individuals adjust their travel paths according to the structure and predictability of the environment. This context-dependent flexibility highlights that route planning might arise as a dynamic behavioral response aimed at maintaining efficient travel and securing access to key nutritional resources under varying ecological conditions.

Although fixed feeding resources, such as fruits, consistently emerge as key elements guiding primate movement (Abreu et al., 2021; Asensio et al., 2011; de Guinea et al., 2019; Gómez-Posada et al., 2019; Janson, 2016; Nagy-Reis & Setz, 2017; Trapanese et al., 2019), not all resources offer the same energetic or nutritional value. Variation in resource nutritional composition and seasonal availability can strongly influence feeding decisions (Irwin et al., 2025; Joanna et al., 2024; Lauer et al., 2025). By providing a fine-scale assessment of the seasonal availability, nutritional composition, and spatial distribution of the main food items used by frugivorous–faunivorous BLTs (i.e., fruits and invertebrates), together with detailed observations of group behavior in a seasonal forest fragment, our findings reveal intrinsic foraging strategies shaped by nutritional and temporal dynamics. We show, for the first time, that BLTs preferentially targeted energy-rich fruits, increased prey foraging during the dry season when resources are scarcer and consumed high-energy foods early in the day—patterns that reflect a finely tuned balance between energetic demands and the spatiotemporal distribution of food resources. These results demonstrate that foraging strategies—and the movement decisions that support them—are influenced not only by the location of feeding sites but

also by the quality and seasonality of available resources and individual metabolic needs. This highlights the importance of integrating nutritional ecology and individual state with movement analyses to achieve a deeper understanding of how primates navigate, particularly in resource-limited and fluctuating habitats.

Finally, by integrating seasonal, high-resolution information of forest structure, resource distribution and quality, social cues, risk perception, and the energetic costs associated with movement into advanced movement models (Potts & Borger, 2022), we provide, in the last chapter of this thesis, a detailed understanding of how BLTs make fine-scale movement decisions within a seasonal forest fragment. In line with the importance of resource quality and distribution highlighted above, our results show that forest structure—captured by canopy height—and the spatial distribution of known, and likely preferred, fruit-feeding trees, consistently oriented movement across seasons. Additionally, associations between movement patterns and estimated energy expenditure were stronger during the rainy season, whereas social cues and risk perception—particularly alarm calls—became more influential in the dry season, when reduced canopy cover and lower resource availability may heighten perceived risk and inter-group competition. Together, these findings reveal a decision-making process that integrates spatial memory, habitat structure, perception of predation risk, and social information, demonstrating that BLT movement is shaped by a flexible interplay of ecological and social factors that shifts with seasonal dynamics.

Taken together, our findings illustrate how primates flexibly combine ecological, cognitive, and social information to navigate dynamic and heterogeneous environments. They also highlight the value of studying movement across scales—from cross-species comparisons to fine-scale seasonal analyses—to capture the full spectrum of behavioral strategies used by primates facing changing environmental pressures. In conclusion, this thesis demonstrates that primate movement is shaped by a dynamic integration of environmental, cognitive, social, and nutritional factors, with species and populations adjusting their strategies according to local conditions. For the black lion tamarin, this flexibility appears critical for navigating fragmented, seasonal habitats and securing access to key resources. By combining comparative approaches with detailed field studies and emerging analytical tools, this work contributes to a broader understanding of how

primates make movement decisions in complex landscapes and offers valuable insights for the conservation of species increasingly threatened by habitat loss and environmental change.

Looking forward, future research should investigate how individual-level differences—such as age, sex, reproductive state, or social rank—influence movement strategies within the same environmental context. For BLTs, examining whether individual experience and personality affect group decision-making, how learning shapes route fidelity and the use of landmarks across development, and whether groups differ in the extent and structure of their spatial knowledge would provide deeper insight into the cognitive and social foundations of route planning. Such information is fundamental for population management, particularly in the context of translocation or reintroduction programs. Moreover, linking fine-scale movement decisions to broader conservation outcomes remains essential. Understanding how primates navigate increasingly fragmented and human-modified forests, together with their feeding preferences and foraging strategies, can directly inform corridor design, habitat restoration, and protected area management. Integrating movement ecology with landscape genetics, population viability analyses, and long-term demographic monitoring will be critical for assessing how behavioral flexibility contributes to population persistence in rapidly changing environments. As landscapes continue to transform under the combined pressures of climate change and human activity, such research will be vital for predicting species responses and for developing conservation strategies grounded in a robust understanding of primate movement, cognition, and adaptability.

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