I. PROJECT TITLE, PRINICIPLE INVESTIGATOR AND LOCATION

Project Title: The Biomechanics of Arboreal Stability in Primates: An Integrated Analysis
Principle Investigator: Jesse W. Young, Professor, Dept of Anatomy and Neurobiology
Location: Comparative Biomechanics Laboratory, D103; Department of Anatomy and Neurobiology, NEOMED

II. ABSTRACT

Organismal biologists have long maintained a keen interest in the adaptations that allow some animals – such as primates – to successfully invade the small-branch arboreal niche, where maintaining stability is of paramount importance. Decades of comparative and experimental research have identified *morphological features* (e.g., clawless grasping extremities and long, mobile tails) and *behavioral mechanisms* (e.g., the maintenance of a low and flat center of mass and the use of distinctive gait patterns) that arguably facilitate stability on narrow and compliant substrates. Although these studies have greatly expanded our knowledge of primate locomotor adaptation and evolution, we nonetheless have an incomplete understanding of the mechanisms by which primates actually keep balance during arboreal locomotion. This research will remedy this gap in our understanding by testing a novel mechanical model that relates postcranial anatomy, grasping performance, and locomotor behavior to direct measures of balance performance on narrow substrates. Project research will focus on a previously collected dataset on locomotion in rhesus macaque monkeys (*Macaca mulatta*), in which synchronous kinematic, kinetic, and whole-body mechanical data during locomotion were measured during movement on simulated arboreal substrates. Analyses of these data will be compared with existing data on locomotor stability in squirrel monkeys (*Saimiri boliviensis*), marmoset monkeys (*Callithrix jacchus*), and gray tree squirrels (*Sciurus carolinensis*) to better understand the adaptive significance of typical primate morphology and quadrupedal locomotor behavior.

III. BACKGROUND AND RATIONALE

The origins and subsequent diversification of primates are intimately linked with arboreality. The arboreal habitat is inherently discontinuous, multidimensional, and frequently unstable. Arboreal primates therefore face a host of locomotor challenges not encountered by more terrestrial mammals – a fact attested to by the frequency of long bone fractures due to falling in free-ranging arboreal primates. Decades of comparative and experimental research have identified *morphological features* (e.g., clawless grasping extremities and long mobile tails) and *behavioral mechanisms* (e.g., the maintenance of a low and flat center of mass and the use of distinctive gait patterns) that arguably facilitate stability on narrow substrates. Nevertheless, despite the central role that concepts of stability have played in theories of primate locomotor evolution, we still lack direct measures of balance performance during arboreal locomotion. Without such data, we will be unable to fully explore the links between *morphology* (locomotor anatomy and behavior), *function* (the production of forces and torques) and *performance* (the maintenance of arboreal stability). Organizing research questions along this *morphology-function-performance* axis is a crucial step in establishing the adaptations.

IV. GOALS AND OBJECTIVES

The primary goal of this project is to use a newly developed mechanical model of arboreal stability and novel experimental techniques to explicitly test long-standing hypotheses about the adaptive nature of primate grasping and locomotor mechanics. The Young Laboratory has made significant progress over the past decade investigating the mechanical strategies primates use to maintain stability when moving across narrow substrates, demonstrating the unique roles for tail movements, grasping forces, and gait patterns in the maintenance of arboreal stability (Chadwell and Young 2015; Young et al. 2015; Young et al. 2016; Dunham et al. 2019; Dunham et al. 2020; Young et al. 2021). The research the summer fellow will carry out will continue this work through investigation of locomotor mechanics in macaques. Macaques are much larger than the previously studied species, outweighing squirrels, marmosets, and squirrel monkeys by an order of magnitude. Adding macaques to the dataset will provide valuable comparative data with which we will be able to understand how body size influences the mechanisms primates use to maintain arboreal balance.

V. INVESTIGATIVE METHODS

Integrated locomotor dynamics, including three-dimensional kinematics, single-limb force and torque production, and whole-body CoM mechanics were measured while monkeys were moving freely at steady speeds across 2.5cm, 5cm, and 10cm diameter PVC pipes. Locomotion was filmed with four high-speed cameras, two cameras on each side of the runway, allowing us to reconstruct three-dimensional movement trajectories for the whole animal, as well as code footfall patterns and other details of limb placement. Single-limb force and torque production and whole-body CoM mechanics were quantified using six custom-built force transducers.

VI. DATA ANALYSES

Locomotor data will be analyzed using ProAnalyst Motion Analysis software. Locomotor data will be combined with anatomical data on body mass distribution in macaques to quantify changes in whole-body angular momentum about the pole (our primary metric of stability) instantaneously during the stride. Subsequent data processing will be performed using custom MATLAB routines.

Our primary metric of stability during locomotion is the net change in angular momentum of the center of mass about the support (abbreviated as ΔL_{sup}). ΔL_{sup} is a direct measure of lateral stability – if ΔL_{sup} becomes too large, the animal will be unable to arrest its angular movement and will fall from the support. Additional metrics that will be calculated from the locomotor data include center of mass height and variability during the stride, and assorted measures of the stabilizing torques (i.e., twisting forces) that the animals apply to maintain balance.

Variation in locomotor measures associated substrate diameter, as well as possible associations between locomotor measures (i.e., between center of mass height and ΔL_{sup}) will be assessed using mixed-effects analyses of variance (ANOVA), analyses of covariance (ANCOVA), or regressions depending on the categorical or continuous nature of the predictor variables. The mixed-effects approach (Pinheiro and Bates 2000), allows us to appropriately adjust degrees of freedom and error terms to account for random variation among individuals and experimental days. All statistical analyses will be done using R data analysis software (R Core Team 2022).

VII. CONTRIBUTION TO OVERALL PROJECT

Analyses of macaque locomotor data will contribute to Young Lab research efforts over the past decade to understand the mechanistic underpinnings of primate arboreal stability (i.e., Chadwell and Young 2015; Young et al. 2015; Young et al. 2016; Dunham et al. 2019; Dunham et al. 2020; Young et al. 2021).. Potential research products will include 1) a student presentation at the annual NEOMED student research conference, 2) student authorship on a research presentation at the annual conference of the American Association of Biological Anthropologists, and 3) student authorship on an eventual manuscript summarizing research findings. Project data will also serve as pilot data to support future NSF grant applications.

Summer Research Fellow Training/Mentoring Plan

Over my 13 years at NEOMED, I have mentored scores of research trainees, seven postdoctoral research fellows, two graduate students, and 39 pre-doctoral trainees (i.e., medical students, undergraduate students, and high school students). I am committed to fostering a positive, rewarding research experience for all students in my laboratory. In the current context, this goal will be achieved through the mentoring program described below.

First, the fellow will be trained to participate in every phase data analysis, interpretation, and dissemination. This involvement will promote mastery of several skills necessary to accomplish holistic biomechanical research, such as the analysis of quantitative data and the use of common software packages (e.g., MATLAB, R, and ProAnalyst). Opportunities for medical students to gain experience with *in vivo* biomechanical research are rare, and the skills gained through involvement with this project should substantially broaden the fellow's expertise. Additionally, I will mentor the fellow in a structured literature review, providing the student with the necessary theoretical and empirical background to understand the impetus for our research and the chosen methodology for addressing the research questions. All project findings will be disseminated through presentations at professional conferences, peer-reviewed journal articles, and other scientific media. Where merited, the fellow will be given authorship on all presentations and publications relating to this project, even after the student is no longer actively working in my laboratory.

The student will be given the opportunity to participate in regular brown bag seminars and journals clubs sponsored by the NEOMED Skeletal Biology Research Focus Area. Additionally, the fellow will participate in all Young Laboratory meetings.

REFERENCES

Chadwell BA, and Young JW. 2015. Angular momentum and arboreal stability in common marmosets (*Callithrix jacchus*). Am J Phys Anthropol 156:565-576.

Dunham NT, McNamara A, Shapiro LJ, Phelps T, Wolfe AN, and Young JW. 2019. Locomotor kinematics of tree squirrels (*Sciurus carolinensis*) in free-ranging and laboratory environments: Implications for primate locomotion and evolution. Journal of Experimental Zoology Part A Ecological Genetics and Physiology 331:103-119.

Dunham NT, McNamara A, Shapiro LJ, Phelps T, and Young JW. 2020. Asymmetrical gait kinematics of free-ranging callitrichines in response to changes in substrate diameter and orientation. J Exp Biol 223:jeb217562. DOI:217510.211242/jeb.217562.

Pinheiro JC, and Bates DM. 2000. Mixed-Effects Models in S and S-PLUS. New York, NY: Springer.

R Core Team. 2022. R: a language and environment for statistical computing. 4.2.0, "Vigorous Calisthenics" ed. Vienna, Austria: R Foundation for Statistical Computing (https://www.R-project.org/).

Young JW, Chadwell BA, Dunham NT, McNamara A, Phelps T, Hieronymus T, and Shapiro LJ. 2021. The stabilizing function of the tail during arboreal quadrupedalism. Integr Comp Biol DOI: 10.1093/icb/icab096.

Young JW, Russo GA, Fellmann CD, Thatikunta MA, and Chadwell BA. 2015. Tail function during arboreal quadrupedalism in squirrel monkeys (Saimiri boliviensis) and tamarins (Saguinus oedipus). J Exp Zool A Ecol Genet Physiol 323(8):556-566.

Young JW, Stricklen BM, and Chadwell BA. 2016. Effects of support diameter and compliance on common marmoset (*Callithrix jacchus*) gait kinematics. The Journal of Experimental Biology 219:2659-2672.