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Introduction

The connection between food and foraging is a main theme in studies of feeding ecology.^{1,5} Individuals should seek foods that maximize energetic return while minimizing the energetic expenditure of travel.^{6,7} Accordingly, foraging behavior should have a direct relationship with energy gain. However, animals may shift their foraging behavior to reduce the cost of competition over limited resources,⁸ especially if they have low priority of access to highly sought-after foods.

The relationship between foraging and energy gain might be stronger for large and dominant primate consumers, though this is not the case for small and subordinate species. While large species may benefit from priority of access to energy-rich foods, small species seek alternative sources of foods to overcome food shortages.

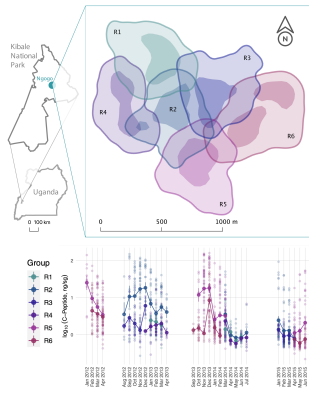
The effect of large-bodied competitors on smaller primate energy gain has never been measured directly. **Here we demonstrate the effect of inter-species feeding competition on foraging patterns and energy gain in red-tailed monkeys.**

Methods

Red-tailed monkeys in Kibale National Park, Uganda have a high degree of dietary overlap with chimpanzees (*Pan troglodytes*).⁹⁻¹³

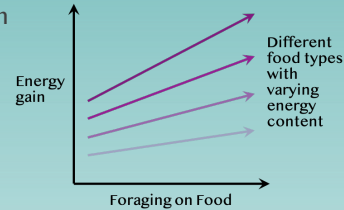
- Urine samples (N = 1271) collected noninvasively from 95 individuals.
- Phenology of preferred chimpanzee foods used as proxy for their presence and the competitive pressure they exert on red-tailed monkeys.¹⁴⁻¹⁹ Chimpanzee competition index was calculated as a subset of the habitat-wide phenology that included measurements made only within the each red-tailed monkey group home range.

- Foraging was recorded during group scans, conducted every half hour.
- Radioimmunoassay of C-peptide of insulin, a biomarker of energy.²⁰⁻²¹
- Specific gravity to standardize sample concentration.²²
- Set of multilevel models using an Information-Theory approach.²³
- Assessed C-peptide values with respect to percent time spent foraging on various food types (ripe and unripe fruit, flowers, young leaves, and insects).



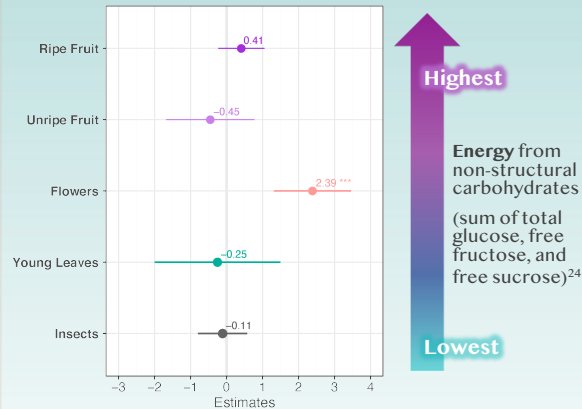
Prediction 1

Red-tail energy gain (C-peptide values) will increase when red-tails forage more on energy-rich foods



Results:

The effect of foraging on energy balance (C-peptide, ng/sg)



Red-tail monkey energy balance does not increase when foraging on energy-rich foods.
Ripe fruit, an energy-rich resource, does not contribute to red-tailed monkey energy gain.

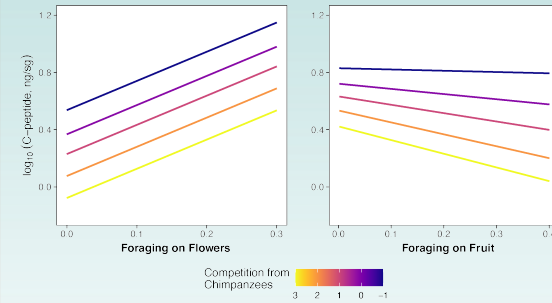
Prediction 2

Red-tail energy balance (C-peptide values) will decrease when they experience more feeding competition from chimpanzees

Predictors	Models						
	Null	1	2	3	4	5	6
All plant parts		*					
Ripe fruit		○	○	○			
Ripe and unripe fruit				○			○
Flowers					*	*	*
All other plant parts					*	*	*
Number of foraging scans		*	*	*	*	*	*
Chimpanzee competition index		○	○	○	○		
Random effects							
month of observation		:	:	:	:	:	:
group identity		:	:	:	:	:	:

Results:

The effect of competition on energy balance (C-peptide, ng/sg)



Competition from chimpanzees weakens the relationship between foraging and energy balance.

Though a high degree of competition reduces energy gain, red-tailed monkeys benefit by foraging on foods not sought out by a larger competitor.

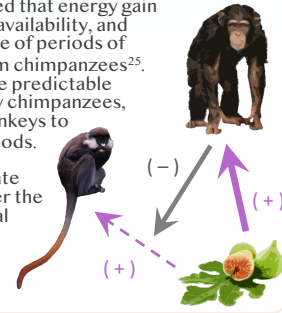
Conclusion

Our study demonstrates that foraging behavior is not necessarily indicative of energy gain for some consumers, largely due to between-species competition. We expected a positive relationship between fruit feeding and energy balance.

Substantial differences in body size may lead to asymmetries in access to preferred food resources. When larger competitors are present within a red-tail monkey home range and are foraging on high-quality foods, the smaller-bodied consumer gains energy only when feeding on foods not sought out by chimpanzees.

Our previous analysis of these red-tailed monkeys showed that energy gain does not follow food availability, and instead occurs outside of periods of high competition from chimpanzees.²⁵ This is likely due to the predictable pursuit of ripe fruit by chimpanzees, forcing red-tailed monkeys to forage on alternate foods.

These findings illustrate the need to reconsider the suite of environmental pressures that shape primate feeding strategies.



Acknowledgements

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