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Alexander D. Wright

Gary W. Barrett
gbarrett@uga.edu

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GOLDEN MOUSE (*OCHROTOMYS NUTTALLI*) AND WHITE-FOOTED MOUSE (*PEROMYSCUS LEUCOPUS*) DIETARY RESOURCE PARTITIONING UNDER EXPERIMENTAL FIELD CONDITIONS

Alexander D. Wright and Gary W. Barrett*

Eugene P. Odum School of Ecology
University of Georgia
Athens, GA 30602

*Corresponding Author: gbarrett@uga.edu

ABSTRACT

Ochrotomys nuttalli and *Peromyscus leucopus* are two small-mammal species that have similar life histories. This results in a relationship with a high degree of sociality between the two species, including extreme niche overlap. We investigated differences in diet preference and daily caloric intake under experimental field conditions in order to clarify this close relationship. Diets were based on reported food preferences in their natural environment. Five food resources were provided to 20 adult individuals (10 male, 10 female) of each species for three consecutive days. Individuals were contained in separate covered mesocosm tanks located in a riparian forest ecosystem. White-footed mice consumed more energy per day than golden mice (0.89 and $0.70 \text{ kcal} \cdot \text{g live wt}^{-1}$, respectively), which is considerably less (2.38 and $1.48 \text{ kcal} \cdot \text{g live wt}^{-1}$, respectively) than those reported by Gibbes and Barrett (1) when fed identical diets under controlled, laboratory conditions (22°C). This study also suggests that nest cavities and soundscape assist in mitigating environmental perturbations, such as food scarcity and predation, in their natural habitat.

Keywords: dietary resource partitioning, *Ochrotomys nuttalli*, *Peromyscus leucopus*, mesocosm, soundscape

INTRODUCTION

Past investigations of similar small-mammal species have examined the roles of competition (2, 3, 4), and niche partitioning (5, 6). However, only recently has ecological facilitation via shared resources been considered important among species of plants and animals (7, 8). This study queried how dietary resource partitioning might partially explain the coexistence of two species of small mammals with similar life histories. The golden mouse (*Ochrotomys nuttalli*) and white-footed mouse (*Peromyscus leucopus*) have similar life histories, body masses, nest-site preferences, food preferences,

periods of activity, home-range sizes, and are semi-arboreal (9, 10, 11). It has been shown, however, that the species differ in how they inhabit three-dimensional space with white-footed mice found more frequently at ground level and golden mice building globular or communal nests aboveground (2).

Additionally, these two species have been double-captured in the same live trap (13), and adult scrotal males have been observed in the same nest box together on different occasions (11). The competition exclusion principle (*i.e.*, that no two species can occupy the same niche) does not explain this observed coexistence and, therefore, their close social relationship in their natural environment warrants additional study. In a previous study (12), *P. leucopus* was removed from experimental grids to observe how its removal would affect *O. nuttalli* abundance. These researchers observed no significant difference in abundance between experimental and control grids. To further investigate the relationship, we addressed the differences in caloric intake and diet preferences in semi-natural conditions to quantify both small-mammal species' dietary behavior.

Several studies have compared the bioenergetics of white-footed mice (*P. leucopus*) and golden mice (*O. nuttalli*) under experimental laboratory conditions (1, 14, 15). However, this is the first comparative study quantifying the bioenergetics of these two species under field mesocosm conditions. We investigated the differences in caloric intake and diet preferences of both species by offering five different diets that are considered important in the diet of *O. nuttalli* and *P. leucopus* (9, 15, 16, 17, 18, 19, 20, 21, 22). All of these diets are abundant seasonally within our experimental site. Three of them, flowering dogwood fruits (*Cornus florida*), water oak acorns (*Quercus nigra*), and white oak acorns (*Q. alba*), are from native species. However, Chinese privet seeds (*Ligustrum sinense*) and staghorn sumac seeds (*Rhus typhina*) are from invasive species. We hypothesized that the three native diets would rank higher as dietary food preferences than the two nonnative diets, particularly *C. florida* and *Q. nigra* due to the caloric and food quality of these two diets. We also hypothesized that the animals fed under experimental field conditions would consume a higher caloric diet compared with the animals fed under laboratory conditions in the Gibbes and Barrett (1) experiment due to the much lower ambient temperatures experienced by the mice in their natural environment, and their endothermic nature.

MATERIALS AND METHODS

This study was conducted during spring, 2010, at the HorseShoe Bend (HSB) Ecology Experimental Research Site in proximity to Athens, GA (33°57' N, 83°23' W). HSB is a 14.2-ha forested peninsula created by the meandering North Oconee River. Five food resources, reported as important in the diet of *O. nuttalli* and *P. leucopus*, were collected in the fall of 2009, and then stored in a refrigerator before the feeding experiment. These diets were Chinese privet seeds (*L. sinense*), flowering dogwood fruits (*C. florida*), staghorn sumac seeds (*R. typhina*), water oak acorns (*Q. nigra*), and white

oak acorns (*Q. alba*). Table I summarizes the caloric values and percentage protein for each food item. Ten adults of each species (5 male, 5 female) were collected from nest boxes or live traps at HSB. At HSB each animal was released into one of five cylindrical mesocosm tanks (80 cm in diameter, 88 cm in depth) located in the forest riparian habitat. Each mesocosm tank was covered by a sheet of outdoor plywood, and contained a nest box (18.5 cm in width, 27.5 cm in length, and 20.5 cm in height), including nonabsorbent cotton (nesting material), situated in the center. Each nest box was positioned 5 cm above the bottom of the tank with a central entrance/escape portal (3.5 cm in diameter) located at the base of the nest box. Around the edge of the tank, located 72° apart, were five ceramic food dishes; each dish contained one of the five food items. Each animal was acclimated in the mesocosm tank, which included water and each diet, for 24 hours.

Table I. Summary of caloric values (Kcal • g live wt⁻¹ ± SD) and percentage protein for each food item based on 5 samples per diet.

Diet	Caloric value	Percentage protein
<i>Quercus nigra</i>	5.2 ± 0.17 ^a	3.99 ± 0.10
<i>Quercus alba</i>	3.6 ± 0.03 ^a	4.68 ± 0.07
<i>Cornus florida</i>	5.2 ± 0.12	7.90 ± 0.03
<i>Ligustrum sinense</i>	4.8 ± 0.13	10.46 ± 0.03
<i>Rhus typhina</i>	4.6 ± 0.18	5.93 ± 0.23

Note: After Gibbes and Barrett (1)

^aAcorn minus outer pericarp shell

Individual feeding studies were conducted for three consecutive days between 23 January and 6 April 2010 following the one-day acclimation period. At the beginning of each day, each of the five dietary options (~ 5 g per container, weighed to the nearest 0.1 g) was placed into the tank. After 24 h, the remaining food from each diet was weighed and recorded. Weight of the seeds and fruits remaining was subtracted from the weight of seeds and fruit initially placed in each dish to determine the amount of food consumed (Kcal • g live wt⁻¹ • day⁻¹). Five petri dishes containing 10 g of flowering dogwood and Chinese privet were placed in a drying oven at 40°C for 72 h to determine the water content in both diets. Ambient maximum/minimum temperature data were collected from the weather station at Athens-Ben Epps Airport (AHN). Thermometers also were placed in the mesocosm tanks to measure maximum/minimum temperatures inside the tanks. We followed guidelines approved by The American Society of Mammalogists for the Use of Wild Animals in Research (23) and The University of Georgia Animal Care and Use Committee (AUP #A2010 7-116).

This study was a “split-plot” design because we were interested in (a) comparing rates of ingestion for each small-mammal species and sex, and (b) the dietary preference and rate of ingestion for individual mouse. We performed an ANOVA to identify significant predictors of consumption (*i.e.*, species, sex, and diet). The criterion for statistical significance was $P \leq 0.05$.

RESULTS

The ranking of food preferences based on Kcal consumed ($\text{Kcal} \cdot \text{g live wt}^{-1} \cdot \text{day}^{-1}$) for male golden mice was water oak > white oak > flowering dogwood > Chinese privet > staghorn sumac, and for male white-footed mice the ranking of food preferences was water oak > white oak > Chinese privet > flowering dogwood > staghorn sumac. For female golden mice the food preference ranking was water oak > white oak > Chinese privet > staghorn sumac > flowering dogwood, and for female white-footed mice the food preference ranking was water oak > white oak > flowering dogwood > Chinese privet > staghorn sumac. The rate of ingestion for male *P. leucopus* (0.91 ± 0.18 SD $\text{Kcal} \cdot \text{g live wt}^{-1} \cdot \text{day}^{-1}$) was greater than male *O. nuttalli* (0.72 ± 0.12 SD $\text{Kcal} \cdot \text{g live wt}^{-1} \cdot \text{day}^{-1}$), the rate of ingestion for female *P. leucopus* (0.86 ± 0.22 SD $\text{Kcal} \cdot \text{g live wt}^{-1} \cdot \text{day}^{-1}$) was also greater than female *O. nuttalli* (0.68 ± 0.09 SD $\text{Kcal} \cdot \text{g live wt}^{-1} \cdot \text{day}^{-1}$). The average daily ambient high temperature for male *O. nuttalli* was 20°C and the average low was 4.1° C, and for female *O. nuttalli* the average high was 21°C and the average low was 4.8°C. For male *P. leucopus* the average high was 16.5°C and the average low was 4.9°C; for female *P. leucopus* the average high was 14.4°C and the average low was 3.5°C.

The most parsimonious model identified for these data indicated species and diet as the two statistically significant predictors of caloric consumption (the $P \leq 0.05$ level of significance). There was no significant interaction found between species and diet, indicating the two species of small mammals have similar preferences regarding the proportion of caloric consumption from each diet. *P. leucopus* consumed significantly more daily calories per diet on average than *O. nuttalli* (0.89 and 0.70 $\text{kcal} \cdot \text{g live wt}^{-1}$, respectively). *Q. nigra* was preferred to all other diets for both species, and *Q. alba* was preferred to *C. florida*, *L. sinense*, and *R. typhina* for both species (Fig.1).

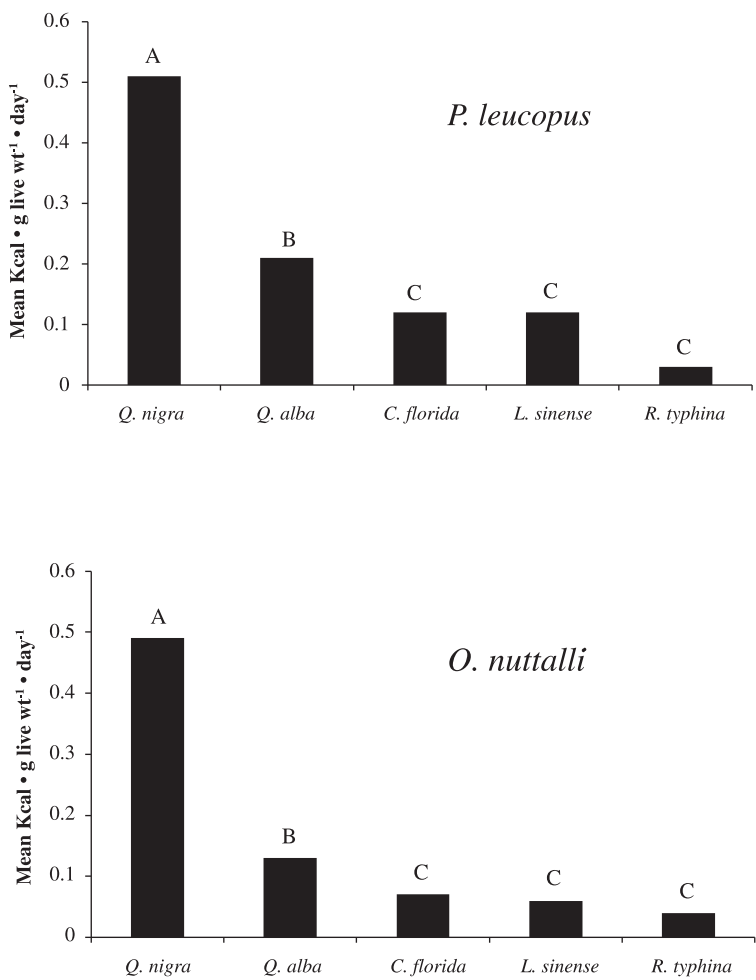


Figure 1. Bar graphs show dietary ranking for *P. leucopus* and *O. nuttalli* expressed as mean caloric intake (Kcal • g live wt⁻¹ • day⁻¹). Bars with letters in common are not significantly different ($P > 0.05$).

DISCUSSION

Several studies have focused on the bioenergetics of the white-footed mouse and the golden mouse (14, 15, 24, 25, 26, 27). Each of these studies was conducted under laboratory conditions, typically in metabolism units at room temperature (~ 20-22°C). Only Layne and Dolan (28) attempted to investigate bioenergetics of *O. nuttalli* in varying ambient temperatures and to compare these data with *P. leucopus*. The objective of our investigation was to compare the bioenergetics of *P. leucopus* and *O. nuttalli* under natural, mesocosm field conditions. We hypothesized that both species would exhibit

higher rates of food ingestion under natural ambient temperatures ranging from 4.1°C at night to 21.0°C during daytime hours.

To our surprise, the ingestion values were considerably less (0.89 and 0.70 Kcal • g live wt⁻¹ • day⁻¹) than those reported by Gibbes and Barrett (1) for *P. leucopus* and *O. nuttalli* (2.38 and 1.48 Kcal • g live wt⁻¹ • day⁻¹) when fed identical diets under controlled laboratory mesocosm conditions (22°C). These values, however, were similar to the ingestion values (0.82 and 0.61 Kcal • g live wt⁻¹ • day⁻¹ for *P. leucopus* and *O. nuttalli*, respectively) measured at 20°C by Knuth and Barrett (14). Table II is a summary of ingestion values for *O. nuttalli* and *P. leucopus* when fed a variety of diets under controlled laboratory conditions. Our study is the first to use a mesocosm established in a riparian forest habitat and exposed to natural ambient temperature conditions and functioning within a natural biophony soundscape (29).

Table II. Summary of ingestion values (Kcal • g live wt⁻¹ • day⁻¹) for *O. nuttalli* and *P. leucopus* based on a diversity of diets when fed under controlled laboratory conditions.

Treatment	Rate of ingestion	Diet	Citation
Grouped <i>O. nuttalli</i>	0.41	Husked sunflower seeds	25
Ungrouped <i>O. nuttalli</i>	0.50	Husked sunflower seeds	25
<i>O. nuttalli</i>	0.61	<i>Rubus frondosus</i> , <i>Prunus serotina</i> , <i>Zea</i>	14
<i>P. leucopus</i>	0.82	<i>mays</i> , <i>Lonicera mackii</i> , and <i>Rhus typhina</i>	14
<i>O. nuttalli</i>	0.80	Purina lab chow (75%) Sunflower seeds (25%)	24
<i>O. nuttalli</i>	0.09	Smooth sumac (1 year old)	27
<i>O. nuttalli</i>	0.95	Japanese honeysuckle berries	26
<i>O. nuttalli</i>	0.42	Eastern red cedar berries	26
<i>O. nuttalli</i>	1.06	Water oak acorns and	15
<i>P. leucopus</i>	1.72	Privet berries	15
<i>O. nuttalli</i>	1.48	Water oak and white oak acorns,	1
<i>P. leucopus</i>	2.38	staghorn sumac, privet seeds, and flowering dogwood fruits	1

Our rates of ingestion values (0.70 Kcal • g live wt⁻¹ • day⁻¹ for *O. nuttalli* and 0.89 Kcal • g live wt⁻¹ • day⁻¹ for *P. leucopus*) under field conditions were considerably less than those ingestion values reported by O'Malley *et al.* (15)

and Gibbes and Barrett (1) under controlled laboratory conditions (20-22°C). Individual mice of both species participating in our study, even under colder nocturnal conditions, collected water oak acorns (their diet of preference) and mostly consumed this dietary resource while in the their nest box; the nest-box cavity had numerous acorn shells each morning. *Q. nigra* shared the highest caloric value (5.2 Kcal • g dry wt⁻¹) of the five diets, while also an easily cached and consumed food resource. Over 90% of the assimilated energy by each species is used for respiration (14). Therefore, we hypothesized that under natural ambient temperatures (the average daily minimum temperature was 4.5°C for *O. nuttalli* and *P. leucopus*), individuals would have higher average rates of ingestion compared to individuals under controlled laboratory conditions of 20-22°C in order to maintain body temperatures necessary for important metabolic processes. However, that was not what we observed. The natural environment appears to have a different effect on the behavior of the study individuals. For example, both species spent less time foraging, though more time foraging cacheable diets and feeding in their insulated nest boxes. They also heard predators, such as owls, and instinctively sought refuge in the nest boxes. This observation helps to explain why these species of small mammals cache acorns in nest cavities during winter months - a strategy that provides a food resource during months of food scarcity, while avoiding avian predators in low foliage cover. We recommend that future bioenergetics or behavioral studies be conducted under natural field conditions.

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