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Influence of Resource Abundance on Echimyid Rodent Interactions

Casey A. Krause¹, Gregory H. Adler², Laxman M. Hedge³,
Erica H. Kennedy⁴, and Thomas D. Lambert^{1*}

Abstract - We studied inter- and intraspecific interactions between two morphologically-similar echimyid rodents *Proechimys semispinosus* (Tome's Spiny Rat) and *Hoplomys gymnurus* (Armored Rat) in central Panama. Due to their cryptic nature and nocturnal activity patterns, many aspects of the natural history of echimyids remain poorly documented, despite their being some of the most abundant mammal species in Neotropical forests. We performed paired behavioral trials with one individual having prior access to a resource during periods of resource abundance and scarcity. Species pairings demonstrated differences in aggression, but refuted seasonality and resource presence as main factors influencing aggression, suggesting other influencing factors.

Introduction

Aggressive interactions are energetically costly and risky; thus, individuals increase their fitness by avoiding direct hostilities. Dominance hierarchies, both within and between species, help to reduce the frequency and intensity of agonistic interactions, thereby allowing individuals to assess the likelihood of winning the interaction before the interaction occurs. In seasonally-fluctuating environments, changes in the availability of a shared resource may alter species interactions and resource use (Barger and Kitaysky 2011, Correa and Winemiller 2014, Venner et al. 2011). When periods of resource scarcity occur, resource competition increases. During these times of scarcity, the strength of the dominance hierarchy is predicted to be greatest (Isbell and Young 2002, Michel et al. 2016, Sterck et al. 1997) and species may alter their use of the resource to reduce competition and overlap (Correa and Winemiller 2014, Pianka 1974). However, during periods of scarcity, the relative importance of resources to the individual is increased, and for non-social species, inter- and intraspecific encounters will become more frequent. The increase in the value of the resource might increase the likelihood of an aggressive interaction. Despite the theoretical predictions, studies have had mixed results when searching for a relationship between resource abundance and the strength of dominance hierarchies (Michel et al. 2016, Wikberg et al. 2013, Wright et al. 2014).

To test this relationship, we studied two species of echimyid rodents that are known to have similar resource use and overlapping habitats with seasonal variations in resource availability. These two species are *Proechimys semispinosus* (Tomes) (Tome's Spiny Rat) and *Hoplomys gymnurus* (Thomas) (Armored Rat). Both species are nocturnal and morphologically similar and often occur sympatrically in central Panama (Adler et al. 1998, Buchanan and Howell 1965, Endries and Adler 2005, Fleming 1971, Tomblin and Adler 1998). Due to the seasonality of their environment and main dietary resources, we predict that behavioral changes should occur between seasons. Previous studies have focused on

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encounters between the 2 species, demonstrating that the Tome's Spiny Rat is generally more aggressive than and behaviorally dominant to the Armored Rat during encounters (Alberico and Gonzales 1993, Dupre 2012, Dupre et al. 2015). While some seasonal comparisons have been made, such comparisons did not have a resource present (Dupre 2012, Dupre et al. 2015). However, anecdotal observations collected during a previous study showed increased aggression by the Armored Rat and potentially a reversal of the behavioral dominance when it had prior access to a resource. In this study, we examine whether there are seasonal differences in their encounters when a resource is present.

Methods

Data collection occurred during 2 consecutive wet (June and July, 2011 and 2012) and dry (January, 2012 and 2013) seasons in both Soberania National Park and Barro Colorado Nature Monument in central Panama. Central Panama experiences seasonality in rainfall, with an 8-month wet season from May to December, punctuated by an intense 4-month dry season from December through April, during which less than 10% of annual rainfall occurs (Windsor 1990). This seasonality results in predictable patterns in fruit and seed availability. From the end of the dry season into the beginning of the wet season, fruit production increases to where there is an abundance. This production decreases by the end of the wet season and beginning of the dry season, resulting in a period of severe resource scarcity (Adler 1998, Adler and Lambert 2008, Foster 1982, Poulin et al. 1999). Individuals of both species were captured for behavioral trials using Tomahawk Live traps (41 X 13 X 13 cm), handling and trapping techniques following the American Society of Mammalogists' guidelines (Sikes et al. 2011). Traps were checked every morning and captured rodents were identified, sexed, weighed, and fitted with numbered ear tags for individual identification. Individuals that were to be used in the behavioral trials were then taken to a protected holding facility where they were kept separately in covered cages and provided with fresh plantain. The rodents were brought back to the holding facility at around mid-day; thus, individuals were not held without access to food for no more than a few hours (time of capture until approximately noon). Individuals were kept no longer than one night to reduce the harmful effects of stress. Individuals were used in the behavioral trial only once, recaptured individuals were immediately released, ensuring that subjects involved in the study were experiencing a novel situation.

Behavioral trials were conducted by selecting 2 individual rodents, placing them in an enclosure separated by an opaque barrier for a 5' acclimation period, during which time one individual had access to a food resource. After the acclimation period the barrier was removed, and interactions were recorded for a 20' trial period. These dyadic behavioral trials were performed starting 1 hour after sunset in a 93 X 84 X 77 cm Plexiglass® enclosure. This enclosure consisted of 4 sides with an open top and bottom and an opaque partition to separate the rodents at the start and end of each trial. The open bottom was placed on natural substrate, such as mowed grass or bare earth. The open top allowed for trials to be video recorded with a camera (DCR-TRV22; Sony Co.) and infrared light (SL-20IR; Sima Products Co.) stabilized on a tripod above the enclosure. Pairings were determined based on what species were caught the night before and how many of each type of pairing had previously been performed. Which individual had initial access to the resource was randomly selected. Due to their year-round availability and consumption by both species, ripe plantains (*Musa* sp.) were used as the resource in the trials.

After video recording the trials, the videos were analyzed for three specific interactive behaviors using the coding program, Noldus: Observer XT program (8.0, Noldus Informa-

tion Technology). Due to the different lengths of time for each trial, standardization of the behavior counts was performed. The raw count for each behavior was standardized by dividing the count by the trial duration in seconds and multiplying that by 10,000 (e.g., Dupre 2012, Dupre et al. 2015). Each behavior was defined by specific movements and the directionality of those movements. For each behavior, one bout was counted by the initiation of that behavior after a period of no movement, immediately after ceasing the actions of a different behavior, or if that behavior was being performed and stopped for 5" before restarting. If the behavior lasted longer than 10", it was counted as a bout and as a new bout for every 10" increment that it continued.

The three main behaviors analyzed were aggression, retreat, and approach, with aggression being the focal behavior (e.g., Dupre et al. 2015) (Table 1). Behavioral rates were compared using 8 explanatory variables, by both bout and individual. For individuals, the 8 explanatory variables were categorized as whether the individual had the resource (yes or no), the species of the individual (Tome's Spiny Rat (Ps) or Armored Rat (Hg)), the season in which that trial took place (wet or dry), the type of pairing in which that individual participated (Ps/Ps, Ps/Hg, or Hg/Hg), the individual's age (young or adult), the individual's sex (female or male), their weight difference class based on the weight difference between the two rodents in that trial (WDC) (1 = 1–75 g, 2 = 76–150 g, and 3 = 151 g +), and whether the individual was reproductive (reproductive or non-reproductive). The explanatory variables for the bouts of the behaviors were based on age of the pairings (young/young, young/adult, adult/adult), the sex of the pairings (male/male, male/female, female/female), and the reproductive state of the pairings (reproductive/reproductive, reproductive/non-reproductive, non-reproductive/non-reproductive).

Comparisons for each of the behaviors to the explanatory variables were made to determine if any of those variables influenced the frequency of the 3 behaviors during a trial. For instance, we wanted to determine if the pairing type caused different frequencies of aggression for each species. All behaviors were tested for normality using the Cramer-von Mises test. The data were non-normal due to the inflations in zero, so the non-parametric Kruskal-Wallis rank sums test was used to compare the behaviors, with each of the explanatory variables using an alpha of 0.05 to assess statistical significance (Dupre 2012, Dupre et al. 2015, Johnson 1999).

Table 1. Descriptions for each of the interactive behaviors performed by individuals during trials.

Behavioral Category	Description
Aggression	
<i>Lunge</i>	Rapid movement towards the other individual
<i>Mount</i>	To climb on the back of the other from behind
<i>Stance</i>	Standing on hind legs with paws in a boxing position. While in this position one can bite, "punch", or place its paws on the arms or shoulders of the other individual (Alberico and Gonzalez 1993)
Approach	To move within 2" of the other individual
Retreat	A responsive movement away from an immediate action performed by the other individual

Results

Of the 51 dyadic trials performed, 16 were interspecific, seven were paired Armored Rats, and 28 were paired Tome's Spiny Rats. Species pairing was the only explanatory variable with rate of aggression showing significant variation for individuals ($\chi^2 = 16.3070$, $df = 2$, $p\text{-value} = 0.0003$), and in bouts ($\chi^2 = 10.6960$, $df = 2$, $p\text{-value} = 0.0048$). Interspecific pairings had the highest mean aggression of 29.66 ± 72.78 , while Tome's Spiny Rat pairings had a mean of 2.27 ± 6.86 , and Armored Rat pairs had zero acts of aggression (Fig. 1). Levels of aggression were not different during interspecific bouts ($\chi^2 = 2.9376$ $df = 1$, $p\text{-value} = 0.0865$). However, post hoc testing demonstrated that the Tome's Spiny Rat was the more aggressive species based on a higher mean and a greater variance (Fig. 2).

Rates of aggression did not differ between seasons for either individuals ($\chi^2 = 0.9156$ $df = 1$, $p\text{-value} = 0.3386$) or in bouts ($\chi^2 = 0.7675$, $df = 1$, $p\text{-value} = 0.3810$). Retreat also did not differ between seasons for individuals ($\chi^2 = 0.1715$, $df = 1$, $p\text{-value} = 0.6788$) or in bouts ($\chi^2 = 0.1587$, $df = 1$, $p\text{-value} = 0.6904$). Approach was different between seasons, with higher rates during the dry season for both individuals ($\chi^2 = 6.0869$, $df = 1$, $p\text{-value} = 0.01362$) and bouts ($\chi^2 = 5.2250$, $df = 1$, $p\text{-value} = 0.02223$) (Table 2).

Discussion

Our findings supported previous studies in demonstrating that species pairings produced varying yet predictable levels of aggression (Alberico and Gonzalez 1993, Dupre 2012, Dupre et al. 2015). As predicted, the two species exhibited higher levels of aggression towards each other than they did intraspecifically. These findings suggest that interspecific encounters are more likely to result in aggression and consequently cost more to the individuals. Therefore, partitioning habitat between species would be more likely than within species. The higher level of aggression shown by the Tome's Spiny Rat also suggests that it is the

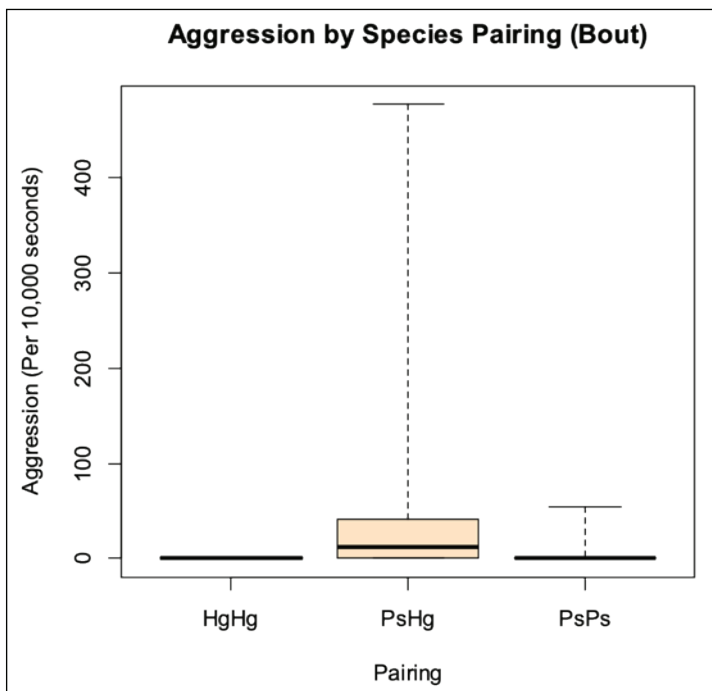


Figure 1. Number of aggressive acts per 10,000 second period for bouts within the three pairing types. Pairing types included Tome's Spiny Rat / Tome's Spiny Rat (PsPs), Tome's Spiny Rat / Armored Rat (PsHg), and Armored Rat / Armored Rat (HgHg).

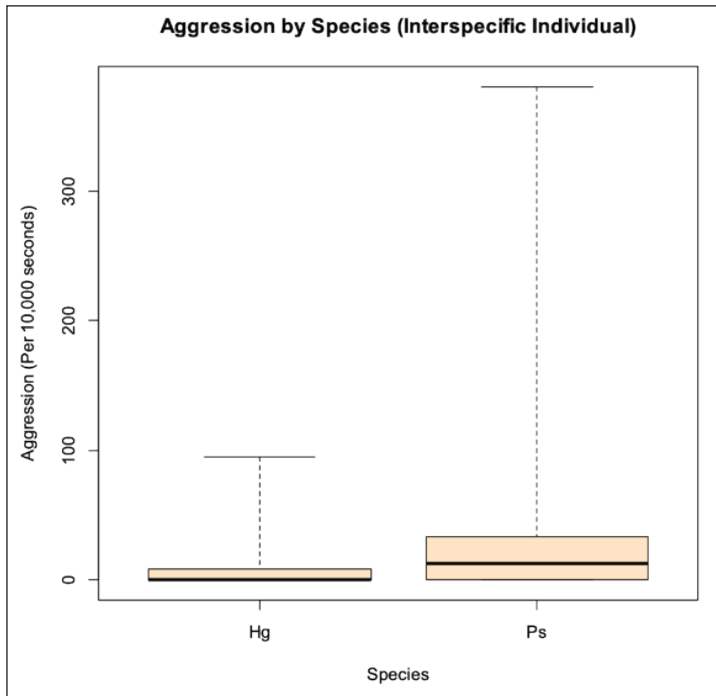


Figure 2. Box-plot showing the number of aggressive acts per 10,000 second period for individuals of the two species Tome’s Spiny Rat (Ps) and Armored Rat (Hg). Individuals scored were from interspecific pairings.

Table 2. Summary of the Kruskal-Wallis rank sum test for each of the three behaviors along with the eight explanatory variables and grouped by individual and bout. The explanatory variables were categorized as resource (yes or no), species (Tome’s Spiny Rat or Armored Rat), season (wet or dry), pairing (Ps/Ps, Ps/Hg, or Hg/Hg), age (young or adult), sex (female or male), weight difference class (WDC) (1 = 1-75 g, 2 = 76-150 g, and 3 = 151 g +), and reproductive (reproductive or non-reproductive). Bouts also included pairings of age (young/young, young/adult, adult/adult), sex (male/male, male/female, female/female), and reproductive state (reproductive/reproductive, reproductive/non-reproductive, non-reproductive/non-reproductive).

Test	Aggression		Approach		Retreat	
	Indiv.	Bout	Indiv.	Bout	Indiv.	Bout
Resource	p > 0.05		p > 0.05		p > 0.05	
Species	p > 0.05		p > 0.05		p > 0.05	
Season	p > 0.05	p > 0.05	p < 0.05*	p < 0.05*	p > 0.05	p > 0.05
Pairing	p < 0.05*	p < 0.05*	p > 0.05	p > 0.05	p > 0.05	p > 0.05
Age/Pairing	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p < 0.05*	p > 0.05
Sex/Pairing	p > 0.05	p > 0.05	p > 0.05	p < 0.05*	p > 0.05	p > 0.05
WDC	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05
Repro/Pairing	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05

more aggressive of the two species. If their current habitat were to drastically change, we could expect the more aggressive Tome's Spiny Rat to competitively exclude the Armored Rat through interference competition, due not only to their higher levels of aggression but also to their more generalized use of habitat (Adler 1996, Fleming 1971).

Seasonality did not alter the interactions of the two species in terms of aggression or retreat. This result suggests that these species have different strategies to reduce overlap during resource-limited periods and therefore do not need to be aggressive. Individuals did, however, show an increase in approach during the dry season. This form of behavior is considered investigative because they are shortening the distance between each other while not demonstrating aggression. This behavior could be performed either to gain information about the other individual or to demonstrate affiliation (Moy et al. 2004). The lack of changes in aggression due to seasonal fluctuations in resources suggests that stabilizing strategies have already been developed to maintain coexistence. Subordinate species use subtle changes in behavior and use of space to avoid direct conflict over resources (Monterroso et al. 2020, Vanak et al. 2013). It is possible that similar mechanisms are at work here, and further investigation into which strategies are used and how these strategies change with season should be conducted.

Continued research on resource partitioning strategies for both species would further assist in understanding interspecific relationships. Studies using more controlled environments should also be performed to determine if fluctuations in certain resources alter how individuals interact with one another. Research should aim to understand each species' intraspecific regulatory behaviors. Not only does more research need to be conducted to understand this specific relationship, but further understanding their ability to coexist could improve our understanding of species coexistence in general.

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