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Patch depletion used as an index of within-group scramble competition to investigate group size in Paraguayan black howlers (*Alouatta caraya*)

The ecological constraints model suggests that food patches are depleted in a manner related to group size, and larger groups experience more intragroup competition compared to small groups (Teichroeb and Sicotte 2009, Markham et al. 2015, Chapman et al. 2002). Due to the superabundance of leaves it has been traditionally presumed that folivorous primates do not experience within-group competition in a significant capacity, particularly in regards to limiting population size (Chapman and Rothman 2009) and it is this assumption from which the folivore paradox arises. This inference stems primarily from studies finding no relationship between group size and day range (Fashing 2001), as larger groups would be required to increase their daily travel distance to fulfill the nutritional requirements of the group members (Altmann 1974; Chapman 2000; Clutton-Brock and Harvey 1977). The existence of smaller folivorous primate groups living in an environment without food depletion contradicts the traditional socioecological model regarding the benefits of aggregation into larger groups. These include infant care such as the decreased infanticide by foreign males (Treves 2001) and defense against predation and intergroup competition (Aguiar et al. 2008). Meanwhile, the costs primarily originate from intragroup competition arising from limited resources (Markham et al. 2015). Prior to applying foraging models to the primates' behaviour it is essential to first determine whether food depletion is, in fact, absent (as the models suggest). The answer to this question may provide insight as to why some primates prefer smaller group size.

Snaith and Chapman (2005) found evidence of limited food and intragroup competition of red colobus (Procolobus rufomitratus) in Kibale. Their project design was based upon two predictions: (1) patch depletion will occur if food availability limits group size and (2) in a depletable patch feeding time will increase with group and patch size. Furthermore, their methods allow for the control of confounding factors such as satiation, an issue that has plagued other primatological studies such as Grether et al. (1992). Their results demonstrated that red colobus monkeys do deplete patches when feeding on young leaves and do experience within-group scramble competition. However, red colobus form large groups, therefore these

conclusions may not be representative of smaller folivorous groups. Tombak et al. (2011) conversely found lower food competition among guerezas (Colobus guereza), a folivorous species that form small groups. Their evidence indicates the guerezas satiate on young leaves and leave a patch prior to depletion, however within-group competition may still be a factor in the difference between red colobus and guerezas' group size. This evidence implies that current socioecological interpretations misrepresent the feeding habits and competitive characteristics of folivorous primates. Multiple studies have demonstrated the selective feeding of folivores, as seen in Asian colobines (Yeager and Kool 2000), guerezas feeding selectively on species with clumped distributions (Harris 2006), and howler monkey's preference for young leaves and high quality food items (Glander 1981). Identifying whether folivorous primates such as the *Alouatta caraya* experience patch depletion and within-group scramble competition is a step towards refining current socioecological models.

Howler monkeys (*Alouatta* sp.) are primarily folivorous yet they demonstrate selective feeding behaviour preferring young leaves, fruits, and flowers over mature leaves (Glander 1981) providing the opportunity for patch depletion and within-group scramble competition (Chapman and Chapman 2000; Janson and Goldsmith 1995). Patch occupancy (amount of time spent in a feeding tree, PO) and presence of preferred food items have been positively correlated in black howler monkeys (*Alouatta pigra*) (Plante et al., 2014). Furthermore, another study found that black-and-gold howlers (*A. caraya*) with larger group sizes compared to brown howlers (*Alouatta guariba clamitans*) travelled for a greater proportion of time (Agostini et al. 2012), suggesting the potential presence of food competition. Likewise, studies of mantled howler monkeys in Panama and Costa Rica have identified a relationship between howler group size and both food patch size (Leighton and Leighton 1982) and density of food resources (Gaulin et al. 1980). Therefore there is precedence for ecological constraint on group size in *Alouatta* species. Using the same methodology proposed by Snaith and Chapman (2005), two groups of black-and-gold howler monkeys (*Alouatta caraya*) living in separate habitats will be evaluated for presence of patch depletion and within-group scramble competition. Of the two group's habitats, one is an urban area consisting of local's gardens, a dirt road, and a grazing area for cows; the second consists of two isolated forest patches transected by a road. Investigation of the depletion and competition between the two groups will provide insight as to the impact of urban intrusion upon group size. If food availability is eliminated as a factor limiting group size, future studies of these two howler groups will have the opportunity to investigate the folivore paradox under a new light

with the findings of this paper in mind. Ultimately, this research will add to the growing discussion of factors underlying primate social organization in the face of current socioecological theory.

Methodology

We studied black-and-gold howler monkeys in two locations: Pilar (26°52'8"S, 58°17'36"W), the capital city of the Paraguayan department of Ñeembucú and Estancia Santa Ana (26°85’2”S, 58°04’2”W), a cattle ranch 27km outside of Pilar. These two sites lie within the Humid Chaco, and experience two primary seasons: summer (October - March) and winter (May - August).

Data collection occurred over 3 months in 2019, July to September, and groups were selected based on habitat type and ability to find them before they woke up. The group situated in Pilar are the “Police group”, whilst the group at Estancia Santa Ana are the “Santa Ana” group.

Data collection in a focal food patch (defined as a single tree) occurred opportunistically, beginning when monkeys were seen entering a patch to feed. Patch occupancy of a single tree was defined as total amount of time spent feeding in the tree over the course of the entire day and therefore began when the first monkey started eating in the tree until the last monkey to eat in the tree left. Once the first monkey left or finished eating, data collection continued with another monkey in the patch, with preference for adults. At every 5 minutes total number of individuals (group size) and number of individuals feeding (feeding group size) in the tree was recorded. Distance moved (meters) by the focal monkey every 3 minutes was recorded to represent feeding effort. Feeding gain was indexed as intake rate, measured by number of times a food item was put into mouth (bites) per 1 minute. Diameter at breast height (DBH) was recorded for every tree from which feeding data was collected and provided an indication of food abundance. Furthermore, percentage of tree covered by each food item (mature leaves [ML], young leaves [YL], flower [FL], seeds [SE], fruit [FR]) was visually approximated.

The null hypothesis that patch depletion is not present amongst the two groups of howler monkeys would be supported if there is no significant (or a negative) association between feeding effort and feeding gain. This suggest satiation is occurring, whereby decreased leads to decreased feeding gain. If patch depletion is present (the alternative hypothesis) feeding gain

(bites/min) is predicted to co-occur with a constant or increase in feeding effort (m/3 min). Patch depletion suggests the monkeys may be subject to within-group scramble competition, and this is predicted to manifest as a decrease in patch occupancy with increase in group size. Intake rate for the first and fourth quarter of every patch occupancy was calculated and compared using the Mann Whitney U test and Welch Two Sample t-test. All instances of patch occupancies with fewer than six data points for intake rate were excluded from analysis.

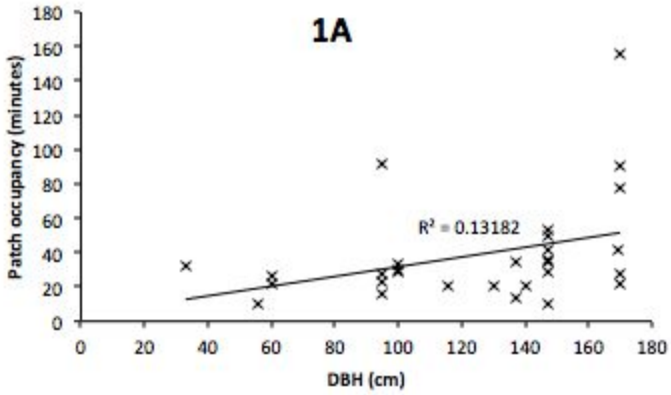
Scramble competition was examined by comparing feeding group size and patch size (measured as diameter at breast height) with patch occupancy. If scramble competition is a factor limiting group size, then group size and patch occupancy would be inversely proportional whereby an increase in the former would lead to a decrease in the latter. Likewise, scramble competition would cause a proportional relationship between patch size and patch occupancy. No relationship between these two variables and patch occupancy will support the null hypothesis that scramble competition is absent. The interaction between DBH, feeding group size, and patch occupancy were analysed according to a multiple linear regression.

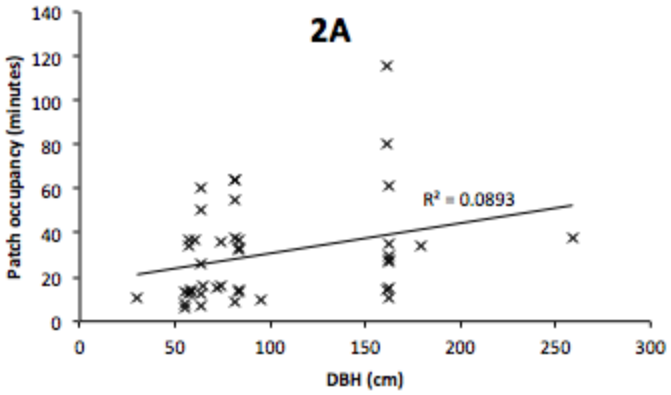
Results

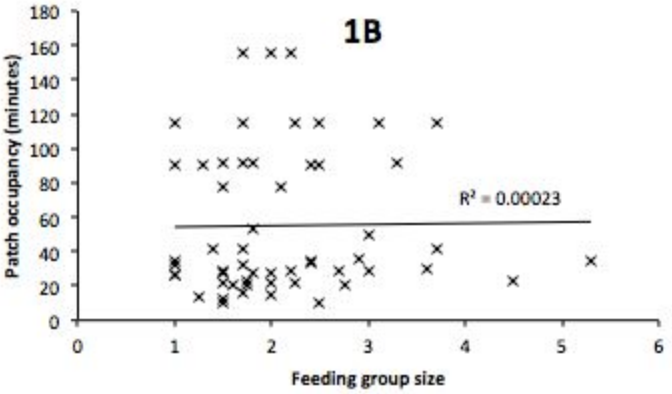
The Santa Ana group has a mean patch occupancy of 62 minutes, and consumed mature leaves for 12% of their time spent feeding, young leaves for 61%, flowers for 21%, seeds for 2% and fruit for 2%. This group had an equal percentage of tree cover of young leaves and mature leaves at 38%,19% for flowers, 3% for seeds, and 0.2% for fruit. Feeding group size ranged from 1 to 5 individuals, with an average of 2 monkeys feeding in a tree at the same time. Conversely, the Police group's mean patch occupancy was 48 minutes. They consumed mature leaves for 63% of their time feeding, young leaves for 16%, flowers for 6%, and no consumption of fruit. Feeding group size ranged between 1 and 6 with an average of 2 individuals.

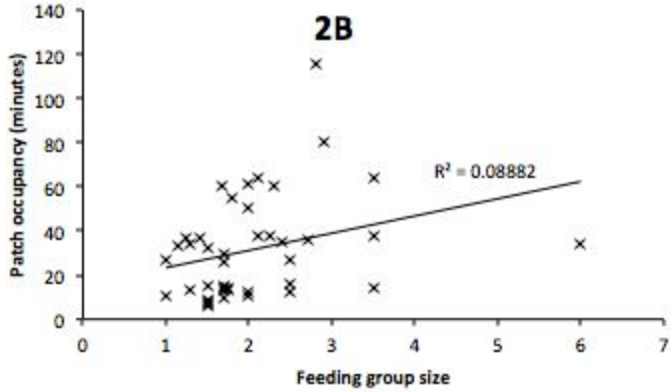
The Santa Ana howlers have a significant decrease in intake over the 1st and 4th quarter (start rate $x=3.07$ bites/min, end rate $x=2.23$, $p<0.03$). There is no significant difference between the distance moved in quarter 1 and 4. Likewise, the Police group also has a significant intake decrease between 1st and 4th quarter (start rate $x=7.47$ bites/min, end rate $x=5.57$, $p<0.01$). The distance moved between quarter 1 and 4 does not significantly change.

Within the Santa Ana group, a linear relationship exists between DBH, feeding group size, and patch occupancy according to residuals vs fitted plots. Whilst DBH has a significant impact on patch occupancy ($p<0.001$), feeding group size does not impact PO ($p=0.5$). However when *combined*, these variables together do have a significant impact on PO ($p<0.001$). The Police group howlers show a significant impact on PO for DBH ($p<0.001$), feeding group size ($p<0.001$), and these two variables combined ($p<0.001$). Though there is significance in both groups, the relationship is very weak, with R^2 values of 0.1 and below (Graph 1A, B, 2A, B).









Graph 1 Effect of (A) diameter at breast height (cm) of feeding tree and (B) feeding group size on Santa Ana group patch occupancy.

Graph 2 Effect of (A) diameter at breast height (cm) of feeding tree and (B) feeding group size on Police group patch occupancy.

Conclusion

The null hypothesis that howler monkeys do not deplete patches can be supported as food intake does not decrease as feeding effort remains constant or increases. With no significant

distance moved whilst feeding intake decreases, the howler monkeys are likely satiating themselves. The alternative hypothesis for within-group scramble competition stated that patch occupancy would decrease as group size increased. Within the Santa Ana group, feeding group size had no impact on patch occupancy. Police group, on the other hand, had a significant impact - however it was positive indicating that an increase in group size would also increase patch occupancy. Furthermore, this relationship was weak and as a result was not likely the main factor contributing to patch occupancy. The relationship between DBH and PO was both significant yet similarly weak to feeding group size, in both groups. This suggests that food abundance was also not a large factor contributing to patch occupancy, supporting the findings that patch depletion did not occur, and as a result the howler's do not experience within-group scramble competition.

The reasons for small group size amongst the howlers can not be attributed to ecological constraint according to the results of this study. There are, however, alternative reasons that can be speculated about, such as lack of intergroup competition. Both groups live in an location whereby they do not interact with other monkey groups. As a result, the protective benefit of large group sizes become redundant. There are also additional dangers facing these monkeys that a large group size would not protect against. Whilst the Santa Ana group are considerably less habituated than the Police group, both have territories transected by a road. This requires the monkeys to leave the canopies and run across the ground. I personally observed the entire Santa Ana group climb through a fence and run across the road - one monkey crossed just a few seconds before a car drove past. Whilst the Police group's road is used less frequently, they are considerably more exposed to humans, cattle, dogs, cats, and powerlines. These factors may have contributed to their smaller group sizes through mortality.

The folivore paradox, questioning why folivores live in small groups despite a presumed abundance of food, remains relevant when investigating Pilar's *Alouatta caraya*. This study has found they do not experience food depletion or within-group scramble competition, suggesting their group size is not ecologically constrained. This opens up other avenues of research to determine why they remain in smaller group sizes of 10-15, including home range size limitation, infanticide, or external dangers.

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