

UNIVERSITY OF CALGARY

The Nature of Intergroup Interactions in the Black Howling
Monkey of Belize

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Abstract

The socioecological model relates female social systems in a predictable manner to the distribution of resources in the habitat. Between group competition for resources is thought to be the main pressure affecting female social systems in primates. There is extensive evidence in support of this model in many primate; however, it does not account for the variance in others. Howling monkeys are generally thought to consume leaves: low quality abundant resources that are not associated with intergroup competition. Black howling monkeys (*A. pigra*) of Belize display high levels of between group competition, the function of which is not clear. The current study examines three hypotheses: resource defence, male mate defence, and female resistance to immigration. Results indicate that while resource defence is a partial function of between group agonism, male mate defence also plays a role. Female responses to encounters with solitary males indicate that infanticide pressure may also be a factor shaping howler social systems. Ecological pressures play a role in howler social structure, but are not acting alone. It is likely that several factors are contributing to the existing social patterns in black howling monkeys.

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Chapter 1: Introduction

In the past several years, evolutionary and behavioural theory in primatology has shifted from a focus on old-world species, to a broader perspective. It has become apparent with the growing number of studies on new world monkeys, that the socioecological model, which links environmental pressures in predictable ways to primate social structure, does not currently explain all of the reported variation in the social structure of new world species (Sterck et al. 1997). In particular, the genus *Alouatta* are reported to have aspects of social structure which are not explained by the current model. Being the best studied genus of new world primates to date, the genus *Alouatta* proves to be a challenging case, as their combination of habitat type, group structure, and female social systems seems to be an exception to the predictions of the model. Howlers feed on a wide variety of foods, which are believed to be evenly dispersed throughout the habitat. The socioecological model predicts low levels of competition between groups under these conditions. This, however, does not appear to be the case, as intergroup competition is widely documented for howling monkeys. Further research into the nature of intergroup conflict in

the genus *Alouatta* is necessary, in order to determine the function of intergroup agonism. This is a study of the nature of intergroup interactions in the black howling monkey (*A. pigra*) of Belize.

The socioecology model:

Primate ecology, and the current ecological, and socioecological models stem from early studies of primates which link environmental pressures to aspects of primate social structure. One early study of howling monkeys by Carpenter (1934) examines the habitat and social behaviour of howling monkeys. Crook & Gartlan (1966) argue that various environmental pressures can explain differences in social organisation. Crook and Gartlan's model established important connections and provided a framework for subsequent studies, and modifications of the ecological model. In a further development by Denham (1971), energy constraints were proposed as an explanation for various group sizes and compositions. The ecological model proposed by Wrangham (1980) suggests that the distribution of females -the sex that has higher investment in reproduction and offspring -will be determined by the distribution of resources. A female's reproductive success is dependent on her ability to reproduce and to ensure the survival of her

offspring. In order to ensure survival of her offspring, she and her offspring must have access to resources. The distribution of resources will thus affect the distribution of females.

In habitats where food is distributed evenly, and is abundant, groups are less likely to compete. In habitats where food is patchily distributed and defensible, female primates are expected to group together in order to cooperatively defend resources against neighbouring groups. In cases of high between group competition, females will form coalitions with kin in their natal groups and will be better able to defend resources than if they acted alone. Also, by forming coalitions with kin, females are ensuring that those who share their genetic material will also benefit, and this increases their reproductive success. The resulting female social structure is one of female residence where a stable dominance hierarchy exists, and is tied to kin relationships, referred to as a female-bonded social system.

The distribution of males is expected to be less driven by resource access, and more by the need to find breeding opportunities, as access to reproductive females

limits a male's reproductive success. Male distribution is thus a function of the distribution of females.

Van Schaik (1992) proposes a modification of Wrangham's (1980) model to include within group competitive regimes, incorporating the role of predator pressure on female social structure. The model is mainly discussed in the context of old world monkeys, in particular the cercopithecoid group.

Sterck et al. (1997) expand the model by including a discussion of additional selective pressures on females, such as infanticide and habitat saturation. The first modification suggested by Sterck et al. (1997) is to abandon the traditional terminology of female-bonded, and non-female bonded societies, in favour of new terminology which contains more specific information. Four types of social systems are suggested, based on levels of between group contest competition (BGC), and within group contest competition (WGC). Contest competition is direct competition between individuals for resources. This is contrasted with scramble competition which is indirect competition for access to an evenly distributed resource.

The following table (adapted from Sterck et al. 1997) demonstrates the four possible social systems suggested.

Table 1. Contest competition and resulting social strategies.

WGC	BGC	Social Response
Low	Low	Female dispersal-egalitarian
Low	High	Female resident-egalitarian
High	Low	Female resident-nepotistic-despotic
High	High	Female resident-nepotistic-tolerant

It is important to note that the four predicted social systems do not account for variation evident in many primate species, such as howling monkeys (Chivers 1969, Crockett and Eisenberg 1987, Glander 1992, Clarke et al. 1997), and gorillas (Stewart and Alexander 1987, Sicotte 1996).

Sterck et al. 1997 advance the possibility that factors other than resource distribution are influencing female social relationships, as not all social systems can be explained with the current ecological model.

Habitat saturation may lead to changes in the risk to emigrating females. A species that normally displays low BGC and female transfer may change to a resident system in a saturated habitat, due to increased competition between groups. In other words, if the habitat is saturated, low

BGC can become high BGC. If the habitat reaches maximum capacity, scramble competition may become so high that it approaches contest competition, causing BGC to become a factor. Groups would be resistant to immigrants, and may form coalitionary bonds to defend limited resources, or to collectively deter immigrants. A system of forced emigration may also result as it would be less costly to evict an individual than to allow the group to grow and for a natural group fission to occur.

Another factor which Sterck et al. suggest influences primate social systems is infanticide pressure. Infanticide has significant effects on the reproductive success of females it follows that females should develop defence strategies to minimize infanticide risk. Infanticide pressure may account for several aspects of primate social systems, such as permanent male-female pairs in gregarious primates, where females seek out the company of males who will act to defend females and offspring against potentially infanticidal males. Gorillas have a social system of permanent uni-male multi-female groupings which may support this hypothesis. Gorillas appear to have developed a dispersal system which virtually eliminates predation risk for transferring females, as transfers occur

directly between groups during intergroup encounters. (Stewart and Alexander 1987, Sicotte 1996).

Given that there is evidence for factors other than food distribution and abundance influencing the evolution of primate social systems, and that the ecological theory does not account for the variation observed in Howlers, it is likely that the BGC in howling monkeys is not simply a function of resource defence.

Between group competition:

As stated above, it is expected that primates who exploit a habitat that has defensible resources will show contest competition between groups. Direct contest competition in most cases takes the form of an agonistic intergroup encounter.

Behaviours during intergroup encounters vary between species. Vervet monkeys show active physically-aggressive defence of their relatively small home ranges, with both male and female participation (Cheney 1987). In contrast, mangabeys show high levels of range overlap, and rarely display agonistic behaviours between groups, and when contest does occur over such resources as fruiting trees, both males and females participate (Waser 1976). Encounters

between groups of mountain gorillas most often involve males displaying to extragroup males, while females and young actively avoid involvement (Sicotte 1996).

Certain behaviours are commonly associated with intergroup encounters, such as vocalisations or loud calls. While some species seem to lack such behaviours, such as Japanese macaques, a large number of species have characteristic loud calls (Cheney 1987). These often take the form of vocalisations that can act either to alert others to a group's presence and thereby, mediate spacing (Chivers 1969, Whitehead 1987a 1987b, Pope 1992) or to attract groups to actively compete for and defend a range (Terborgh 1983, Cheney 1987).

Further behaviours which may indicate between group contest competition include specific patterns of range use, and range overlap. Heavy use of range periphery, and low levels of range overlap are indications of group range defence (Cheney 1987, Fedigan, in press). However, it is important to note that while the ranging behaviour of primates may be an indication of high BGC, it is also tightly tied to the search for and exploitation of food

sources, and may therefore be a stronger indication of the distribution of food in the range, rather than BGC.

While the ecological model summarised above relates BGC with resource defence, it is possible that intergroup competition may also be a result of mate defence. van Schaik et al. (1992) indicate that intergroup agonism in S.E. Asian langurs is a function primarily of male mate defence, and secondarily, resource defence. Likewise, Steenbeek (1999) states that there are two major functions of between group competition, resource defence, and mate defence in wild homas langurs.

Intergroup encounters: the case of *Alouatta*

Several behavioural elements must be examined in order to fully understand the nature of intergroup behaviour in howling monkeys.

Vocalisations:

The most common behaviour associated with agonistic intergroup interactions in howlers is vocal behaviour. Several authors have documented the relationships between vocalisations and the spacing between groups (Chivers 1969, Gittins 1980, Sekulic 1982a,b, Larose 1993, Whitehead 1987a,b). An early observational study of howler vocal

behaviour by Chivers (1969), suggests that long calls of howlers signal others in the area as to the location of the group. Likewise, in listening to other groups' calls, the monkeys are better able to estimate the positions of other groups, thereby spacing themselves to minimise competitive costs, such as direct contest competition. Sekulic (1982a,b) later examined the seasonal variation in patterns of long calls and group spacing. It was determined that roaring was more frequent and intense during the dry season, when food was presumably more patchily distributed, suggesting a link between food competition and vocal interactions between groups. Gittins (1980) argues, however, that loud calls may alert neighbouring monkeys that the group is in a distant part of their range, allowing them to sneak into the range and exploit resources, and that long calls may instead function in mate defence. Experimental studies by Whitehead (1987a,b) show that recorded howler vocalisations of two different types consistently elicited different reactions from the monkeys when played back to them. Recorded long calls by males played back to a group of howlers caused males to withdraw from the area. This further supports the idea that vocalisations function to mediate space between groups in

the genus *Alouatta*, and specifically that vocalisations have the effect of repelling neighbouring groups.

All of the above studies also note that encounters between groups in close proximity resulted in more intense bouts of howling than those interactions occurred at a greater distance. Similar patterns of increased intensity of vocal behaviour with increased proximity have also been observed in the preliminary observations of a population of black howling monkeys in South-eastern Belize. Vocal behaviour is thus widely documented to be associated with between group competition in howling monkeys.

Ranging Patterns:

Range use by howlers is reported to vary. Peetz et al. (1992), report that a group of *A. seniculus* showed heavy peripheral range use, and increased core area use with increased incidence of predation on group members. A second group of *A. seniculus* (Sekulic 1982b), showed extensive use of the core area of their range, and had 63% overlap with ranges of neighbouring groups. Chapman (1990) reports primarily core-use ranging for *A. palliata*, with 57% of ranging occurring outside the core, but not concentrated on the periphery. Garcia-Chiarello (1993)

states that *A. fusca* used the range uniformly, and had a 22% overlap with neighbouring groups. The variation in patterns of range use reported for the genus *Alouatta* suggests that there is variation in intergroup competition between species. The range use observed in preliminary studies of the Belizean black howler show small ranges that are used uniformly.

Diet and Feeding Behaviour:

The diet of howling monkeys is consistently reported as folivore-frugivore. In most cases, the majority of the diet is composed of leafy material with some fruit consumption. Some researchers report a mainly frugivorous diet; this is, however, an exception to the general pattern. The following table summarises the reported diets for several species of the genus *Alouatta*.

Table 2: Majority and priority diets of various species of the genus *Alouatta*.

<u>Species</u>	<u>Main diet</u>	<u>Priority food</u>	<u>Source</u>
<i>A. seniculus</i>	Fruit, leaves	Bagassa fruit	Simmen 1992
<i>A. seniculus</i>	Fruit, leaves	Leaves	Julliot 1996, 1994

<i>A. caraya</i>	Fruit, leaves, flowers	Fruit	Oliveira-Filho & Galetti 1996
<i>A. palliata</i>	Leaves	Papilionacea	Bilgener 1994
<i>A. palliata</i> & <i>A. seniculus</i>	Leaves, fruit, flowers	Leaves	Crockett & Rudran 1987a,b
<i>A. palliata</i>	Leaves, buds, no fruit	Leaves	Tomblin & Cranford 1994
<i>A. caraya</i>	Leaves, exotic orange	Leaves	Bicca-Marques & Calegario-Marques 1994b
<i>A. palliata</i>	Leaves, figs, fruit	Young leaves	Chapman 1990
<i>A. palliata</i>	Leaves, fruit	Young leaves	Enqvist & Richard 1991
<i>A. palliata</i>	Leaves, Fruit	Young leaves	Estrada & Estrada 1986
<i>A. seniculus</i>	Leaves, fruit flowers	Young leaves	Braza et Al. 1983
<i>A. seniculus</i>	Leaves, fruit, flowers	Leaves	Ungar 1990
<i>A. seniculus</i>	Leaves, fruit, flowers	Young leaves	Julliot & Sabatier 1993

Preliminary observations of a population of black howlers in South-eastern Belize show that 82% of the material consumed was fruit (Chaput 1999, thesis). This figure varies greatly from the expected diet of mostly

leaves. The diet in this population of howlers suggests that the majority of food sources are fruiting trees which are defensible, and may be linked to high levels of between group competition.

Group Size:

In an analysis of the relationships between group size and food patch size, Leighton and Leighton (1982), found that the size of feeding parties of mantled howling monkeys was related to the size of the feeding patch. The larger the patch, the larger the group that exploited the patch. Smaller food patches were associated with smaller feeding aggregates, and higher levels of competition. Patch size must be gauged relative to group size. A patch that can accommodate all members of the group would be considered larger than one in which only a few members of the group are able to feed (Koenig et al. 1998). Howlers in Belize were found to reside in groups of 7 to 10 individuals (Chaput 1999, thesis). The groups generally foraged as a whole. They were not observed to have high levels of feeding competition within the group in the form of agonism, but some observations indicate a link between feeding and intergroup agonism.

Social Structure:

All members of the genus *Alouatta* are reported to live mainly in multi-male, multi-female groups, with a small portion living in smaller uni-female, uni-male groups (Crockett & Eisenberg 1987). Some researchers report sightings of solitary animals, both males and females; however, these cases are consistently reported to be individuals in the process of transferring to a new group (Clarke et al. 1997, Calegario-Marques & Bicca-Marques 1996). Patterns of transfer reported by Calegario-Marques & Bicca-Marques (1996), Glander (1992), and Crockett & Pope (1993) state that both females and males emigrate from their natal troops, with females being the more common emigrants. In the case of female emigration, the emigrant is usually evicted from the group, and before joining a new group, she must first become the dominant female. This pattern is not one that is common among old-world monkey species (Strier 1994). Sterck et al. (1997) argue that forced eviction of females may be a result of habitat saturation, and an indication of pressures affecting female social systems, other than resource distribution.

The social activity between howling monkeys within the group also vary from the general patterns predicted by the ecological model. Described as energy minimisers (Crockett 1987), howlers spend a relatively low proportion of time engaged in social activity and a large proportion of their time resting (Crockett 1987). Nevertheless, female howlers are reported to form stable dominance hierarchies, which are not nepotistic (Zucker & Clarke 1998).

There is evidence that reproductive success is related to the rank of a female, indicating that male howlers may breed preferentially (Clarke & Glander 1997). It is also possible, however, that increased reproductive success is due to increased resource acquisition, or acquisition of higher quality resources. In either case, the reproductive success of a female in an established group would be negatively affected with the immigration of a new female.

Observations of male howler interactions include low levels of social grooming, play behaviour, and agonism with a dominance hierarchy that is less stable than that of females (Zucker & Clarke 1986, Strier 1994b).

Little is known about the breeding patterns of *A. pigra*. In other howler species, it is reported that for *A. palliata*, and *A. seniculus* although breeding is not

seasonal, and births can occur in any month, there are often clusters of births in the dry season (Clarke et al. 1997, Clarke and Glander 1984)

For red and mantled howlers, obtaining and maintaining a position in a breeding group are crucial to high female reproductive success. Clarke and Glander (1984) indicate wide variance in reproductive success for female mantled howler monkeys (measured as percentage of surviving offspring), varying from 0 to 100%. The variation in reproductive success was linked to female rank. Mid-ranking females showed the highest rate of success. At the time of conception of the first infant, all the females in the study but one were top ranking. This indicates a high level of competition among females.

One pattern that appears to be common to howling monkeys is that of female dispersal. Transferring between groups is a high risk activity, as the threat of predation for a single animal is much higher than for a group member (Clarke et al. 1997, Glander 1992), and food sources are not as easily exploited alone (Leighton & Leighton 1982). There is also evidence that females do not willingly leave the natal group, but rather are evicted by resident adult females (Glander 1992). To enter into a new group, an

immigrating female must become dominant over all resident females, or she will not be allowed to stay by the resident females (Glander 1992, Zucker and Clarke 1998). The option of forming a new group with other emigrants, from different groups, does exist; however, it requires the formation of social bonds with strangers, and the population density to be low enough to allow for a new group's presence. Contrarily, it also requires that the population density must be high enough to produce an excess of females. Given the costs and level of difficulty associated with female emigration, and the fact that female rank is linked to resource acquisition, females should defend their rank, and discourage new immigrants. The limited number of positions in a group, once occupied, would be threatened by extra-group females.

This phenomenon may also be consistent with diana monkeys, who have a similar pattern of forced female emigration (Hill 1994). The analysis of territorial behaviour in diana monkeys indicates that females are the primary instigators of intergroup agonism, suggesting that females in this species may be defending access to limited breeding opportunities.

Overall, the social structure of howling monkey groups is very different from the common pattern of female philopatry, and male dispersal seen among the old-world monkeys (DiFiore and Rendall 1994). The unusual pattern of between group competition and female social systems seen in howlers indicates that functions of between group competition, other than just the defence of resources, may be a factor for the black howling monkey (*A. pigra*) of Belize. I observed intergroup interactions among the howling monkey population in the Monkey River Belize area in an effort to determine which of the following 3 functions between group competition might serve: Male Mate defence; Female resistance to immigration; Resource defence.

Male Mate defence:

The agonistic interactions between groups of black howlers may be a function of the males in a group defending their reproductive access to females from extragroup males. A limited number of females present in a group denotes a limited number of breeding opportunities for the males. Extragroup males (especially those who are not members of an established group) in proximity to the females in a

group threaten a resident male's access to those females. Males would then direct agonism toward extragroup males. This type of agonistic intergroup behaviour is seen among hamadryas baboons, and is suggested to be a major function of intergroup competition in langurs (Wrangham 1980, van Shaik 1996, Steenbeek 1999). The defence of breeding opportunities between males will involve males as primary actors, as their reproductive interests are at stake in the presence of extragroup males.

If the function of BGC is male mate defence, then I expect the following:

- A. Males are the initiators and primary participants in agonism between groups.
- B. Females are relatively inactive in such an encounter.
- C. The rate and intensity of intergroup agonism does not necessarily increase at or near defensible or monopolisable food sources.
- E. Incidence and intensity of male involvement in intergroup agonism is greater in interactions with solitary or extragroup males, than in encounters with established breeding groups.

Female resistance to immigration.

A limited number of females may successfully reside in a group at any given time. If new females immigrate, the rank of existing females is affected, and the reproductive success of females is also affected. Females may thus actively deter new immigrants, in order to maintain rank, and ensure reproductive success.

If intergroup agonism is a function of female resistance to immigration, I would expect that:

- A. Females are the initiators and primary participants in the agonism between groups. The defence of group position involves females as primary actors, as their reproductive interests are at stake in the presence of female competitors.
- B. Males are relatively inactive in such an encounter.
- C. The incidence and intensity of intergroup agonism does not necessarily increase at or near defensible or monopolisable food sources.
- D. Incidence and intensity of female participation in intergroup agonism will be greater in interactions with

solitary or extragroup females than with established breeding groups.

Resource Defence.

While howling monkey behaviour and social systems across the genus are not likely solely due to competition for resources, it is still a possibility in populations that feed on high quality, defensible resources. Preliminary observations of the study population indicate a high proportion of fruit in the diet. Fruit is a high quality resource, and seasonally fruiting trees are defensible.

If the function of between group agonism is resource defence, I expect the following:

A. Females are the initiators of agonism and both males and females engage in agonistic interactions when another group is present or in close proximity (van Shaik et al. 1992). The defence of resources is important to both sexes, as they both require food for survival however, females are more limited by resources due to higher investment in offspring, and so are more likely to initiate agonism.

B. An increase in the incidence and intensity of agonistic interactions will correspond to patchily distributed food sources, such as fruiting trees, in areas of range overlap.

C. The use of range periphery will be high, and the amount of overlap between ranges will be low: Fedigan (in press) shows that high use of range periphery is linked to resource defence in BGC.

Chapter 2, Methods:

Four groups of howling monkeys were followed and observed on a regular basis along the northern shore of Monkey River in Belize, west of the river mouth, and south of a road which runs parallel to the river. The area occupied by the groups is a semi-deciduous, flooded forest. The forest is relatively young, as the area was used as a banana plantation until 1950. Three additional groups were observed opportunistically during intergroup encounters. Both within and between group behaviour, as well as characteristics of the food supply were measured. Two researchers collected these three types of data (further detailed below) during the four-month period from January to May 2000. Initial location and identification of the groups was completed with the assistance of a local guide, from January 8-11, 2000, following which, the research team collected data Mondays through Fridays. Weekends were reserved for calculations and obtaining supplies. Each identified group of monkeys was sampled on a separate day, beginning January 12, 2000. On a daily basis, the team of researchers each located one group of monkeys, performed a direct count census, and collected

ten-minute focal animal behavioural data on all members of the groups. The target groups were sampled on a rotating schedule. Ecological line-transect censuses were conducted randomly throughout the ranges of the target groups. Researchers worked independently of one another, so as to maximise the probability of one researcher hearing, or witnessing an intergroup encounter. Researchers maintained contact via hand-held two-way radio. In the event of an intergroup encounter that only one researcher was present to witness, the second researcher was radioed to move to the location of the encounter. Due to the rarity of intergroup encounters, the observations during these events is necessarily opportunistic, and always took priority over focal animal data collection.

Within Group Data Collection:

Within group behavioural data were collected in a series of ten-minute focal animal samples as part of a long-term project data base. The information obtained from focal animal samples used for this study includes range size, patterns of range use, and identification of food sources. In conducting focal animal sessions for the long-term project, the researchers were able to track the

animals movements in order to map ranges and patterns of range use, and were more likely to witness intergroup encounters if the animals were kept in visual range.

With the assistance of local guides, a series of trails were cut and flagged. The position of each flag was calculated using a compass and range finder. The trails were then mapped. When each group of monkeys was located, their position relative to the pre-determined flag points was calculated, and mapped. When the group changed position, their new location was also plotted. Range size and location was calculated as a combination of the total area seen to be used by the primates, and any areas that the group would need to pass through to reach an area where they were seen. Range overlap was calculated as the percentage of the range shared by both groups involved.

Researchers rotated through the age-sex classes in order to obtain information on as much of the group as possible, and to ensure that all age-sex classes were represented. If an animal left the visible range of the observer for more than 10 % of any ten-minute focal session, the sample was discarded. On average, ten focal animal sessions per researcher per day were collected. A record of the location of the focal animals and the group

with respect to previously mapped reference points was recorded in order to ascertain range use.

The following ethogram was used for daily data collection, in both intragroup and intergroup contexts:

State Behaviours

Allogroom: Individual directs any or all of the following at another individual; combing through fur, brushing flies or other objects away from fur or skin using hands feet or tail, for a measurable duration.

Autogroom: Individual directs any or all of the following at self; combing through fur, brushing flies or other objects away from fur or skin using hands feet or tail, for a measurable duration.

Dorsal/Ventral carry: Adult individual locomotes while infant is clinging to dorsum or ventrum.

Dorsal/Ventral cling: Infant clings to fur of adult individual on dorsum or ventrum.

Embrace: Individual wraps arms around another individual.

Feed on: The act of searching for or selecting from available food. Can include sweeping branches and leaves

with hands, feet, mouth or tail, and or inspecting food objects using vision, olfaction, touch and/or taste; and the act of ingesting food and/or drink through the mouth and swallowing. Includes mastication and other means of processing, which are noted. The species and plant part consumed is noted.

Hanging: Individual supports all of body weight with tail, below level of the supporting structure.

Inactive: Individual lies on ventrum dorsum or side, or sits with little or no movement, eyes may be open or closed. Individual is not in physical contact with any other animal.

Locomote: Individual propels self from any one location to any other, includes walking, running, leaping.

Non-social play: Individual engages in somewhat exaggerated actions with no other individuals. May include grappling with branches or other objects, swinging from hands feet or tail. May or may not be accompanied by a play-face, or soft vocalisations.

Nurse: Adult female allows dependant offspring to suckle.

Out of Sight: Individual is not within the visual range of the observer.

Sit in body contact: Individual is in physical contact with another individual but fails to engage in allogroom, social play, or embrace.

Sit near: Individual A approaches individual B and sits, lies or relaxes posture within at most 1m of individual B, but does not engage in physical contact.

Social play: Individual engages in somewhat exaggerated actions with one or more other individuals. May include grappling, gentle biting, slapping, chases swinging from hands feet or tail while in physical contact with another individual. May or may not be accompanied by a play-face, or soft vocalisations.

Suckle: Dependent offspring places mouth to mother's breast to obtain nourishment.

Vigilance: Individual directs vision intensely in specific direction. May be accompanied by the stiffening of body posture.

Vocalise: Individual produces sound from vocal chords but does not engage in other activities.

Vocalise-(other): Individual produces sound from vocal chords, while engaging in any other activity. (Other behaviour category is noted).

Event Behaviours:

Approach: Individual A propels self toward individual B. social behaviour may ensue.

Branch shake: Individual uses part or all of body to move branches in surrounding area, but does not engage in feeding.

Branch throw: Individual physically displaces branch, and propels it away from the body. May or may not be directed at other animals or data collector.

Eliminate: Animal engages in urination or defecation.

Leave: Individual propels self away from one or more individuals.

Lunge: Individual A propels self in a rapid and direct manner toward individual B.

Muzzle: Individual places face and/or lips to other individual's face or lips.

Push: Individual A places hands on individual B and exerts force through the straightening of arms away from the body.

Quick vocalisation: Individual produces sound from vocal chords of immeasurable duration.

Slap: Individual swings hand foot or tail rapidly, and makes brief physical contact with another individual.

Ecological characteristics of the ranges:

Information about the types of foods eaten by howlers, and the distribution of these foods was obtained by way of random line transect censuses throughout the ranges. A list of tree species consumed by the monkeys in prior study periods, as well as those eaten in the current study was used. Line transects of various lengths, depending upon the accessibility of the area, with margins set according to the visibility in the forest were used to calculate the sample size which was subsequently utilised to calculate population estimates with King's equation (Skorupa 1987, See equation 1). The phenology of the trees being censused was noted under the following categories presence or absence of leaves, young leaves, unripe fruit, ripe fruit, flowers, buds, seeds/pods.

Equation 1: $N = nA/2rL$

Where: N =Population Density Estimate, n =sample, r =sighting distance, and L =transect length.

Intergroup, and group-individual interactions:

For the purpose of this study, an intergroup encounter is defined as the occurrence of two groups coming within 30m of one another. A group-individual encounter is a group and a solitary animal coming within 30m of one another.

For each intergroup encounter, or group-individual encounter, ad-libitum data were collected with particular emphasis on the location of the interaction, the age-sex class of the initiators of the interaction, the age and sex of the primary participants, whether or not the group was in a food source, if the group was eating during the encounter, the type of food source if present (including whether unripe fruit, ripe fruit, young leaves, mature leaves, flowers, or seed pods were present), the intensity and direction of agonism.

Using audio recorders, the researchers described the behaviours outlined in the ethogram, and variables listed above. If both researchers were present at the time of the interaction, each one recorded data on one of the groups

involved. If only one was present the data was collected on only one group. The audio recorder maximised the ability of researchers to maintain visual contact with animals while describing the behaviours. The time at which the interaction began and ended were noted. Immediately following the encounter, a line transect census was conducted, to determine the possible role of food sources in the encounter.

Analysis:

Data were compiled and entered into a database previously established for this study group. Intergroup data were compiled by encounter. The following variables were noted for each encounter: The age-sex composition of the group, the initiator of the encounter, the primary participant, whether the encounter was between two groups or an individual and a group, whether the group was in a food source or not, and if so the food species, what type of food it contained, the state of the food (ripe vs. unripe, young vs. mature), if the food was being consumed during the encounter, the group's use of range periphery, the amount of overlap of the two ranges, the average intensities of each age sex class, an average intensity rating overall, and average rates of agonistic behaviours for each of the age sex classes. Agonistic behaviours include vocalisations, branch shaking, branch throwing, lunges, pushing, vocalise-locomote, vocalise-branch shake, vocalise-branch throw, or vocalise lunge.

While some of the above categories of analysis are self-explanatory, others require elaboration.

Initiator: the age sex class of the first animal to engage in agonistic behaviour, once two groups, or a group and an individual were within 30m of one another.

Primary participant: the age sex class of the animal who displayed the highest number of agonistic behaviours during the encounter.

Average intensities: An intensity rating was assigned to each of the agonistic behaviours as follows. Vocalisation=1, head bob=3, body bob=4, branch shaking=5, branch throwing=6, lunges=7, pushing=8, slapping=9, biting=10, vocalise-locomote=2, vocalise-head bob=4, vocalise body bob=5, vocalise-branch shake=6, vocalise-branch throw=7, or vocalise lunge=8, vocalise push=9, vocalise slap=10. Average intensity was then calculated by age-sex class according to Equation 1 (adapted from Martin and Bateson 1986, Roper 1984).

$$\text{Equation 2: } A = \frac{\sum(BI)}{T}$$

Average intensity (A) is the sum of the average number of occurrences of agonistic behaviours (B), multiplied by their respective intensity rating (I), divided by the total time of the encounter (T). The average intensity is

therefore an average rate calculation that takes into account the intensity rating of each agonistic behaviour.

Due to the small sample size, non-parametric tests were used to explore possible significant differences in the behaviours between different variables, as these tests use mean ranks rather than actual means for comparison. This is useful in investigating preliminary data such as these. For tests with two grouping variables, the Mann-Whitney U test was performed and a 95% confidence interval used. For tests with greater than two grouping variables, the Kruskal-Wallis test was performed, and a 95% confidence interval used.

Chapter 3, Results:

A total of 16 encounters were observed in the period from January to May 2000. Encounters were rare, occurring 0.07 times per hour of observation. Fourteen of the encounters were between two groups, and 2 were encounters between a group and a solitary animal, one being an adult male and one an adult female. Of the 16 encounters, 69% involved one of the three groups (group 1, group 2, and group 3) which were followed regularly, and the remaining 31% involved groups or individuals from the surrounding area. Group 1 is comprised of 10 individuals: 4 adult males, 4 adult females, and two juveniles. Group 2 has 10 members: 4 adult males, 3 adult females, and 3 juveniles. Group three is the smallest with 9 members: 3 adult males, three adult females, and three juveniles.

Intergroup encounters most often took the form of two groups occupying separate trees, directing howling and other agonism at each other. The entire group occupied one tree more often than being spread apart in more than one tree, although this did occur occasionally. All encounters witnessed occurred in trees, as opposed to on the ground, although in some cases one of the groups would come to the ground prior to the encounter, in order to gain proximity

to the other through a clearing. The observers in most cases were between 3 and 10 meters away from the monkeys involved in the encounters.

Overall the average intensities of agonistic behaviours during the encounters were generally higher for adult males, and lower for adult females and juveniles. Adult males engaged in agonistic behaviours in more of the encounters than did adult females and juveniles. The rates of agonistic behaviours varied, and average intensities were calculated from incorporating the rates and the level of intensity of the behaviours. Table 3 summarises the average intensities for all age sex classes, in the encounters observed.

Table 3. Sex differences in intensities of agonistic behaviour by encounter

Encounter	Group or Solitary	Adult Males	Adult Females	Juveniles
1	2 groups	0.07	0	0
2	2 groups	1.79	0.26	0
3	2 groups	0.52	0	0
4	2 groups	0.59	0	0
5	2 groups	0.63	0.07	0.13
6	2 groups	1.05	0	0.07
7	2 groups	0	0.02	0
8	SM & Grp	0.43	-	-

9	2 groups	1.69	0.08	0
10	2 groups	0.13	0	0
11	2 groups	1.05	0.4	0
12	2 groups	2.66	0	0
13	2 groups	0.88	0	0
14	Grp & SM	0.62	0.97	0
15	Grp & SF	0	0	0
16	SF & Grp	-	0	-
Mean		0.81	0.10	0.07

Resource defence hypothesis:

It was expected that adult females and adult males would both participate in agonism if resource defence is the function of between group agonism. Males and females did both display agonistic behaviours, but not in the manner predicted. In 100% of the encounters where the beginning of the encounter was witnessed (N=7), adult males were the initiators. In all of the agonistic encounters observed, adult males were the primary participants. Female reproductive success is limited by resources, and females are expected to defend resources more actively than males. Female participation in intergroup agonism was, however, lower than that for males, as can be seen in Table 3.

If the function of between group agonism is resource defence, intergroup encounters should occur in non-random locations, and be associated with food trees. In 92.9% of encounters, the observed group was in a food source at the time of the encounter. However, this is comparable to the time spent in a food source while not engaged in intergroup contact. In 7.1% of encounters the animals were in a non-food tree, but there was a food tree within 10m of the tree occupied by the group. The following table (Table 4) outlines the differences in intensities of agonistic behaviours for all age sex classes in food trees and non-food trees.

Table 4: Differences in Overall Intensities by Tree Type

Age-Sex Class	Food Source	Non Food Source
Adult Male	0.86	0.07
Adult Female	0.13	0
Juvenile	0.01	0

The overall intensity of adult male agonism was higher than that of adult females both in food sources and in non-food sources. No statistically significant differences in the intensities of agonistic behaviours were found for any age-sex class during encounters at a food

source, compared with encounters at non-food sources, so differences seen may be due to chance. However, the type of food source, i.e. patchy and defensible foods, vs. evenly-distributed non-defensible foods, may be associated with different behaviours, i.e.; the fact that a tree is a food source, may not make it worth defending.

If intergroup encounters are related to resource defence, patchy defensible resources such as fruiting trees, are expected to be linked to a higher incidence and intensity of agonistic behaviour between groups. Forty-six percent of the encounters observed took place in fruiting trees. The overall intensities of agonistic behaviours during encounters which took place in fruiting trees, compared with non-fruiting trees, is shown in Table 5.

Table 5: Differences in Overall Intensities of Agonism at fruiting trees.

Age-Sex Class	Fruiting Trees	Non Fruiting Trees
Adult Male	0.82	0.77
Adult Female	0.28	0.03
Juvenile	0	0.04

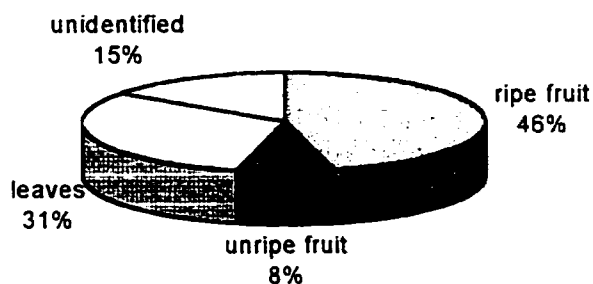
As shown above, the overall intensities of agonism for adults are higher in encounters which occurred in fruiting

trees. It is more notable with the Adult females, whose overall intensity of agonistic behaviour was over nine times greater in a fruiting tree than in a non-fruiting tree. Adult males also showed higher intensities. The intensities for juveniles are interestingly the opposite of adults, and are higher in non-fruiting tree encounters. This is likely due to a small sample size, as juveniles were only observed to display agonistic behaviours twice during the entire study period.

Although not statistically significant, females did show higher intensities of agonism in encounters occurring in ripe fruit trees, than at other food sources.

Some other differences in behaviour were also noted during encounters in fruiting trees. Of the encounters which took place in food sources, the animals in the group engaged in feeding behaviour in 35.7% of cases. Adult females and juveniles were more likely to engage in feeding behaviour during the encounter if the group was in a ripe fruiting tree. Figure 1 shows the proportion of encounters that took place in different food tree types.

Figure 1.

Proportion of Encounter Food Types

In 83.3% of the cases where ripe fruit was available during an encounter, feeding behaviour occurred, whereas no feeding behaviour was seen in cases where only unripe fruit leaves, or other food items were available. All age-sex classes displayed feeding behaviour, and females were the most likely to feed during encounters.

While the trees occupied by the groups during encounters provide information about the proximate trigger for intergroup agonism, trees in the immediate area of the encounter may also be worth engaging in contest competition. The line-transect censuses conducted immediately following the encounters provide information about the food sources surrounding the group during the

encounter. The tree species occupied during encounters varied, as did the tree species found in the vicinity of an encounter. The following table summarises the tree species involved in encounters, and the respective densities at the encounter sites, and in the ranges overall (see Table 6).

Table 6: Tree species densities.

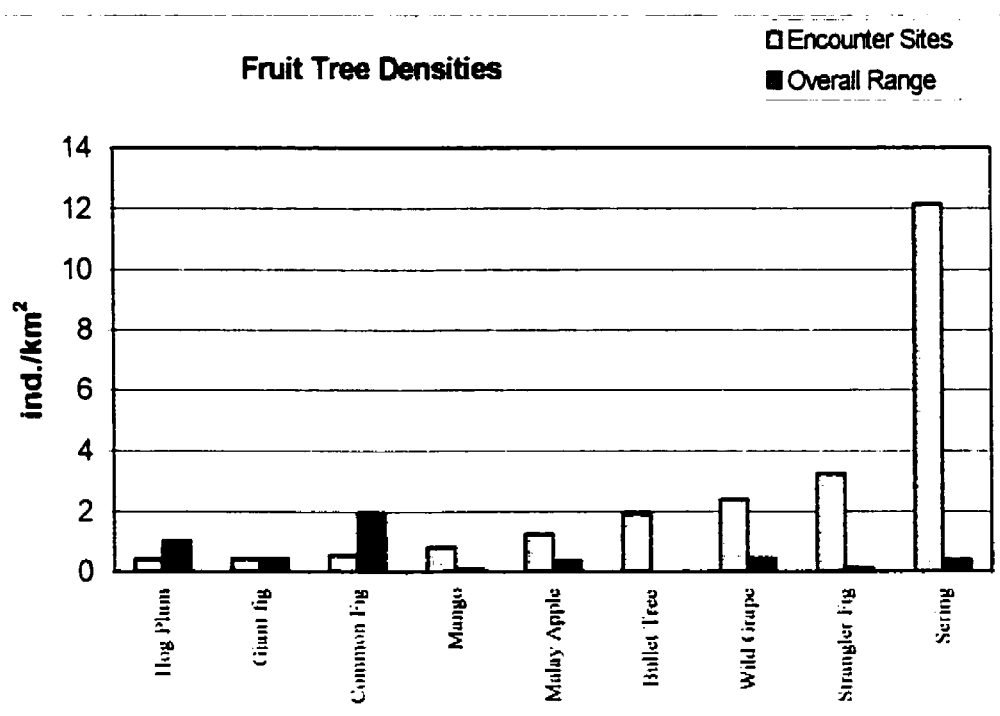
Species Local name (scientific name)	Plant part eaten	Encounter site density. (N/km ²)	Density over whole range. (N/km ²)
Freshwater Moho	Flower/ seed	0.28	0.2
Bucut (<i>Leguminosae sp.</i>)	seed pod	0.33	0.18
Hog plum (<i>Spondias mombin</i>)	ripe fruit/ leaves	0.43	1.02
Giant Fig (<i>Ficus sp.</i>)	unripe fruit/ leaves	0.45	0.45
Common Fig (<i>Ficus sp.</i>)	fruit/ leaves	0.54	1.94
Mango (<i>Mangifera indica</i>)	ripe fruit	0.83	0.11
Provision (<i>Pachira aquatica</i>)	leaves	0.95	0.26
Malay Apple (<i>Eugenia malaccensis</i>)	ripe fruit	1.25	0.36
Turtlebone (<i>Mouriri myrtilloides</i>)	leaves/ flowers	1.34	1.36
Cochito (<i>Simarouba glauca</i>)	ripe fruit/leaves	1.69	0.25
Bullet (<i>Ximenia americana</i>)	ripe fruit	1.90	0
Kojoton (<i>Stemmadenia donnelli-smithii</i>)	leaves	2.05	1.38

Cowai (<i>Pterocarpus belizensis</i>)	leaves	2.40	1.75
Wild Grape (<i>Vitis tiliifolia</i>)	ripe fruit/leaves	2.40	0.45
Strangler Fig (<i>Ficus crassiuscula</i>)	fruit/ leaves	3.23	0.12
Black Bay Cedar (<i>Gauzuma ulmifolia</i>)	leaves/ ripe fruit	3.53	0.35
Banac (<i>Virolia kosechnye</i>)	leaves	4.22	3.73
Inga (<i>Inga edulis</i>)	leaves	4.42	1.83
Yellow Bay Cedar (<i>Cedrella mexicana</i>)	leaves	7.13	1.35
Trumpet (<i>Cecropia obtusifolia</i>)	leaves	8.30	8.26
Sering (<i>Miconia argentea</i>)	ripe fruit	12.13	0.38

Several species were present in higher densities at encounter sites. Some of these were sources of leaves, and others, sources of fruit. Most of the ripe fruit trees were found in higher densities at encounter sites than in the range overall. The most notable difference is the density of Sering trees. At encounter sites, the population density of Sering is 12.13 individuals per km², more than twelve

times the overall density of 0.38 individuals per km². Figure 2 demonstrates the differences in densities for fruit trees between encounter sites, and in the ranges overall.

Figure 2: Fruit tree densities at encounter sites, and in the range overall.



The density of fruit trees was significantly higher at encounter sites than in other areas of the range (exact sig. 0.038, $p < 0.05$). It is unlikely that the observed increase in population density for fruit trees at encounter

sites is due to chance. Therefore it can be assumed that the encounters observed did not take place in random locations, independent of the location of fruit trees.

Ranging behaviour was expected to be concentrated on the periphery if the groups were engaging in resource defence. Refer to Figure 3 for a map of the ranges. Of the three groups that were followed regularly, and for which the ranges are known, range use was concentrated on the periphery for groups one and two, and was more uniform for three. There was no range overlap for groups 2 and 3. For groups one and two, the calculation of range overlap was affected by a field, approximately 102m wide, which is situated between the areas where groups one and two are normally located. The majority of the field was never occupied by either group. Group two was seen to cross the field on two separate occasions, however even though the animals crossed the field, they did so in a narrow band of trees at the water's edge, and never ventured into the

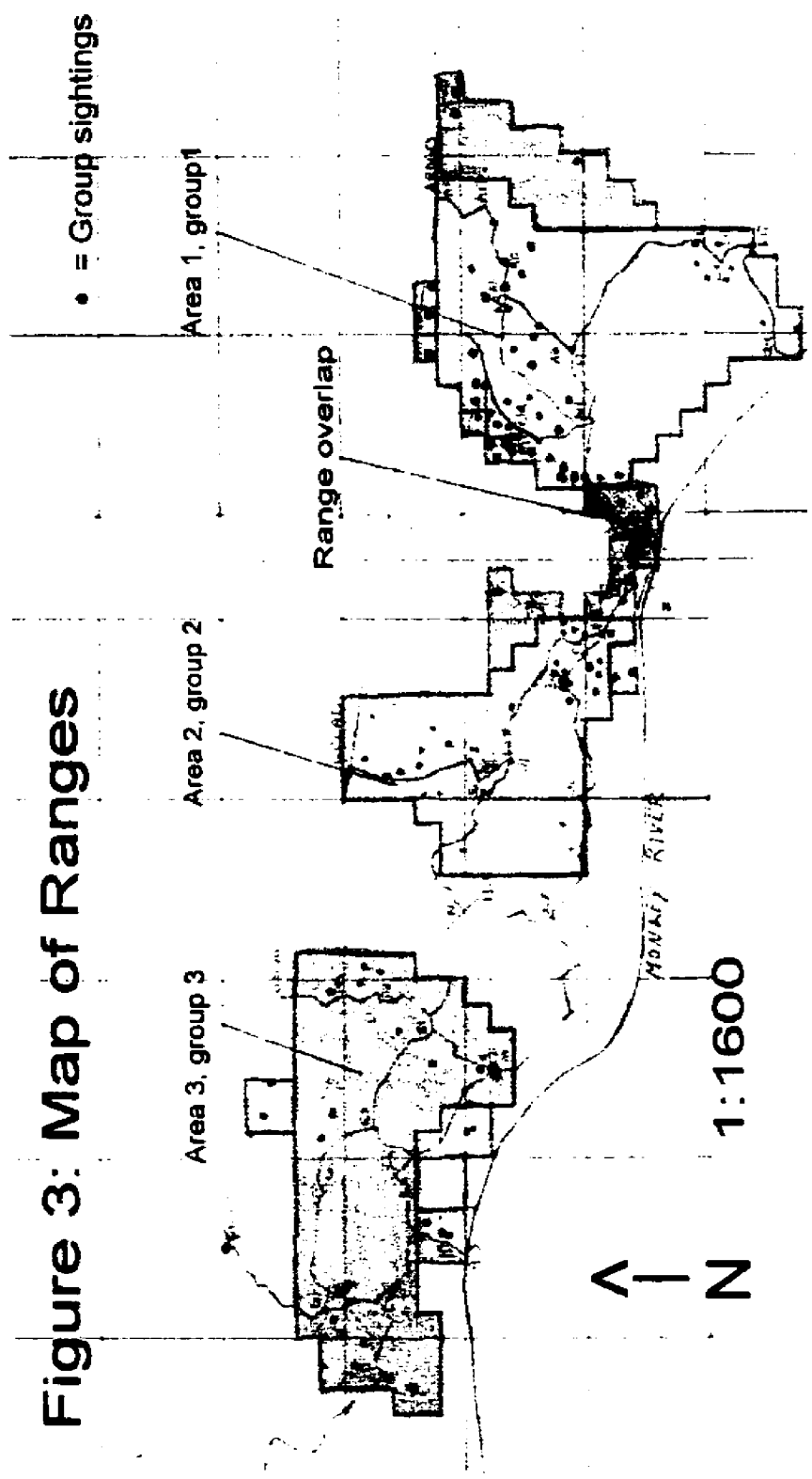


Figure 3: Map of Ranges

field itself. The area of the field was not included in the calculation of range overlap. The total area of the trees used to cross the field were included in the range size calculation. The overlap for ranges one and two was 5%.

Of the encounters for which the ranges of the groups were known, 83.3% occurred on the periphery of the range. The only encounters not occurring on the periphery of a known range were those involving a group and solitary female, and no agonistic behaviour was observed.

Contrary to the predictions of the resource defence hypothesis, adult males were the initiators and primary participants in agonistic behaviours in most encounters. Both males and females did participate in agonism during intergroup encounters, which is consistent with predictions. While not statistically significant, females did show higher average intensities of agonistic behaviours in encounters which occurred at ripe fruit trees, and females were more likely to feed during encounters at ripe fruit trees. The location of encounters was not random, and significantly higher densities of fruiting trees were found at encounter sites, than in other areas of the range. Range periphery use, and range overlap was observed for two of the three groups.

Male mate defence hypothesis:

If Male mate defence is the primary function of between group competition, adult males are predicted to be the initiators and primary participants in agonism. Recall that adult males were the initiators of all encounters for which the beginning was witnessed, and primary participants in agonism in all of the encounters observed.

The rates of agonistic behaviours during encounters were consistently higher for adult males than for adult females. Females were predicted to be relatively inactive in encounters if the main function of intergroup agonism is male mate defence. Although females did participate in agonistic interactions during encounters the average intensities of female agonistic behaviours were 0.10 which is lower than for adult males at 0.81. Juveniles were inactive in most of the encounters, and had the lowest average intensities of agonistic behaviour of any age-sex class with an overall intensity of 0.07.

It is expected that if male mate defence is the primary function of intergroup agonism that the incidence and intensity of between group agonism should be independent of patchy defensible food sources, such as

fruiting trees. While not significant, there was an increased intensity of agonism by adults, seen in encounters which occurred at ripe fruiting trees. Also, if the main function of intergroup agonism is male mate defence, it was expected that the encounters would occur in locations of the range which are independent of fruiting trees. However, there is a significantly higher density of some species of ripe fruit trees at encounter sites, showing that there is a pattern of intergroup encounters occurring in areas with higher population densities of ripe fruit trees which does not support the prediction.

Adult males are expected to display higher average intensities of agonism toward solitary males, than males who are in an established breeding group. Males who are in an established group would not be as likely to attempt to mate with females of another group as a solitary male would be, as bonds with females would already exist in his own group, and attempting to mate with unknown females would require a greater investment.

Different intensity ratings for adult male agonism were observed across encounters. It was predicted that if the primary function of intergroup agonism was male mate defence, that the intensity of adult male agonism would be

higher when directed at a solitary male. No significant differences in intensity of agonistic behaviours of adult males were found between encounters with groups, an encounter with a solitary male, or an encounter with a solitary female.

The prediction that adult males would be the initiators and primary participants in agonistic behaviours was met. Females showed lower intensities of agonism than males which also supports the predictions if the main function of intergroup agonism is male mate defence. The prediction that Encounters would occur independently of food sources, and the prediction that males would show higher levels of intensity when encountering a solitary male were not met.

Female resistance to immigration hypothesis:

If the primary function of between group competition is female resistance to immigration, females are expected to initiate, and be the primary participants of agonism. Low rates and average intensities of agonistic behaviours were observed for Adult females ranging from 0 in most cases, to 0.97 in an encounter with a solitary male. The overall intensity of agonism for adult females is 0.10. Females were never observed as the initiators, or the

primary participants in agonistic behaviours during any of the encounters observed. Adult males were predicted to be relatively inactive in encounters if the main function of intergroup agonism is female resistance to immigration, but males were the primary participants in all agonistic encounters, and the initiators in all cases where the beginning of the encounter was witnessed.

The incidence and intensity of female agonistic behaviour is expected to be higher in encounters with solitary females, than encounters with females in established groups. Female transfer in Howlers is not known to take place during intergroup encounters as it does in Gorillas (Sicotte 1996), so a solitary or transferring female is at greater risk of predation than one who is a member of a group, and is a potential immigrant to groups that she encounters. A female in an established group is not as likely to transfer to a new group, as there are high social costs for an immigrating female. The average intensity of agonistic behaviour for adult females in an encounter with a solitary female was 0 (N=1). No agonistic behaviours were observed during the encounter between a group and a solitary female, for any age-sex class. It was not clear if the female was attempting entry into the

group, however, she stayed in close proximity to the group for several hours.

The highest average intensity of agonistic behaviour for adult females, of 0.97, was observed in an encounter between a group and a solitary male. The average intensity of agonism for females was more than two times higher than the next highest average intensity value of 0.4, which occurred in an encounter between two groups. A trend for higher intensities of agonism for females during encounters with solitary males, as opposed to groups or solitary females is evident, although no statistically significant differences are seen.

It is possible that the composition of the group may affect adult female behaviour. Perhaps any one-male group would elicit the same response from females as a solitary male. To explore this possibility, a Kruskal-Wallis test was performed to assess if there is a significant difference in behaviour for any age-sex class when the composition of the target group is taken into account, and none were found. The composition of the target group in an encounter, in terms of number of adult females, and number of adult males, is not associated with statistically

significant differences in intensities of agonistic behaviour for any age-sex class.

None of the predictions for the female resistance to immigration hypothesis are met.

Chapter 4: Discussion

The current study examined the behaviours of black howling monkeys during intergroup encounters, over a four-month period in light of three possible functions; resource defence, male mate defence, and female resistance to immigration. Resource defence should be associated with adult females as initiators and primary participants in intergroup agonism, and a higher incidence and intensity of agonism in encounters that occur in conjunction with patchy defensible resources such as fruiting trees. Male mate defence should be associated with males as initiators and primary participants of agonism during encounters. Encounters should occur independently of food sources. Female resistance to immigration should be associated with females as initiators and primary participants in intergroup agonism, and encounters occurring independently of food sources.

Resource Defence:

It was predicted that both males and females would participate in intergroup agonism, as both require food for survival, but that females would be more active in

encounters, as their reproductive success is more directly limited by access to resources. Results show, however, that adult males were always the primary participants in agonistic interactions, and were the initiators wherever this could accurately be determined. Adult females participated in agonistic behaviours during most encounters, but had lower average intensities of agonistic behaviours. Lower intensities of agonistic behaviours for females may suggest lower interest in the encounter than that of males. In some cases females did not participate at all in the encounter, and even slept on some occasions. This is not predicted for females who are acting in the interest of resource defence, however it does not rule out the possibility.

A pattern of males as primary participants in intergroup encounters is documented in diana monkeys. Hill (1994) argues that female diana monkeys solicit the agonistic support of males during intergroup encounters. Female diana monkeys will often vocalise at the beginning of an encounter, encouraging males to participate and take over. Females may thus be attaching themselves to males who display the ability to aid in the defence of resources. Females immigrating into a range with high quality

resources would benefit, and philopatric males would benefit from defending a high quality range as this would attract females, and increase his chances of higher reproductive success.

The high intensities of agonism displayed by males in the current study suggest that it is possible that males are defending resources however, contrary to the pattern reported for diana monkeys, female howlers were never observed as the initiators of agonism during an encounter and are thus not likely soliciting agonistic support in the same manner. The function of the behaviours observed remains unclear.

If the primary function of intergroup agonism is resource defence, then it is expected that intergroup encounters will correspond with food sources, in particular those that are patchily distributed, and defensible -such as ripe fruit trees. Over 90% of the encounters observed occurred when one or both groups were in a food source. This corresponds to the prediction of a higher incidence of agonism at food sources, and indicates a link between intergroup agonism and resource defence. However, the proportion of encounters occurring at a food source is not in and of itself an indication of resource defence. More

information about the type of food available is needed to explore this link. In this case, the proportion of time spent in food sources on a daily basis is similar to the proportion of encounters that occurred at food sources. This pattern may simply be a function of the trees available to the monkeys in the range, rather than a choice of trees to occupy during encounters. No statistically significant differences in average intensities of agonistic behaviours were found between encounters at a food source and encounters at a non-food source. This suggests that simply being a food source may not be enough to make a tree worth defending, so the fact that an agonistic encounter occurs at a food source does not necessarily correspond to the predictions of the resource defence hypothesis.

High-density, dispersed resources of low quality are not monopolisable and/or not worth defending, as contest is costly, and benefits must outweigh the costs. However, a more patchily distributed, high-quality food source, such as a seasonally fruiting tree is defensible, and worth defending (Koenig et al. 1997). If intergroup agonism in howlers serves primarily in the defence of resources, it would be expected that there would be a link between those food sources which are of high priority and defensible, and

intergroup agonism. Encounters occurred in trees of various food types.

Recall that ripe fruit was available in 46% of the encounters that occurred in a food source, more than any other food type. When ripe fruit was present, the animals were more likely to engage in feeding during the encounter. Ripe fruit was consumed during 83.3% of the encounters where it was available, mainly by adult females and juveniles, while other food types (leaves, flowers and seeds/pods) were never consumed during encounters. This suggests that ripe fruits may be of higher priority than food which was not consumed during the encounter. If the presence of another group threatens the occupants' chances of consuming the food available in the tree, it would be beneficial for the monkeys, especially adult females, to consume available food while they can.

Because females are more directly limited by resources, their behaviour during encounters involving high priority defensible resources would provide clues as to whether or not intergroup agonism functions in resource defence. Adult females displayed higher average intensities of agonistic behaviours at ripe fruit trees compared with non-ripe fruit trees, indicating that the ripe fruit trees

were linked to a greater energy expenditure. Though differences were not statistically significant, the trend for females to display higher average intensities of agonistic behaviours at ripe fruit trees indicates that resource defence may play a role in the function of intergroup agonism. The data obtained during this study are not adequate to determine if the primary function of intergroup agonism is resource defence, however, the links between ripe fruit trees and increased intensity of agonism suggests that the resource defence hypothesis is warranted further investigation.

If encounters were not linked to resource defence, it would be expected that agonistic encounters would occur at locations that are independent of high priority food sources. Koenig et al. (1988) found that high priority food sources were associated with contest competition in a population of langurs. Howlers and langurs are commonly reported to be folivores, who do not engage in contest competition for food (Julliot 1994, 1996, Tomblin & Cranford 1994, Koenig 1998). However, previous studies of the current study population indicates both a high level of fruit consumption, and agonistic intergroup encounters (Chaput 1999, unpubl.) This further suggests that there may

be a link between intergroup agonism and the defence of resources. Although there were no significant differences in the intensity of agonism when the group was in a fruit tree, or a non- fruit tree, it is possible that the trees in the surrounding area are contributing to the proximate trigger for agonistic interactions between groups. The tree occupied by the groups during an encounter may be the food patch being contested, but food sources in the area immediately surrounding the group may also be worth defending by contest competition. For example, I noticed that in an encounter between two groups, the trees that were occupied were both sources for leaves, but that there was a patch of ripe malay apple trees situated between the two groups. Malay apples are eaten by the howlers while ripe, and are not widely dispersed. It is possible that the malay apples were the patch being contested, even though the trees occupied by the groups contained other food types.

In order to explore the possibility of ripe fruit trees in the immediate vicinity of encounter sites being the objects of contest competition, the population densities obtained by ecological line transect censuses were compared. When the population densities of food trees

at encounter sites were compared to those measured at random locations throughout the range, I found that certain food sources were present in higher densities at encounter sites. In particular, the densities of seasonally fruiting trees were significantly higher (see Figure 2). This indicates that the current study groups are engaging in agonistic encounters more frequently at seasonally fruiting trees, and that encounter location is not independent of high-quality resources. This indicates that the areas where agonistic interactions occurred contained food sources worth defending. The location of an intergroup encounter is therefore not random, and it is likely that the ripe fruit trees in question are of high priority, and may be a proximate trigger for intergroup agonism. This lends support to the resource defence hypothesis and indicates that resource defence is at least a partial function of between group competition.

All of the encounters that occurred in seasonally fruiting trees and in which the ranges of the participants were known took place at the periphery of the range. If the resources in the range of the monkeys are being defended in intergroup encounters, it is expected that the monkeys would actively deter other groups from entering the range.

Range overlap would thus be low, and animals would be expected to concentrate range use on the range periphery, or borders of ranges shared with other groups, in order to ensure that neighbouring groups do not enter the range and exploit resources.

Range use by howlers is reported to vary. *A. seniculus*, according to Sekulic (1982b), showed extensive use of the core area of their range, and had 63% overlap with ranges of neighbouring groups. Chapman (1990) reports primarily core-use ranging for a group of *A. palliata*, with 57% of ranging occurring outside the core, but not concentrated on the periphery. Chiarello Garcia (1993) states that the group of *A. fusca* studied, used the range uniformly, and had a 22% overlap with neighbouring groups. In the current study, the only groups for which the ranges were known had either 0% overlap, or 5% overlap with neighbouring groups. When compared with range overlap in other species of *Alouatta*, this is very low. This may indicate further support for the resource defence hypothesis, however, while ranging behaviour may be an indication of resource defence, it is also tightly tied to the search for and exploitation of food sources, and may therefore not be as strong an indication of resource

defence, but rather the distribution of food in the range. In future studies in the area, a map of all food trees will be constructed, and this matter will be better assessed. Also, the current study may not have been long enough to accurately assess range size and use. For the period of study, the ranging behaviour of two of the three target groups was concentrated on the edge of the ranges where they bordered areas occupied by other groups of monkeys, and the third group used the range more uniformly. But, Ostro et al. (1999) in their studies of *A. pigra* in Belize argue that studying the movements of the group for a full year was not sufficient time to determine the sizes of home ranges.

There was no significant difference in behaviours of adult females, or adult males, during encounters in fruiting trees; however, juveniles showed significantly higher average intensities. This could be due to the small sample size, and would require further exploration before any conclusions can be drawn. There is also very little data published on the behaviour of juvenile howling monkeys in intergroup encounters, and it is therefore difficult to interpret the results obtained in such a short study, as there is little available for comparison.

The predictions for the resource defence hypothesis are not entirely met. Adult females did not behave in the manner predicted. They were not the primary participants, and often showed little or no participation in interactions with other groups. The prediction that increased incidence of agonism between groups would be seen at ripe fruiting trees was met, and links between intergroup agonism and defensible high quality resources are present, indicating that resource defence is likely at least a partial function of intergroup agonism.

Male mate defence:

If male mate defence is a function of intergroup agonism, males are expected to be initiators and primary participants in intergroup agonism. In the current study, adult males consistently showed higher incidence and intensity of agonistic behaviour than other age-sex classes, being the initiators for all encounters for which the beginning was witnessed, and the primary participants in all agonistic encounters observed. This pattern of involvement for adult males in between group competition suggests that the male mate defence hypothesis is possibly at work in the study population.

The most common agonistic behaviour displayed by males was vocalisations. While howler long calls are thought to function in intergroup spacing (Chivers 1969, Whitehead et al. 1994) the nature of howler calls as deterrents may not be a resource defence strategy, as suggested. There is evidence in langur populations that the function of long calls may be more directly related to mate defence (Steenbeek 1999). It is possible that this is also the case for howlers. Because loud vocalisations advertise the location of the group, it may allow neighbouring groups to sneak into a range undetected. This counters the resource defence hypothesis, and lends itself more to a mate-defence hypothesis (Gittins 1980). Cheney (1987) states that there are two types of intergroup calls in nonhuman primates. One type attracts neighbouring groups, and usually leads to a direct physical competition between the groups, and is often associated with high quality food sources. The other acts to deter neighbouring groups. In Playback experiments, male howler calls consistently elicited a withdrawal response from other males (Whitehead et al. 1994). Howler calls act to deter other groups. The males observed in the current study did not noticeably vocalise directly at other groups until they were in visual range, indicating that

they were not advertising the location of the group, but rather actively deterring other howlers.

Adult females were expected to be relatively inactive in such an encounter. as indicated above, the average intensities of agonistic behaviours of adult females were much lower than for males. Adult females did not participate in all agonistic encounters, and in some cases they were inactive for the duration of the encounter. This is in line with the predictions of the male mate defence hypothesis.

Average intensities of agonistic behaviour directed at solitary males were expected to be higher for adult males if mate defence is a function of between group competition. Male reproductive success is limited by the males access to breeding partners, and is threatened more by solitary males than by males who are in an established breeding group. Higher average intensities of adult male agonism were not observed in encounters with solitary males in the current study. No statistically significant differences were seen in adult males average intensities regardless of the target type (group vs. solitary male vs. solitary female), or the composition of the groups (number of adult males, or number of adult females in the target group). This does not match

the predictions for the male mate defence hypothesis. A solitary male should pose more of a threat to the reproductive success of the male in an established group, as solitary males are more likely to seek copulations with females in the group than males in an established breeding group.

Predictions for the mate defence hypothesis are partially met. Males met the prediction as initiators and primary participants in agonism between groups. Females also met predictions with lower average intensities of between group agonism than males, and in some cases did not participate in encounters. But encounters did not take place in locations independent of defensible food sources as predicted, nor did the intensity of adult male agonism increase during the encounter with a solitary male.

If mate defence is the only function of between group agonism, encounters should occur at locations in the range that are independent of high quality resources. As discussed above, this is not the case. In light of the current data, it is possible that mate defence, and resource defence are both partial functions of intergroup agonism. Determining this, and the extent to which each is

contributing to intergroup competitive regimes is unclear, and will require a more in-depth investigation.

Female resistance to immigration:

If the function of intergroup agonism is female resistance to immigration, females are expected to be initiators and primary participants in agonistic encounters. Adult females were never observed to be the initiators or the primary participants in intergroup encounters. During most of the encounters, females remained relatively inactive, and displayed agonism at much lower average intensities than adult males. Females engaged in feeding behaviour during 35% of encounters, and in some cases remained completely inactive for the duration of the encounter. Females generally remained in the centre of the group with adult males between them and the target groups. These behaviours, along with the adult male behaviours discussed above, do not support the female resistance to immigration hypothesis. However, they may further suggest that male mate defence is a partial function of between group agonism in the study groups.

The incidence and intensity of adult female agonism was predicted to be higher in encounters with solitary

females, as they are more likely to be immigrants than females who are in an established breeding group. Transferring to a new group includes increased predation risk, a loss of group foraging, and the costs of forming new social bonds. A female in an established breeding group would thus benefit from remaining in the group, but a solitary female would benefit from joining the group. The predicted female behaviour was not observed. However, it remains unclear if females are transferring in this species, as little research on immigration patterns has been conducted to date. There was no agonistic behaviour for any age-sex class in encounter (N=1) between a group and a solitary female. The encounter took place in the interior of the group's range, and the solitary female was virtually ignored. This does not meet the predictions of the female resistance to immigration hypothesis, however the predictions were all formed assuming that females in this population transfer. If this is not the case, it may be the reason for the unexpected behaviour. However, if there is no female transfer in this population, the solitary female would have to have been away from her group for several hours, and the group was not detected by the researchers. The lack of agonism from adult females suggests

that solitary females are not actively resisting immigrants in the study population. Although there is evidence for a system of female forced emigration in the genus *Alouatta*, there is no evidence in the current study that females in an established group are resistant to the immigration of new females.

The data examined in light of this hypothesis suggest that it is unlikely that between group competition functions in deterring female immigration. None of the predictions of the females resistance to immigration hypothesis were observed.

Infanticide Pressure

The socioecology model attributes social structure to ecological pressures. There is evidence that the function of between group agonism in some species is primarily male mate defence (Van Shaik et al. 1992, Steenbeek 1999). As not all primate social structures can be explained by the model, it is possible that there are other pressures acting on females, and thus on males, which may explain the variance in primate social systems.

One aspect of observed adult female behaviour was not predicted for any of the hypotheses, and may indicate an

additional pressure on females. The intensity rates of females in encounters were generally low, and often zero. One encounter observed involved a solitary adult male coming in contact with a group on the periphery of the group's range. In this encounter, the rates and intensity of adult female agonism were much higher- more than twice the next highest intensity- than in other encounters. None of the hypotheses developed for this project predict such behaviours. An additional pressure acting on adult females must be present to explain this phenomenon.

Sterck et al. (1997) discuss habitat saturation and infanticide as pressures acting on females in addition to the distribution of resources. Infanticide, hypothesised to be a sexually selected male reproductive strategy, negatively affects the reproductive success of females. Where infanticide occurs, females should evolve strategies to avoid infanticidal costs.

Infanticide is known to occur in howling monkeys (Crockett 1984, Clarke et al. 1994, Agoramcoorthy & Rudran 1995). Infanticidal males are generally solitary males who take over a group, and kill resident infants. Groups with higher numbers of females are more often targets for infanticidal males (Agoramcoorthy and Rudran 1995, Steenbeek

1999b). A multi-female group with dependent offspring is therefore a potential target for infanticidal males, and should exhibit behaviours to reduce infanticide risk.

The current study group displayed behaviours which are indicative of infanticide avoidance strategies. The high intensity of agonism for adult females in a group with three infants, coming in contact with a solitary male, may indicate a female response to infanticide. One possible defence strategy for females is to elicit males as protectors against infanticidal males. If females are choosing males as protectors, it can be argued that the higher intensities of agonism observed may be an indication of a lack of male success as protectors. However, the intensities and rates of agonism for adult males was still higher than for adult females, and they were consistently the initiators and primary participants in encounters. So while female intensities were notably higher, males were still the primary actors in deterring the solitary male. The trend of higher intensities for adult females in this case is not a statistically significant difference, however it is a hypothesis requiring further investigation.

Chapter 5: Conclusion

Based on this preliminary study of 16 intergroup encounters, the function of intergroup agonism in the black howling monkey population of Monkey River, Belize, does not appear to be explained by any one functional model. The links between agonism and seasonally fruiting trees, particularly for females, suggest that resource defence is partially a function of intergroup agonism. Some of the predictions for the male mate defence hypothesis are met: adult males are consistently the primary participants and appear to be the initiators of agonism, suggesting that male mate defence is partially the function of between group agonism. The female resistance to immigration hypothesis is not supported by the data from the current study. Increased female agonism in encounters with solitary males indicates that infanticide may be another major pressure acting on howling monkey females.

There are well-established links between resource distribution and female social systems among primates. It is probable, however that these pressures are not acting alone. Additional pressures, such as infanticide, and male competition, may be influencing female social systems in

howling monkeys, and possibly in other species whose social systems are not explained by the socioecology model.

The current study supports several possible trends which may support the resource defence, male mate defence, and infanticide pressure hypotheses, but it is limited due to a small sample size, and the rarity of intergroup encounters. Future studies of a long-term nature, including identification and measuring of the ranges, and the infanticide pressure hypothesis would be required in order to shed more light on the above hypotheses, and aid in clarifying the functions of intergroup agonism in howling monkeys.

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