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Ranging behavior of translocated and established groups of black howler monkeys *Alouatta pigra* in Belize, Central America

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Abstract

We studied the ranging behavior of translocated and non-translocated groups of *Alouatta pigra* in Belize, Central America from March 1994 to May 1995. Home range size, day-range length and monthly range size were determined for all groups. In high density populations, home range size and day-range length increased with group size. Home range size increased with translocation to a low density population, but day-range length did not, and neither were affected by group size. These patterns are consistent with differences in the distribution of important food resources in the two areas. The costs of translocation to *A. pigra* were not revealed by variation in ranging patterns between newly translocated and previously established groups but may be evident in the intensity of range use. Previously established groups use their ranges more intensively than newly translocated groups while the new groups explored the release site and then began to reuse areas explored earlier. Newly translocated groups generally established their home ranges six months after translocation but continued some exploration one year after they were moved. This suggests that a full year of monitoring is not necessarily sufficient to determine the size and location of the home ranges of translocated monkeys, but that monitoring should continue through all seasonal phases of food abundance.

Keywords: *Alouatta pigra*; Translocation; Home range; Day-range; Population density

1. Introduction

Translocation has been defined as the "deliberate and mediated movement of wild individuals or populations from one part of their range to another" (IUCN/SSC, 1995). This procedure can potentially preserve populations of animals whose habitats are threatened, repopulate areas after local extinctions or with low population densities, and augment genetic diversity in existing gene pools (Konstant and Mittermeier, 1982; Caldecott and Kavanagh, 1983). Although a number of translocations of primates have occurred (Mittermeier et al., 1976; Konstant and Mittermeier, 1982; Southwick et al., 1984; Strum and Southwick, 1986; de Vries, 1991; Richard-Hansen and Vie, 1996), there have been few follow-up studies of translocated animals. When post-translocation monitoring has taken place, the studies have usually lasted for less than a year although a few have lasted longer (e.g. *Papio anubis*: Strum and Southwick, 1986; *Macaca mulatta*: Strum and Southwick, 1986; *Alouatta palliata*: de Vries, 1991; Rodriguez-Luna et al., 1993; *Cercopithecus mitis*: Stoinski et al., 1996). Post-release monitoring is considered a vital part of any translocation or reintroduction project (Stanley Price, 1989; Griffith et al., 1989; Chivers, 1991; IUCN/SSC, 1995) and has often been conducted when the translocation has not occurred as the result of a crisis situation, as is often the case with primates (Griffith et al., 1989; Stanley Price, 1989; Kleiman et al., 1991).

From 1992 to 1994, the Wildlife Conservation Society (Bronx, NY), Community Conservation Consultants (Gays Mills, WI), and the Belize Audubon Society (Belize City, Belize), translocated 62 black howler

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monkeys *Alouatta pigra* from the Community Baboon Sanctuary (CBS) in northern Belize to the Cockscomb Basin Wildlife Sanctuary (CBWS) in southern Belize (Horwich et al., 1993; Koontz et al., 1994; Koontz, 1997). This translocation is unique among primate translocations in that the primary objective is to re-establish a viable population of a species in an area where it had become locally extinct rather than to rescue specific groups from habitat destruction or other threats. In February, 1994 we began a study of the ecological response of *A. pigra* to translocation.

The translocated groups in our study were faced with both a change in habitat and population density, while group size and composition were held constant. This provided a semi-natural experiment on the effects of habitat and population density on the ranging behavior of black howler monkeys. The aim of this study was: (1) to increase understanding of the processes of adjustment by howler monkeys to translocation in order to make it a more effective conservation tool; (2) to gain a better understanding of the behavioral ecology of howler monkeys by examining their response to a controlled change in environmental conditions.

There are large differences in local population densities within the CBS, and between the CBS and the CBWS. Comparisons within and between these sites allowed us to investigate the importance of population density and group size on home range size and other variables associated with the use of space, such as day-range length and the amount of area used on a monthly basis. The translocation event enabled us to conduct a rare experimental analysis of this relationship.

To examine the effects of translocation on the ranging behavior of the monkeys, we studied groups before and after translocation. We also contrast the behavior of groups newly translocated into CBWS with that of groups translocated 2 years earlier, in an attempt to determine: (1) the length of time necessary for translocated monkeys to adjust to a new area, (2) the size of the area required by the groups, and (3) the patterns by which groups establish themselves in a home range.

Translocation of groups of monkeys is, in many respects, similar to (involuntary) locational dispersal in which animals disperse to an unfamiliar location (Isbell and Van Vuren, 1996) without experiencing social dispersal. If there are costs to the monkeys associated with translocation as a result of not knowing the location of food sources we predicted they would be manifested as longer day-range lengths, as has been previously reported for dispersing howler monkeys (Pope, 1989), and perhaps increased mortality through predation (Isbell et al., 1990). Based upon findings for other dispersing primates (Isbell et al., 1990), we also predicted newly translocated groups would occupy inferior habitat when compared with groups that have been living in CBWS for several years.

Until now, no follow-up study of primates has compared the behavior of a primate group before and after translocation or made extensive comparisons between the behavior of translocated groups and the resident population. Given the potential benefits associated with the ability to successfully move wildlife populations it is likely that translocation will be used more often in the future. Empirical data of the type reported here are necessary for improving our ability to design and monitor future primate translocations.

2. Methods

2.1. Donor and receptor sites

2.1.1. Community Baboon Sanctuary

The Community Baboon Sanctuary consists of a 47 km^2 area located along the Belize River, Belize at 17°33′N, 88°35′W. The eight villages which comprise the sanctuary are agricultural communities where the landowners have pledged to follow farming practices that will allow the howler monkeys to survive on their land (Horwich and Lyon, 1990). The habitat is a patchwork of secondary forest types in various stages of succession along the Belize River, interspersed with cattle pastures and plantations. The CBS had a distinct dry season from January to May 1994 and 1995 when rainfall averaged 48 mm per month. Rainfall peaked in September and averaged 218 mm per month for the rest of the year. During this study, temperature ranged from a mean monthly minimum of 20°C in January 1995 to a mean monthly maximum of 32°C in May 1994.

The forests within the sanctuary are semi-deciduous broad-leaved forests found in a band of variable width along both sides of the Belize river (Horwich and Lyon, 1990). Three distinct forest types have been identified in CBS: riverine forest; mixed broad-leaved forest and swamp forest (Horwich and Lyon, 1990).

Riverine forest occurs in a narrow band on the banks of the Belize river and is seasonally flooded. It contains at least 60 tree species (Silver, 1997; Silver et al., 1998). The trees are often taller (12–20 m) than those found elsewhere because clearing and logging within 18 m of a river is forbidden under Belizean law. Mixed broad-leaved secondary forest is found adjacent to the riverine forest. The canopy is low (8–12 m) and frequently broken. The forest was flooded from October 1994 through January 1995 during this study. This area continues to be both logged and grazed by cattle. Cohune palms *Orbigyna cohune* are common, often dominating areas alongside stream beds.

In low-lying areas within the mixed broad-leaved forest are well-defined swamp forests with low canopies (5–10 m). The swamps are dominated by palms *Bactris* spp. and bamboo, with *Erythrina* sp., *Inga* spp. and

Lonchocarpus spp. forming the canopy. During this study the swamps flooded from October 1994 to February 1995.

2.1.2. Cockscomb Basin Wildlife Sanctuary

The Cockscomb Basin Wildlife Sanctuary consists of a 400 km^2 area on the eastern slope of the Maya Mountains in south central Belize, Central America. The sanctuary is located 15 km from the Caribbean Sea at 16°49′N, 88°47′W and 160 km south of CBS. The sanctuary includes the watersheds of two major rivers divided by a series of hills (< 1000 m a.s.l.) which separate the sanctuary into the east and west basins. Our study was conducted entirely in the east basin. The two basins are surrounded by mountains. Elevations range from 50 m to 1120 m (Kamstra, 1987). The east basin is comparatively flat, with 75% of the area lying below 200 m (Kamstra, 1987). The climate in CBWS follows the same seasonal pattern reported for the CBS. Dry season rainfall averaged 59 mm per month and in the rainy season an average of 309 mm of rain fell per month. Temperature data were collected on a daily basis at the Melinda forest station, 28 km from the sanctuary headquarters and averaged 25–28°C (Silver, 1997).

The east basin is covered with a mixture of evergreen and semi-evergreen broadleaf tropical forest (Kamstra, 1987). The most common trees in the forest are *Pourouma bicolor* and *Orbignya cohune*, which make up 24% of the trees in the basin. Other common tree species include *Cordia bicolor*, *Protium copal* and *Pterocarpus* sp. (Silver, 1997).

The basin was logged from 1888 to 1961. In 1961, the eye of hurricane Hattie passed over the basin. According to some reports (cited in Kamstra, 1987), this hurricane leveled 90% of the canopy. After this major logging operations ceased, although selective logging continued until the mid 1980s. Patches of undisturbed forests remain in a few sheltered valleys of the west basin(Kamstra, 1987), but the forests of the east basin consist primarily of various stages of disturbed and secondary growth.

2.2. Study groups of A. pigra

From February 1994 to May 1994 we studied six groups of *A. pigra* in two forest patches within CBS (Fig. 1), three groups at each site. In May 1994, four of these groups (T1–T4) were translocated to the Cockscomb Basin Wildlife Sanctuary 160 km to the south, while the other two (C1 and C2) remained in CBS. From May 1994 to May 1995, we studied groups T1 and T2 in CBWS and the two groups in CBS (C1 and C2). During this period we also studied two previously established groups (E1 and E2) that were translocated into CBWS in 1992 and 1993.

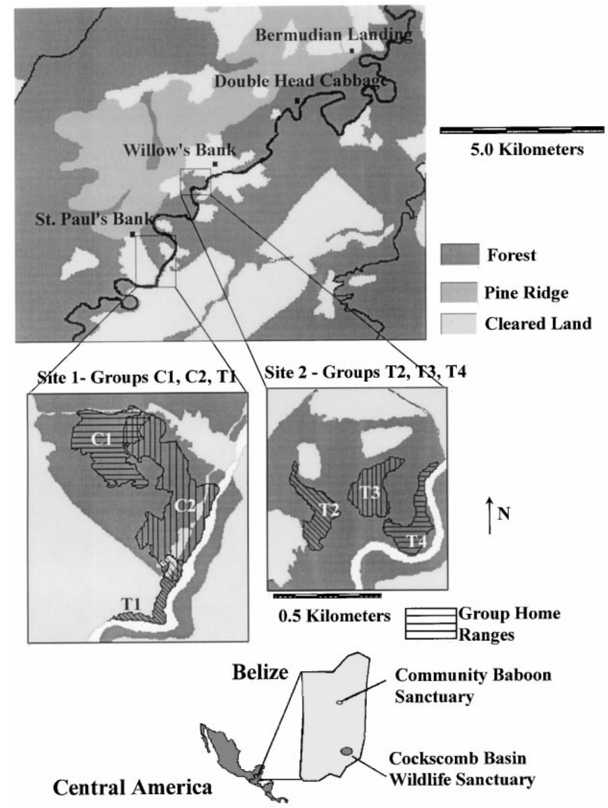

Fig. 1. Vegetation types and location of study sites and study groups within the Community Baboon Sanctuary (CBS), Belize.

With the exception of group T1, all study groups were reproductive prior to translocation. During this study infants were born to all groups. Study groups were predominantly single male with one or two females (Table 1). Group E1 was translocated into CBWS as an intact social group. Group E2 consists of two females and their offspring who left their original groups when they were translocated in 1992. In September 1993 they were joined by a male from a third group that was translocated in May 1993. Because the two adult females of the group were in CBWS for two years prior to this study, and the group stayed within the area

Table 1
Mean age–sex composition of study groups of *Alouatta pigra* in the Community Baboon Sanctuary and the Cockscomb Basin Wildlife Sanctuary, March 1994–May 1995

Group	Location studied	Year translocated	Adult males	Adult females	Immatures	Infants
C1	CBS	–	1	2	2	2
C2	CBS	–	1	3	4.5	1.5
E1	CBWS	1992	1	2	2	2
E2	CBWS	1992/1993	1	2	1	2
T1	CBS/CBWS	1994	1	2	0.5	0.5
T2	CBS/CBWS	1994	1	1	1	1
T3	CBS	1994	1.5	1.5	1	0
T4	CBS	1994	2	2	2	2

explored by the females in 1992–1993, we treated this group as fully established.

2.3. Data collection

In the 3 months prior to translocation, we followed the six study groups for 3 days a month from dawn until dusk. After translocation we followed each of the study groups for 4 days a month for a full year. During data collection, we recorded the location of the center of the group every 15 min relative to a position tag. These position tags had previously been placed every 20 to 50 m along the trails (Ostro, 1998). If the monkeys moved away from these known positions, we placed new tags along their travel path.

2.4. Vegetation sampling

We laid 14 100×10 m belt transects in CBWS within the home ranges of the study groups. Eight transects were within the ranges of the translocated groups and six in the ranges of the established groups. Ten belt transects that totaled 1000 m in length in CBS were also established. Methods and results of vegetation sampling, food resource distribution and phenology study are described in detail in Silver (1997) and Silver et al. (1998). All trees on the transects that were >30 cm in circumference were measured and identified. We compared tree density and DBH, species diversity and relative coverage in CBS and CBWS and in established and translocated group ranges.

2.5. Data analysis

Since all resident groups in each study area were known to us, we were able to calculate local population densities by dividing the number of individuals whose entire home ranges were known within each study site by the total area of the study site. We calculated population density separately for the two sites within CBS due to the distance between them (Fig. 1), and differences in the social structure and behavior of groups at the two sites (Ostro, 1998). We calculated day-range length by summing the distances between the location points each day.

We estimated home range size using digitized polygons (Ostro, 1998; Ostro et al., 1999), presenting home range sizes only for groups that were studied for 1 year or more (Groups E1, E2, C1, C2, and T1,T2 in CBWS). When we compared range sizes of groups prior to translocation with those of any other group we used 3 months of data to ensure that differences in range size were not due to different sample sizes. We compared the home range sizes (1) of groups before and after translocation, (2) of translocated and established groups and (3) of groups in CBS and groups in CBWS. Location data collected by F. Koontz in 1992–1993 (unpublished data) were used to construct minimum convex polygons for the first year home ranges of groups E1 and E2.

For analyses of range use we used 20×20 m grid cells as units. We chose this cell size because the average spread of the groups was 16 m and the mean distance moved every 15 min was 11 m. We calculated the size of monthly ranges and the percentage of the total range used by the groups per month. Using the number of times each cell was entered, we calculated the usage frequencies of individual cells within the ranges and compared the intensity of range use between translocated and established groups.

To determine temporal patterns of home range development we classified each grid cell entered in a month as (1) new (not previously entered) or (2) previously entered. We examined differences between groups in the number of new cells entered on a monthly basis. We also calculated the ratio of new to previously entered cells each month. When the ratio of previously entered to new cells exceeded 1 for more than 5 months, we considered the groups to have established themselves in an area.

2.6. Statistical analyses

Differences between vegetation in established and translocated group ranges were tested with the Mann–Whitney U test. We used Spearman's rank correlation to determine the effects of population density and group size on home range size and day-range length, and to examine relationships between fruit abundance and day-range length. We compared day-range lengths of groups before and after translocation with a paired Student's t test. Day-range lengths were log transformed and amount of new area used per month were square root transformed to approximate normal distributions. Differences between day-range lengths of translocated and established groups, and the size of new areas entered each month were tested with repeated measures ANOVA. We were unable successfully to transform monthly range sizes so differences between groups were tested using Friedman's ANOVA. A chi-square test was used to test the significance of differences in usage frequencies of cells between established and translocated groups.

3. Results

3.1. Vegetation

There were considerable differences in vegetation characteristics between the donor and receptor sites. Tree density and species richness and diversity were lower in CBS than in CBWS. However, despite the highly disturbed nature of the site, mean DBH and the relative coverage of food species were higher in CBS (Table 2). In CBS fruit is generally more abundant and available year round while in CBWS there is a much more pronounced seasonality to fruit abundance (Silver, 1997, Fig. 2). The distribution of fruit at the two sites is also very different. In CBS the fruit species eaten most by the howler monkeys (*Ficus americana*) account for < 1% of the relative coverage of the forest, and has a clumped distribution. In CBWS, the fruit species eaten most by the monkeys (*Pourouma bicolor*, *Simarauba glauca* and *Cordia bicolor*) account for > 16% of the relative coverage of the forest and is widely and evenly distributed in season.

Newly translocated howler monkeys were quickly able to find suitable areas in which to establish their home ranges. In fact, we were unable to distinguish significant differences between the quality of translocated and established group ranges in tree density ($U_{8,6} = 19$, $p = 0.5$), relative coverage of food species ($U_{8,6} = 13$, $p = 0.16$), species diversity ($U_{8,6} = 13$, $p = 0.16$) or species richness ($U_{8,6} = 18$, $p = 0.48$). Trees in the ranges of established groups were slightly larger than those in translocated group ranges ($U_{8,6} = 9$, p < 0.053) (Table 2).

3.2. Population density and home range size

In CBS, population density in site 1 was less than half the density in Site 2 (Table 3). Yearly home range sizes from site 1 in CBS (Groups C1 and C2) averaged 9.6 ha (Table 3). Three month range size of the groups in site 2 with the highest population density were very similar, but varied widely in site 1. Overall, 3 month range size increased with group size ($r_s = 0.96$, $n = 6$, $p < 0.003$) in CBS, suggesting that while food is more generally abundant than in CBWS it may nonetheless be limited by the small size of the home ranges.

Population density in CBWS was much lower at three individuals/km^2 (Table 3), and yearly home range sizes were larger, averaging 18.7 ha. Three month range size increased six-fold after translocation in group T1 and four-fold in T2. Yearly home range sizes of groups T1 and T2 were greater than those of groups E1 and E2 (Table 3). Within CBWS, range size did not increase with group size ($r_s = -0.2$, $n = 4$, $p = 0.8$) suggesting that while the quality of the habitat may not be as good as the donor site, food is not limiting in CBWS. Overall, estimates of home range size were inversely related to population density, ($r_s = -0.68$, $n = 10$, $p < 0.03$) (Fig. 3).

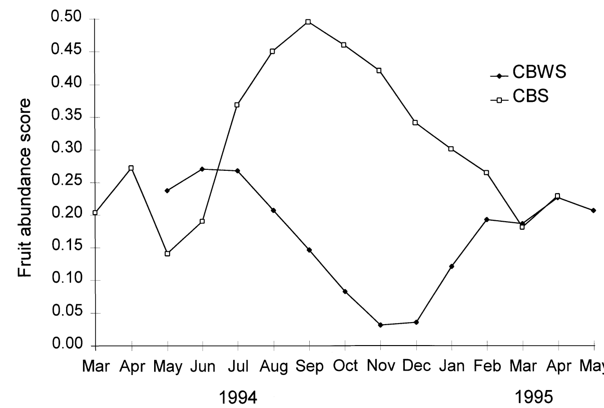

Fig. 2. Monthly patterns of fruit abundance in the Community Baboon Sanctuary (CBS) and the Cockscomb Basin Wildlife Sanctuary (CBWS) from 1994 to 1995. Fruit abundance score based upon phenology study and relative coverage of fruit trees in CBS and CBWS (Silver, 1997).

3.3. Day-range length

Another indication of food limitation in CBS was that day-range length increased significantly with group size ($r_s = 0.84$, $n = 6$, $p < 0.04$). This relationship was not evident in CBWS ($r_s = 0.\ 4$, $n = 4$, $p < 0.6$). Day-range length did not vary strongly with fruit abundance in CBS ($r_s = 0.29$, $n = 14$, $p = 0.32$), perhaps because *Ficus spp*. (the primary fruit sources) have asynchronous phenological cycles (Janzen, 1979). However, there was a significant seasonal effect on monthly day-range length in CBWS ($F_{12,48} = 3.9$, $p < 0.001$) and day-range length increased with fruit abundance across all groups ($r_s = 0.61$, $p < 0.03$) although not all individual groups showed a significant response. We found no significant

Table 2
Differences in vegetation characteristics (mean ± 1 standard error) (1) between the Community Baboon Sanctuary and the Cockscomb Basin Wildlife Sanctuary and (2) within the Cockscomb Basin Wildlife Sanctuary between transects in established and newly translocated group ranges

	(1) Between sites		(2) Between transects (+1SE)	
Variable	CBS (1.0 ha)	CBWS (1.4ha)	Established groups ($n = 6$)	Translocated groups ($n = 8$)
Tree density (trees/ha)	551	642	671 ± 58	607 ± 56
Species richness	60	89	26 ± 3	23 ± 1
Species diversity (H′) [a]	1.43	1.59	4.9 ± 0.3	4.6 ± 0.1
Mean DBH (cm)	28.0	24.3	23 ± 1	26 ± 1
Relative coverage of food species [b]	0.84	0.54	0.46 ± 0.05	0.60 ± 0.07

[a] Measured by the Shannon–Weaver diversity index.
[b] Relative coverage calculated from Brower et al. (1990).

Table 3
Population density of study sites, group size, yearly and 3 month range sizes, and day-range lengths (±1 standard error) of all study groups in CBS and CBWS from 1994 to 1995

Group	Location	Time studied	PD	GS	YHR	3MO	DRL (±1 SE)
Pre-translocation							
T1	CBS Site 1	March–May 1994	47	3.0	nd	2.0	417±85
T2	CBS Site 2	March–May 1994	124	4.5	nd	3.3	410±151
T3	CBS Site 2	March–May 1994	124	4.5	nd	3.1	497±192
T4	CBS Site 2	March–May 1994	124	7.5	nd	3.5	673±207
Post-Translocation							
T1	CBWS	May 1994–May 1995	3	4.0	21.0	7.4	412±181
T2	CBWS	May 1994–May 1995	3	4.0	24.5	8.4	465±191
E1	CBWS	May 1994–May 1995	3	6.0	9.3	6.3	441±176
E2	CBWS	May 1994–May 1995	3	4.5	20.2	8.7	567±263
Not Translocated							
C1	CBS Site 1	March 1994–May 1995	47	6.0	10.4	3.3	520±185
C2	CBS Site 1	March 1994–May 1995	47	9.5	15.8	7.9	648±230

PD = Population Density (individuals/km^2). GS = Group Size. YHR = yearly home range size (ha). 3MO = Area used in a 3 month period (ha). DRL = mean day-range length (m). nd = no data.

difference between the mean day-range lengths of groups T1 ($t=0.15$, $p=0.88$), and T2 ($t=1.42$, $p=0.2$) in CBS and their day-range lengths in CBWS.

Despite their generally smaller home ranges, groups in CBS had significantly longer day-range lengths than groups in CBWS ($F_{2,17}=5.25$, $p<0.02$). This may be due to the larger size of the groups studied in CBS. There were no significant difference between the day-range lengths of the newly translocated and established groups in CBWS.

3.4. Home range use

Newly translocated groups did not use significantly more area on a monthly basis than established groups ($t=5.31$, $p=0.15$) (Table 4). However, because the home ranges of the established groups are smaller than those of the translocated groups, E1 and E2 tend to use a greater *percentage* of their range on a monthly basis (Table 4). T1 and T2 tended to shift the location of their monthly ranges, exploring more areas than established groups. T1 and T2 entered cells only once or twice more frequently (~315 times) than established groups (~200 times). Conversely, established groups used parts of their home range significantly more intensively than translocated groups ($\chi^2=62.45$, $df=10$, $p<0.01$). For example, group E1 entered 41 grid cells (20×20 m) more than five times while neither translocated groups used more than 11 cells this intensively (Fig. 4). Only established groups visited any cell more than 13 times. The majority of the most frequently visited cells in all group ranges had been visited at least once by the fourth month of the study.

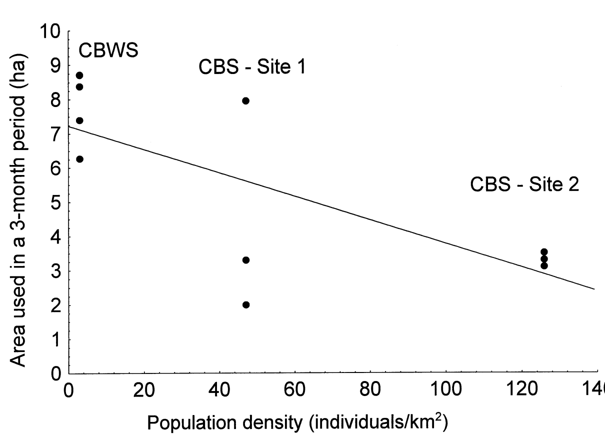

Fig. 3. Correlation between population density and amount of area used in a 3-month period for all study groups ($r_s=-0.68$, $n=10$, $p<0.03$).

3.5. Home range development

One of the established groups (E1) used significantly less new area than all other groups ($F_{2,10}=12.23$, $p<0.001$). The patterns of group E2, however, were more similar to those of the newly translocated groups. There was, however, a significant interaction effect between treatment and month ($F_{11,22}=3.41$, $p<0.007$) which is due, at least in part, to the large increase in new area entered by groups T1 and T2 in the last month of the study while neither established group showed such an increase (Fig. 5). This increase in exploration coincides with an increase in fruit abundance in these months.

Home range establishment occurred in the sixth month for all of the groups (Fig. 6). After this month the newly translocated groups began to refine their ranges, excluding less suitable areas. However, only fully established groups (E1, E2, C1 and C2) consistently maintained a ratio of >1 for the remainder of the study.

Table 4
Size (ha) of monthly ranges and % of yearly home range used monthly by study groups

	Area used per month				% Home range used per month			
Month	E1	E2	T1	T2	E1	E2	T1	T2
May	2.8	1.8	2.0	3.6	33	11	11	18
June	2.3	3.7	3.3	2.3	27	22	18	11
July	2.5	1.9	2.4	2.2	29	11	13	11
August	2.2	2.9	3.0	2.5	25	17	17	12
September	2.9	3.2	2.6	2.2	33	19	15	11
October	1.8	2.0	1.8	2.5	21	12	10	12
November	2.0	3.4	2.0	2.6	24	20	11	13
December	0.7	3.2	2.4	2.0	8	19	14	10
January	0.9	3.5	2.7	2.8	10	21	15	14
February	2.9	5.1	2.1	2.5	33	30	12	12
March	3.8	4.2	1.8	2.0	44	25	10	10
April	3.0	3.8	4.0	5.7	35	22	23	28

The ratio of previously entered to new cells also approached unity much faster for these groups, with mean values >0.5 by June or July, whereas the translocated groups did not reach this point until September.

Measured by minimum convex polygons, groups E1 and E2 used a much smaller area during this, their third year in CBWS than in their first year (E1: 58.4 ha, year 1; 20.2 ha, year 3; E2 173.7 ha, year 1; 62.4 ha, year 3).

4. Discussion

4.1. Ranging behavior

The ranging behavior documented in this study is consistent with the adaptable behavior of howler monkeys and their ability to thrive in different habitats that has been noted by other authors (e.g. Crockett and Eisenberg, 1987; Neville et al., 1988). Population density, however, may be as important a determinant of habitat quality as the vegetation characteristics of an area. Groups of *A. pigra* in CBS in northern Belize live in smaller home ranges and at much higher densities than groups in CBWS. Population density was found to affect home range size when all groups and sites are considered together, as with *Alouatta* species in general (Crockett and Eisenberg, 1987). Groups of *A. pigra* in CBS are territorial (Horwich, 1983; Ostro, 1998) and maintain exclusive home ranges with high levels of inter-group aggression (Ostro, 1998). As with other primates, the home ranges of howler monkeys living at high densities may be compressed by the presence of surrounding groups (Dunbar, 1987; Dobson and Lyles, 1989). The increase of home range size with group size in CBS may result from the defendable area (and therefore the food resources) being limited by the high numbers of surrounding groups.

In CBWS the low population density results in home ranges that are less compressed and the monkeys are able to use a much larger area with fewer intergroup encounters (Ostro, 1998). The lower overall diversity and abundance of food sources in CBWS (possibly indicating a lower quality habitat in CBWS) may also contribute to the larger home range sizes of the groups in CBWS. Dunbar (1987) and (Chapman, 1988a, Chapman, 1988b) theorized that groups living in relatively impoverished habitats would need larger supplying areas. However, differences in habitat quality alone may not account for the differences in home range size between the two areas. In addition, high rates of reproduction and infant survival in CBWS (Koontz, unpublished data) contradict the suggestion that CBWS is an impoverished habitat.

Differences between donor and receptor sites are also highlighted by variation in the relationships between day-range length and group size. Isbell (1991) suggests

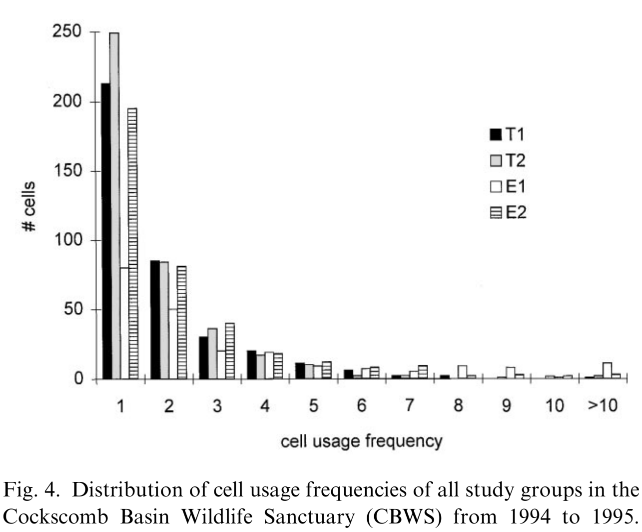

Fig. 4. Distribution of cell usage frequencies of all study groups in the Cockscomb Basin Wildlife Sanctuary (CBWS) from 1994 to 1995. E = Established groups, T = Newly translocated groups.

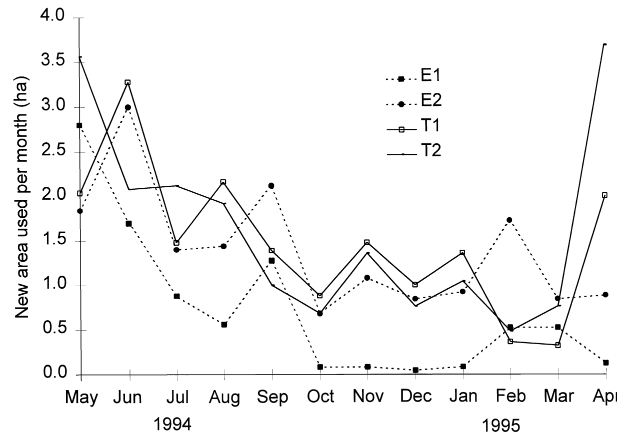

Fig. 5. New area (in ha) used by study groups in the Cockscomb Basin Wildlife Sanctuary (CBWS) from 1994 to 1995. E = Established groups, T = Newly translocated groups.

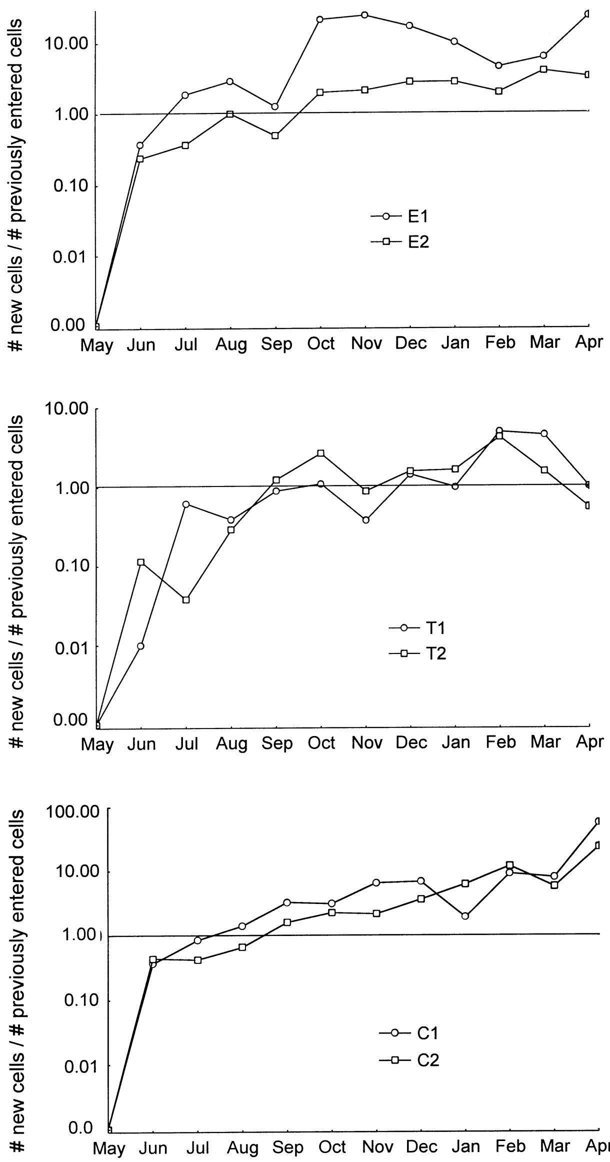

Fig. 6. Ratio of new cells entered to cells previously entered within the yearly home ranges of the study groups in the Community Baboon Sanctuary (CBS) and the Cockscomb Basin Wildlife Sanctuary (CBWS) from 1994 to 1995. E = Established groups, T = Newly translocated groups, C = CBS groups.

that the relationship of day-range length to group size is sensitive to patterns of food distribution where populations feeding on clumped resources show a positive relationship between group size and day-range length but not those that feed on dispersed resources. There appear to be such differences in the distribution of food (particularly fruit) resources between the CBS and CBWS. In CBS fruit resources are highly clumped, while the most important fruit resources in CBWS are also common trees in the forest (Silver, 1997). Consequently, when these species are in fruit in CBWS, this resource is abundant and evenly distributed, a pattern more commonly attributed to foliage resources (Clutton-Brock, 1974; Clutton-Brock and Harvey, 1977; Isbell, 1991; Yeager and Kool, 1998). At the same time, the ranging behavior of the groups corresponds more closely to Isbell's (1991) predictions for folivorous groups.

4.2. Translocation and range use

In the year following translocation, groups appear to systematically explore their release area. We expected that during the year they would refine their ranges by excluding less suitable areas and they did tend to do so. However, although the most frequently used areas had been fully explored by the sixth month after the translocation, the complete process of selection and refinement may take longer than one year, as indicated by the large amount of new area groups T1 and T2 added to their ranges in March, and particularly April 1995 (Fig. 5). The resumption of range expansion by these groups coincides with the highest level of fruit abundance in 9 months (Silver, 1997). Since some aspects of ranging behavior are correlated with fruit abundance, we suggest groups should only be termed 'established' when the ratio of new to previously entered cells remains >1 through all phases of fruit abundance. Consequently, monitoring programs should continue through a complete phenological cycle in order to assess changes of ranging behavior that occur in response to changes in food abundance.

The larger areas used overall by the newly translocated groups can be attributed to exploration by the new arrivals. This may only be evident in the first year post-translocation. The reduction in range size by groups E1 and E2 after their first year can be ascribed to range refinement in their second and third years in CBWS. Their range sizes may also have been affected by the increase in population density in CBWS caused by the introduction of newly translocated groups. Since E1 and E2 were moved, another eleven groups have been translocated into the area. This corresponds with at least a three-fold increase in population density from their first year in CBWS. Much of the outer boundaries of the first year's range of E1 and E2 is now within the home ranges of other groups.

The presence of other established groups is likely to have affected the home range size of groups T1 and T2 in their first year, restricting their exploration of surrounding areas. Groups T1 and T2 were among the last groups to be introduced into the basin. Because no other groups of monkeys will be translocated into the area we now expect only gradual increases in population density. Under the scenario of exploration and range refinement, we expect the ranges of groups T1 and T2 to decrease over time. However, because of the restrictions in their initial explorations placed on them by the presence of adjacent troops, we do not expect a reduction in range size as large as that which occurred for groups E1 and E2.

It is worth noting that group E2 only defended their territory as a group 6 months prior to the translocation of T1 and T2. This group also exhibits ranging characteristics that are often midway between the translocated groups and group E1. The overall range size, new area used on a monthly basis and distribution of cell usage frequencies of this group is more similar to translocated groups than to those of E1. This same pattern also holds true for their feeding behavior and activity budgets (Silver, 1997).

The key differences between established and translocated groups do not lie in the amount of area they explore on a daily basis, but in how they use the area they do travel in. Presumably, established groups have a greater knowledge of the travel paths and the location and relative quality of food resources within their ranges. As a result, they cover a larger proportion of their total range on a monthly basis and use their area more intensively, returning to the same locations more frequently than the translocated groups. New arrivals need to satisfy their daily nutritional needs, while at the same time increasing their knowledge from which they base their ranging decisions. This is reflected in a greater degree of exploration when compared to the established troops, particularly when food resources are widely available. These differences can be expected to remain until new arrivals have acquired sufficient information from which to make ranging decisions.

The overall costs of this translocation to the monkeys are not easily discerned. We were unable to find statistically significant differences in any measure of ranging behavior between established and translocated groups. Day-range lengths were not higher in newly translocated groups and translocated groups did not experience higher mortality than established groups. Differences in habitat quality between the ranges of the established and translocated troops were indiscernible except the slight difference in tree size within the ranges of established groups. Milton (1980) suggested that *Alouatta* may be "travel minimizers" and that their activity may be limited by their relatively low energy diet. The similarities in ranging behavior between translocated and established groups presented here appear to support this view. Researchers have suggested that howler monkeys adjust their diet to the availability of different food resources (Milton, 1980) or that they are "facultative folivores" (Silver et al., 1998). Because howler monkeys are able to adjust their behavior in order to minimize the costs of sudden changes in habitat they are excellent candidates for translocations and reintroductions. Howler monkeys may also provide a model for translocations of other taxa that exhibit similar dietary and behavioral characteristics.

With high annual variability and supra-annual phenological cycles of tropical forests, this process of adjusting ranging behavior to suit changes in their environment may take several annual cycles. Home range sizes estimated in the first year post-translocation may be much larger than those the animals eventually use. As a result, a 1-year follow-up of translocated animals may be the *minimum* time necessary to characterize the ranging patterns of newly established groups or to evaluate the short-term success or failure of a translocation project.

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