

# Habitat selection by translocated black howler monkeys in Belize

Linde E. T. Ostro<sup>1,3</sup>, Scott C. Silver<sup>1,3</sup>, Fred W. Koontz<sup>1</sup> and Truman P. Young<sup>2</sup>

<sup>1</sup> Science Resource Center, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY, 10460, USA

<sup>2</sup> Department of Environmental Horticulture, University of California, Davis, CA 95616, USA

<sup>3</sup> Louis Calder Biological Station and Department of Biology, Fordham University, Armonk, NY 10504, USA

(Received 28 April 1999; accepted 29 November 1999)

## Abstract

Habitat selection by translocated black howler monkeys (*Alouatta pigra*) was studied in Belize, Central America. Ranging patterns of two recently translocated groups were contrasted with those of two groups in the same area with established home ranges, on a yearly and monthly basis. All groups concentrated their activities along stream beds at elevations below 200 m. Newly translocated groups increased the percentage of their monthly ranges in riverine areas (within 100 m of a water source) over the year of the study (with the exception of the last month) while established groups did not. Areas used more than five times by the monkeys contained larger trees and a greater relative coverage of major food species than low-use areas even though they had a lower overall species richness and diversity. These monkeys may be selecting habitat within the forest based upon vegetative differences and ranging patterns may be affected by patterns of food availability.

## INTRODUCTION

Translocation is being increasingly used by the conservation community to rescue threatened animals from habitat destruction, repopulate areas with low densities or to augment genetic diversity in existing gene pools (Mackinnon, 1976; Konstant & Mittermeier, 1982; Caldecott & Kavanagh, 1983; Griffith *et al.*, 1989; Woodruff, 1989). The increasing need for intensive management of species in national parks and refuges (Conway, 1989; Woodruff, 1989; Foose, 1991) also suggests that translocations will need to be used more often as a management tool. However, this technique can be extremely expensive (Kleiman *et al.*, 1991), requires intensive monitoring if conducted properly (Stanley Price, 1989; Griffith *et al.*, 1989; Chivers, 1991; IUCN/SSC, 1995) and has long been known to be stressful to the animals involved (Haarhoorn, 1962; Caldecott & Kavanagh, 1983; de Vries, 1991).

In view of these factors it is imperative that we study the relatively few successful primate translocations so that future movements of wild animals can be conducted properly. One factor that can dictate the success or failure of a translocation is the proper selection of a release site (Griffith *et al.*, 1989). Release into unfavourable habitat can result in increased dispersal or even loss of the animals, while prior knowledge of the preferred habi-

tats of the study animals can help avoid a needless waste of resources. A study of habitat selection can also help prioritize areas for conservation efforts by targeting those habitats that are most important for particular species. We present a study of habitat selection by four groups of translocated black howler monkeys (*Alouatta pigra*) in Belize, Central America. This study was conducted in the hope that determining the habitat characteristics that are important to *A. pigra* would improve our ability to determine the most suitable areas for habitat protection and release sites for future translocations of howler monkeys.

Populations of *A. pigra* are found throughout Belize and in parts of southern Mexico and northern Guatemala. Like other species in the genus, *A. pigra* is generally found in riparian forests at elevations below 400 meters (Bolin, 1981; Horwich & Johnson, 1986; Crockett & Eisenberg, 1987). An exception to this is the population in Tikal, Guatemala, which lacks true riparian habitat, although the low-lying forests are seasonally flooded (Schlichte, 1978). The species was originally depicted as a fruit specialist (Coelho *et al.*, 1976; Schlichte, 1978) but has more recently been described as a facultative folivore, whose diet is as frugivorous as possible and as folivorous as necessary (Silver *et al.*, 1998).

From May 1992 to May 1994, 14 groups of *A. pigra* were translocated from the Community Baboon Sanctuary in northern Belize to the Cockscomb Basin Wildlife Sanctuary (CBWS) in southern Belize (for

details of the translocation, see Horwich *et al.*, 1993; Koontz *et al.*, 1994; Koontz & Ostro, 2000). The CBWS consists of 400 km<sup>2</sup> of continuous evergreen and semi-evergreen broadleaf tropical forest (Kamstra, 1987). While CBWS contains the watershed of two river systems in the East and West Basins, like Tikal the forest lacks clearly defined riparian or gallery forest. The monkeys were released into the East Basin: the watershed of the South Stann Creek river. Elevations within CBWS range from 80 m to 1120 m above sea level (a.s.l.).

From May 1994 to May 1995 habitat selection by two groups of recently translocated monkeys and two groups with established home ranges in CBWS was studied. Our intention was to characterize and compare the areas that the monkeys used extensively with those areas that were explored and subsequently not used. We were particularly interested in the effects of elevation and proximity to watercourses on the ranging patterns of the monkeys in CBWS.

It was hypothesized that the use of habitat below 120 m would be disproportionate to the amount of lowland habitat in the study area, and that the use of riverine areas would be disproportionate to the amount of riverine habitat in the study area. Furthermore, it was predicted that areas used most by the monkeys would be characterized by differences in vegetation. It was also predicted that if the groups were selecting particular habitat types, recently translocated (new) groups would increase the percentage of their monthly range spent in these habitats over time, but established groups that were translocated 2 years previously, would not show such an increase.

## METHODS

### Data collection

From May 1994 to May 1995 the ranging behaviour of four groups of *A. pigra* was studied in CBWS (Ostro *et al.*, 1999a, b). Two of the study groups of *A. pigra* were translocated to CBWS in May 1994 (T1 and T2), and two groups had been moved to CBWS in previous years (E1 and E2). Group E1 had been translocated to CBWS as an intact group in 1992, E2 was a group that had formed in CBWS from females that had been translocated in 1992 and were joined by a male translocated in 1993. Both of these groups were considered to have established stable home ranges since the majority of group members had been consistently found within the same areas for 2 years prior to this study (Ostro *et al.*, 1999a). The age–sex composition of the study groups is described in Ostro *et al.* (1999a).

Each study group was followed for two consecutive data collection periods at the beginning and end of each month (a data collection period lasted from the time the monkeys were first contacted to the same time the following day). The home ranges of the study groups were located within the CBWS trail system. Prior to this study the 23 km trail system had been mapped using a hand-line and compass, and tags placed every 50 m along the trails (Koontz *et al.*, 1994). Universal Transverse

Mercator co-ordinates were calculated for each of these positions. Differentially corrected Global Positioning System (GPS) readings were taken at trail intersections to gauge the accuracy of the co-ordinates and indicated that the trail tags were accurate within a 20 m radius (C. Miller, pers comm.). Using a Geographic Information System (GIS), a 1 km grid was superimposed upon the trail system and the 9 km<sup>2</sup> area where the group ranges were located was defined as the study area. This GIS is based on digitized topographic maps issued by the government of Belize. Using a hand-line and compass the group's distance (to the nearest metre) and direction from known points was recorded every 15 minutes. All group location points were entered into the GIS.

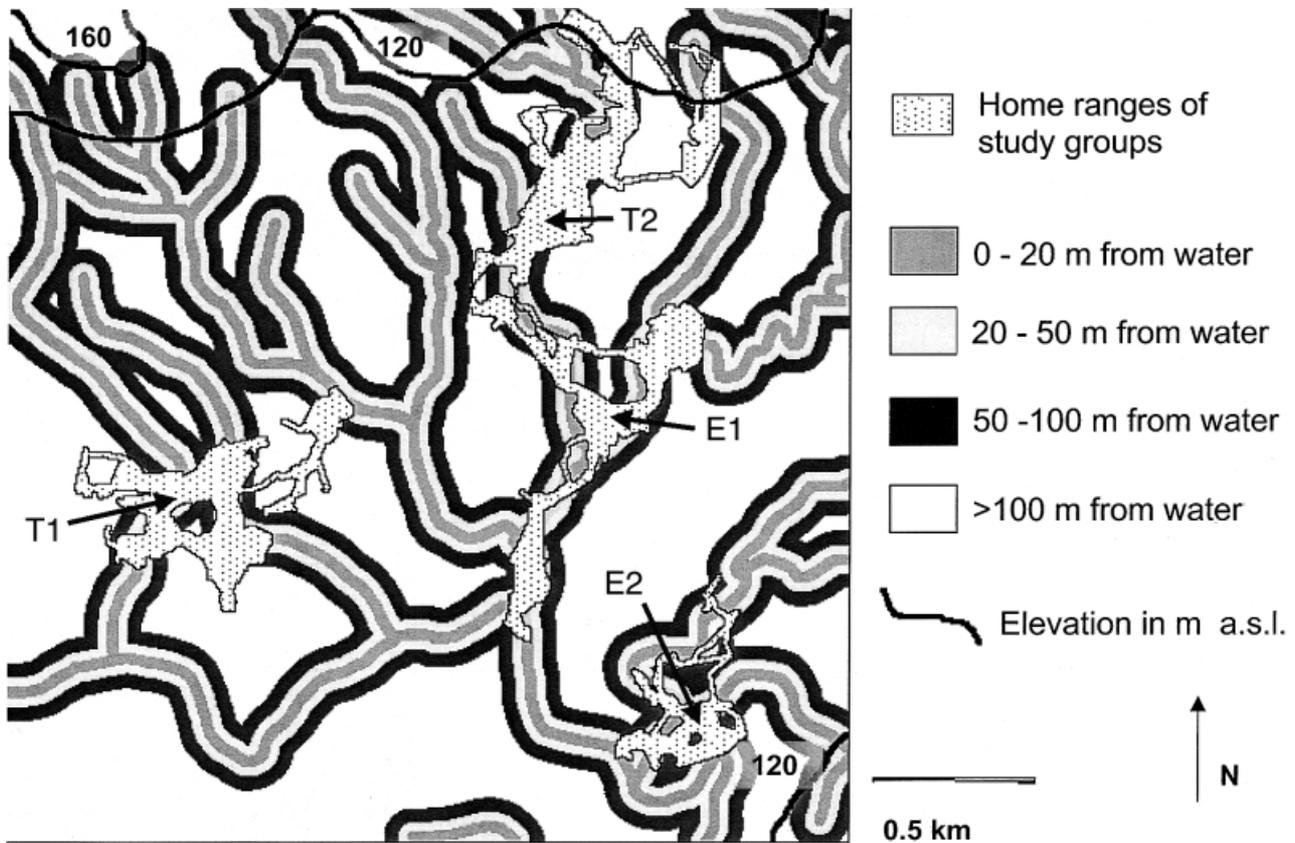
### Data analysis

Over the year of the study an average of 2500 location points was collected for each group. The data were highly autocorrelated so we used a subset of the data points for each group created using Shoener's (1980)  $t^2/r^2$  ratio. Using this subset and the GIS, areas were arbitrarily delineated as: (1) low-use areas (visited once only), (2) medium-use areas (visited 2–5 times) and (3) high-use areas (visited more than five times) within the home ranges of the monkeys. All high-use areas were located within 100 m of a stream so the percentage of the monthly ranges that were found in 100 m riverine and non-riverine areas was calculated, and a Spearman's rank correlation was used to determine whether the percentage of monthly ranges within riverine zones increased significantly over time.

The home ranges of the monkeys were delineated using digitized polygons (Ostro *et al.*, 1999b). Using the GIS, the location data were overlaid on topographic maps of CBWS (Fig. 1). The proportion of different elevations in the study area was calculated and  $\chi^2$  was used to test whether the location points of monkey groups were distributed disproportionately at different elevations. The GIS was also used to digitize buffers of 0–20 m, 21–50 m, 51–100 m, 101–150 m, 151–200 m, 201–250 m and >250 m width centred on every watercourse and to calculate the percentage of each 'riverine zone' within the study area. The percentage of the study areas within each of the zones was calculated and this was used to generate the expected numbers of observations within them for each group. The subset of location data was then overlaid on to the riverine zones of all widths and the observed number of points in each riverine zone for each group was calculated. A  $\chi^2$  test was used to determine whether the group location points were randomly distributed within the study area.

### Vegetation sampling

Fourteen 100 m × 10 m belt transects were established in CBWS. Once the home ranges of the monkeys had been determined, known points that lay within low-use and high-use areas in the home ranges of the groups could also be determined. Low- and high-use points were



**Fig. 1.** Home ranges of the study groups from May 1994–May 1995 in the Cockscomb Basin Wildlife Sanctuary, overlaid on 0–20 m, 21–50 m and 51–100 m riverine zones. Also shown are elevations of 80–120 m, 120–160 m and 160–200 m above sea level (a.s.l.).

chosen out of a hat to determine the starting points for the transects, and the direction was also randomized. Eight transects were located in high-use areas (two from each group), while one transect from each of the established groups and two transects from each of the newly translocated group transects were in low-use areas.

Voucher specimens were collected from each tree species and identified at the New York Botanical Gardens. Tree size (diameter at breast height, DBH), tree density, species richness and diversity (Shannon–Weaver Index) of each species was measured. Relative coverage was also measured using the formula adapted from Brower, Zar & von Ende (1990):

$$\text{Coverage } (C_i) = \sum \text{relative stem areas for species}_i$$

$$\text{Relative coverage } (RC_i) = \frac{(C_i)}{\text{sum of coverage for all species}}$$

Methods of vegetation sampling are described in detail in Silver *et al.* (1998). A *t*-test was used to determine the significance of differences in tree size, and the Mann–Whitney U test was used to analyze differences in other variables.

Data from a concurrent study of the feeding ecology of translocated howler monkeys (Silver, 1997) were used to determine important food species (those whose individual usage exceeded 1% of yearly feeding time). The

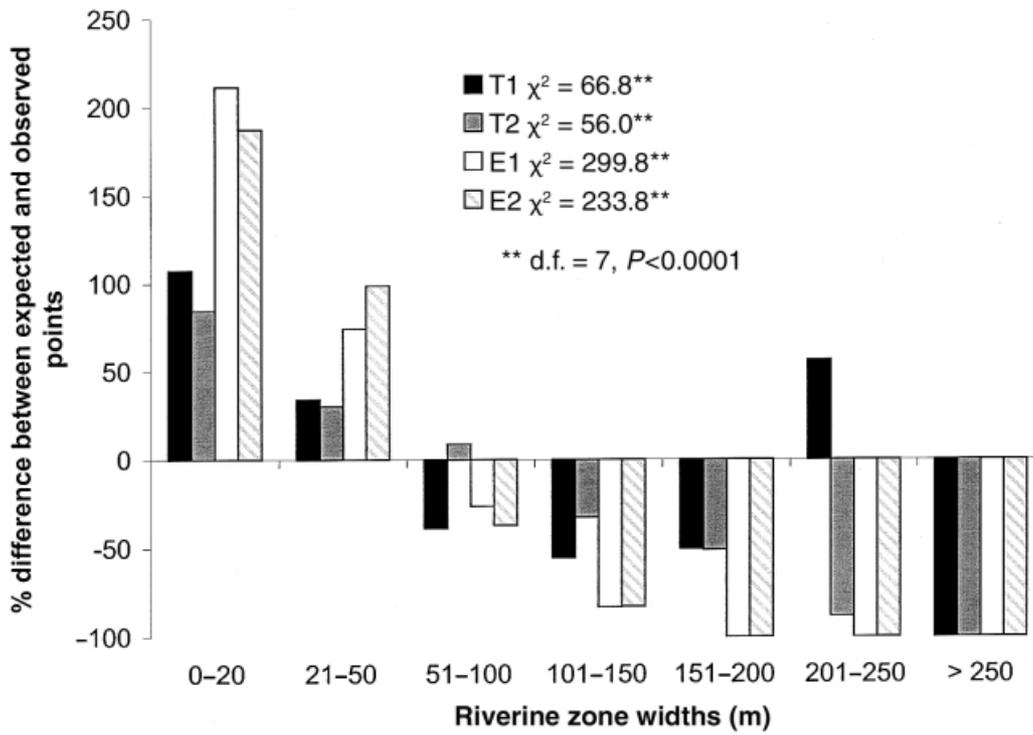
combined relative coverage of these species in high-use and low-use areas was compared using a Mann–Whitney U test.

## RESULTS

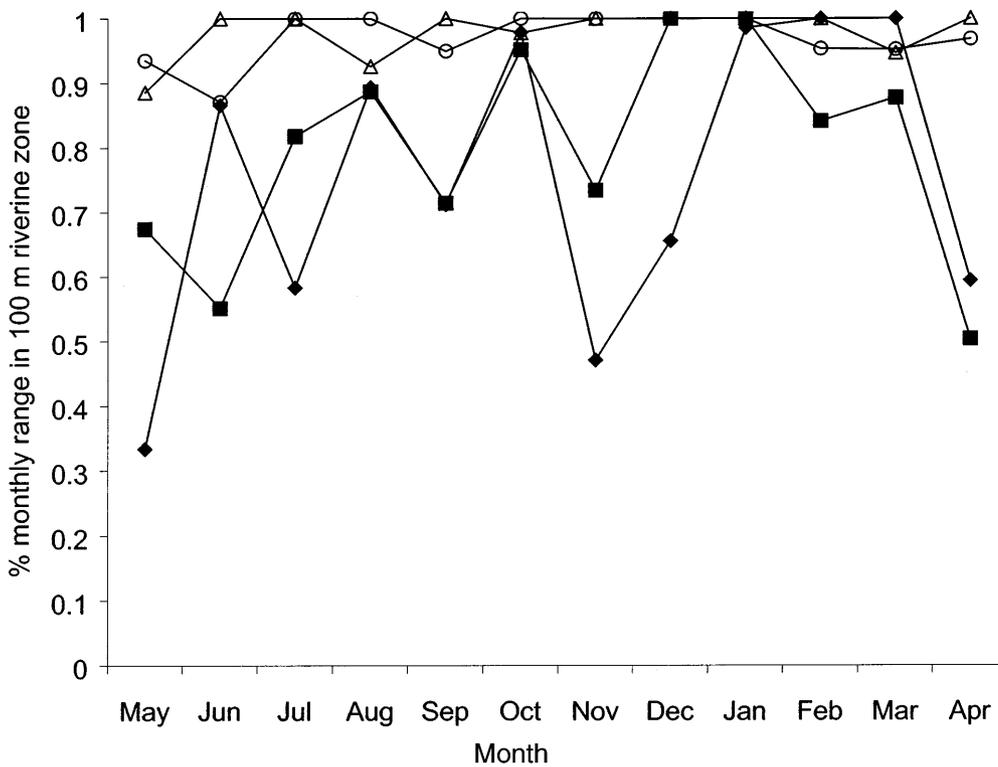
### Topographic features

Elevations in the study area (the 9 km<sup>2</sup> area that encompassed the group home ranges) ranged from 80 m to 200 m a.s.l. and 24.3% of the study area was >120 m a.s.l. (Fig. 1). All groups were released between 80 m and 120 m a.s.l. and < 2 km from higher elevations. The study groups all established their home ranges within 3 km of their release sites. This was typical of the majority of the translocated groups ( $n = 14$ ), although three non-study groups travelled up to 9 km in the first year following translocation (Koontz & Ostro, 2000). All study groups were found in areas below 120 m significantly more often than expected (in all cases  $\chi^2 > 42$ , d.f. = 1,  $P < 0.01$ ). In fact, three groups stayed entirely within areas between 80 m and 120 m a.s.l. throughout the study while the fourth group (T2) used areas between 120 m and 160 m in the first 2 months and on the last day of the study only.

The study groups tended to range in the forests located along stream beds (Fig. 1). The distribution of location



**Fig. 2.** Percentage difference between the frequency of observed and expected location points in riverine zones of 0–20 m, 21–50 m, 51–100 m, 101–150 m, 151–200 m, 201–250 m and >250 m for newly translocated groups (T1 and T2) and established groups (E1 and E2).



**Fig. 3.** Percentage of monthly range within 100 m river zones of two newly translocated groups (T1 and T2) and two established groups (E1 and E2). ◆, T1; ■, T2; △, E1; ⊙, E2.

points within the study area deviated significantly from randomness for all groups (in all cases  $\chi^2 > 56$ , d.f. = 7,  $P < 0.0001$ ; Fig. 2). The number of location points observed in the 0–20 m and 21–50 m riverine zones was far greater than expected for all study groups, although there was a larger effect from the established groups (Fig. 2).

The percentage of T1 and T2's home range within 100 m riverine zones generally increased over time until the last month of the study (Fig. 3), at which time both the phenological patterns in the forest and the ranging patterns changed dramatically (Ostro *et al.*, 1999a). If the last month is not considered, the correlation between the number of months since translocation and the percentage of monthly range within riverine zones is significant for both groups (T1:  $r_s = 0.62$ ,  $P < 0.05$ ; T2:  $r_s = 0.68$ ,  $P < 0.05$ ). Established groups did not significantly increase the amount of area within river zones over time (E1:  $r_s = 0.23$ ,  $P > 0.49$ ; E2:  $r_s = 0.31$ ,  $P > 0.34$ ).

### Vegetation

Habitats in high-use areas were characterized by significantly larger trees, lower species richness and a higher relative coverage of food species than habitat in low-use areas (Table 1). Six of the 11 major food species (42% of yearly feeding time) had greater relative coverage in high-use areas, and four species (23% of yearly feeding time) had approximately equal coverage in high- and

low-use areas (Fig. 4). High-use areas also showed a strong tendency to be characterized by lower tree density, although the difference was not statistically significant (Table 1).

### DISCUSSION

In CBWS, all the groups established home ranges at lower elevations although they could have ranged in areas above 120 m a.s.l. Group T2 was released on the edge of the higher elevations, but after the first 8 weeks in CBWS they remained below 120 m a.s.l. At least one of the established groups (E1) had also explored higher elevations during their first year of release (F. W. Koontz, unpublished results), but they were never seen in these areas during this study. In their survey of the geographic distribution of *A. pigra*, Horwich & Johnson (1986) did not find any monkeys above 400 m in elevation. The 300–400 m mountains surrounding the sanctuary, combined with extensive agricultural development at the lowland entrance to the basin may explain why local populations did not recolonize CBWS after their extirpation in 1978 (Koontz *et al.*, 1994). Transects were not established above 120 m in this study, but Kamstra (1987) describes distinct differences in vegetation between the slope forest above 200 m and the typical lowland broadleaf forest. At the highest elevations of the eastern basin, the forest gives way to pineland interspersed with savanna, grasslands and fern glades – habitat in which howler monkeys have never been

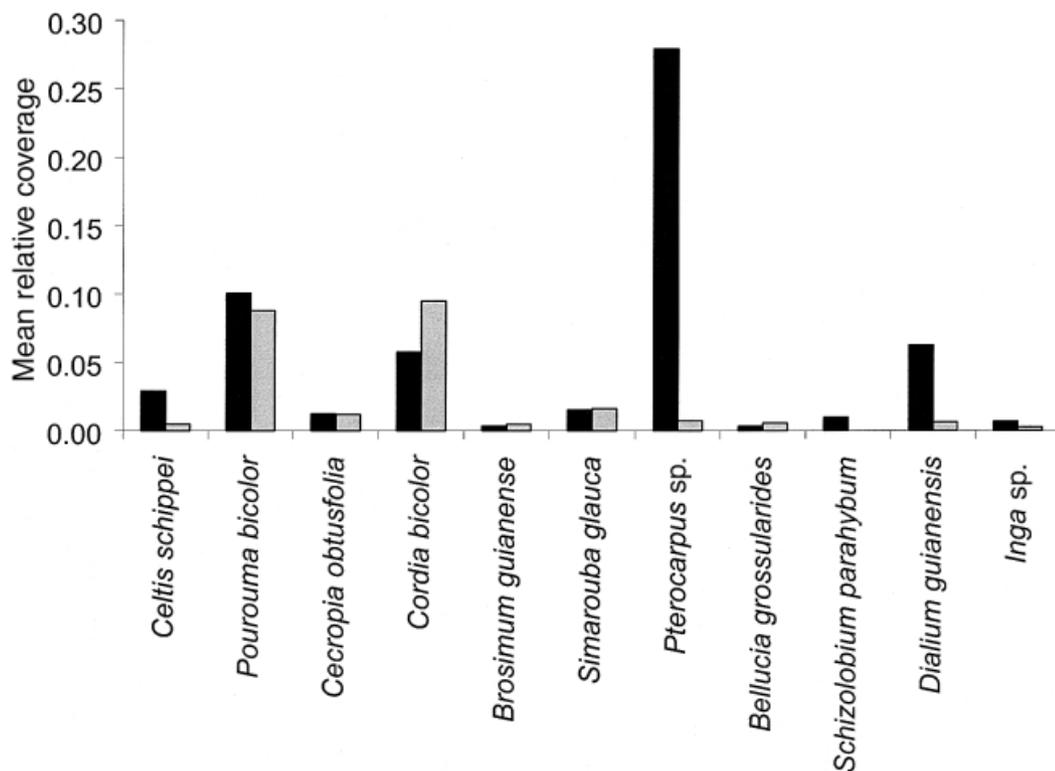


Fig. 4. Mean relative coverage of the 11 tree species used as major food sources that are found on transects in riverine and non-riverine zones. Species are presented in order of dietary preference. ■, Riverine; □, non-riverine.

**Table 1.** Differences in vegetation ( $\pm$  SEM) and Mann–Whitney U test scores between transects in high-use ( $n = 8$ ) and low-use ( $n = 6$ ) areas within *Alouatta pigra* home ranges in the Cockscomb Basin Wildlife Sanctuary

Variable	Riverine zone	Non-riverine zone	Z	P
Tree density (trees/ha)	59.2 ( $\pm$ 3.8)	73.6 ( $\pm$ 8.0)	-1.94	0.053
Species richness	22.2 ( $\pm$ 3.5)	29.2 ( $\pm$ 1.6)	-2.13	0.032
Species diversity (H')	2.7 ( $\pm$ 0.1)	2.0 ( $\pm$ 0.1)	-1.81	0.071
Mean DBH (cm)	26.1 ( $\pm$ 1.5)	20.8 ( $\pm$ 0.6)	-2.07	0.039
Mean relative coverage (%) of major food species ( $n = 11$ ).	57.9 ( $\pm$ 6.5)	28.6 ( $\pm$ 2.4)	-1.94	0.002

DBH, diameter at breast height.

observed. These data highlight the importance of maintaining lowland corridors of forested areas if populations of howler monkeys (and other animals that may be restricted by elevation) are to disperse successfully, or to recolonize areas that have lost their normal populations.

Within the lowland forest areas, the shape of the home ranges appears to be dictated by the course of the streams and rivers (Fig. 1). The analysis of riverine zones of different widths suggests that all of the study groups concentrate their activities in riverine zones that range from 0–100 m in width (Fig. 2). Established groups and one translocated group (T1) had a far greater than expected number of location points only in riverine zones of 0–20 m and 2–50 m while group T2 also used 51–100 m areas more than expected. The process of selecting riverine areas takes some time and by the end of the study newly translocated groups had not yet fully modified their ranging patterns to select only riparian habitats. However, the significant correlation between amount of time spent in riverine zones and time since translocation suggests that this process was occurring during this study.

Multiple patterns suggest that the areas within 100 m of streams provide the most important habitats for the monkeys: (1) all of the high-use transects were located entirely within 100 m riverine zones; (2) all of the low-use transects were located  $> 100$  m from a stream; (3) the greatest discrepancy between observed and expected frequencies of location data occurred when the riverine zone was between 0 and 20 m. Although, it is important to note that some high-use areas occurred between 50 and 100 m for all of the study groups.

To a casual observer, the forest within 100 m of a stream is not obviously different from the rest of the lowland forest in CBWS. The streams are usually so narrow that they rarely cause a gap in the canopy and the monkeys were never seen to drink from them. However, the greater DBH and the overall higher relative coverage of many major food sources in the high-use areas indicate that there is a greater abundance of high quality foods there. Although the difference in mean DBH of trees in riverine and non-riverine areas is relatively small, when translated into canopy volume, the difference becomes larger. Extremely subtle variations may dictate the suitability of habitat to a species so it is important not only to save large areas of habitat but also as many different variations as possible within the broad habitat type.

The possibility exists that the monkeys selected riverine areas for a reason other than an increased presence of their major food sources and large trees. There could be differences in the phytochemical, water, or mineral content of foods found in trees growing next to the stream beds. However, since both the definition of major food sources and the determination of habitat preferences are ultimately based upon time, a relationship between these two measures must be regarded with caution. Nevertheless, the monkeys were not restricted to riverine areas by their diet. Most of their food species plants were found throughout the forest although they were less common outside riverine areas (Fig. 4). In fact, only one major food species (*Schizolobium parahybum*) was not found outside the 100 m riverine zone.

There was only slight seasonal variation in the percentage of the monthly range of the established groups found in riverine areas. This variation coincides with the location of foods most commonly eaten on a monthly basis. Food availability in CBWS was determined on the basis of a phenology study of the howler monkey food species from 1994–1995 (Silver, 1997). From November to January when the monkeys rely most heavily upon mature leaves as a food source use of the riverine areas peaked for these groups. The two most important sources of mature leaves (*Celtis schippei* and *Cecropia* spp. (Silver, 1997) are more common in the high-use areas.

Seasonal changes in the availability of foods present new challenges regarding the location of food items to translocated monkeys. Each change in season means meeting nutritional requirements with new food choices in new locations, and constant adjustments in habitat use. The recently translocated groups, with less complete knowledge of their habitat, responded to changes in the seasonal availability of food by changing their ranging behaviour. When food availability was high in the riverine areas, translocated groups increased the percentage of their monthly ranges in these areas. However, when tree species common in non-river areas were fruiting (e.g. *Simauruba glauca* in April, 1995), the two newly translocated groups resumed exploration of the forest around their release areas and spent more time away from the riverine zones (Ostro *et al.*, 1999a). The availability of a widely distributed high-energy food resource outside the riverine areas may have allowed these groups to resume expanding their home ranges. Howler monkeys are extremely flexible in their diets, switching from fruit to leaves and flowers as they become available

(Silver *et al.*, 1998). However, other taxa may not be as flexible in their behaviour. For this reason, it is vital that translocation efforts be monitored for a *minimum* of 1 year, through all seasonal changes to ensure that the subjects are able to find food as the levels of resources change.

Horwich *et al.* (1993) speculated that the presence of mountains surrounding the CBWS may have prevented black howler monkeys from recolonizing the basin following the local extinction of the species in the late 1970s. This study supports their concept of *A. pigra* as a species with a strong preference for low-lying areas. Prior studies have already indicated that black howler monkeys exhibit a preference for gallery forest (Bolin, 1981; Horwich & Johnson, 1986), and the Belizean law forbidding clearing or logging within 18 m of a river may be one reason why Belize still has healthy populations of *A. pigra*. This study highlights the importance of preserving large, mature trees and riparian habitat even within continuous forests. Future translocations of *A. pigra* should select release sites close to streams or rivers with many large trees to minimize dispersal following translocation.

### Acknowledgements

We thank F. Koontz, R. Horwich and the Belize Audubon Society who granted us permission to conduct research on the translocation project. The assistance of Ernesto Saqui, William Shoh, Eligorio Sho, Monique Teich, Mark Robertshaw, Ernest Ostro and the wardens of CBWS was invaluable. J. Wehr, L. Isbell and C. Yeager as well as A. Plumpre and P. Walsh provided advice and comments on this study. This research was funded in part by The Wildlife Conservation Society and their assistance is gratefully acknowledged.

### REFERENCES

- Bolin, I. (1981). Male parental behavior in black howler monkeys (*Alouatta palliata pigra*) in Belize and Guatemala. *Primates* **22**: 349–360.
- Brower, J. E., Zar, J. H. & von Ende, C. N. (1990). *Field and laboratory methods for general ecology*. 3rd edn. Dubuque, IA: Wm. C. Brown Publishers.
- Caldecott, J. & Kavanagh, M. (1983). Can translocations help wild primates? *Oryx* **17**: 135–139.
- Chivers, D. J. (1991). Guidelines for re-introductions: procedures and problems. *Symp. Zool. Soc. Lond.* **62**: 89–1002.
- Coelho, A. M. Jr, Bramblett, C. A., Quick, L. B. & Bramblett, S. (1976). Resource availability and population density in primates: a socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates* **17**: 63–80.
- Conway, W. G. (1989). The prospects for sustaining species and their evolution. In *Conservation for the twenty-first century*: 199–210. Western, D. & Pearl, M. C. (Eds). New York: Oxford University Press.
- Crockett, C. M. & Eisenberg, J. F. (1987). Howlers: variations in group size and demography. In *Primate Societies*: 54–69. Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). Chicago: University of Chicago Press.
- de Vries, A. (1991). *Translocation of mantled howling monkeys (Alouatta palliata) in Guanacaste, Costa Rica*. MSc thesis: University of Calgary, Alberta.
- Foose, T. J. (1991). Viable population strategies for re-introduction programmes. *Symp. Zool. Soc. Lond.* **62**: 165–173.
- Griffith, B., Scott, J. M., Carpenter, J. W. & Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science* **245**: 477–480.
- Haarhoorn, A. M. (1962). Translocation as a means of preserving wild animals, *Oryx* **6**: 215–227.
- Horwich, R. H. & Johnson, E. D. (1986). Geographical distribution of the black howler (*Alouatta pigra*) in Central America. *Primates* **27**: 53–62.
- Horwich, R. H., Koontz, F. W., Saqui, E., Saqui, H. & Glander, K. (1993). A reintroduction program for the conservation of the black howler monkey in Belize. *Endang. Spec. Update* **10**: 1–6.
- IUCN/SSC (1995). *IUCN/SSC guidelines for re-introductions*. Gland, Switzerland: IUCN/SSC Re-introduction Specialist Group.
- Kamstra, J. (1987). *An ecological survey of the Cockscomb Basin, Belize*. MSc thesis: York University, Ontario.
- Kleiman, D. G., Beck, B. B., Dietz, J. M. & Dietz, L. A. (1991). Costs of a re-introduction and criteria for success: accounting and accountability in the golden lion tamarin conservation program. *Symp. Zool. Soc. Lond.* **62**: 125–144.
- Konstant, W. R. & Mittermeier, R. A. (1982). Introduction, reintroduction and translocation of neotropical primates: past experiences and future possibilities. *Int. Zoo Yrbk* **22**: 69–77.
- Koontz, F. W., Horwich, R. H., Saqui, E., Saqui, H., Glander, K., Koontz, C. & Westrom, W. (1994). Reintroduction of black howler monkeys (*Alouatta pigra*) into the Cockscomb Basin Wildlife Sanctuary, Belize. In *American zoo and aquarium association annual conference proceedings*: 104–111. Bethesda, MD: American Zoo and Aquarium Association.
- Koontz, F. W. & Ostro, L. E. T. (2000) Translocation of black howler monkeys (*Alouatta pigra*) in Belize: a multidisciplinary team approach for effective wildlife conservation. *AZA Field Conserv. Man.* In press.
- Mackinnon, J. (1976). Mountain gorillas and bonobos. *Oryx* **13**: 372–382.
- Ostro, L. E. T., Silver, S. C., Koontz, F. W., Young, T. P. & Horwich, R. (1999a). Ranging behavior of translocated and established groups of black howler monkeys (*Alouatta pigra*) in Belize, Central America. *Biol. Conserv.* **87**: 181–190.
- Ostro, L. E. T., Young, T. P., Silver, S. C. & Koontz, F. W. (1999b). A geographic information system method for estimating home range size. *J. Wildl. Mgmt.* **63**: 748–755.
- Schlichte, H. (1978). A preliminary report on the habitat utilization of a group of howler monkeys (*Alouatta villosa pigra*) in the national park of Tikal, Guatemala. In *The ecology of arboreal folivores*: 551–561. Montgomery G. G. (Ed.). Washington, DC: Smithsonian Institution Press.
- Schoener, T. W. (1980). An empirically based estimate for home range. *Theoret. Pop. Biol.* **20**: 281–325.
- Silver, S. C. (1997). *The feeding ecology of translocated howler monkeys (Alouatta pigra) in Belize, Central America*. PhD thesis: Fordham University, New York.
- Silver, S. C., Ostro, L. E. T., Yeager, C. P. & Horwich, R. (1998). The feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. *Am. J. Primatol.* **45**: 263–279.
- Stanley Price, M. R. (1989). *Animal re-introductions: the Arabian oryx in Oman*. Cambridge: Cambridge University Press.
- Woodruff, D. S. (1989). The problems of conserving genes and species. In *Conservation for the twenty-first century*: 76–89. Western, D. & Pearl, M. C. (Eds). New York: Oxford University Press.

