Passages within a Discontinuous Canopy: Bridging in the Red Howler Monkey (*Alouatta seniculus*)

**Key Words**
*Alouatta seniculus*  
Howler monkey  
Bridging  
Rain forest canopy  
Habitat structure  
Positional behaviour  
Locomotion  
Postcranial morphology  
Prehensile tail

**Introduction**

The instability and fragility of the available supports, the tortuous form of potential pathways and discontinuities of the rain forest canopy compel arboreal mammals to develop particular positional and anatomical adaptations [1, 2]. A major problem is to achieve passages between discontinuous supports while searching for feeding sites [2]. This problem is solved in different ways by different arboreal mammals. A common and successful solution involves bridging the gaps.

Bridging is a way of forming passages between discontinuous supports in which all appendages are used (including the prehensile tail) in deforming either actively or passively one or both of the supports concerned. During bridging, in contrast to leaping or dropping, the animal maintains contact with the supports by grasping each with at least one appendage.

This paper presents a qualitative and preliminary quantitative description of bridging as demonstrated by the slow-moving red howler monkey (*Alouatta seniculus*).

**Study Site and Methods**

The data presented here were collected at the 'Station des Nouragues' site in French Guiana characterized by terra firme wet rain forest [3], using focal individual instant sampling [4]. The variables recorded were (a) support size [small (<2 cm)], medium
(2–10 cm), large (10–15 cm) and very large (>15 cm)],
(b) canopy level [emergent (>30 m), upper (25–30 m),
middle (20–25 m) and lower (15–20 m) canopy],
(c) tail use [no use, tail placed above the centre of gravi-
ty of the animal (CG) and tail placed below CG],
(d) position of the forelimbs with respect to the shoulder
girdle (above, level or below),
(e) direction of move-
ment (ascending, horizontal or descending),
(f) last appendage to release the initial support and
(g) tree quadrant (periphery or central area of tree crown).
Videotapes of the red howler’s behaviour in the same
forest were also consulted in order to determine the
nature of movements involved.

Results

Bridging represents a large proportion of
the locomotor repertoire of the red howler and
especially during travel (12.3%, n = 1,191)
while the percentage diminishes significantly
during feeding (7.3%, n = 372). The howler
bridges gaps more frequently in the upper
canopy (73.5%, n = 147), a stratum that is
extensively used [5], and between tree crown
peripheries (89.6%, n = 48). Consequently,
both initial and terminal supports are preferen-
tially small- and medium-sized (fig. 1). The
role of the prehensile tail is essential in stabi-
zizing and securing the body, grasping above
the CG of the animal and being the last ap-
pendage to release the initial support (fig. 1).

When confronted with a gap, the howler
will either continue to move or stop and
observe. In the first case, it may continue to
clamber upon the slender supports, grasping
firmly with abducted limbs held in semi-
extension, and thus cross the gap (37.5%, n =

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It may also launch itself into an incomplete leap to grasp and haul in an oscillating terminal support (4.2%, n = 48). However, in most cases, the howler stops and stabilizes itself before initiating a passage attempt. To do so, it may suspend itself by tail and feet and use a pendulum-like mechanism to reach the terminal support to pull it towards it (27.1%, n = 48). If in an above-branch pronograde posture, it may extend its torso and forelimbs slowly, maintaining a firm grasp with tail and feet, in order to pull in the terminal support (18.8%, n = 48). Lastly, it may perform an incomplete leap (with tail and feet grasping the initial support) to position its extended torso and forelimbs on the support which then oscillates under the impact of the animal’s weight (12.5%, n = 48). With all techniques used, the forelimbs are semi-extended and placed level with the shoulder (fig. 1). Once the howler has moved to the new terminal support, it continues to walk, climb or clamber more frequently (60.4%, n = 48) than it waits for stabilization of the oscillating support (39.6%, n = 48).

**Discussion**

The howler monkey is a large ceboid characterized by a lethargic nature, slow and deliberate pronograde locomotion, a high proportion of climbing [5–11] and a postcranial morphology associated with frequent rotation, abduction, flexion and pronation in limb articulations [12–16]. Its large body mass, lack of pronounced locomotor specializations and notable adaptations for reaching, grasping and pulling supports [17] compel it to use secure locomotor modes to pass between canopy gaps surrounded by slender, flexible supports. Accordingly, leaping is confined to larger gaps, tail-swinging is used for smaller gaps on stable supports, and dropping, pulling-up and vertical descent are used for rapid vertical crossings.

As the high canopy is characterized by flexible and discontinuous supports, the use of bridging is essential during locomotion within it. Moreover, during these bridging attempts, the howler uses the flexibility of the slender supports and probably transforms their potential energy into kinetic energy to cross the gap. This is particularly important during travel in search of feeding sites. When travelling long distances between feeding trees, the howler is obliged to move within many tree crowns, and, therefore, gaps and small supports increase in number, especially in the crown peripheries. On the other hand, when moving within the same feeding tree, any gaps can commonly be crossed by climbing or clambering, as the crown of a single tree may be relatively ‘coherent’ due to its intrinsic architecture [18]. Consequently, the proportion of bridging decreases significantly during feeding [6].

Bridging demands several adaptations, as it is strongly linked to slow and cautious arboREAL walking and clambering [17]. Animals must have a long reach, be agile and flexible and present an appropriate osteomuscular configuration [19]. During bridging, forelimbs are placed above or at the same height as the shoulder, thus complying with anatomical observations revealing considerable freedom of movement at the shoulder girdle [15, 16]. The elbows are frequently abducted and consistently semi-extended. The fingers are flexed, assuring a firm grip. Bending, compressive and tensile forces are exerted on the forelimbs [8]. Hindlimbs are kept extended at the hip joint, thus stabilizing the animal [14]. They are rotated, abducted and kept semi-extended at the knee joint. The toes grasp firmly [13].

The prehensile tail of the howler weighs approximately as much as a limb and is heavi-
ly muscled [20]. During bridging, it is loaded under tension and grasps the initial support securely. The naked extremity as well as its strong flexor musculature assure a firm grip. It thus stabilizes the body and rotates it to diverse orientations due to the well-developed and widely attached proximal caudal muscles [12]. This permits the howler to explore the space in front of it and choose the most suitable pathway. The tail is then the last to release the initial support, avoiding any risk of a fall that could be lethal. Lastly, the body is extended in order to enhance the accessibility of the new support.

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