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LOCOMOTION BEHAVIOR OF THE LETTERED ARACARI (*PTEROGLOSSUS INSCRIPTUS*) (RAMPHASTIDAE)

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Resumo. – Comportamento locomotor do Araçari-letrado (*Pteroglossus inscriptus*) (Ramphastidae). – Embora seja de amplo conhecimento que as aves locomovem-se, preferencialmente, por saltos no ambiente arborícola, pouca atenção tem sido dada a tal comportamento locomotor e aos parâmetros cinemáticos relacionados ao seu deslocamento. Assim, o Araçari-letrado (*Pteroglossus inscriptus*), um dos menores ranfastídeos de distribuição sul-americana, teve seu deslocamento em poleiros, de dois diferentes diâmetros (fino e grosso), registrado por meio de uma câmara de vídeo digital de alta velocidade (a 250 ou 500 imagens/s). Os vídeos foram analisados, imagem por imagem, e os parâmetros locomotores estimados. Observou-se que tal deslocamento, durante os experimentos, foi sempre efetuado por meio de saltos defasados, a uma velocidade média de 1,68 ms^{-1} (± 0,40 ms^{-1}), cuja freqüência dos movimentos foi de 3,9 Hz (± 0,48); tais saltos não são executados com ambos os pés movimentando-se simultaneamente, ou seja, ocorre sempre uma fase relativa entre cada um deles de 0,044 s (± 0,014 s) durante a fase de apoio dos pés, representando cerca de 15% (± 6%) do ciclo locomotor. Além disso, o Araçari-letrado inverte regularmente a seqüência de apoio dos pés durante seu deslocamento: o pé que primeiro perde o contacto com o poleiro, durante o salto, é o segundo a se apoiar novamente, ao mesmo tempo em que a posição da cauda também se alterna, posicionando-se do mesmo lado deste pé. Tal aspecto não fora registrado para outras aves, assim como as características dos parâmetros locomotores durante o deslocamento arborícola do Araçari-letrado diferem daquelas encontradas para saltadores terrícolas em velocidades equivalentes.

Abstract. – It is known that birds move by hopping in arboreal environments, but little attention has been given to the kinematics of such means of displacement. We have registered the movement patterns of a small South American ramphastid bird, the Lettered Aracari (*Pteroglossus inscriptus*), in branches of two different diameters (small and large) by means of a high-speed video camera (250 or 500 images/s). The locomotion parameters were estimated from the analysis of individual images. The displacement of birds takes place through out-of-phase hopping at an average speed of 1.68 ms^{-1} with movement frequency of 3.9 Hz (SD = 0.48). The two feet do not move simultaneously, but always with a relative phase of 0.044 s (SD = 0.014) between them during the phase of foot support contact, which represents about 15% (SD = 6%) of the locomotion cycle. In addition, Lettered Aracaris regularly change the sequence of foot support contacts during displacement. The trailing foot that looses contact with the perch during the hop is the second to touchdown again; at the same time the tail position also changes, moving towards the same side as this foot on touching the branch. Such aspect had not been registered for other birds; the characteristics of locomotion parameters during the arboreal displacements of the Lettered Aracari also differ from those found for ground hoppers with equivalent speeds. *Accepted 22 January 2006.*

Key words: Ramphastidae, *Pteroglossus inscriptus,* aracari, arboreal locomotion, hopping, kinematics.

INTRODUCTION

Birds live in all possible environments (terrestrial, aquatic, and arboreal), using different modes of locomotion. Terrestrial locomotion modes have been studied in some groups of birds (Dagg 1977, Hayes & Alexander 1983, Gatesy & Biewener 1991, Vestappen & Aerts 2000, Vestappen *et al.* 2000, Reilly 2000, Abourachid 2000, 2001; Abourachid & Renous 2000). Birds moving on the ground use three kinds of gait: walking, running, and hopping (Hayes & Alexander 1983). Hopping gaits of birds have been studied by Hayes & Alexander (1983) in four species of crows (Corvidae) and in Zebra Finches (*Taeniopygia guttata*), and by Vestappen *et al.* (2000) in Black-billed Magpies (*Pica pica*) when moving on the ground. These birds walk at a low speed, run at an intermediate speed and hop either at an intermediate on faster speed, using an out-of-phase hop, the movement of both feet being asynchronous, with one foot set down after the other.

Arboreal locomotion plays an important role in many bird groups, since trees constitute their living habitat. Analysis of arboreal locomotion is difficult under natural conditions for practical reasons; indeed, it is difficult to film birds moving in trees for further quantitative frame analysis. As far as we know, there exists no available kinematical data on birds moving in trees in the literature.

It has been known for a long time that the Ramphastidae move among tree branches to perform various activities including foraging. With exception of observations made by Mikich (1991) on a couple of captive Toco Toucans (R*amphastos toco*), little is known on the locomotion abilities of toucans and aracaris, typical arboreal birds which hop more than fly (e.g., von Ihering 1968, Sick 1997).

Toucans and aracaris are a group of endemic birds of the Neotropical region (Haffer 1974). The distinguishing characteristics of toucans and aracaris include a large, light, pneumatic, and bright-colored bill that may exceed body length in some species. They are zygodactylous and arboreal, inhabiting the canopy of wet and flooded forests; some species are however typical of dry mountain forests, with Toco Toucan being the only ramphastid living in open country areas. Toucans and aracaris are basically frugivorous, being thus considered very important seed dispersers; occasionally they feed on small animals, invertebrates and eggs (Short & Horne 2002). The Ramphastidae are represented by six (Haffer 1974, Meyer de Schauensee 1982, Sibley & Ahlquist 1990, Short & Horne 2002) or five genera, due to the switching of *Baillonius bailloni* to the genus *Pteroglossus* (*P. bailloni*) (Kimura *et al.* 2004), and 33 (Haffer 1974) or 34 species (Short & Horne 2001, 2002).

We present here a description of the gait pattern of the Lettered Aracari (*Pteroglossus inscriptus*) when moving on tree branches.

MATERIAL AND METHODS

We studied six Lettered Aracaris (3 females and 3 males) in their usual enclosure at the "Criadouro Científico e Cultural Poços de Caldas" (Poços de Caldas, MG, Brazil), well adapted to life in captivity, but in similar conditions to natural environments.

The Lettered Aracari is one of the smallest species of *Pteroglossus* together with *P. viridis*, which together form a superspecies, being characterized by the yellow sides of their jaws, transversed by many irregular black lines in the nominate form (*P. i. inscriptus*). The male has black neck, throat and head, whereas the female exibits chesnut brown throat and neck with a black crown. This species occurs in the Amazonian region (except in its northeastern portion) as well as in the Guyanas (Haffer 1974). There are also early records of its pres-

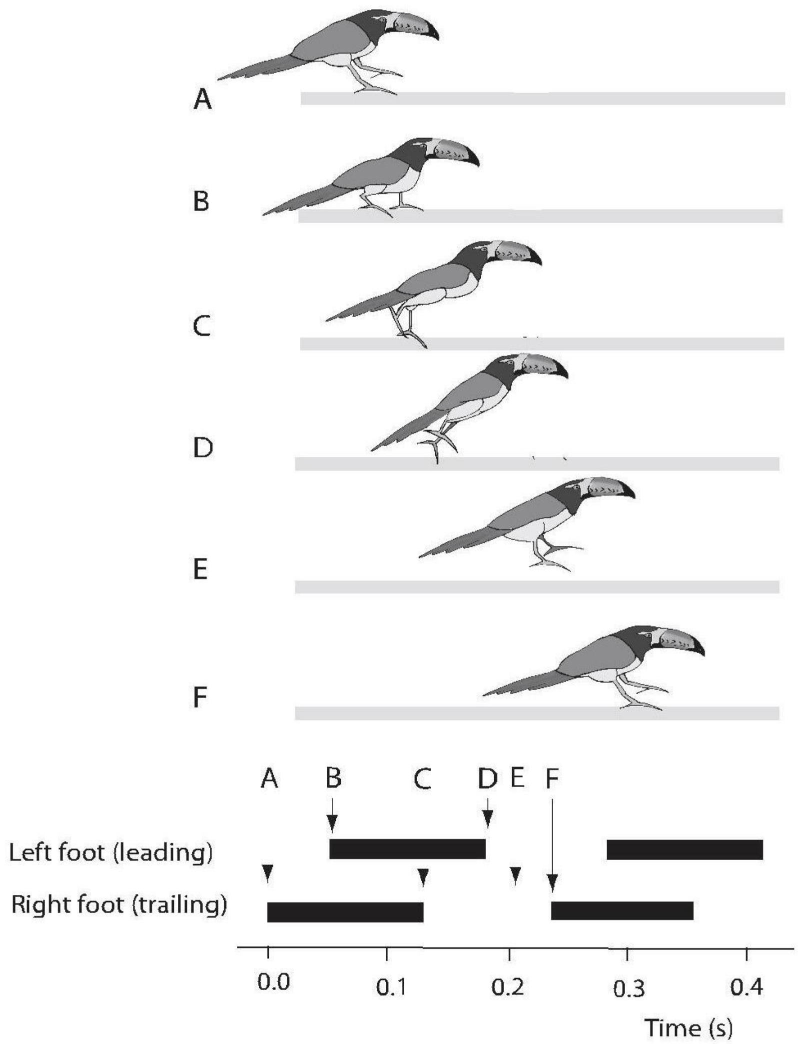

FIG. 1. Out-of-phase hopping of the Lettered Aracari (*Pteroglossus inscriptus*) on a small diameter branch: A) touchdown of the right foot, B) touchdown of the left foot, C) right foot leaves the branch, D) left foot leaves the branch, E) no foot on the branch, F) right foot touchdowns the branch again. Bottom: Gait diagram representing relative duration of the stance (dark lines) and swing (space between two dark lines) phases of each foot. Mean speed: 1.49 ms^{-1} (± 0.12 ms^{-1}).

ence in the isolated forests of Pernambuco and Alagoas states (Brazil), suggesting that the Atlantic rainforest was linked to the Amazon rainforest not so long ago (Alvarenga 2004). The Lettered Aracari lives in forested regions and primary lowland forests, occasionally reaching mountain subtropical forests along the Andes (1000–1200 m a.s.l. or higher) (Short & Horne 2002). As other ramphastids, Lettered Aracaris usually form noisy groups, with 3 to 10 individuals hopping conspicuously from branch to branch or follow-

TABLE 1. Results of Kruskal-Wallis (KW) tests performed to compare the kinematic parameters of displacement of the Lettered Aracari (*Pteroglossus inscriptus*) on large (lb) and small (sb) branches, and with leading foot change (lfc).

Kinematic parameters	KW test value	*P* value	Conclusion
Relative phase	2.661	0.264	sb = lb = lfc
Frequency	6.584	0.030	sb lfc
Stride length	0.764	0.682	sb = lb = lfc
Stance duration	8.040	0.012	sb lfc
Swing duration	5.974	0.434	lb lfc
Duty factor	6.310	0.035	sb lb lfc (?)
Stride cycle duration	6.584	0.030	sb lfc
Asynchronous touchdown	2.022	0.364	sb = lb = lfc
Asynchronous takeoff	2.498	0.287	sb = lb = lfc
Speed	2.699	0.259	sb = lb = lfc

ing each other in a single line from tree to tree.

We filmed the birds under experimental conditions that simulate as far as possible natural conditions, using a high-speed video camera (Redlake Motion Scope) and a digital cassette (DVCAM Sony DSR-PD100P). Sequences of 8 s each were recorded at a speed of 250 or 500 frames/s. The enclosure dimensions were 5 m long, 2 m wide and 2.5 m high. The movements of the aracaris took place on several branches, parallel to the ground, with two different diameters (2 cm and 9 cm). Distances were estimated using a scale near the branches during the filming of birds.

The films were analyzed frame by frame, and sequences with birds moving straight and perpendicular to the camera at a steady speed were selected; the other sequences, in which the birds stopped, hopped to another branch or flew, were discarded.

Instants of touchdown, when the foot is on the branch, and takeoff, when the foot no longer touches the branch, were recorded with an error of 2 frames (0.01s) (Fig. 1). Stride lengths were measured (with a precision of 0.05 m) as the distance between two successive touchdowns of the same foot (distance travelled by the center of mass during a complete locomotor cycle). Stride cycle duration corresponds to the time lag between two successive touchdowns, allowing for calculating stride frequency as the inverse function (number of complete cycles over a period of one second). Swing phase duration is the time lag between takeoff and the next touchdown (foot off the support). Stance phase duration is defined as the time lag between touchdown and the next takeoff (foot is on support contact). These last two parameters were recorded in time units of second. The relative phase (Hayes & Alexander 1983) (time lag between the touchdown of both feet as a percent of stride duration) and the duty factor (duration of foot support contact as a percent of stride duration) were also calculated. The speed (frequency x stride length) is given in meters per second (ms^{-1}). Gait diagrams of the sequences analysed are shown in Figure 1.

Twenty locomotion cycles were analyzed from 13 different sequences, involving four individuals in displacement. Their kinematical parameters were estimated each from nine measurements taken with the birds on a large (thick) branch, six on a small (thin) branch (normal displacement), and five with the birds

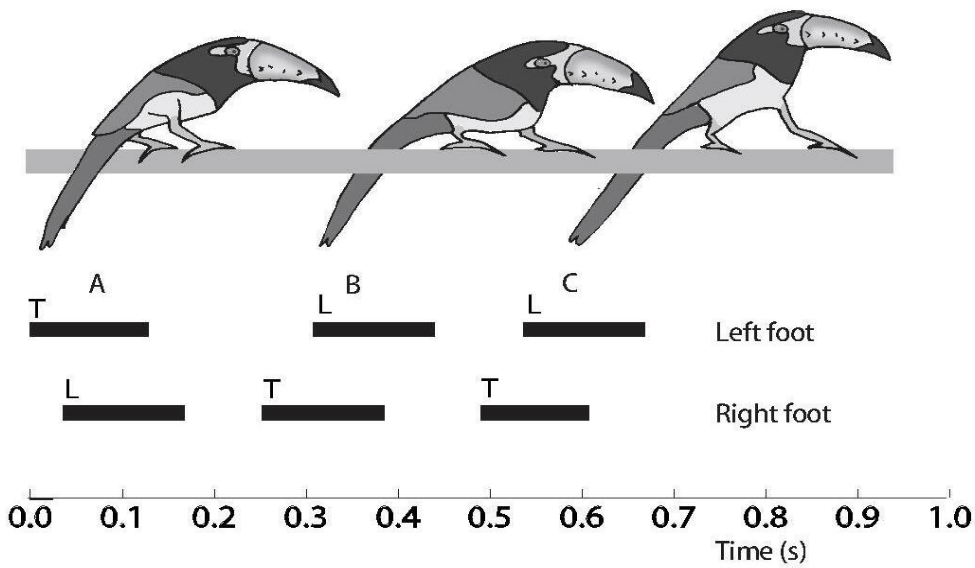

FIG. 2. Leading foot change during the out-of-phase hopping of the Lettered Aracari (*Pteroglossus inscriptus*). During the first hop (from A to B) the feet order changes and the tail changes from one side of the branch to the other. The stance duration (dark lines on the gait diagram: T – trailing foot, L – leading foot) does not change whereas the swing phase duration (space between the dark lines) of the left foot is longer than the swing phase duration of the right foot. In the second hop (from B to C) the bird does not change the position of both feet and tail (cf. Fig.1). Mean speed: 1.75 ms^{-1} (± 0.39 ms^{-1}).

displaying leading foot change on both types of branches: the foot which touched the support first (trailing foot, *sensu* Hildebrand 1988: 494) changed during the swing phase so as to become the leading foot (second foot to touch the support, in front of the trailing foot). The data from these three groups (birds on large branches, on small branches, and when displaying leading foot change) were compared using the Kruskal-Wallis (KW) test, a non-parametric analysis of variance. In cases in which the null hypothesis of equality of medians was rejected (KW test value corresponding to a probability level less than 0.05), a multiple comparisons test (Dunn's test) was applied to detect the groups responsible for the significant value of the KW test (roughly a chi-squared distribution, in the present case with 3–1 = 2 d.f.).

RESULTS

The results and conclusions drawn from the statistical analysis we performed are summarized in Table 1.

Although in many instances the parameter estimated with the birds on large (lb) or small (sb) branches was significantly different from the pattern exhibited when the birds displayed leading foot change (lfc), only in two instances (stance duration and duty factor) behavior differences were detected between the two types of branches (small vs large). In the case of the duty factor the conclusion is ambiguous because the KW test value indicated the presence of statistically significant differences but the multiple comparisons test failed to locate them, probably due to the high degree of dispersion of the variable in at least one out of the three groups.

In spite of the fact that the above-mentioned statistical KW test uses ranks, corresponding therefore to a test of medians instead of means, in the following lines, the statistical parameters of the measurements are given as mean ± 1 SD estimated using the whole data set collected from birds on both types of branches, with the exception of the two measurements indicated in the previous paragraph, and from the parameters with trailing foot change (5 stride cycles).

On the two supports used for analysis, the speed of displacement of the Lettered Aracari ranged between 1.23 ms^{-1} and 2.69 ms^{-1} with a mean speed of 1.68 ms^{-1} (± 0.40 ms^{-1}). On the large branch diameter, mean speed was 1.76 ms^{-1} (± 0.5 ms^{-1}), on the small one this was 1.49 ms^{-1} (± 0.12 ms^{-1}), during bird leading foot change, this was 1.75 ms^{-1} (± 0.39 ms^{-1}). The mean frequency of movements was 3.9 Hz (± 0.48): 3.85 Hz (± 0.4) on the large branch, 3.7 Hz (± 0.5) on the small branch, and 4.2 Hz (± 0.2) at leading foot change. Aracaris move by out-of-phase hopping, the two feet not moving simultaneously, but always with a relative phase (time lag between touchdown of the two feet) corresponding to 15% (± 6%) of the stride duration on a large branch and on a small branch. The same relative phase occurs for the swing phase.

Lettered Aracari shows two modes of out-of-phase hopping that alternate in the same sequence of displacement. For 75% of strides the order of foot placements on the branch during each stance phase is preserved during the swing phase and the following stance phase (Fig. 1). In fact, this displacement corresponds to a series of repeated identical postures. For 25% of strides, *P. inscriptus* changes the position of the trailing foot during displacement (Fig. 2): the trailing foot swing phase is longer so that it touches the branch after the leading foot. In this case, the order of foot placement changes with the successive touchdowns, the foot switch occurring during the swing phase. The tail position follows this foot switch, changing its placement in relation to the branch on the leading foot side.

In the normal displacement, the mean time lag between asynchronous touchdowns of feet lasts 0.041 s (± 0.014 s), ranging from 0.012 s to 0.064 s. This time (or relative phase) represents 15.5% (± 5.6%) of the stride cycle duration of each foot. However, when the measurement is made between the takeoff of the feet, the mean time lag between the beginnings of the swing of the feet lasts 0.048 s (± 0.009 s), ranging from 0.032 s to 0.064 s. The mean stance phase lasts 0.12 s (± 0.01 s) on the large branch and 0.16 s (± 0.02 s) on the small one, corresponding to 45% (± 7%) of the cycle duration (duty factor) on the large branch and to 57% (± 3%) on the small one. The swing phase on the two branch diameters lasts for 0.13 s (± 0.03 s). Since only the stance phase and duty factor (dependent of the stance phase duration) on the two different branch diameters are different, we can suppose that the time contact of the feet changes with the diameter of perches during the displacement.

In the leading foot change, a difference appears in the swing phase duration of both feet. The swing duration of the trailing foot that becomes the leading foot in the following touchdown is longer – 0.16 s – whereas the mean duration of the leading foot that will touch down on the branch first (thus becoming trailing foot) is shorter – 0.08 s (± 0.01 s) (Fig. 2). No significant differences exist for stride length (0.41 ± 0.09 m), stance duration (0.13 ± 0.04 s), mean time lag between asynchronous touchdowns of feet (0.05 ± 0.01 s), mean time lag between asynchronous takeoffs (0.05 ± 0.02 s) and the relative phase (21 ± 8%) in relationship with the values obtained in the non-leading foot change (normal displacement). Frequency (4.2 ± 0.2 Hz) is higher than that observed on the small branch

(3.7 ± 0.5 Hz). The mean stride duration (0.24 ± 0.01 s) was significantly lower than that of the small branch (0.27 ± 0.3 s); the duty factor shows a relative different value (56% ± 17%) from that of the large branch (46% ± 7%).

DISCUSSION

The arboreal behavior of ramphastids moving along branches by means of hops has been the object of many studies (e.g., von Ihering 1968, Sick 1997) and of many direct observation performed in natural environments. Mikich (1991), analyzing the behavior of Toco Toucan, mentions that toucans hop by means of an impulse given simultaneously by the two hindlimbs. In fact, we observe asynchronous movements of the hindlimbs in the Lettered Aracari, a remarkable time lag being visible between the touchdowns (or takeoffs) of each foot only with high speed filming, as they last only a few milliseconds. In general, this time is unperceivable to the human eyesight. Preliminary high speed frame analyses of Toco Toucans in captivity (pers. observ.) also show such an asynchronous functioning of the hindlimbs when this ramphastid hops. The Ramphastidae seem to be characterized by an out-of-phase hopping. Moreover, the Lettered Aracari is able to inverse the position of its feet on the branch during the displacement.

During displacement on small diameter branches, the aracaris develop lower speed than on the large diameter branches. This can explain the stance phase duration and the duty factor significantly higher on the small one.

The comparison between the arboreal out-of-phase hopping of the Ramphastidae and the hopping of the terrestrial birds brings about interesting questions. Corvids (crows and magpies) (Hayes & Alexander 1983, Vestappen & Aerts 2000) walk generally at a low speed. The stance phase is longer than the swing phase (duty factor > 0.5) when the birds walk with bipedal alternate gait. They run when the stance phase is shorter than the swing phase (duty factor <0.5). However, corvids always used an out-of-phase hopping gait with a duty factor less than 0.5, as an alternative to the run, and a hop for fast gait. The speed of the Lettered Aracari (mean value around 1.6 ms^{-1}) corresponds to an intermediate value between the running and hopping of corvids. However, considering the stance phase longer than the swing phase (duty factor > 0.5) on the small branch, the out-of-phase hopping of the Lettered Aracari can be considered as a slow gait, an alternative to the walk of the Corvidae.

In ravens and magpies, the relative phase ranges from 14% to 40% of the stride cycle duration, decreasing with speed. The relative phase used by the aracaris (about 15%) is comprised in the range of the relative phase difference used in fast hop of crows. Moreover, the frequency of limb movements of the Lettered Aracari (around 3.9 Hz) is higher than the one reported for corvids [from 2.5 Hz for Common Ravens (*Corvus corax*) to 3.3 Hz for Black-billed Magpies (*Pica pica*)]. Thus in the out-of-phase hopping, the slow gait has the same kinematic parameters as the high speed gaits of terrestrial birds. It is clear that this original association of kinematic parameters of the Lettered Aracari could be ascribed to arboreal behavior.

Furthermore, corvids were not reported to change the feet order during hopping. The arboreal hop of the Lettered Aracari is thus not comparable to the terrestrial hop of the crows. This is not really surprising since the position of the trunk is not the same in both conditions: during the terrestrial hop, the body faces the direction of displacement, whereas, during the arboreal hop, the body is oblique to it. It would be interesting to compare the arboreal walking displacement of other groups of birds, e.g., the Psittacidae, to that of ground walking birds.

CONCLUSIONS

Out-of-phase hopping is the natural means of displacement of the Lettered Aracari on perch branches. Displacement by walking was never observed by us on branches under experimental conditions. During hopping there is always a delay between the beginning of the stance phase of one of the limbs and the beginning of the same phase of the other limb, that lasts for 0.044 s (± 0.013 s). Lettered Aracari can change its feet position on branches associating it with the tail placement in relation to the branch at the same side of the leading foot.

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