



How many for dinner? Recruitment and monitoring by glances in capuchins

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Received: 23 February 2007 / Accepted: 12 June 2007 / Published online: 24 July 2007
Japan Monkey Centre and Springer 2007


Abstract Group members present physical and physiological differences according to their age, sex or social status, which could generate motivation differences among group members during travel.

among individuals during travel. In spite of these divergences of interest among individuals, the group succeeds more often than not in making a collective decision about departure time and which direction to take. To reach a consensus decision, animals should exchange information relating to characteristics of group movement through different communication channels.

Keywords Recruitment Monitoring
Visual communication *Cebus capucinus*
Collective movement

Introduction
The main purpose of this study is to understand the function of behaviour patterns displayed during movements of white-faced capuchins (*Cebus capucinus*). We designed experiments in which we provoked collective movements involving a binary choice. During experiments, a video camera recorded the behaviour of each capuchin, which enabled us to determine which individuals displayed a behavioural pattern during travel and how this behaviour influenced the other group members.

We found that looking backwards seemed to permit the recruitment of group mates during collective movement. This behaviour also seemed to allow the quantification of the number of followers, since the emitter modified its locomotion speed according to this number. In this preliminary study, we showed that visual behaviour was used to recruit and monitor group mates during collective movement between two or more mutually exclusive actions with the specific aim of reaching a consensus, are called "consensus decisions" (Conradt and Ruxton 2005).

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To reach such a consensus, individuals should exchange information through different communication channels. To coordinate group movement, the signals used vary depending on the function of grouping, the precision required, and the mode of locomotion (Bradbury and Vehrencamp 1998) as well as on the surrounding visibility (e.g. vegetation density) and background noise. Early

studies on collective movements in primates revealed that

individuals involved in the decision-making process used

intentional movements to communicate (Hall and DeVore

1965; Kummer 1968). These signals are visual (gorilla:

Schaller 1963; Harcourt 1979; *Macaca sylvanus*

Mehlman 1996; *Pan paniscus*; Ingmannson 1996) or vocal

(*Alouata palliata*; Carpenter 1934; *Chlorocebus aethiops*

Struhsaker 1967; *Lophocebus albigena*; Waser 1977; *Cal-*

licebus moloch; Robinson 1979; *Cebus capucinus*; Boinski

1993; Boinski and Campbell 1995). However, these studies

are descriptive and few authors have reported quantitative

data to address the question of the function, i.e. the com-

sequences of such communication signals, on the behav-

our of conspecifics.

In semi-free-ranging conditions, an initial study on

white-faced capuchins (Leca et al. 2003) demonstrated

that the initiator of a group movement uses behavioural

patterns such as "looking backwards" (looking back

towards the other group members) and "pauses" during

locomotion (stops of <10 s), combined with trills, a tra-

vel coordination call (Boinski 1993; Boinski and Camp-

bell 1995). Leca et al. (2003) demonstrated that start

attempts include twice as many occurrences of looking

backwards than trills. Thus, visual communication ap-

pears more important than described in previous be-

havioural studies (Boinski and Campbell 1995). However, almost

all the preceding studies have focused on vocal rather

than visual communication. This lack of empirical data

could be explained by the field conditions: when vege-

tation is very dense, it is difficult for observers to

quantify this type of visual behaviour displayed between

individuals. Complementary studies in better observati-

on conditions are thus necessary for taking into account

such important behaviour.

In their study, Leca et al. (2003) focused on behavioural

patterns displayed at the beginning of the group movement.

They did not evaluate the impact of such behaviour on the

followers or, thus, the nature of the behaviour, i.e. re-

cruitment or monitoring. The main purpose of this pre-

liminary study is to understand the function of these

behavioural patterns. To follow a collective movement

from its beginning to its end, we need to know in advance

the points of departure and arrival, and thus be able to

observe all behaviour emitted during a group movement. In

this study, all these factors have been controlled by

designing experiments where collective movements are

provoked. Firstly, we determine which individuals dis-

played a behavioural pattern during direction choice and

throughout the journey until the point of arrival. Secondly,

we determine the influence of initiator behaviour on the

other group members with the aim of understanding if this

behaviour is used to recruit and/or monitor other member

of the group.

Subjects and environment

The group of white-faced capuchins was established in

1989 at the Louis Pasteur University Primate Centre,

Strasbourg, France. During our study, the group contained

12 individuals of three separate lineages: six males (aged 1,

3, 5, 7, 11 and 20 years or more) and six females (4, 5, 5,

10, 12 and 20 years or more).

The group was kept in a 1-acre outdoor enclosure with

natural vegetation and uneven ground with free access to

an indoor shelter (Fig. 1). Commercial primate pellets and

water were available ad libitum. Fresh fruit and vegetables

were provided once a week but not during the testing

period.

Observation procedure

Observations took place between 0900 and 1200 h and

between 1400 and 1800 h from April to November 2004.

All observations were conducted before sunset. We

conducted 68 trials in which capuchins were trained to

move on hearing a whistle and then to choose from two

opposite areas in their park. In their enclosure, animals

spontaneously used a special zone for social activities

and resting, referred to here as the "departure zone"

(Fig. 1). The two areas from which the capuchins could

choose were natural foraging areas situated 60 m away

from the departure zone. A trough was placed in each of

the areas (T1 and T2, Fig. 1) but was not visible from

the departure zone because of the park relief and the

conditions are thus necessary for taking into account

such important behaviour.

Experimental set-up

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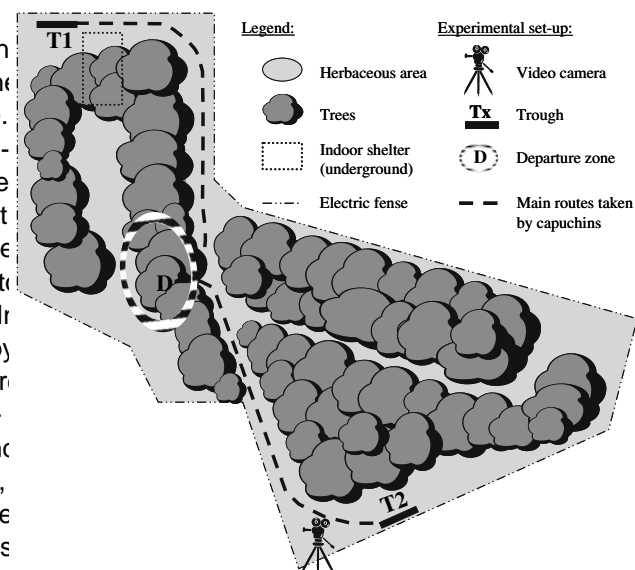


Fig. 1 Enclosure and experimental set-up

vegetation separating the departure zone from the troughs. In order to record behaviours displayed on the route taken by capuchins from the departure to the arrival area, we installed a video camera fitted with a wide-angle lens close to T2 (Fig. 1). We showed that during these experiments, capuchins collectively chose the direction to take (Meunier et al. 2006). Data were collected when the collective choice of the group was T2, i.e. 29 trials. In 17ve tests, only some of the data were entirely available, and these 17ve trials were thus discarded from the analyses.

In the experiments, only one randomly selected trough contained 17gs (a very appetising resource). The other trough contained commercial primate pellets (available ad libitum in the indoor enclosure and thus little preferred by capuchins). This enabled us to retain conflicting interests and divergences among individuals concerning the direction to take. Four conditions were used: T1 and T2 contained 17gs, T1 and T2 contained pellets, T1 contained 17gs and T2 pellets, and T1 contained pellets and T2 17gs. Each condition was used the same number of times and the order of the conditions was randomised. However, the same condition was not used more than twice successively to prevent learning of reward position and development of location bias. The troughs were long enough (2 m) to allow all the monkeys to eat simultaneously. When all animals were grouped in the departure zone, the whistle was sounded, and the troughs were opened simultaneously. A maximum of two trials per day were performed.

Video processing

One of us, H.M., scored video tapes and recorded instantaneous (every 1 s) focal animal sampling (Altmann 1974): (1) the relative position (first, second, third, etc.) of each capuchin in the line of moving monkeys, from front to back, to indicate progression rank and (2) the number of followers, i.e., the number of individuals having left the departure area and chosen T2, except for the initiator. H.M. also noted all the behavioural patterns displayed by each individual using the all occurrences of some behaviours sampling method (Altmann 1974). For each type of behaviour recorded, H.M. noted its corresponding latency (in seconds from the whistle). Behavioural patterns recorded included looking backwards (orientation of head back towards the other group members), brief stop during locomotion (stops ≤ 2 s), and the speed of each capuchin at each second. To evaluate this speed, H.M. distinguished three locomotion patterns: stop (>2 s), walking, and trotting/running. All changes in locomotion patterns were noted. No vocalisations were emitted by capuchins on the route taken from the departure to the arrival area.

According to these preliminary results, we focused on the first individual who occupied the first position during the 24 trials. Moreover, one individual recruited other group members during movement, but occupied this position in 18 movements out of 24. This individual was the second male of the hierarchy. The three other individuals occupying the first position were the alpha male (four times), an adult subordinate female (once) and a sub-adult male, in the middle position of the hierarchy (once).

The first individual and the consequence of its behaviour on the number of followers

Does the number of followers affect the first individual's behaviour?

Who is first? Only four individuals occupied the first position during the 24 trials. Moreover, one individual recruited other group members during movement, but occupied this position in 18 movements out of 24. This individual was the second male of the hierarchy. The three other individuals occupying the first position were the alpha male (four times), an adult subordinate female (once) and a sub-adult male, in the middle position of the hierarchy (once).

Impact of looking backwards on the number of followers displayed at rest (i.e. 49 out of 55 backward looks). The higher the number of followers, the lower the first individual's probability of remaining still after looking backwards ($r^2 = 0.928, P = 0.008, \text{Fig. 3}$). This probability follows a threshold function ($r^2 = 0.998$), the threshold value (S) being 2 (Fig. 3):

$$P = \frac{0.58}{1 + \left(\frac{F}{S}\right)^7}$$

during the same collective movement. We only considered backward looks separated by a minimum of 5 s to test the effect of looking backwards on the number of followers 2 s after its occurrence. We found a significant effect of looking backwards on the number of followers (sign test, $N_{\text{negative differences}} = 1; N_{\text{positive differences}} = 15; N_{\text{ties}} = 19; P = 0.001$). The number of followers was higher after a backward look than at the time of its occurrence. When the number of followers increased after a backward look, the mean increase was 1.2 ± 0.1 followers.

In a complementary qualitative analysis, we considered the results for the three other first individuals. The alpha male displayed 14 backward looks; in three cases, the number of followers was higher after a backward look than at the time of its occurrence, no decrease in this number was observed, and 11 cases with no change were recorded.

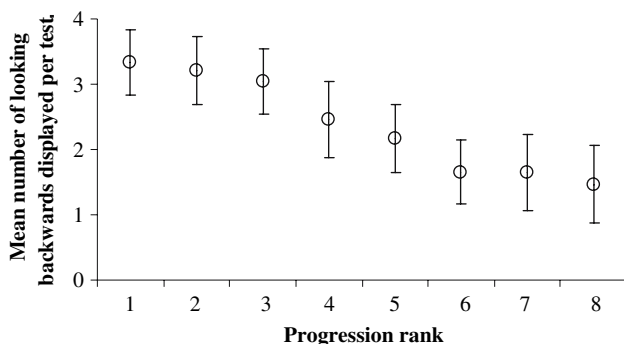


Fig. 2 Mean number of backward looks displayed per test for each progression rank

This last result means that the leader changed its behaviour (remaining still or moving) according to the critical value of two followers. If the number of followers is smaller than two, the probability of remaining still is high (0.7) and if the number is greater than 2, the probability abruptly falls

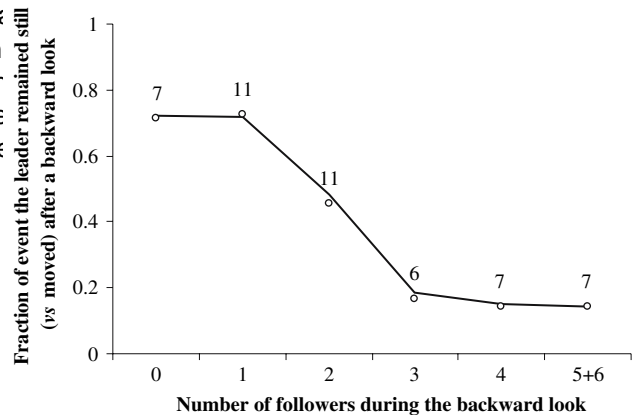


Fig. 3 Fraction of events in which the leader remained still (vs. moved) after a backward look according to the number of followers perceived during the backward look. The line illustrates the threshold function fitting our experimental data. The numbers above the points indicate the number of backward looks on which the percentage is based, i.e. the number of backward looks displayed for each of the possible numbers of followers

Discussion

The only signals observed in this study were backward looks and brief stops. Looking backwards was the most frequently displayed type of behaviour, and we stated that its occurrence was not equally distributed among group members. We showed that looking backwards was displayed at a much higher rate at the leading edge of the travelling group than in following positions, as Boinski and Campbell (1995) found for trills in the same species.

The discrepancy between wild and semi-free-ranging conditions may be responsible for the absence of trills in this specific experimental context. In our conditions, visual signals rather than vocal signals could thereby be preferentially used. Moreover, the positions of the troughs were known to the monkeys, and there was no need to indicate the context of spontaneous moves where only the leader knew where it would go, trills could be emitted (Leca et al. 2003).

We found that the number of followers was higher after a backward look than before, and that the higher the number of followers, the less the first individual remained still after looking backwards. Our interpretation is that looking backwards permits the recruitment of other group members during collective movement and that the number of followers present at the time of looking backwards influences the behaviour of the leader, since it modifies locomotion speed according to this number. We confirm the results of Leca et al. (2003) who showed that, in white-faced capuchins, glances towards other group members were a revealing feature of leadership patterns. Moreover, our results on this recruitment function are in agreement with the hypothesis of Menzel (1971) that describes looking backwards in chimpanzees during travel, in which the author judges that this behaviour pattern is not necessarily species-specific, in any strict sense.

The observed decrease in waiting behaviour (i.e. remaining still after looking backwards), coupled with the increase in the number of followers, shows that while the first individual decides on its destination, it does not continue its journey without other group members. This result suggests the first individual adapts its behaviour to the situation at any given time (i.e. the number of followers perceived). The decrease in waiting behaviour is not linear according to the increase in the number of followers but follows a threshold function, which means that the leader seems to change its behaviour according to an 'all or nothing' process. After a backward look, this threshold function consists of remaining still if the number of followers is less than 2 and moving if it is higher than 2, and

displays a variable response for two followers, the threshold value. By looking backwards several times throughout its travel, the leader thereby monitors the progress of group movement and thus modulates its distance from other group members. This pattern of looking backwards and waiting for other group members illustrates well the trade-off between the motivation to travel to reach food and the benefits of remaining in a group. Thereby, looking backwards seems to be an intentional behaviour of monitoring followers' response to the leader's behaviour and its modulation as a function of the number of followers conditions may be responsible for the absence of trills in this specific experimental context. In our conditions, visual signals rather than vocal signals could thereby be preferentially used. Moreover, the positions of the troughs were known to the monkeys, and there was no need to indicate the context of spontaneous moves where only the leader knew where it would go, trills could be emitted (Leca et al. 2003).

Looking backwards could contribute to the emergence of consensus decision making. However, to demonstrate such a role of looking backwards, evidence is required that, given a choice of individuals to follow, most group members will follow the one that emits the most occasions of looking backwards, and complementary experiments thus seem necessary. We are aware that our results are limited to one social group, and supplementary data from other groups are required. However, these preliminary results suggest how a group of white-faced capuchins may manage to maintain cohesion and coordinate group movement among members during travel.

Acknowledgements We are grateful to the Louis Pasteur University Primate Centre, Strasbourg, France, and to Pierre Uhrich for technical support for the experiments. We also thank Arianna De Marco for determining the hierarchy of this group, Bernard Thierry for statistical advice and Guillaume Salmon for his help collecting some of the data. H.M. appreciates helpful comments and discussion with Pau Molina-Vila. J.L.D. is a research associate sponsored by the Belgian National Funds for Scientific Research. We also thank the three anonymous reviewers for insightful comments on the manuscript. We wish to thank Ruth Knowles for English corrections on the manuscript. Observations and experiments were made in accordance with the CNRS guidelines.

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