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BRIEF REPORTS

# Patterns of Lateralized Hand Use in an Arboreal Primate, *Simias concolor*

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Studies of hand use in nonhuman primates suggest that several species exhibit hand preferences for a variety of tasks. The majority of studies, however, focus on the lateralized hand use of captive nonhuman primate populations. Although captive settings offer a more controlled environment for assessing hand preferences, studies of wild populations provide important insights into how handedness is affected by natural environmental conditions and thus potential insights into the evolution of handedness. To investigate handedness in a population of wild nonhuman primates, we studied patterns of lateralized hand use during feeding in four simakobu monkeys (*Simias concolor*), an arboreal species inhabiting the Mentawai Islands, Indonesia. Our data show that individual variation in hand preferences for feeding existed among our study animals. In addition, each simakobu expressed a significant hand preference for supporting itself on a branch during feeding, an uncoordinated bimanual task. This bias was most prevalent when the branch used for support was a main branch rather than a terminal branch. When both hands were employed in a coordinated bimanual feeding activity (bimanual manipulation), only two subjects showed a significant bias for feeding. Our data suggest that these individuals are more likely to express significant hand preferences when feeding from stable, rather than precarious, positions within the canopy. Am. J. Primatol. 56:231–236, 2002. 

**Key words: handedness; simakobu monkey; bimanual hand use; Mentawai Islands**

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## INTRODUCTION

Numerous studies provide evidence that nonhuman primates (hereafter primates) exhibit hand preferences for a variety of tasks [for review see Ward & Hopkins, 1993]. The extent of such hand preferences, however, is variable both between and within species [McGrew & Marchant, 1997]. For example, captive chimpanzees (*Pan troglodytes*) exhibit a consistent population-level right-hand preference across a variety of different tasks [Hopkins, 1996; Hopkins & Fernandez-Carriba, 2000; Hopkins & Morris, 1993], while wild populations typically exhibit only individual-level hand preferences (i.e., each individual may have a preference for using either the right or left hand, but the preference is not consistent across all individuals in the population) [Boesch, 1991; Sugiyama et al., 1993; Marchant & McGrew, 1996; McGrew & Marchant, 2001]. The exact reason for this dichotomy is unknown, but the observed variation may result from methodological differences [Marchant & McGrew, 1996; Hopkins & Fernandez-Carriba, 2000] or occur because studies of wild and captive chimpanzees are not exploring comparable aspects of manual behavior. Rectifying the basis of this difference is imperative because both captive and wild studies are critical to our understanding of lateralized hand use. Whereas captive studies are able to investigate how discrete aspects of behavior (e.g., postural modifications during feeding, bimanual hand use, etc.) influence hand preferences, studies of wild populations are key to understanding how hand use is affected by natural conditions, and thus lend insights into the evolution of handedness. Studies of handedness are likely to benefit from incorporating the strengths of both lines of research by documenting how discrete behavioral actions influence patterns of lateralized hand use in wild primates.

Here we present data on how multiple factors affect patterns of lateralized hand use during feeding in four wild simakobu monkeys (*Simias concolor*). This highly endangered, arboreal species inhabits the dense tropical rainforests of the Mentawai Islands, Indonesia—an archipelago situated off the west coast of Sumatra. The simakobu is a monotypic colobine known to live in small social groups of two or three adult animals, and subsists on a diet consisting of leaves, fruits, and flowers [Tilson, 1977; Tenaza & Fuentes, 1995] (Paciulli, unpublished results). The Mentawai Islands are home to four primate species endemic only to this archipelago: the simakobu, the Mentawai macaque (*Macaca pagensis*), the Mentawai Island langur (*Presbytis potenziani*), and the Kloss gibbon (*Hylobates klossii*) [Miller, 1903].

This study had two specific goals. The first goal was to document hand preferences during feeding in a wild, arboreal colobine, a group of primates for which few data on handedness exist. With the exception of one study of an arboreal primate species [e.g., Panger, 1997], the majority of studies on hand use in wild monkey populations investigate terrestrial species [Hauser et al., 1991; Mittra et al., 1997; Harrison & Byrne, 2000]. The second goal was to record how the actions of the nonfeeding hand influenced the degree of expressed handedness during feeding in the same species. This aspect of the study was important for documenting whether these factors exert the same influence on both captive and wild primates. These data are important for advancing our understanding of how external factors influence hand preference, and thus may contribute to a better understanding of the reported differences in hand use between captive and wild populations.

## METHODS

### Study Population

We recorded hand preferences of four simakobu monkeys (*Simias concolor*) from two social groups inhabiting the forest surrounding Betumonga Research

Station (BRS), Indonesia. One group consisted of two males (M1, M2) and one female (F1). The other group consisted of a single male (M3) and a single female (F2; no data were collected on this female due to lack of habituation). All individuals included in this study were considered adults. BRS is located in an area of mixed disturbed and undisturbed tropical rainforest on North Pagai Island in the Mentawai Island Archipelago [for a more detailed description of this area see Fuentes, 1996].

### Data Collection and Analysis

We collected data during daily focal animal follows between 6:00 and 18:00 hr from July through October 1996. We recorded hand use during feeding bouts, which were defined as any instance during which an individual extended the arm from the body, touched a food item (e.g., leaf, fruit, insect, etc.) and returned the food item to its mouth. Each bout involved a single reach towards a food item. A modification of 1-min focal animal sampling was used [Altmann, 1974]. A single focal animal was followed and hand use was recorded at 1-min intervals. Specifically, when the alarm sounded on the researcher's watch the next clear observation of hand use while feeding was recorded. If a feeding bout was already in progress at the time the alarm sounded, data were not collected until the bout was completed and a new feeding bout began. This technique was used in order to gain a randomized sample of statistically independent behaviors.

We also collected data on whether individual hand preferences were affected when the hand not engaged in feeding was involved in one of the following activities: *support*, *bimanual manipulation*, or *free* from any activity. When both hands were engaged in an action, we considered the hand touching the food item to be dominant and the other hand subordinate. We defined "support" as an individual placing one hand on a substrate while the other hand reached for a food item. "Bimanual manipulation" was defined as instances in which both hands were engaged in obtaining a food item. These situations typically occurred when one hand pulled a small branch towards the individual (the subordinate hand) while the other hand reached for a food item from that branch (the dominant hand). The nonfeeding hand was said to be "free" when it was not engaged in any activity during the feeding bout.

During instances when the hand was used to support the body, the substrate used for support was recorded as either a terminal (less than 3 cm in diameter) or main (greater than 3 cm in diameter) branch. On occasion, the dominant hand could be seen clearly, but the subordinate hand was obscured by foliage. During these instances, the observer recorded the activity of the subordinate hand as "unknown."

To determine lateral biases, the total number of left hand reaches was compared to the total number of right-hand reaches. A binomial test was used for within-subjects comparisons of individual activities. All tests were two-tailed, with the alpha level set at $P < 0.05$. An individual was said to be "lateralized" or to exhibit a "hand preference" when that individual used one hand significantly more than the other (i.e., $P < 0.05$).

## RESULTS

We recorded data on hand preferences during feeding bouts in four simakobu monkeys. A summary of all data reported here is shown in Table I. Our data did not reveal any consistent between-individual hand preferences for feeding. F1 used her right hand during feeding 70% of the time ($P = 0.0001$), and M1 pre-

**TABLE I. Number of Feeding Bouts Recorded for Each Task**

| | F1 | | M1 | | M2 | | M3 | |
|---|---|---|---|---|---|---|---|---|
| | L | R | L | R | L | R | L | R |
| Overall feeding | 41 | 93[a] | 17 | 48[a] | 37 | 27 | 101 | 93 |
| Support | 21 | 50[a] | 12 | 30[a] | 22[a] | 3 | 56[a] | 32 |
| Main branch | 10 | 30[a] | 4 | 18[a] | 11[a] | 0 | 29[a] | 11 |
| Terminal branch | 11 | 20 | 8 | 11 | 11 | 3 | 27 | 21 |
| Bimanual manipulation | 14 | 34[a] | 4 | 8 | 5 | 1 | 39 | 30 |
| Free | 6 | 9 | 0 | 8[a] | 9 | 23[a] | 5 | 13 |

[a]Denotes statistically significant difference.
R, right hand; L, left hand.

ferred to use his right hand for feeding 71% of the time ($P = 0.0002$). In contrast, both M2 and M3 failed to show significant hand preferences for feeding.

Each individual did, however, exhibit a significant individual hand preference for feeding while simultaneously using the nonfeeding hand for support. The lone female, F1, expressed a right-hand preference for feeding while using the other hand for support ($P = 0.0009$). M1 had a right-hand preference for feeding while supporting himself with the nonfeeding hand ($P = 0.003$), whereas M2 and M3 both exhibited left-hand preferences for feeding while supporting themselves on a substrate (M2: $P = 0.0002$; M3: $P = 0.01$).

Results from observations of bimanual manipulation revealed a different pattern. Although F1 expressed significant right-hand preference during bimanual manipulation ($P = 0.002$), none of the other individuals showed any hand preference. However, during instances in which the nonfeeding hand was free from any activity, two individuals showed significant hand preferences (M1: $P = 0.007$; M2: $P = 0.03$), while F1 and M3 showed no preference for either hand.

Overall, each of the monkeys exhibited a significant preference for feeding while supporting themselves on main branches, but a significant bias was not observed when the supporting substrate was a terminal branch. Both F1 and M1 exhibited right-hand preferences for feeding while supporting on main branches ($P = 0.003$ and $P = 0.01$, respectively), but showed no preference when using terminal branches for support. Similarly, M2 and M3 exhibited left-hand preferences for feeding while supporting themselves on main branches ($P = 0.001$ and $P = 0.007$, respectively), but displayed no preference on terminal branches.

## DISCUSSION

In this study, we described hand preferences in the natural behavioral repertoire of wild, arboreal simakobu monkeys. Given the small sample size, however, it is impossible to determine whether the pattern of handedness in our subjects is representative of the population or species as a whole. As such, it is premature to assert what level of handedness this species exhibits in the McGrew and Marchant [1997] framework. We did, however, observe a lack of consistency among individuals in hand preferences for feeding, a finding that is consistent with results from other studies of wild monkey populations [Mittra et al., 1997; Panger 1997; Harrison & Byrne, 2000]. Since studies of captive primates frequently report that a variety of different factors can influence an individual's hand preference, the lack of a single hand preference across all individuals may not be representative of the complex nature of hand use dur-

ing feeding. To address this possibility, we also documented the effect that the hand which was not engaged in feeding had on handedness in these simakobu.

Hopkins [1995] argues that bimanual hand use can be divided into two distinct categories: coordinated and uncoordinated. An uncoordinated bimanual action occurs when both hands perform actions independently of each other, while a coordinated bimanual action is described as instances during which both hands work together to achieve a unitary goal, such as food procurement. Based on these definitions, "support" in our usage can be considered an uncoordinated bimanual activity, and "bimanual manipulation" a coordinated bimanual activity. Our results indicate that simakobu monkeys show a stronger lateral bias during instances in which the nonfeeding hand was used to support the body than when both hands were engaged in bimanual manipulation, a result that is inconsistent with studies of several other species (*Gorilla g. beringei* [Byrne & Byrne, 1991], *Cercopithecus aethiops* [Harrison & Byrne, 2000], and *Pan troglodytes* [Hopkins, 1995]). Typically, coordinated, rather than uncoordinated, bimanual activities elicit stronger hand preferences. There are several possible explanations for this difference. The failure to find a significant bias for coordinated bimanual manipulation in this study may be species-specific or due to an ecological difference in this study population. Specifically, all other studies of bimanual hand use focused on terrestrial subjects. In contrast, simakobu monkeys are entirely arboreal. It is possible that an arboreal niche imposes pressures on individuals that affects how both hands are used while feeding. Further, although we considered support during feeding to be an uncoordinated bimanual activity, it may be that that this behavior is in fact a coordinated action. Although both hands are engaged in separate activities, they are working together towards a common goal. These data do not allow us to distinguish between these possibilities, but future studies will consider this problem.

Overall, results showed that, as with many captive populations, an individual simakobu's tendency to exhibit hand preferences during feeding is influenced by numerous external factors. In addition to the influence that the nonfeeding hand has on handedness, data reveal that the study animals exhibited increased hand preference when feeding in stable positions within the canopy rather than in precarious ones. Specifically, all four simakobu showed a significant hand preference for feeding when supporting themselves on main branches, but no preference while supporting themselves on terminal branches. One explanation for this difference pertains to the arboreal nature of this species. Injury and death due to a fall provide a significant pressure on arboreal animals to constantly maintain a state of balance in the canopy [Fleagle, 1998]. Thus, one would expect arboreal species to evolve morphological and/or behavioral adaptations in response to this pressure. As in the case of simakobu monkeys, it is possible that the risk of falling causes an individual to modify a preexisting hand preferences to insure that he or she is situated securely within the canopy. In other words, the dominant hand, previously used for reaching for food when stability was not an issue, may at times be better suited for supporting the individual when it is situated in precarious positions within the canopy. If such external environmental factors can influence hand use, it is possible that some of the observed differences between captive and wild populations may result from ecological variation between the two settings. To elucidate this possibility more clearly, laterality studies of wild primate populations should investigate aspects of manual behavior that are comparable to those studied in captive populations.

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