

Constraints on Great Apes' Imitation: Model and Action Selectivity in Rehabilitant Orangutan (*Pongo pygmaeus*) Imitation

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We discuss selectivity in great ape imitation, on the basis of an observational study of spontaneous imitation in free-ranging rehabilitant orangutans (*Pongo pygmaeus*). Research on great ape imitation has neglected selectivity, although comparative evidence suggests it may be important. We observed orangutans in central Indonesian Borneo and assessed patterns in the models and actions they spontaneously imitated. The patterns we found resembled those reported in humans. Orangutans preferred models with whom they had positive affective relationships (e.g., important caregiver or older sibling) and actions that reflected their current competence, were receptively familiar, and were relevant to tasks that faced them. Both developmental and individual variability were found. We discuss the probable functions of imitation for great apes and the role of selectivity in directing it. We also make suggestions for more effective elicitation of imitation.

After a hiatus in interest of some 30 years, imitation has returned to prominence in debates and research on cognitive processes and social transmission in nonhuman primates. It represents an important process in the realm of social cognition and one of a constellation of capacities suggested to distinguish monkey, great ape, and human mentality. Despite its key importance, however, imitation in great apes remains poorly understood; for example, research has emphasized imitation's role in enhancing intellectual competence and its underlying cognitive mechanisms to the relative neglect of other mechanisms, such as motivation, or its functions (Galef, 1988; Mitchell, 1987; Pallaud, 1988; Yando, Seitz, & Zigler, 1978). In this study we consider one

neglected facet of great apes' imitation, motivational factors that influence what and whom to imitate.

Concepts in Imitation

It is important to establish conventions at the outset because of the complexity of imitation and the plethora of terminologies proposed. Complexities arise because imitative behavior can be generated by various mental processes (e.g., contagion, local enhancement, matched dependent learning, or imitative learning; see Aronfreed, 1969; Galef, 1988; Mitchell, 1987; Whiten & Ham, 1992). Some imitative processes generate new behavior, others, merely per-

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The study was funded by the Glendon College Research Fund and the Natural Sciences and Engineering Research Council (President's Fund, Operating Grant OGPIN 012). The long term project that made the work possible was funded by Wilkie Brothers Foundation, L. S. B. Leakey Foundation, National Geographic Society, van Tienhaven Foundation, Herz Foundation, Jane and Justin Dart Foundation, World Wildlife Fund, P. T. Georgia Pacific Indonesia, New York and Chicago Zoological Societies, Weyerhaeuser Foundation, Huffco Indonesia, and the Guggenheim Memorial Foundation. Support from L. S. B. Leakey enabled the project to begin. We are very grateful to these Indonesian sponsoring organizations and the persons associated with them for making the work possible: Perlindungan Hutan dan Pelestarian Alam Branch, Forestry Department; Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences); and Fakultas Biologi, Universitas Nasional (UNAS).

We thank Mr. W. Russon, Mr. Dede Wahyudi, Mr. T. Hainald, Dr. Salim Usman, Mrs. C. Grimm, Ms. V. Gobeil, and Mrs. J. Fitchen of Simon Fraser University, Ms. C. Russell of York University, Earthwatch, and field staff of the Orangutan Research and Conservation Project for their assistance. For the

long term project, we thank Dr. Soedjarwo, Mr. Siswojo Sarodja, Mr. Prijono Hardjosento, Mr. Walman Sinaga, Mr. Lukito Daryadi, Mr. Wartono Kadri, Dr. Rubini Atmadwidjaja, Dr. Bachtiar Rifai, Ms. Sjamsian Achmad, Mrs. Moertini Atmowidjojo, Mr. Napitapulu, and Mr. J. Bima for their support; the government of Kalimantan Tengah, in particular Mr. R. Sylvanus and Mr. W. Gara, former governors, Governor Gatot Amrih, and Mr. G. T. Binti, for encouragement and support; Mrs. J. Travis, Mrs. N. Sulaiman, Mrs. A. Masters, Dr. M. Payne, Ambassador E. Masters, Mrs. M. G. Smith, Mrs. M. Pechanec, Mrs. S. Johnson, Mrs. O. Kemp, Dr. J. Westermann, Mrs. B. Whittey, Mrs. K. Rust, Mr. and Mrs. F. O'Brien, Mr. J. Short, Mrs. H. S. Lokey, Mr. and Mrs. R. Allen, Mr. and Mrs. D. J. Postma, and particularly Mr. R. Wilkie and Mr. L. Wilkie for their support; former Universitas Nasional students Mr. Jaumat Dulhaja, Mr. Suharto Djojsudarmo, Mr. Endang Soekara, Mr. Barita Manulang, and Mr. Yatna Supriatna for their contribution; and Mr. Ahmad for collecting data. We especially thank Mr. Bohap bin Jalan and Dr. Gary Shapiro for their continuing dedication.

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formance of preexisting behavior; even imitation that generates new behavior can derive from either experiential or symbolically mediated processes (e.g., local enhancement vs. imitative learning). Imitative behavior does not unambiguously reflect what was acquired by imitation or which imitative processes generated acquisition (e.g., Bandura, 1977; Galef, 1988; Visalberghi & Frigaszy, 1990; Yando et al., 1978). Correspondingly, as a point of departure, we adopted the convention of using the term *imitation* for incidents in which an observer replicates a model's behavior and the replication is contingent on observing the modeling (Russon & Galdikas, 1993; see also Hall, 1968; Nadel, 1986; Yando et al., 1978).

There is little dispute that observers' intellectual capabilities constrain imitation. There are also strong arguments that motivation plays a key role. Evidence for motivational influence is that human imitation tends to decrease from childhood to adulthood despite increasing imitative capabilities (Yando et al., 1978). Motivation may be influenced by demonstrated actions and, because imitation is a social process, by social factors. Because normally various actions can be imitated but only some of them ever are, one probable role of motivation is selectivity, that is, the nature of imitation that actually occurs, within the scope of imitators' abilities (Yando et al., 1978). Potential roles for selectivity in great ape imitation are discussed in light of relevant research on humans.

Social Factors in Human Imitation

Humans have been described as imitative generalists: Even infants can be induced to imitate quite unlikely models doing equally unlikely things (Meltzoff, 1988b, 1988c; Meltzoff & Moore, 1992). Commonly, however, humans show preferences in the models and actions they deign to imitate.

The imitator-model relationship, especially its affective nature, has long been considered influential in imitation (e.g., Freud, 1933/1964; Yando et al., 1978). Especially significant is attachment to the model; this increases the likelihood that youngsters will imitate, especially unusual actions (McCabe & Uzgiris, 1983; Valentine, 1930). Model choice based on peer dominance or friendships and on fear of the model as well as deliberate nonimitation of disliked or mistrusted models have been found (Hartrup & Coates, 1970; Nadel, 1986; Russon & Waite, 1991; Uzgiris, 1981; Yando et al., 1978). Even transient or impersonal social factors can influence the direction imitation takes. A model's social position, especially its prestige, competence, or dominance, can foster imitation (Bandura, 1971). The tone of interactions with a model can influence children, especially ones of affection or nurturance (e.g., youngsters imitated warm and friendly over distant and cold adult strangers; Flanders, 1968; Valentine, 1930; infants imitated skilled experimenters; Meltzoff, 1988c; Meltzoff & Moore, 1992). Children may elect to imitate or not according to their understanding of models' or situational expectations (Yando et al., 1978).

Action-Related Factors in Human Imitation

Three factors are of interest. First, competence is considered to guide selection of which actions to imitate (Aronfreed, 1969; Bates, 1979; Masur, 1988; Yando et al., 1978). It is accepted that competence constrains imitation, because of observers' limited abilities to represent the ensemble of discriminative contingencies involved in a demonstration. Competence may also motivate: Imitators select challenging actions, those at levels just beyond their abilities, and may not attempt actions that are more difficult or too easy (Yando et al., 1978). Interest may reflect such competence motivation: Children seem to prefer operating at the cutting edge of their abilities, selecting problems or domains that reflect their current learning focus and level (Yando et al., 1978). Second, when imitation is used to solve problems, relevance to the problem may affect observers' selection of which demonstrated actions to imitate (Yando et al., 1978). Third, demonstrations of receptively familiar behavior elicit imitation more readily than those of novel actions (Meltzoff, 1988a; Valentine, 1930). These three factors are distinct but not mutually exclusive.

Developmental Influences

Discussions of motivational factors are incomplete without considering development. Which affective relationships are important change with age (Nadel, 1986; Yando et al., 1978), as do cognitive capacities (Piaget, 1962). Who motivates an infant to imitate may not motivate an adult; what challenges a juvenile is impossibly complex for an infant but boring for an adolescent. Such developmentally based changes are known across most of the motivational factors discussed. For example, older but not younger children imitate task-relevant over task-irrelevant actions, and older children may prefer models in affiliative over attachment relationships (Nadel, 1986; Nadel, Baudonnicre, & Fontaine, 1988; Speidel & Nelson, 1989; Yando et al., 1978).

Motivation in Great Apes' Imitation

If imitation is this closely channeled in humans, whose capacities are considered the most flexible, it seems unlikely that it would operate more freely in nonhuman primates. This suggestion is not novel. Various researchers have suggested that experimental failures to elicit sophisticated imitation in great apes may be due partly to test conditions that inhibit, not motivate, imitation (Cheney & Seyfarth, 1990; Hall, 1968; Huffman, 1984; Nishida, 1986). Social and action-based factors are both probable motivators of imitation in nonhuman primates, which are distinguished for their sociality and cognitive flexibility (e.g., Byrne & Whiten, 1988; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987). Boesch (1992) suggested that nonhuman primate imitation "presupposes a natural and trustful relationship between two individuals that should motivate one of them to copy a specific behavior of the other" (p. 149) and that models' prestige may affect their effectiveness. For

Mitchell (1994) and Galef (1992), almost all nonhuman primate imitation is based on identification with the model; for example, Plooij (1978) described an adolescent male chimpanzee that imitated an adult male the adolescent followed constantly, like a favorite. In regard to actions, Custance (1992) reported that in her replication of the "do what I do" experiments (Hayes & Hayes, 1952), her chimpanzee subjects occasionally refused to imitate a demonstrated action by walking out, apparently because the action was too difficult. Kohler (1927) argued, from his extensive experimentation, that chimpanzees could not imitate a problem's solution unless they already understood the crucial relationships involved.

Empirical research does suggest that nonhuman primate imitation is socially directed; it follows kinship, affective relationship, and social status lines (e.g., Huffman, 1984; Kawai, 1975; Russon, 1990; for overviews, see Meador, Rumbaugh, Pate & Bard, 1987; Pallaud, 1988; Walters & Seyfarth, 1987). Socialization may play an important role. Those great apes who have shown signs of imitative learning were raised by humans (Tomasello, Kruger, & Ratner, 1993; Whiten & Ham, 1992), and chimpanzee and orangutan imitation has been rather easily elicited once they have been trained to understand "do what I do" instructions (Custance, 1992; Hayes & Hayes, 1952; Miles, Mitchell, & Harper, 1992). Nonhuman imitation may also selectively focus on activities that are near imitators' competence levels, receptively familiar, and instrumentally valuable (Pepperberg, 1988; Visalberghi & Fragaszy, 1990). Developmental variation is probable in nonhuman primate affective relationships (Harlow & Harlow, 1965; Tuttle, 1986) and cognitive competencies, including imitation (Dumas & Doré, 1986; Mathieu & Bergeron, 1981; Mignault, 1985; Miles, 1990; Russon, 1990; Visalberghi, 1992). Age does influence model choice (Huffman, 1984) and perhaps whether model or activity cues are favored (Meador et al., 1987).

We explored patterns of model- and action-based selectivity in great apes' imitation in an observational study of spontaneous imitation in free-living rehabilitant orangutans. We designed an observational study because goals for the rehabilitants preclude experimental intervention, and in any case, our questions concern spontaneous behavior and choice. As an observational study, this project offers at best suggestive material. It can be valuable in offering a larger, more representative sample than those normally achieved in experimental studies and a better view of the cues that orangutans themselves use to guide their imitation.

Method

The imitation data derive from the same data base and methods used in a related study (Russon & Galdikas, 1993). We sketch common methodological features briefly and describe in detail those specific to this study.

Subjects

Subjects were formerly captive orangutans (*Pongo pygmaeus*) and their offspring associated with the Orangutan Research and

Conservation Project's rehabilitation program at Camp Leakey, Tanjung Puting National Park, Central Indonesian Borneo. Rehabilitation offers individualized support that ranges from supplementary provisioning to forest skills training for orangutans released from captivity into the forest. Almost all former captives are orphans, but the conditions and duration of their captivity vary considerably: Orphans arrive as young as 2 or 3 months of age; commonly, they arrive as older infants or juveniles, some recently orphaned and some who were raised from infancy with humans; and a few arrive as subadults after many years of captivity. All but youngsters under protective nursery care are free-living. They range through the forest; intermittently and for variable periods of time, some pass through the base camp. Some that had extensive human contact show residual interest and considerable expertise with human affairs. Rehabilitants' offspring are raised normally by their biological mothers. To sample the richest behavior, we selected the few adult and adolescent rehabilitants that frequented camp and forest environments. Because most had dependent offspring, data included the offspring.

Setting

The subjects were observed in Camp Leakey and the surrounding forest. The camp comprises buildings (dining hall, herbarium, ranger hut, and living quarters), a dock, and an observation tower. At the time of the study, it was staffed by 10–20 Indonesians who maintained the camp, followed wild orangutans, and cared for rehabilitants. It is situated on about 1 ha of tropical rain forest along the Sekonyer Kanan River. The surrounding forest consists mostly of lowland dipterocarp and peat swamp forests interrupted by a few abandoned rice fields; a 35-km² study area is transected by a well-developed trail system.

Data Collection

We collected data in two 3-month field trips in the 1989 and 1990 dry seasons. A rehabilitant's behavior was sampled when the individual was found while we were searching the forest, the standard subject selection method in research on free-ranging orangutans. Most data were collected in focal-subject follows (in 1989, half-day follows, in camp, and in 1990, full-day follows, that is, from rising to nesting, in the forest or in camp). In 1990, we also collected 25 hr of video data on 10 orphans, 1½–5 years old, under nursery care (5- to 30-min sample per subject in the nursery peer group setting). Within the bounds of field conditions, we balanced each subject's video samples over the 3 months and waking hours of the day.

Observation comprised continuous descriptive notes on the focal orangutan's behavior during the follow, with concentration on all imitation with the focal orangutan as imitator or model. Most follows were made by Anne E. Russon. In 1990, research students and Earthwatch research volunteers contributed. We accepted reports from inexperienced observers when we could substantiate them as reliable (see Russon & Galdikas, 1993). Birute M. F. Galdikas contributed additional data (some incidents of imitation and background) and interpretations as part of her long-term project.

Ad lib observation and discussions with staff provided adjunct data on orangutans' relationships and background, camp activity patterns, availability of tools, and so forth. We used staff reports when they proved reliable, as with reports from inexperienced observers. We assessed relationships other than kinship and parenting (such as friendship, dominance, and consortship) by infor-

mal, extensive observation and judgments by Galdikas and knowledgeable camp staff. These adjunct data ultimately allowed us to estimate the familiarity of the imitated action and orangutans' previous opportunities to learn it by experiential learning; they permitted inferences about the possible processes that guided the observed imitation and those that guided its acquisition.

Imitation. Identifying imitation requires establishing match and contingency between an imitator's and a model's actions. Field conditions precluded using the precise criteria developed for imitation experimentally (e.g., Meltzoff, 1988b; Meltzoff & Gopnik, 1989; Zentall & Galef, 1988), so we relied on markers for imitation in spontaneous behavior (Russon & Galdikas, 1993). Our interest was in the actions imitators (not researchers) chose; these were not controllable or predictable, so our criteria were relational rather than concrete.

Criteria for matching are well-established for immediate imitation, when imitator's and model's actions co-occur (Masur, 1988; Meltzoff & Gopnik, 1989; Nadel, 1986). A match is identified under the following conditions. First, some demonstrated features are replicated (much imitation only partially replicates the original; Galef, 1988; Pallaud, 1988); we considered this satisfied when observers could describe the demonstration and the features replicated. Second, the imitator perceived the model's actions; we considered this established if the model's actions were salient and within the imitator's sensory field. Third, the imitator's actions closely follow the model's in time; given orangutans' slow pace, we allowed a maximum delay of 2 min. In deferred imitation, when the imitator's actions occur separately from the model's, matching is identified by the precision of the replication, particularly its details (Hall, 1968; Nadel, 1986). The closer the similarity between imitation and demonstration, the less likely it is that the imitation arose independently. Matching can be determined by observers' direct knowledge of a demonstration that the imitator observed (Ratner, 1989; Snow, 1981) or general knowledge of the imitator's similarity to actions characteristic of and peculiar to the imitator's sociocultural context (Meltzoff, 1988a). We required observers to specify the relevant demonstration (model, occurrence, action sequence, and imitator's opportunities to observe) and features matched.

Establishing contingency requires showing a low probability of spontaneous production of the imitative actions without demonstration (e.g., Meltzoff & Gopnik, 1989). Our operational criteria were that the imitative actions were rare, their performance constituted an abrupt change in behavior immediately after demonstration, or the imitator had not performed them in the previous 10 min despite opportunities or incentives to do so (Hall, 1968; Nadel, 1986).

For every imitation we identified, we described in detail its action sequence and that of the demonstration, imitator and model identities, ages, and contextual factors (others present, their actions, and initiating and terminating conditions).

Parenting relationships. A parental, attachmentlike relationship was identified if imitator and model were biologically parent and offspring, if knowledgeable long-term staff or Galdikas judged an orangutan dyad to be an adoptive parent-offspring relationship, in which the older orangutan had taken on caregiving responsibilities for the younger, or if the model was a designated human caregiver for that orangutan.

Nonparenting relationships: Dominance, friendship, and consortship. Following Hinde (1979), we saw relationships as representing enduring and consistent patterns in partners' encounters. Short-term direct assessments of rehabilitants' relationships were problematic: Many of these rehabilitants' relationships derived from encounters prior to our study (e.g., adult friendships from

contacts during youth), and orangutans are semisolitary, interacting infrequently and even avoiding social contact (Galdikas, 1985). Indeed, we saw no or very few social encounters for some orangutan dyads. We therefore relied heavily on judgments from knowledgeable humans about rehabilitants' relationships. Our procedures were admittedly informal and heavily dependent on human judgment, but we were careful to identify a relationship only after several consistent assessments. Because affective relationships may play an important role in selectivity, we present our assessments in the spirit of offering suggestive material that may benefit more carefully controlled studies.

Dominance has been given varied formal definitions (Walters & Seyfarth, 1987), but the central concept is consistent: asymmetry in dyadic social encounters, for which outcomes are regularly more advantageous for one partner than for the other. We used agonism as well as other sources of asymmetry to assess dominance (e.g., undisputed object, place, or partner possession encounters, aggressive or submissive gestures, pursuits, contact soliciting, or disturbing a partner's activity; see Russon & Waite, 1991). Friendships were nonsexual affiliative relationships characterized by relaxed, prosocial encounters rather than competitive ones (e.g., Smuts, 1987); we identified rehabilitant friendships through mutual preference (travelling, foraging or resting together, play, grooming, or sharing). Consortships were temporary relationships between sexually mature males and receptive females; the two traveled together with frequent sexual encounters, the male defended the female against other males, often aggressively, and the relationship terminated when the female became pregnant (Galdikas, 1979; Tuttle, 1986). Consortships were assessed by current behavior.

Results

We accumulated 395 hr of live observation for 349 imitations by 26 orangutans (6 adult females and their dependent offspring, 2 infants and 6 juveniles; 3 adolescent females; 7 infant and juvenile orphans; and 2 subadult males). Video samples produced 11 more imitations by 6 young orphans (3 among the original 26). Imitation reports came from Russon (191), Galdikas (21), students (76), and inexperienced observers (72).

The analyses take into account that our data concern performance, but selectivity factors may reflect internal processes, and these may act interactively rather than independently. For each factor we first established measures for relevant internal processes and identified data subsets in which the factor's independent influence would be evident. For example, competence concerns cognitive abilities, which we assessed through the range and complexity of the routines imitated; competence as constraint or motivator would be evident in the subset of most complex imitations. For each analysis we describe these measures and subsets and then our findings. Caveats are that the distributions reported for selectivity are suggestive only because of uneven sampling across age and sex classes and that video samples provided too few incidents of imitation to support distribution-related analyses.

Model Selection

Many models were available. Up to 30 rehabilitant and wild orangutans congregated at feeding, and rehabilitants

encountered one another in the forest. Human visitors resident in camp included staff, researchers, volunteers, and students, and transient visitors, Indonesian and foreign, passed through almost daily; all were readily accessible in the camp and surrounding forest. Models were identifiable for all imitations, so we examined the whole data set for model-based patterns. To link these analyses with those on action factors, we also examined 54 cases that suggested imitative learning (see Russon & Galdikas, 1993).

Species-level model preferences. Models were orangutans in 59.2% of imitations, humans in 40.3%, and an infant pigtail macaque in 0.5%. No orangutan imitated only humans, 14 imitated only orangutans, and 13 imitated both. We explored species-level model preferences in the subset of imitations performed by 7 orangutans that imitated both humans and orangutans and for whom we had substantial, systematic data in 1990; the 1989 sampling favored camp settings, so models were predominantly humans (Table 1). The pattern suggested was preference for orangutan models in subjects with closer, more extensive, or more effective relationships with orangutans than with humans (commonly, offspring vs. rehabilitants; dominants vs. subordinates; reproductively or chronologically older rehabilitants vs. younger ones).

We further explored imitator qualities related to species preference by comparing the 14 orangutans that imitated only orangutans with the 15 that sometimes imitated humans. The former were 1 adult female rehabilitant and 14 offspring. The rehabilitant spent little time near camp and avoided humans; its models were other rehabilitants, mostly orangutans with which it had been raised and which were considered its friends. All offspring but 2 (see Table 1) imitated only orangutans even if their mothers imitated humans. Those who sometimes imitated humans were 13 rehabilitants raised by humans, several from early infancy, and the 2 offspring just mentioned.

Patterns were similar in the set that suggested imitative learning. In 47 of 54 cases, imitators were individually identified: Eight rehabilitants imitated human models only, 1 offspring imitated its rehabilitant orangutan mother only, and 1 offspring imitated both (the eldest daughter of a rehabilitant; both had ample contact with humans and orangutans). Models were orangutans in 5.6% cases and humans in 94.4%. These figures probably show strong bi-

ases because of the inherent difficulty of identifying orangutan-modeled imitative learning: It commonly involves species-typical behavior, so ruling out individual learning is problematic.

Because of these species-based patterns and because relationship possibilities differed between species, we separated further model-related analyses by species.

Affective relationships with human models. Orangutans imitated humans in 88 cases in which imitator and model were identified. The imitated models (individuals or groups) were their designated caregivers (68.2%), researchers or students (13.6%), other resident visitors (12.5%), camp cooks (4.5%), and a friend, Frederick, son of Birute M. F. Galdikas (1.2%). In cases that suggested imitative learning (51 of 54), imitators were 8 rehabilitants and 1 offspring. Preference was even stronger for models that represented major caregivers (80.4%); other models were camp cooks (5.9%), resident visitors (7.8%), or Frederick (2%); 4% were unidentifiable.

For contrast, we examined stranger models. Many strangers, both resident and transient visitors (research volunteers, day-use drop-in tourists, and officials), had contact with the rehabilitants. Resident visitors stayed in camp, commonly at least 2 weeks, and regularly encountered the rehabilitant community; transient ones did not stay in camp, returned at most 3 or 4 times, and had less contact. No orangutans were seen imitating transient strangers. One adolescent female rehabilitant (Davida) did imitate newly arrived resident visitors; she actively cultivated that group for food, companionship, and support.

On the basis of observability or salience, transient strangers ought to have been among the most frequent models, but they were never chosen. Neither was availability the key: Orangutans rarely imitated camp cooks, very commonly available; young orphan rehabilitants imitated their caregivers even if that relationship was very recently established; and Davida imitated some strangers apparently because she was familiar with and preferred their group.

Affective relationships with orangutan models. Orangutans imitated orangutan models in 174 cases in which both partners were identified. Model choices were biological or adoptive parents (68.4%), friends (20.1%), offspring (5.2%), siblings (4.6%), and sexual partners (1.7%). For quantitative views we used data from systematic follows on

Table 1
Species Preferences for Models in Orangutans That Imitated Both Humans and Orangutans

Imitator	Type	Sex	Age	Offspring ^a	Dominance ^b	No. imitations to orangutans	No. imitations to humans
Davida	Rehabilitant	Female	Adolescent	0	Low	5	9 ^c
Supinah	Rehabilitant	Female	Adult	died, 2½	Low	3	50 ^c
Princess	Rehabilitant	Female	Adult	4½, pregnant	Low	10	11
Siswoyo	Rehabilitant	Female	Adult	>13	High	5	5
Unyuk	Rehabilitant	Female	Adult	6½	High	4 ^c	1
Siswi	Offspring	Female	Adolescent	died, pregnant	High	21 ^c	7
Sugarjito	Offspring	Male	Infant	0		15 ^c	7

Note. Data were collected in 1990.

^a Age in years of oldest offspring in June 1990; 0 indicates nulliparous. ^b Female dominance status. ^c Model species preference.

focal orangutans (164 cases; 5 adult females and 2 adolescents). These data accurately represent relationships for focal subjects and reasonably accurately for their infants, which rarely leave their mothers or interact with others, but the data are biased for older offspring that increasingly spend time away from their mothers and change their range of social partners. The bias overrepresents mother-modeled and underrepresents other-modeled imitation. With this bias in mind, we assessed relationship factors in choices of orangutan models (Table 2).

Patterns appear age-dependent. The 4 infants 1½–4 years old preferred mothers as models. In a rare instance, one chose siblings; another chose its own and its mother's friends. The two juveniles chose their mothers but equally often chose friends; one also chose siblings. Given our bias, this suggests that juveniles may be shifting to affiliation-based rather than attachment-based model choice. Both adolescents were focal subjects. Siswi, the eldest offspring of a rehabilitant, preferred her mother, then friends, acquaintances, or siblings. In a few isolated cases, she imitated her current sexual partner and an adult female who was probably dominant to her. Davida, an orphan rehabilitant, rarely imitated orangutans; when she did, her models were friends or acquaintances, and all cases involved food. The 5 adult female rehabilitants included 2 who strongly preferred orangutan over human models. These 5 females imitated orangutan models that were their friends (often, earlier peer group companions), their own offspring, and subordinate youngsters (over food).

For directionality, we examined systematically sampled orangutan relationships in which imitation occurred both

ways (Table 3). Offspring always copied their mothers more than the reverse. The sibling set imitated one other rather often, with at best a slight preference for sibling models that were older or closer in age. In friendships, no clear pattern emerged (older vs. younger and dominant vs. subordinate).

There were some other minor patterns. On a few occasions subadult males imitated sexually interesting females. Once a subadult male imitated a subordinate subadult during an agonistic chase, apparently as a sort of intimidation. In the video samples young orphans imitated their nursery peer companions and adult female rehabilitants that visited their group more than their human caregivers (9 and 6 vs. 4 cases).

We found only 3 incidents that suggested imitative learning from orangutan models. The 2 orangutans involved imitated their biological mothers.

Dominance. Imitator–model relationships had dominance dimensions in 311 cases (145 human modeled and 166 orangutan modeled). Galdikas and male staff persons tended to dominate the rehabilitants and their offspring, whereas most other humans, including Russon, female staff persons, and visitors, dominated juvenile and younger orangutans at best. Dominant humans modeled 58% of human-modeled imitations; another 31% cases involved actions also commonly demonstrated by these dominant humans. Between orangutans, mothers were dominant over offspring, and older partners, over younger ones. Some orangutan friendships could be co-assessed for dominance. In mother–offspring imitation (123 cases), models were almost exclusively the dominant partner, the mother (92.7%). With friends and siblings (35 and 8 cases), imita-

Table 2
Relationship-Based Preferences for Orangutan Models: Frequency of Imitation by Relationship With Model

Family group and imitator	Age group	Model					Total
		Mother	Offspring	Sibling	Friend	Other	
Family A							
Kuspati*	Adult		0		2	0	2
Kris	Infant	10			0	0	10
Family B							
Princess*	Adult		3		9	1	1
Prince	Infant	5		0	3	1	9
Family C							
Supinah*	Adult		1		0	2	3
SiDyDy	Infant	71			0	0	71
Family D							
Siswoyo*	Adult		5		0	0	5
Sugarjito	Infant	14		3	0	0	17
Simon	Juvenile	2		3	4	0	9
Siswi*	Adolescent	10		2	6	6	24
Family E							
Unyuk*	Adult		0		0	4	4
Uranus	Juvenile	2			2	0	4
Family F							
Davida*	Adolescent				2	3	5
Total		114	9	8	28	18	164

Note. Other models include an infant pigtail macaque, dominant or subordinate partners, or sexual partners. The adult given for each family group is the mother; nonadults are offspring (and siblings to each other).

* Focal orangutans (dependent offspring were never focal subjects).

Table 3
Model Preference Within Established
Dyadic Relationships

Relationship and dyad	No. imitations to dominant	No. imitations to subordinate
Mother-infant		
Supinah and SiDiDy	71	1
Unyuk and Uranus	2	0
Princess and Prince	5	3
Kuspati and Kris	10	0
Siswoyo and Siswi	10	2
Siswoyo and Simon	2	1
Siswoyo and Sugarjito	14	2
Total	114	9
Siblings		
Siswi and Simon	2	1
Siswi and Sugarjito	0	1
Simon and Sugarjito	3	1
Total	5	3
Friends		
Kuspati and Princess	4	2
Unyuk and Siswi	0	1
Unyuk and Davida	0	1
Unyuk and Princess	0	1
Princess and Davida	0	1
Davida and Princess	2	0
Roger and Nasution	2	0
Siswi and Supinah	1	3
Siswi and Princess	5	5
Siswi and Davida	3	1
Siswi and Prince	1	1
Total	18	16
Grand total	137	28

Note. Dominant indicates mother, older sibling, or dominant partner in friendship or between playmates; subordinate indicates offspring, younger sibling, or subordinate partner in friendship or between playmates. The first partner given is the dominant.

tors chose both dominant (51.4% and 62.5%) and subordinate (42.9% and 37.5%) models; in 2 cases in 2 dyads, the dominance was not clear.

Orangutans imitated subordinate partners in 30 cases. They imitated subordinate friends or siblings almost as often as dominant ones. About half the subordinate-modeled imitation (16 of 30) involved food; by imitating, the dominant shared or coopted the subordinate's discovery. Other cases were using the same object, performing similar manipulations, grooming, scratching, and inspecting genitals.

In the subset that suggested imitative learning, imitators preferred dominant models in that they imitated caregivers and biological parents (81.5%) over others (cooks and visitors; 13%). In 3 final cases (5.5%), we could not determine dominance.

Social anomalies. In 29 imitations, imitator and model had no clear relationship: They were not biologically related, and in our sample they neither frequently interacted nor showed any stable pattern in their encounters. Two factors could account for all but 3 incidents: Models were strangers as individuals but members of a group the imitator preferred (5 of 29), or the modeled actions were important per se (21 of 29; 19 actions pertaining to food, 1 action,

which 1 imitator frequently performed, of wiping its face with a facial tissue, and 1 action that appeared to engage a human companion the imitator preferred). In the last 3 incidents, 2 infants imitated incidental playmates (adult female rehabilitant and infant macaque), and a subadult male imitated a female he appeared to find sexually interesting. Also, 10 of these imitations involved models that had relationships with the imitator's family members, so the models were somewhat familiar to the imitator.

Two failures to imitate suggest the potency of social relationships in imitation. First, Nasution, an orphan rehabilitant about three years old, was approached by her nursery caregiver, who leaned close to her face and stuck out his tongue at her. She immediately imitated while looking at him; they repeated this imitative exchange several times. Russon observed this and tried to join in by sticking out her own tongue at Nasution at the appropriate moment. Nasution watched but did not imitate. Second, Supinah, an adult female, often tried to help camp construction by imitating staff in hammering nails and sawing and chopping wood. When new construction began, Russon expected Supinah to imitate and systematically waited 2 weeks for her to do so. Supinah never did despite ample opportunity. In discussions, Galdikas mentioned that Supinah did not know the man doing the construction, who had been at another site for over a year.

Action Selection

Competence ought to affect imitation near the edges of imitators' abilities: As a motivator, it ought to direct choice to modeled actions just beyond current abilities; as a constraint, it ought to result in performance errors for those same actions. That is, competence ought to affect imitative learning and be most evident there. Task relevance is determined by the task; its role in selectivity also ought to be most evident in imitative learning, where it is not influenced by experience. Familiarity can be assessed across all imitation; its role is most interesting in imitative learning. Our analyses of action factors were then concentrated on a subset of 54 complex imitations that suggested imitative learning (see Russon & Galdikas, 1993). We explored patterns by age because great apes' cognitive capabilities change developmentally. Our sample permitted some developmental tracking but represented juveniles poorly in comparison with other age classes.

Competence. For constraints, we examined the content range (breadth and level) of the 54 incidents of complex imitation. Infants under 3½ years old produced none (they produced only 4 imitations altogether, a narrow range of such simple preexisting actions as mouthing, holding, or pulling an object or protruding tongue). The 6 complex imitations of older infants and juveniles involved novel but simple combinations of a small range of known actions (e.g., bending sugarcane as if to squeeze juice out, wetting and rubbing hair as in shampooing, wiping perineal area with leaf, and chopping earth with hoe); the orangutans made errors, omitted key components, and did not achieve

the modeled goal. Adolescents and adults (48 or 54) coordinated elements from a broader and higher level repertoire of actions on objects and object-object relational operations. Actions were blowing and sucking, holding, pulling and pushing, bending, lifting, collecting and gathering, throwing, dropping, wiggling, scraping and rubbing, manipulating, gesturing (shading eyes), and climbing on and over. Object-object relations were scooping, pouring, drinking from, floating, twisting (wringing, wrapping, winding, untie, and screwing and unscrewing), opening, closing, putting on, inserting, probing, threading, prying, chopping, digging, scraping (drawing, wiping, sawing, and sweeping), hammering (tapping and hitting), hooking, touching together, fanning, and giving. Adolescents' and adults' complex imitations also showed errors of misordering (an orangutan attempted to insert a siphon into a fuel drum before it opened the drum's cap), inadequate coordination (one confused the direction to slide a bar to unlock a door), or botched complex relations (some could not effectively tie a hammock's rope, and others substituted their own simpler solutions). Ranges, age-based variation, and errors are all consistent with competence constraints.

In regard to competence as a motivator for extending existing skills, we looked for novel components. The 6 cases by youngsters over 3½ years old did involve attempts to reproduce novel actions (3 of 6), but they were flawed and did not achieve the results modeled (e.g., bending sugarcane produced no juice, and hoeing earth did not clean paths). In adolescents' and adults' complex imitations (48 of 54), the novelty was in the combinations or uses of basic components rather than in the basic components themselves. Supinah, an adult female, offers a good example: Several of her complex reproductions incorporated the same basic components, but the components were arranged and applied in novel fashion: sharpening an axe blade (dipping a stone in water and rubbing the wet stone back and forth across the blade's surface), sanding blowgun darts (rubbing the dart's flared end across a hairy leaf surface), applying and removing paint (dipping a brush in paint and rubbing it back and forth across a surface and dipping a rag in turpentine and rubbing it back and forth across spilled paint) and washing clothes (dipping a cloth in water, spreading it, and rubbing a brush or soap back and forth across the cloth). Learning is also suggested by the fact that she actively practiced these routines and spontaneously rehearsed them over several days. She knew the basic components (dipping object in liquid or rubbing one object on another) but appeared to acquire sequencing (e.g., wetting and then rubbing) and applications (e.g., stone with axe blade and hairy leaf with dart) imitatively. Most of these adolescent and adult routines failed to achieve their ostensible goals (32 of 48). The novelty and these errors suggest attempts to surpass current constraints, thus competence as a motivator.

We identified interest by individual variation in the routines imitated by adult females, which were ostensibly equal in competence. Although adults imitated similar actions (e.g., several attempted to hang hammocks and unlock

doors), not all of them imitated the same actions or performed given actions with the same frequency or intensity. For example, Supinah and Princess imitated a wide range of tool use, whereas Kuspai imitated no tool use; Princess and Supinah specialized in the intricacies of unlocking doors; Siswoyo and Siswi were drawn to drawing; Davida often put on clothes; Tutut imitated actions that occurred near the river, where she spent much time. Supinah's practicing also suggests interest. Such interest also supports the notion of competence as a motivator.

Task relevance. We first checked if orangutans pay any attention to the task by looking at imitation of tasks important to orangutans and then analyzed task relevance in the original sense, the relation between the problem faced and which components of the modeled behavior strategy are imitated.

Accessing food is acknowledged as the top priority task for orangutans, so we looked at imitations involving food. Although this is a dominant form of orangutan behavior, we could differentiate imitative cases on the basis of contingency (e.g., a 2½-year-old repeatedly passed over one plant for 10 min but ate others nearby, then watched its mother eat it, and immediately ate it). Almost half of our imitations involved food (160 of 360; 44%). Orangutans imitated models in eating the same food (e.g., hairy leaves of a grass), searching for the same food at the same place (e.g., digging for termites at one spot), and using similar methods to process the food (e.g., lathering food against forearm hair, bending sugarcane to squeeze juice out, probing food from a container with a twig, and offering food on a plate). The particular actions reproduced were relevant and effective for accessing food.

With respect to selecting task-relevant components in imitating, youngsters apparently did not. All young infants' imitations (4 cases) involved simple, preexisting actions performed immediately after demonstration, as did most of the older infants' and young juveniles' (preexisting actions, 160 of 168, and immediate imitation, 160 of 168). When youngsters used imitative learning (6 cases), they did reproduce relevant elements (e.g., bending sugarcane is one part of an effective technique for extracting juice) but ignored other critical elements (e.g., the cane was too short) or performed them ineffectively (e.g., the cane was not bent hard enough). In this particular case, the youngster chose the difficult and novel modeled technique over the more common one it normally used effectively, that is, biting off the rind.

In the 48 adolescent and adult cases, the actions reproduced were relevant to the task observed. For example, after orangutans observed models hoe weeds away from camp paths, they used the hoe appropriately (for chopping), chopped effectively at the appropriate target (weedy areas beside paths), and discarded their chopped weeds as models did (piled them in the center of the path). One orangutan correctly reproduced almost every relevant action for siphoning fuel, in its appropriate sequence. Evidence that these orangutans chose actions on the basis of relevance is that on a substantial number of occasions (16 cases), their imitations achieved their ostensible goals. For example,

orangutans successfully replicated techniques for hanging up hammocks, and then rode in them, for untying canoes, and then went for rides in them, for unlocking doors, and then took goods from inside, and for making log bridges across the river, and then crossed on them. The majority of these routines (32 or 48), however, did not effect the ostensible goal. Errors tended to involve absence of critical components (e.g., to siphon, there must be liquid in the originating container) or lack of refinement in performing or coordinating components (e.g., nails must be hammered hard, and a critical amount of kerosene starts, rather than douses, fire). However, at least once an imitator corrected her error by adding a relevant observed component: In Supinah's first imitation of sharpening an axe blade, she simply rubbed the sharpening stone on the blade; in her second attempt, she dipped the stone into a pail of water before she rubbed it on the blade, as the model did. In some cases the errors concerned features that were not observable and so could not be learned imitatively (e.g., if a drum contains fuel, if siphoning requires blowing or sucking, and how much kerosene starts a fire). These patterns suggest task relevance did guide imitation in older orangutans.

Two subsets appeared to discount the role of relevance. First, Supinah twice reproduced nonrelevant components of a demonstrated routine (before she drank, she carefully poured her drink from a mug into a bottle and then shook the bottle; she stroked her painting like models, in wide sweeping arcs and then in up-and-down strokes). Second, some cases were empty nonfunctional routines, often performed after a delay (e.g., making the motions of brushing teeth or siphoning fuel from an empty fuel drum). All were triggered by an opportunity for expression (e.g., finding a toothbrush with toothpaste on it or finding all the tools involved in siphoning; hoes near paths elicited weeding, and tissues elicited wiping the face), whereupon the imitator reenacted the activity demonstrated with those objects or in those contexts.

Receptive familiarity. Familiarity was assessed in terms of how often imitative actions could be observed in the rehabilitants' environment (novel, rare, intermittent, or common). Across all 360 imitations, receptive familiarity was a strong factor: 60% involved actions that could be observed almost daily, 35% involved actions that were intermittently but repeatedly observable, and only less than 1% could be considered novel. For comparability, we examined the imitative learning subset: 81.5% of actions imitated were moderately to very familiar receptively. The 7 imitations of receptively novel actions involved accessing food or other desirables (2 imitations; bridging the river and harvesting cassava) or actions demonstrated by important models (5 imitations e. g., wiggling a marker, examining a sick infant, and washing hair); 3 were elicited by commotions, periods of intense social activity focused on a central activity.

Independent action bases for selection. Orangutans imitated unlikely models in 29 incidents; here, action factors may have acted independently rather than in interaction with model factors. Of these, 65% were food-related, in-

cluding the 2 cases that suggested imitative learning (making log bridges or a fire; bridges gave access to provisions, and such fires were for cooking food). The other 35% involved actions the orangutans knew and preferred or variations on them.

Commutations

An unexpected pattern was imitation triggered by commotions, sudden flurries of activity or exaggerated social attention focused on one central activity (weeding, painting, construction, a burial, blowgun demonstrations, or a medical examination of a sick infant). In all of these, individuals who had important relationships with the imitator were involved in the commotion but not necessarily as models; all demonstrations comprised basic actions familiar to the orangutans but organized or applied in unusual ways.

Discussion

These observational data point to important roles for both social and action factors in directing imitative performances and learning in these orangutans.

Model-related patterns resembled those expected. At the species level, orangutans that had intense contact with humans, especially early in life, preferred human models. This corresponds with findings that most cases that suggest rehabilitant imitative learning involved tools (Russon & Galdikas, 1993) and the most active tool users had close contact with humans from early life (Galdikas, 1982). However, as orangutan lifestyles and relationships were established, imitation correspondingly shifted from humans to orangutans. Models chosen had established relationships with imitators, and preferred relationships varied with development. Most preferred were models to whom imitators were attached, and then friends and other kin; strangers were virtually never imitated. Choices also followed dominance patterns, that is, a tendency to imitate dominants and imitation of subordinates in usurping the latter's discovery (both patterns occur between human infant peers; Russon & Waite, 1991). These model patterns suggest active selection based on relationships rather than simple salience or availability.

This suggests a simple explanation for the observation that human-enculturated but not nonenculturated chimpanzees learn imitatively (Tomasello et al., 1993). This may reflect species- and relationship-based model selectivity: The imitative learning reported appears to have been human modeled, and the human-enculturated chimpanzees likely have better established relationships with humans (having been reared by human caregivers) and better appreciation of expectations of imitation (many were casually reinforced for imitating and regularly anticipated their human caregivers' goals and intentions). Mitchell (1993) concurred.

The action-based patterns found in these orangutans' learning-focused imitation also corresponded well with patterns reported elsewhere. Competence as a constraint was

suggested by our findings that the range of actions imitated was limited but increased with age and that success itself was limited. That imitators attempted to imitate novel combinations or applications of known actions but made errors in doing so, that some of them actively practiced the new routines, and that interests were evident in which actions were imitated all suggest that competence also played a motivating role. Task relevance appeared to play some role in guiding imitation for older orangutans but not younger ones; this resembles the developmental pattern found in humans (Yando et al., 1978). Receptive familiarity characterized the behaviors they imitated, including those that involved learning.

Several unexpected patterns are interesting for the processes they suggest. Commotions could elicit imitation, which suggests that they may have served as social spotlights, drawing orangutans' attention to associated actions and marking them as significant even when the actions were rare or probably irrelevant to orangutan concerns. Imitation appeared to serve as a way of investigating them. Empty imitations, nonfunctional reenactments of observed routines triggered by reencountering the key objects, may express an imitator's understanding of those objects (e.g., toothbrushes are for brushing teeth; twig vs. household brooms are for paths vs. porches). This speculation stems from Piaget's (1952, 1954) and Werner's (1948) notion of knowing through action: That is, objects may not be fully known independent of the actions they afford; acting on them is a way of understanding or recognizing them. When understanding derives from observation, actions are imitative. Imitation is used this way by young children (Meltzoff & Moore, 1992; Speidel & Nelson, 1989).

Sense in Selectivity

Social partners offer important cues to appropriate behavior (e.g., stimulus enhancement or contagion in foraging or predator defense). Social cues are likely important to orangutans, opportunistic foragers in habitats where food distribution is patchy, in space and time (Galdikas & Vasey, 1992; te Boekhorst & Hogeweg, 1992), but some partners offer better cues than others. For example, each adult female occupies a stable home range (Galdikas, 1979), and so knows the area better than nonresidents. Others do use her expertise (males that roam through a female's range follow the resident females; Galdikas & Vasey, 1992); for offspring, selecting mothers as models likewise directs them to expert cues. Action cues ought to also play a significant role. For instance, orangutan foods are notoriously difficult to access and require elaborate processing (Galdikas & Vasey, 1992), and cues to action ought to enhance an observer's foraging success. Familiarity and task relevance highlight actions of most use; competence isolates those within the imitator's grasp.

This rationale for selectivity also applies to imitative learning in great apes. Imitative learning is a powerful process. It uses external cues but brings behavior under internal control, freeing behavior from environmental con-

trol and enabling wider applicability (Meltzoff, 1988b). Great apes increasingly appear capable of imitative learning (Russon & Galdikas, 1993), and their learning range is among the most flexible known, freed of constraints like domain specificity (Cheney & Seyfarth, 1990) and low complexity ceilings (Antinucci, 1989; Dumas & Doré, 1986). This greatly widens the range of behavior they can learn. However, not all behavior observed is worth acquiring, and imitative learning may be effortful rather than easy for great apes (Custance, 1992). This expands the problem of what great apes ought to expend an effort to learn and increases the burden of choice. Factors that can be seen as cuing what to learn are known for simpler learning (e.g., in associative learning, experiences which recur and are reinforced are favored for acquisition). Imitative learning obviates both, but analogous observable cues can flag these features: Receptive familiarity and relevance reflect, respectively, recurrence and instrumental or reinforcement value. Models offer related cues: Those in established relationships with an observer offer more and better opportunities for recurrent observation and hold knowledge more likely of instrumental value for that observer than do others. Selection on the basis of these observable cues will direct observers to those actions worth the effort of acquiring. Such a view makes selectivity a central, not peripheral, component of imitative learning.

Social-Action Balances

The balance between social and action factors that guide imitation is important in debates on the importance of social versus ecological intelligence in primates. Our data suggest that action and model factors probably interacted in guiding much imitation (e.g., commotions); in some circumstances action factors outweighed model ones (e.g., competencies), although in others model factors outweighed action concerns (e.g., youngsters). The balance between the two seemed uneven: Imitation of important behavior like foraging was commonly triggered and directed by models' actions; imitation of simple known actions was common, which suggests that contagion was a prevalent process and in turn that orangutans' attention was on social partners as much as or more than on the physical environment; and youngsters relied on models, not tasks, for cues about what to do and when to do it. In short, we found no indication that action-based, ecological concerns took general priority over social ones in guiding imitation. Our impression is, if anything, the contrary—social forces were perhaps more influential than ecological ones.

Orangutans' favoring social and ecological cues supports views that great ape imitation serves as an efficient and flexible social way for young to acquire adult behavior, as it does in humans (Meltzoff, 1988b). For Parker (1992), this suggests an apprenticeship system in great apes: Learners rely heavily on expert social mediators, perhaps more heavily than on ecological cues early in development when much important learning occurs. An apprenticeship view agrees well with the view that imitation has a fundamental

interpersonal role, along with its instrumental role in humans (Meltzoff & Moore, 1992; Nadel, 1986; Uzgiris, 1981; Yando et al., 1978). Even if apes are not the imitative generalists that humans are, our imitation data suggest that they can and do learn through apprenticeship. These views also place model-based factors at the center of the selectivity forces in imitation.

Implications for Experimentation

Our findings offer suggestions for experimental studies of great ape imitative learning. They suggest that using models without attending to their relationships with observers, using very young subjects, demonstrating actions of little potential relevance to imitators or beyond their capabilities, or offering single demonstrations of novel actions to imitators are all methodological choices that can inhibit use of imitation in great apes. For example, experimenters have demonstrated totally novel actions to great ape subjects with models whose relationships with subjects were not clear (Nagell, Olguin, & Tomasello, 1993; Tomasello, Davis-Dasilva, Camak, & Bard, 1987); the imitation they elicited was of low complexity. Our findings on selectivity predict such poor performance because such conditions may inhibit, not motivate, imitation in great apes. Selectivity factors may account for some of the difficulty experimenters have encountered in eliciting imitative learning in great apes. Greater attention to these factors may lead to greater experimental success.

References

- Antinucci, F. (Ed.). (1989). *Cognitive structures and development in nonhuman primates*. Hillsdale, NJ: Erlbaum.
- Aronfreed, J. (1969). The problem of imitation. In L. P. Lipsitt & H. W. Reese (Eds.), *Advances in child development and behavior* (Vol. 4, pp. 201–319). New York: Academic Press.
- Bandura, A. (1971). Analysis of modelling processes. In A. Bandura (Ed.), *Psychological modelling* (pp. 1–62). Chicago: Aldine-Atherton.
- Bandura, A. (1977). *Social learning theory*. Englewood Cliffs, NJ: Prentice-Hall.
- Bates, E. (1979). *The emergence of symbols: Cognition and communication in infancy*. New York: Academic Press.
- Boesch, C. (1992). Imitation as a measure of attribution. *Behavioral and Brain Sciences*, 15, 149.
- Byrne, R. W., & Whiten, A. (Eds.). (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford, United Kingdom: Clarendon Press.
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Through the mind of another species*. Chicago: University of Chicago Press.
- Custance, D. (1992, August). The cognitive mechanisms underlying the development of self-recognition and imitation: A comparative approach. In K. A. Bard, S. T. Parker, & S. Boysen (Chairs), *Comparative developmental approaches to the study of self-recognition and imitation*. Symposium conducted at the XIVth Congress of the International Primatological Society, Strasbourg, France.
- Dumas, C., & Doré, F. Y. (1986). *Intelligence animale: Recherches Piagetiennes* [Animal intelligence: Piagetian studies]. Sillery, Quebec, Canada: Presses de l'Université de Montréal.
- Flanders, J. P. (1968). A review of research on imitative behavior. *Psychological Bulletin*, 69, 316–337.
- Freud, S. (1964). New introductory lectures on psycho-analysis. In J. Strachey (Ed. and Trans.), *The standard edition of the complete psychological works of Sigmund Freud* (Vol. 22). London: Hogarth Press. (Original work published 1933)
- Galdikas, B. M. F. (1979). Orangutan adaptation at Tanjung Puting Reserve: Mating and ecology. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 197–233). Menlo Park, CA: Benjamin/Cummings.
- Galdikas, B. M. F. (1982). Orangutan tool-use at Tanjung Puting Reserve, central Indonesian Borneo (Kalimantan Tengah). *Journal of Human Evolution*, 10, 19–33.
- Galdikas, B. M. F. (1985). Orangutan sociality at Tanjung Puting. *American Journal of Primatology*, 9, 101–119.
- Galdikas, B. M. F., & Vasey, P. (1992). Why are orangutans so smart? Ecological and social hypotheses. In F. D. Burton (Ed.), *Social processes and mental abilities in nonhuman primates* (pp. 183–224). Lewiston, NY: Edward Mellon Press.
- Galef, B. G., Jr. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In T. R. Zentall & B. G. Galef, Jr. (Eds.), *Social learning* (pp. 3–28). Hillsdale, NJ: Erlbaum.
- Galef, B. G., Jr. (1992). The question of animal culture. *Human Nature*, 3, 157–178.
- Hall, K. R. L. (1968). Social learning in monkeys. In P. Jay (Ed.), *Primates: Studies in adaptation and variability* (pp. 383–397). New York: Holt, Rinehart & Winston.
- Harlow, H. F., & Harlow, M. K. (1965). The affectional systems. In A. Schrier, H. Harlow, & F. Stollnitz (Eds.), *Behavior of non-human primates* (Vol. 2, pp. 287–334). New York: Academic Press.
- Hartup, W. W., & Coates, B. (1970). The role of imitation in childhood socialization. In R. A. Hoppe, G. A. Milton, & E. C. Himmel (Eds.), *Early experiences and the process of socialization* (pp. 109–142). New York: Academic Press.
- Hayes, K. J., & Hayes, C. (1952). Imitation in a home-reared chimpanzee. *Journal of Comparative and Physiological Psychology*, 45, 450–459.
- Hinde, R. A. (1979). *Towards understanding relationships*. London: Academic Press.
- Huffman, M. A. (1984). Stone play of *Macaca fuscata* in Arashiyama B troop: Transmission of a non-adaptive behavior. *Journal of Human Evolution*, 13, 725–735.
- Kawai, M. (1975). Precultural behavior of the Japanese monkey. In G. Kurth, X. Braunschweig, I. Eibl-Eibesfeldt, & X. Percha (Eds.), *Homination and behavior* (pp. 33–35). Stuttgart, FRG: Gustav Fischer Verlag.
- Kohler, W. (1927). *The mentality of apes*. London: Routledge & Kegan Paul.
- Masur, E. F. (1988). Infants' imitation of novel and familiar behaviors. In T. R. Zentall & B. G. Galef, Jr. (Eds.), *Social learning* (pp. 301–318). Hillsdale, NJ: Erlbaum.
- Mathieu, M., & Bergeron, G. (1981). Piagetian assessment of cognitive development in chimpanzees (*Pan troglodytes*). In A. B. Chiarelli & R. S. Corruccini (Eds.), *Primate behavior and sociobiology* (pp. 142–147). Berlin: Springer-Verlag.
- McCabe, M. A., & Uzgiris, I. (1983). Effects of model and action on imitation in infancy. *Merrill-Palmer Quarterly*, 29, 69–82.
- Meador, D. M., Rumbaugh, D. A., Pate, J. L., & Bard, K. A. (1987). Learning, problem solving, cognition, and intelligence. In G. Mitchell & J. Erwin (Eds.), *Comparative primate biology*:

- Vol. 2B. *Behavior, cognition, and motivation* (pp. 17–84). New York: Alan R. Liss.
- Meltzoff, A. N. (1988a). The human infant as “*Homo imitans*.” In T. R. Zentall & B. G. Galef, Jr. (Eds.), *Social learning* (pp. 319–342). Hillsdale, NJ: Erlbaum.
- Meltzoff, A. N. (1988b). Imitation, objects, tools and the rudiments of language in human ontogeny. *Human Evolution*, 3, 45–64.
- Meltzoff, A. N. (1988c). Imitation of televised models by infants. *Child Development*, 59, 1221–1229.
- Meltzoff, A. N., & Gopnik, A. (1989). On linking nonverbal imitation, representation, and language learning in the first two years of life. In G. E. Speidel & K. E. Nelson (Eds.), *The many faces of imitation in language learning* (pp. 23–52). New York: Springer-Verlag.
- Meltzoff, A. N., & Moore, M. K. (1992). Early imitation within a functional framework: The importance of person identity, movement, and development. *Infant Behavior and Development*, 15, 479–505.
- Mignault, C. (1985). Transition between sensorimotor and symbolic activities in nursery-reared chimpanzees (*Pan troglodytes*). *Journal of Human Evolution*, 14, 747–757.
- Miles, H. L. (1990). The cognitive foundations for reference in a signing chimpanzee. In S. T. Parker & K. R. Gibson (Eds.), *“Language” and intelligence in monkeys and apes* (pp. 511–539). New York: Cambridge University Press.
- Miles, H. L., Mitchell, R. W., & Harper, S. E. (1992, August). *Imitation and self-awareness in a signing orangutan*. Paper presented at the XIVth Congress of the International Primatological Society, Strasbourg, France.
- Mitchell, R. W. (1987). A comparative–developmental approach to understanding imitation. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology* (Vol. 7, pp. 183–215). New York: Plenum Press.
- Mitchell, R. W. (1993). Kinesthetic–visual matching, perspective-taking and reflective self-awareness in cultural learning. *Behavioral and Brain Sciences*, 16, 530–531.
- Mitchell, R. W. (1994). The evolution of primate cognition: Simulation, self-knowledge, and knowledge of other minds. In D. Quiatt & J. Itani (Eds.), *Hominid culture in primate perspective* (pp. 177–232). Denver: University Press of Colorado.
- Nadel, J. (1986). *Imitation et communication entre jeunes enfants* [Imitation and communication between young children]. Paris: Presses Universitaires de France.
- Nadel, J., Baudonniere, P.-M., & Fontaine, M. (1988). Imitation et communication au cours de la troisième année [Imitation and communication during the third year]. *Psychologie Française*, 33, 45–50.
- Nagell, K., Olguin, K., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, 107, 174–186.
- Nishida, T. (1986). Local traditions and cultural transmission. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 462–474). Chicago: University of Chicago Press.
- Pallaud, B. (1988). L’imitation chez l’animal [Imitation in animals]. *Psychologie Française*, 33, 51–56.
- Parker, S. T. (1992, August). *Imitation as an adaptation for apprenticeship in foraging and feeding*. Paper presented at the XIVth Congress of the International Primatological Society, Strasbourg, France.
- Pepperberg, I. M. (1988). The importance of social interactions and observation in the acquisition of communicative competence: Possible parallels between avian and human learning. In T. R. Zentall & B. G. Galef, Jr. (Eds.), *Social learning* (pp. 279–300). Hillsdale, NJ: Erlbaum.
- Piaget, J. (1952). *The origins of intelligence in children* (M. Cook, Trans.). New York: Norton.
- Piaget, J. (1954). *The construction of reality in children* (M. Cook, Trans.). New York: Basic Books.
- Piaget, J. (1962). *Play, dreams and imitation in childhood* (C. Gattegno & F. M. Hodgson, Trans.). New York: Norton.
- Plooi, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gesture, and symbol: The emergence of language* (pp. 111–131). London: Academic Press.
- Ratner, N. B. (1989). Atypical language development. In J. Berko-Gleason (Ed.), *The development of language* (2nd ed., pp. 369–406). Columbus, OH: Merrill.
- Russon, A. E. (1990). The development of peer social interaction in infant chimpanzees: Comparative social, Piagetian, and brain perspectives. In S. T. Parker & K. R. Gibson (Eds.), *“Language” and intelligence in monkeys and apes* (pp. 379–419). New York: Cambridge University Press.
- Russon, A. E., & Galdikas, B. M. F. (1993). Imitation in free-ranging rehabilitant orangutans. *Journal of Comparative Psychology*, 107, 147–161.
- Russon, A. E., & Waite, B. E. (1991). Patterns of dominance and imitation in an infant peer group. *Ethology and Sociobiology*, 12, 55–73.
- Smuts, B. B. (1987). Sexual competition and mate choice. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 385–399). Chicago: University of Chicago Press.
- Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (Eds.). (1987). *Primate societies*. Chicago: University of Chicago Press.
- Snow, C. E. (1981). Saying it again: The role of expanded and deferred imitations in language acquisition. In K. E. Nelson (Ed.), *Children’s language* (Vol. 4, pp. 29–58). Hillsdale, NJ: Erlbaum.
- Speidel, G. E., & Nelson, K. E. (Eds.). (1989). *The many faces of imitation in language learning*. New York: Springer-Verlag.
- te Boekhorst, I. J. A., & Hogeweg, P. (1992, August). *Effect of tree size on travel band formation in orangutans*. Paper presented at the XIVth Congress of the International Primatological Society, Strasbourg, France.
- Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution*, 2, 175–183.
- Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, 16, 495–552.
- Tuttle, R. H. (1986). *Apes of the world*. Park Ridge, NJ: Noyes Publications.
- Uzgiris, I. (1981). Two functions of imitation during infancy. *International Journal of Behavioral Development*, 4, 1–12.
- Valentine, C. W. (1930). The psychology of imitation with special reference to early childhood. *British Journal of Psychology*, 21, 105–132.
- Visalberghi, E. (1992, August). *The acquisition of a tool-using behavior in several primate species*. Paper presented at the XIVth Congress of the International Primatological Society, Strasbourg, France.
- Visalberghi, E., & Fragaszy, D. M. (1990). Do monkeys ape? In S. T. Parker & K. R. Gibson (Eds.), *“Language” and intelligence in monkeys and apes* (pp. 247–273). New York: Cambridge University Press.

- Walters, J. R., & Seyfarth, R. M. (1987). Conflict and cooperation. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 306-317). Chicago: University of Chicago Press.
- Werner, N. (1948). *Comparative psychology of mental development*. New York: International Universities Press.
- Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer, & M. Milinski (Eds.), *Advances in the study of behavior* (Vol. 21, pp. 239-283). New York: Academic Press.
- Yando, R., Seitz, V., & Zigler, E. (1978). *Imitation: A developmental perspective*. Hillsdale, NJ: Erlbaum.
- Zentall, T. R., & Galef, B. G., Jr. (Eds.). (1988). *Social learning: Psychological and biological perspectives*. Hillsdale, NJ: Erlbaum.

Received March 29, 1993

Revision received December 10, 1993

Accepted January 24, 1994 ■

Acknowledgment of Ad Hoc Reviewers

The Editor thanks the following persons for reviewing manuscripts. (Numbers in parentheses indicate assistance with more than one manuscript.)

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