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12. If either species of oak suffered greater physiological stress where it is rare, it might be expected to show a lower mean, or a greater coefficient of variation, or both, in the site where it is less abundant. Defoliation could also cause differences in growth rings [P. A. Morrow and V. C. LaMarche, Jr., *Science* **201**, 1244 (1978)], but it might be expected to cause a higher coefficient of variation for both species in the site dominated by scarlet oaks than in the site dominated by white oaks because exceptionally high populations of *Alsophila* occur only in the former site. Because no site-related differences in growth were found for either species, the growth ring data shed no light on either hypothesis.
13. We are grateful to R. Weiss for assistance in the field and to members of the informal plant-herbivore study group at Stony Brook for helpful comments. Supported by NSF grant DEB 76-20232. This is contribution 209 of the Program in Ecology and Evolution of the State University of New York at Stony Brook.

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Abstract. *Three chimpanzees learned to label three edibles as "foods" and three inedibles as "tools." Two chimpanzees could then similarly categorize numerous objects during blind trial 1 tests when shown only objects' names. The language-like skills of the chimpanzee who failed (Lana) illustrates that apes can use symbols in ways that emulate human usage without comprehending their representational function.*

When chimpanzees use signs or lexigrams which they have been taught by human trainers, the question arises as to whether they know what these symbols represent or whether they simply learn contextually appropriate usages, as we have already suggested (*1*). We report on our effort to determine whether or not the abstract symbols used by our chimpanzee subjects were functioning at a representational level. We trained the subjects to label the names of three inedibles (stick, key, and money) as tools, and the names of three edibles (beancake, orange, and bread) as foods. We then presented these chimpanzees with the names of 17 other foods and tools and asked them to categorize these additional names as foods or tools. In order for the chimpanzees to make a categorical judgment of this sort on the first trial, it was necessary for them to recall some representation of the actual object, since the specific names of these foods and tools had never been paired with categorical labels.

Before this study was begun, each of the three chimpanzee subjects—Lana (8 years), Sherman (5 years), and Austin (4 years)—had extensive experience with the Yerkes computer-based language training system (*2*). The original training of these items was similar for Sherman and Austin, but differed for Lana (Table 1). Lana's initial training emphasized symbol sequencing and object naming, while Sherman's and Austin's training emphasized the pragmatic and semantic functions of symbols, and communication between chimpanzees (*2*, *3*). In order to provide Lana with a vocabulary and experience more comparable to that of Sherman and Austin, we introduced to her the eight tools used by Sherman and Austin.

It was necessary for Sherman and Austin to learn to ask for tools which they needed to use before they were able to label these tools divorced from the context of usage (*2*). Lana, by contrast, readily learned to label all the tools long before she could accurately request them as needed. Such disjoint abilities suggest that the chimpanzee's capacity to produce a symbol when an object is desired (for example, to say "key" when a key is needed to open a padlock) may not necessarily be related to the ability to produce the same symbol when asked to name a visible object (for example, to say "key" when the experimenter holds up a key). In the case of Sherman and Austin, the demonstration of an object's function helped them to recall its name. If, for example, they could not recall the name for "key" when it was held up, using a key to unlock a padlock would enable them to recall its name. This was not true of Lana. It seemed that Sherman's and Austin's training led them to link the use of an object and the label of an object together. For Lana, the two skills appeared to remain separate. Before instituting training the categorical classifications of "food" and tool," we conducted blind tests of the abilities of all three animals to use the 11 specific food and tool names which would be the focus of our study. All three chimpanzees scored 100 percent during blind tests of request skills, labeling skills, and receptive skills.

Sorting objects. Categorical sorting of foods and tools was begun by requiring the animals to sort three foods (orange, bread, and beancake) into one bin, and three tools (key, money, and stick) into another. None of the foods or tools resembled each other physically, thereby precluding a match-to-sample response. The dimension for sorting was functional; the foods could be eaten and the tools could not. Training was facilitated in all three cases by emphasis on the functional distinction, which suggested that the animals might be classifying these items along the edible-inedible dimension (Fig. 1).

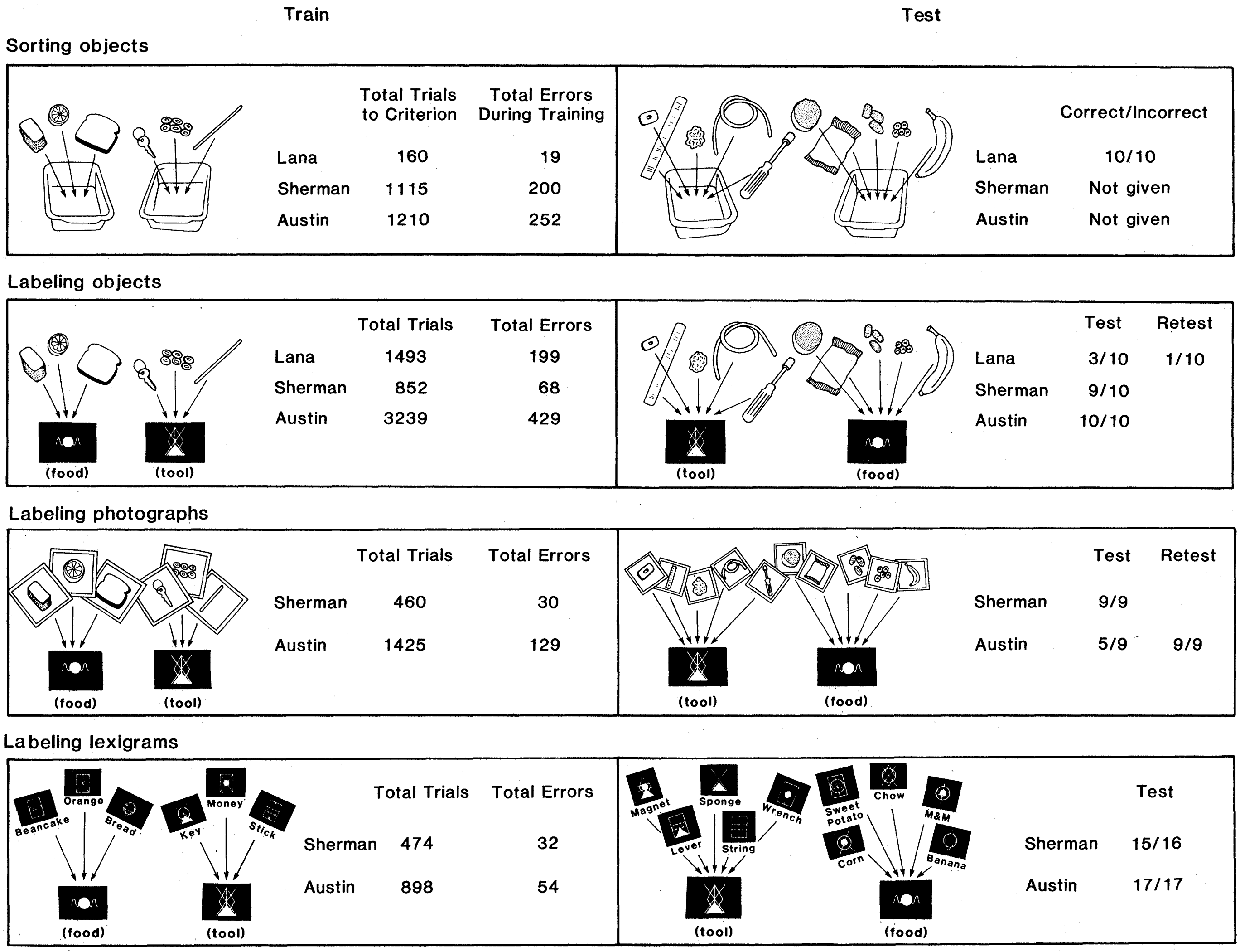
Labeling objects. When the animals reached a sorting criterion of 90 percent or better across 60 trials, we introduced the lexigrams for food and tool. The chimpanzees' task was to sort a food or a tool into the proper bin and then to select the lexigram representing either food or tool. Once the chimpanzees reliably selected a lexigram after sorting each object, the bins were removed and the task then was to label each of the six training objects as they were held up by the experimenter.

Training in this phase continued until the animals met all of the following criteria: (i) ability to label all training items correctly without eating the food or using the tool; (ii) ability to label all training items correctly on trial 1, after food and tool lexigrams were relocated on the keyboard; and (iii) ability to label all training items correctly under the conditions listed above for two consecutive sessions of more than 25 trials at 90 percent (or greater) correct.

It would be possible for the animals to learn the above tasks in either of two ways: (i) by forming a specific association between each item and the appropriate bin or lexigram for that item; or (ii) by formulating a classification rule, "This bin is for items that I eat and the other bin is for items that I do not eat." If such a concept or rule had emerged, then we would expect that the chimpanzees could use these generic symbols to categorize other items with no additional training. We tested the generalizability of this skill by presenting five additional foods and five additional tools. (The chimpanzees knew the specific lexigrams of each of these ten items.) These items were presented once each, in a random order, interspersed with trials of training items. Prior to the presentation of the first novel item, the animals had to respond correctly to the training items for 20 consecutive trials. During the entire test, the experimenter remained outside the room. The chimpanzee approached the door, looked at the object displayed by the experimenter, then reentered the room and labeled the item on the keyboard. The experimenter could see neither the keyboard nor the chimpanzee once the chimpanzee left the doorway. The specific lexigram names of the ten novel exemplars were deactivated during the test, but the other 50 keys remained on. Austin correctly categorized each of the ten novel items on trial 1. Sherman correctly categorized each of the ten novel items except sponge, the tool which he occasionally eats portions of as he uses it. Lana correctly identified only three items. It appeared that Sherman and Austin had acquired a concept of "food" and "tool" that was functionally based, generalizable, and symbolically encoded. Lana had not; she had learned only the specific paired-associative responses required by her training. To be sure, we retested Lana with the novel items to determine whether or not the first test might have been in error. On this second blind test, Lana correctly identified only one novel item. We then returned to the initial sorting procedure. Following the same pretest criterion (20 correct consecutive trials), we began to intersperse randomly the ten novel items used in the two tests described above. This test was also given blind. Lana sorted all ten novel items correctly on trial 1, thereby indicating that her failure on the earlier tests had not been due to an inability to conceptualize the functional relation between the foods and the tools. Rather, it had been due to an inability to encode symbolically this perceived relationship.

To determine whether or not previous training experiences with these particular foods and tools could account for Sherman's and Austin's categorical abilities, we presented them with 28 items (14 foods and 14 tools) with which they were generally familiar, but which had not been used in any specific training paradigm and were, therefore, not associated with lexigrams. Sherman correctly categorized 24 of these 28 items and Austin correctly categorized 25 of 28 items. All but one of the errors resulted from classifying tools used to prepare food (for example, knife and cutting board, which they often lick) as foods (*4*).

Labeling photographs. During this phase of training, we used the same training foods and tools that were used earlier. We began by taping photographs of these objects to the objects themselves. We then held up the training object and its photograph and asked the chimpanzees to label it. Once the animals were responding confidently, we removed the



Train

Test

Sorting objects

	Total Trials to Criterion	Total Errors During Training
Lana	160	19
Sherman	1115	200
Austin	1210	252

	Correct/Incorrect
Lana	10/10
Sherman	Not given
Austin	Not given

Labeling objects

	Total Trials	Total Errors
Lana	1493	199
Sherman	852	68
Austin	3239	429

	Test	Retest
Lana	3/10	1/10
Sherman	9/10	
Austin	10/10	

Labeling photographs

	Total Trials	Total Errors
Sherman	460	30
Austin	1425	129

	Test	Retest
Sherman	9/9	
Austin	5/9	9/9

Labeling lexigrams

	Total Trials	Total Errors
Sherman	474	32
Austin	898	54

	Test
Sherman	15/16
Austin	17/17

Fig. 1. The animals learned the items on the left and were tested, in a blind setting, with the items on the right. The numbers of trials and total errors are given for training and the number of correct trial 1 selections is given for testing. In the final labeling test, 17 different lexigrams, controlled for physical similarity relative to the categorical lexigrams, were used.

Table 1. Symbol training before the present study began.

Skill	Chimpanzee*
1. Use multiple symbols and sequence all symbol productions	L†
2. Use symbol strings to activate movies and slides and to cause people to move about in space	L
3. Request specific foods	L, S, A
4. Label foods while eating other foods	L, S, A
5. Respond to information about hidden foods provided by the symbolically encoded statements of others	S, A
6. Give foods in response to the symbolically encoded requests of others	S, A
7. Cooperatively divide and share food with another chimpanzee by means of symbols	S, A
8. Symbolically request specific tools and use them to procure food‡	S, A
9. Label objects without using them	L, S, A
10. Label colors of objects	L
11. Give either color or name of object as requested	L
12. Give tools in response to symbolically encoded request of others	S, A
13. Cooperatively request of and give tools to another chimpanzee by means of symbols	S, A

*L, Lana; S, Sherman; and A, Austin. †Lana was taught skills 6, 8, and 12 at the beginning of the study so that her vocabulary and basic request, labeling, and receptive capacities would be similar to those of Sherman and Austin. However, her previous training, which had stressed associative skills, led her to use different learning strategies than had been observed in Sherman and Austin. ‡Although tool lexigrams, as a conceptual class, were initially taught after a number of food lexigrams had already been acquired, many additional specific food and tool names were also acquired during coincident time spans, thereby precluding a possible early and recently acquired distinction between foods and tools.

real objects and continued training, presenting only the photographs. When they again reached the training criterion described earlier, we presented them with novel photographs, under the same test conditions described above (*5*).

Sherman correctly labeled all nine novel photographs (100 percent), while Austin labeled only five novel photographs correctly (55 percent) (Fig. 1). This suggested either that Austin had simply learned specific responses to specific photographs, or that when presented with novel photographs, he had, for some reason, not treated these photographs as representations of real objects.

We readministered the blind novel photographs test, believing that it was possible that Austin had treated all the novel photographs simply as pieces of plastic (each photograph is encased in 1/4-inch transparent plastic) and had guessed on these trials instead of looking closely at the object depicted in the photograph in order to make a correct categorical response. The plastic casing surrounding the photographs frequently reflected back enough light to render the enclosed picture invisible at certain angles. Sherman accommodated for this by moving his head to change his line of regard. Austin did not. As Austin came to the door of the room, we encouraged him to look carefully and slowly at each picture and we rotated the angle of the photograph. Under these conditions, Austin correctly identified nine of the nine novel photographs.

Labeling lexigrams. The final phase of the study is the most critical of all, for it alone is unequivocably a test of the referential value of the symbols. This test included the following critical constraints: (i) it required a completely novel response, one never before given by the chimpanzee or by the experimenter when working with the chimpanzee; (ii) it was administered under blind conditions; and (iii) it required that the chimpanzee use one symbol to classify another, thereby forcing him to refer cognitively to the specific referent of one symbol and, based on the recalled characteristics of that referent, assign it to a class of functionally related items. He then had to recall the symbol that has been used to reference that functional relationship in the past and employ it.

Training in this phase began as it had in the previous ones. We returned to the original group of training foods and tools. Initially, the lexigrams for these items were taped to photographs of the items, again to provide a bridge between the levels of stimuli presented. The photographs were then removed and the chimpanzees were shown only the printed lexigrams.

Once the chimpanzees had again reached the training criterion, they were presented with test lexigrams. This test was also administered with the experimenter out of the room, and again novel items were interspersed randomly with training items. It is to be emphasized that prior to this test, these chimpanzees had never been asked to make a categorical assessment of these symbols. In most cases, they had not even been requested to make a categorical assessment of the real objects which these symbols represented. Sherman categorized the novel lexigrams correctly on 15 of 16 trial 1 presentations, and Austin categorized them correctly on 17 of 17 trial 1 presentations (Fig. 1) (*6*). The dimension of lexigram physical similarity was controlled so that if Sherman and Austin chose on that basis they would have been correct only half the time. Between them, only a single error was made on the entire test and that error (sponge was called a food by Sherman) was one which would not have been predicted on the basis of physical similarity (*7, 8*).

Conclusion. The ability to organize sensory input along a dimension of functional similarity does not necessarily give rise to a corresponding ability to organize this information similarly at a symbolic level, as Lana's inability to transfer the food and tool labels to novel exemplars indicates. We suggest that Sherman and Austin were able to treat "food" and "tool" as representational labels, and to expand the use of these labels to novel exemplars because of training which encouraged the appearance of functional symbolic communication between chimpanzees.

Our study offers a paradigm which makes possible, for the first time, an unequivocal determination of the presence or absence of representational symbolic function. We seriously question whether or not any other apes have reached the level of symbolic functioning achieved by Sherman and Austin. Clearly, training of other apes (for example, Nim, Washoe, and Sarah) has emphasized only the skills of associative labeling and combining, and these skills alone do not require either semantic comprehension or representational symbolic ability (*9*).

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3. For Lana, the background color of the symbol originally indicated word class. However, all of the words used in the above study were assigned a single background color to prevent confounding. For Sherman and Austin, background color never indicated word class.
4. Tools included scrub brush, shovel, screwdriver, juice squeezer, ball bearing, locking pin, spoon, saucepan, hammer, sink stopper, knife, scissors, cutting board, and can opener. Foods included ice cube, peanut, celery, peanut butter, jelly, raisins, cabbage, grapefruit, cucumber, chim crackers, turnips, white potatoes, lemon, and cheese.
5. Only Sherman and Austin were continued in this later phase, since Lana's inability to encode referential relationships symbolically implied that it would be fruitless to move from real objects to photographs, in her case.
6. Because the Yerkish symbols are arbitrarily assigned to all objects, it is not possible to decide, simply by looking at the symbol, whether it represents a food or a tool. Austin was given one more than Sherman because one of the test lexigrams was to be used with Sherman in another study.
7. It is possible to unintentionally cue chimpanzees by the way in which one holds objects, touches the chimpanzees, looks at the stimuli, and so forth. In order to make certain that such cuing was not occurring, we reran the final phase of the study with Austin and Sherman. During this retest (i) the experimenter did not know which lexigram the chimpanzee was viewing, and (ii) lexigram presentation was completely random; any lexigram could be followed by itself or by any other lexigram any number of times. No constraints were placed on the number of consecutive food and tool responses. Sherman was correct on 68 of 70 trials, and Austin was correct on 65 of 70 trials.
8. Individuals who are interested in seeing the work reported in this report may purchase a color video cassette from the authors.
9. For more detailed account of this study, see E. S. Savage-Rumbaugh, *Ann. N.Y. Acad. Sci.*, in press.
10. Supported by grants from the National Institute of Child Health and Human Development (HD-06016) and from the Division of Research Resources, National Institutes of Health (RR-00165).

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Nutmeg Dispersal by Tropical Birds

Abstract. *Frugivorous birds preferentially remove fruits from Panamanian* Virola *trees where the ratio of edible aril to indigestible seed is high. A negative correlation between the proportion of the crop removed and mean seed size explains 59 percent of the variance in removal, suggesting that birds minimize ingestion of useless bulk.*

Many tropical trees bear fruits that attract animals (*1*), and many tropical vertebrates consume fruit and either disperse or destroy seeds (*2*). Relationships between frugivores and plants are of general interest in tropical ecology because the mortality of seeds and seedlings under parent trees is density-dependent (*3*) and because dispersal by animals results in a more even distribution of adult trees than passive dissemination by gravity or wind (*4*). Factors promoting efficient seed removal by animals are poorly understood. Synthetic treatments have had to rely upon anecdotal accounts of animal visitation at plant species that vary widely in fruit structure, nutritional reward, and crop size (*2, 3, 5-7*). No one has shown that differences in fruit quality within a population influence seed removal. Here we report dramatic differences in the proportions of seeds removed from individual *Virola surinamensis* (Rol.) Warb. (Myristicaceae) trees that vary in mean aril (pulp) and seed weights. Frugivores preferentially remove fruits from trees producing small seeds; small seed size is generally associated with a high ratio of edible aril to indigestible seed. Partial correlation analysis uniquely distinguishes two attributes of fruits: dispersibility and seed size likely to influence seedling survival.

Virola surinamensis is a canopy tree of the mature wet forest of Barro Colorado Island, Panamá (*8*). Between 20 May and 7 September 1979, 17 trees produced 214 to 10,412 mature fruits (median 2,082) (*9*). Golf ball-sized capsules opened in early morning and midmorning to expose the unit of dispersal, a single seed 2 cm long surrounded by a brilliant red aril (Fig. 1). The hard seed tastes bitter; 15 percent of its 2.0 ± 0.4 g (dry weight) consists of tannins, which inhibit protein activity when ingested by animals (*10, 11*). In contrast, less than 3 percent of the 0.9 ± 0.1 g (dry weight) of the aril consists of tannins. The arils are among the most nutritious known (*12*); edible components include 9.2 ± 1.5 percent usable carbohydrate, 63.1 ± 14.0 percent fat, and 2.5 ± 0.7 percent proteins, leading to an overall energetic reward of 6.5 ± 0.9 kcal per aril (*10*). Six birds swallow the aril and seed and regurgitate the seed in viable condition; one monkey passes intact seeds through the digestive tract (Table 1) (*13*). With the exception of the tityra, a fruit thief that eats arils without ingesting seeds, all birds attempt to swallow all arillate seeds encountered. Selection by birds is of trees, not of fruits within trees. Monkeys actively smell and reject fruits within a tree crown, indicating that their choice is based on a chemical cue (*14*).

Unless fruit thieves intervene (*15*), specialized frugivores should consistently remove fruits with highly nutritious rewards (*2, 5, 16*). The predominance of a small set of highly frugivorous birds meets the first expectation, and the mean level of seed removal of 62 percent (± 19 percent) meets the prediction of efficient dispersal of nutritious fruits. However, proportions of seeds removed from individual trees range from 13 to 91 percent (*9*). Such variation could occur (i) because the quantity of fruit produced influences removal success (*5, 16*), (ii) because nutritional quality of the arils varies from tree to tree, or (iii) because plants offer different expectations of edible reward and indigestible bulk to birds that must swallow fruits (*17*). Large-seeded fruits burden birds with excess weight, and reduce feeding efficiency by filling the crops of the birds with useless bulk (*18*).

The first hypothesis was tested by regressing the proportion of the seeds removed against crop size. Neither linear nor second-order polynomial fits were significant ($P > .25$). Rewards are apparently sufficient to ensure that birds visit small trees and deplete fruits at large ones; variance in crop depletion must be attributable to factors other than crop size.

The second hypothesis presumes that

Fig. 1. A *Virola surinamensis* fruit as presented to birds. The unit of dispersal is a single inedible seed surrounded by an edible aril of brilliant red coloration. Seeds average 20 mm in length by 16 mm in width; arils are 1 mm thick.