RESEARCH ARTICLE

Flexibility and Persistence of Chimpanzee (*Pan Troglodytes*) Foraging Behavior in a Captive Environment

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As a result of environmental variability, animals may be confronted with uncertainty surrounding the presence of, or accessibility to, food resources at a given location or time. While individuals can rely on personal experience to manage this variability, the behavior of members of an individual's social group can also provide information regarding the availability or location of a food resource. The purpose of the present study was to measure how captive chimpanzees individually and collectively adjust their foraging strategies at an artificial termite mound, as the availability of resources provided by the mound varied over a number of weeks. As predicted, fishing activity at the mound was related to resource availability. However, chimpanzees continued to fish at unbaited locations on the days and weeks after a location had last contained food. Consistent with previous studies, our findings show that chimpanzees do not completely abandon previously learned habits despite learning individually and/or socially that the habit is no longer effective. Am. J. Primatol. 74:661–668, 2012.   © 2012 Wiley Periodicals, Inc.

Key words: chimpanzee; termite fishing; learning; optimal foraging; social influences

INTRODUCTION

The physical environment in which an animal lives is inherently variable. One result of environmental variability is that animals may be confronted with uncertainty surrounding the presence of food resources at a given location or time. For chimpanzees (*Pan troglodytes* spp.), this includes seasonal changes in availability of, or accessibility to, preferred foods including termites and several fruits [e.g. Moscovice et al., 2007; Uehara, 1982; Wrangham, 1977; Yamagiwa et al., 2008]. As a result, a foraging or food extraction strategy that is successful on one day may not result in success the next. Natural selection thus favors those individuals that can efficiently adjust their behavior in response to environmental variability.

Behavioral flexibility in response to uncertainty and environmental variability can result from a variety of processes at both the individual and group level. Individuals acquire personal or private information through direct interactions (e.g. trial and error learning) with the environment. Social animals, including chimpanzees, also acquire information by monitoring the behavior of conspecifics [Bonnie & Earley, 2007; Danchin et al., 2004; Laland, 2004; Laland et al., 2011; Thornton & Clutton-Brock, 2011]. By attending to the success (or lack of success) of others, individuals and the groups they belong to can gain additional information regarding resource quality and availability [Bandura, 1977; Valone & Templeton, 2002]. Thus, living in a social group affords an individual the opportunity to acquire information about a variable environment both individually and through the observation of others [Rendell et al., 2011]. While recent theoretical and empirical research has focused on the environmental and social conditions in which individuals should rely on individually acquired vs. socially acquired information [Kendal et al., 2005], our study was not designed to compare these two methods of acquiring information against each other. Rather, in order to focus on naturalistic observations of foraging strategies in a variable environment, we merely acknowledge and appreciate that both may be in play as chimpanzees cope with resource variability in both captive and natural settings.

The ability to acquire new foraging strategies is certainly an important aspect of adjusting behavior

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in response to environmental variability, but so too is the ability to abandon those strategies that are no longer successful. Reversal learning and transfer of training paradigms have been used extensively to test if and how individuals respond when the payoff associated with objects or stimuli can change over time. Chimpanzees, as well as many other animals, typically have little difficulty with this type of task whether information regarding alternative choices is acquired individually [Nissen et al., 1938; Schusterman, 1962], or through the observation of a conspecific partner [Martin et al., 2011]. In addition, Rumbaugh and colleagues have reported that while apes outperform other primates on a discrimination reversal task, the accuracy with which they do so, as measured by the transfer index, may depend on an individual's recent experience with the rewarded stimuli [Rumbaugh, 1970; Rumbaugh & Gill, 1973]. As a result, when determining how individuals respond to environmental variability, it may be important to consider an individual's previous reward history in that environment.

Several recent studies provide evidence that both captive and wild chimpanzees show a remarkable persistence of previously acquired habits related to the acquisition of food [Bonnie, 2007; Hanus et al., 2011; Hrubesch et al., 2009]. However, chimpanzees have recently been shown to be willing to forego an established individual food preference in favor of a group level preference for a strategy resulting in a less preferred food [Hopper et al., 2011]. Importantly, these findings each involve individuals acting within a social context with access to both individual and social information. In one study, a group of captive chimpanzees repeatedly returned plastic tokens to a location that had previously resulted in a reward, even though that behavior had ceased to be rewarded [Bonnie, 2007]. Chimpanzees failed to adapt their behavior despite repeated feedback regarding the success of their personal strategy as well as the strategies used by other members of their social group. On multiple occasions, an individual returned a token to previously rewarded location and received no reward, despite observing another chimpanzee being rewarded for returning a token to a nearby location just moments before. This finding is similar to those reported by others including Hrubesch et al. [2009], Marshall-Pescini and Whiten [2008], and Price et al. [2009] in which chimpanzees showed a marked persistence for initially adopted strategies over other, usually more efficient, techniques. Together, these findings may also explain, in part, the limited evidence for cumulative culture among chimpanzees.

Although these previous findings [Bonnie, 2007; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Price et al., 2009] suggest that chimpanzees are less flexible (and surprisingly persistent) with respect to strategies surrounding the acquisition of food, several methodological factors may account for the reported results. Many of these studies, as well as Hopper et al. [2011], involved experimentally contrived tasks not meant to replicate precisely objects or behaviors, other than food acquisition, that chimpanzees would likely encounter in the wild. As a result, these previous findings are limited in ecological validity. Secondly, both require replication to determine if chimpanzees at other institutions react in a similar way, or if the previous results may be accounted for by individual or group differences in housing, husbandry, or experimental history [Rumbaugh, 1970; Rumbaugh & Gill, 1973]. Finally, social dynamics are known to influence learning in social contexts [Bonnie & de Waal, 2009; Coussi-Korbel & Fragaszy, 1995; Drea & Wallen, 1999; Lonsdorf & Bonnie, 2010], so continued research on learning in social groups is warranted.

The purpose of the present study was to expand upon earlier work to determine if and how a group of captive chimpanzees adjust their foraging strategy at an ecologically relevant artificial termite mound as the availability of resources provided by the mound varied over a number of weeks. In particular, we were interested in recording fishing behaviors at the mound as chimpanzees had access to a food reward at a changing number of locations. This study builds specifically on the research of Bonnie [2007] and Hrubesch et al. [2009] in order to further explore how chimpanzees adapt to variation in food availability.

This study was designed to test the following hypotheses at both the individual and group levels: (1) fishing activity at the mound would be influenced by resource availability; (2) chimpanzees would learn to avoid fishing at hole locations that do not contain food, as measured both by an immediate decrease in and persistent absence of fishing at that location; and (3) likewise, chimpanzees would learn when locations are later replenished, with a similar increase in fishing activity at the hole location with time.

METHOD

Subjects and Housing

Subjects were a group of seven, captive-born chimpanzees (four females and three males) housed at the Regenstein Center for African Apes (RCAA) at Lincoln Park Zoo, Chicago, IL (Table I). The chimpanzees in this study were cared for in facilities complying with United States Department of Agriculture (USDA), Association of Zoos and Aquariums (AZA), and American Society of Primatologists (ASP) principles and standards, and voluntarily participated in all research activities.

The exhibit has an indoor/outdoor design; the indoor exhibit measures 124.5 m^2 and the outdoor exhibit measures 613.2 m^2. Access to the outdoor yard

Subject	Sex	Date of birth (mm/dd/yyyy)	Relatedness
S1	Male (alpha)	11/30/1990	Unrelated
S2	Female	08/18/1984	Mother of S7
S3	Female	09/02/1990	Mother of S5
S4	Female	01/20/1994	Unrelated
S5	Female	09/24/1999	Daughter of S3
S6	Male	02/09/1999	Unrelated
S7	Male	01/22/2000	Son of S2

was temperature dependent, and during the course of the study, the group had outdoor access at varying times depending on the outdoor weather conditions. The indoor exhibit contains climbing structures of varying heights, deep-mulch bedding, and was visible to the general public during daytime hours. Daily meals of fresh produce and biscuits were scattered through the exhibit twice daily, but never within 1 hr of testing. The testing apparatus, located in the indoor exhibit, was presented to the group as a whole without human intervention or demonstration. No animals were trained to complete the task nor received demonstrations of any part of the task. All subjects had successfully learned the fishing task prior to this study [see Lonsdorf et al., 2009], and no changes to the apparatus have been made since.

Apparatus

The artificial termite mound, located in the indoor portion of the exhibit, is a hollow structure with a concrete crust approximately (274 cm wide × 205 cm tall × 15 cm thick). Eight holes, each approximately 2 cm in diameter, are evenly distributed on the mound to which polyvinyl chloride (PVC) tubes on the interior of the mound can be attached (Fig. 1). Only the exterior of the mound is visible to the apes and chimpanzees have no physical or visual access to the tubes located on the interior of the mound. The chimpanzees used natural vegetation (hay, branches, etc.) as tools to extract a food substance from the tubes.

Procedure

The following procedure was reviewed and approved by the Research Committee at Lincoln Park Zoo, and complied with protocols approved by the zoo and its governing bodies. During the study period from July 28, 2008 to March 20, 2009, data were collected each weekday from 12 to 1 p.m. Before each session, research staff filled PVC tubes with ketchup (532 ml) and keeper staff accessed the interior of the mound to attach the tubes behind each hole lo-cation. Tubes were cleaned thoroughly between sessions. To create a baseline condition, tubes containing ketchup were attached at all eight hole locations as had been done for prior experiments [see Lonsdorf et al., 2009]. Prior to this baseline phase, the apparatus had not been baited regularly for several months, thus the baseline phase also served to reestablish the mound as a regular foraging location. On each of the first ten experimental days following the baseline period, tubes were again attached at all eight locations; seven tubes contained ketchup and one tube (always in the same location) was empty. Chimpanzees could continue to fish at all eight locations throughout the study, but had no visible cues as to the location of tubes containing food and which did not. Although chimpanzees may have used olfactory cues to locate a baited tube, close olfactory investigation of the mound was rarely observed. An additional empty tube was introduced after every 10-day phase until none of the eight tubes contained ketchup.

To determine the location of empty tubes for each subsequent phase, we analyzed subject-location preference, measured by the overall frequency of visits to each hole location, from the previous phase. The most preferred location for each phase was excluded until an empty tube was in place at every hole location. We then reversed our procedure and reintroduced a filled tube at a new location every 10 days, starting with the last hole baited, until all eight holes were baited. Individuals involved in data collection and video coding were blind to the location of tubes with ketchup during each phase.

Analysis

For the duration of each data-collection session research staff entered group-scan information at 1-min point samples for 60 min, noting which individuals were present at the mound, to which hole location each individual was closest, and their activity. Activities were defined as fishing with a tool, licking or modifying a tool, poking at a hole, visual investigation of a hole at a distance less than 1 inch, stealing a tool from another individual, or inactive. A mounted video camera recorded all activity within 1 m of the mound and video was later scored for the frequency and duration of all fishing behaviors using Noldus VideoPro 5.0 (Noldus Information Technology, Wageningen, Netherlands). Fishing was defined as any contact to the bait hole using a tool, poking or prodding the bait hole with fingers or toes, inspecting the mound using visual or olfactory senses, or modifying and/or manipulating a tool. Inter-rater reliability for all individuals involved in behavioral scoring was 0.90 or greater.
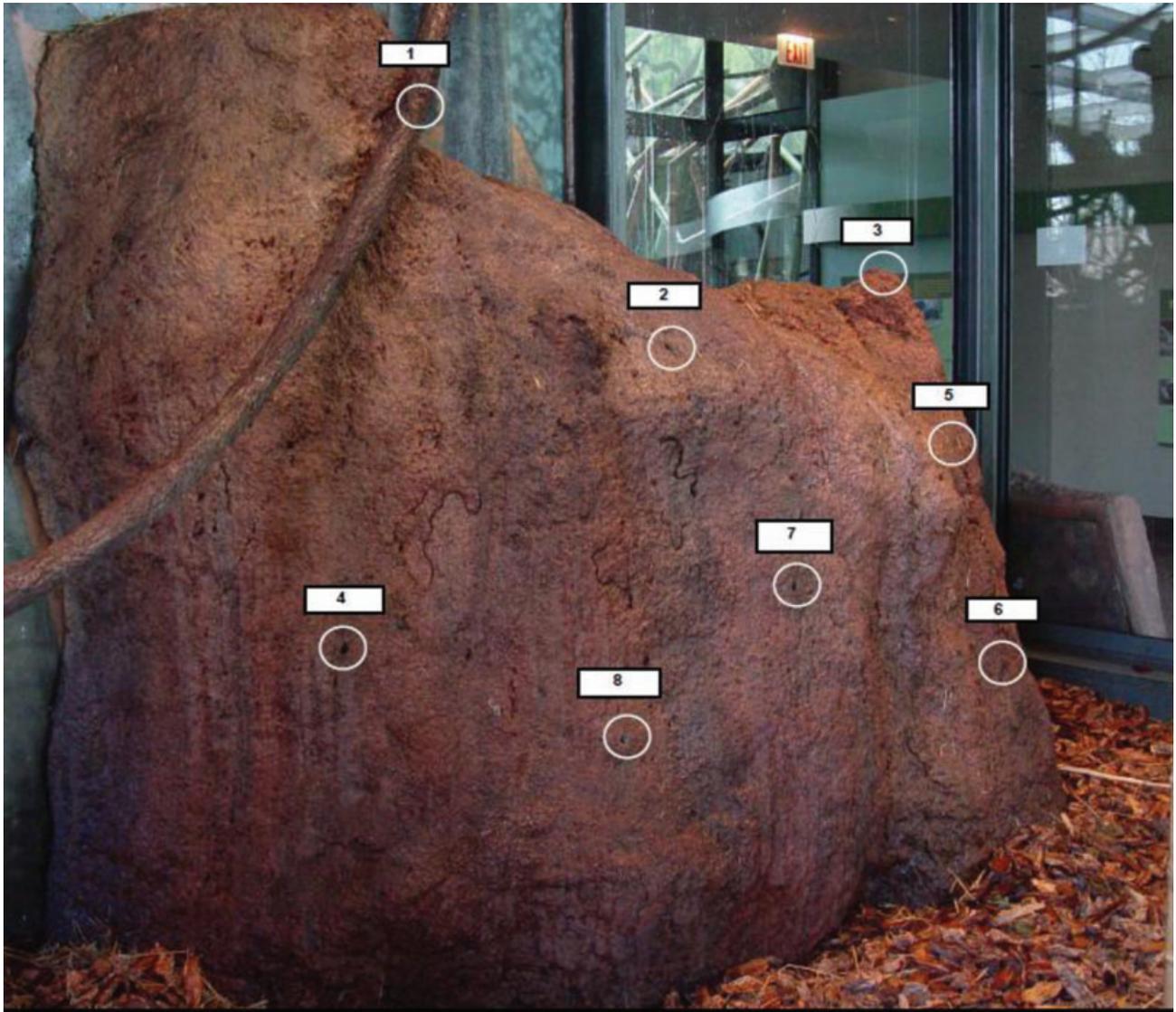
Fig. 1. Artificial termite mound located on exhibit in the Regenstein Center for African Apes at Lincoln Park Zoo. Numbered circles indicate approximate location of a food extraction hole.

RESULTS

We expected that fishing activity at the mound would correlate with resource availability, as defined by the number of hole locations from which ketchup could be obtained. As predicted, as the number of baited hole locations decreased, chimpanzees spent less time engaged in fishing activity at the mound (Fig. 2, days 1–81); likewise, as the number of baited hole locations again increased, chimpanzees spent increasingly more time fishing (Fig. 2, days 82–151). Duration of fishing activity was strongly correlated with the number of baited hole locations for all seven subjects individually (Spearman r = 0.31, 0.37, 0.46, 0.47, 0.52, 0.67, and 0.76, respectively; in all cases $P < 0.001$) and when duration of fishing activity was pooled and analyzed at the group level (Spearman r = 0.78, $P < 0.001$).

To determine whether the chimpanzees would adjust their behavior to avoid fishing at hole locations which no longer contained food (Hypothesis 2), fishing activity at each hole location was compared on the day of and one day prior to when an empty tube was introduced. For this and all subsequent analyses, we used fishing effort, instead of total fishing duration at each location, in order to control for individual variation in total fishing activity in each session. Fishing effort was calculated by dividing the pooled duration of fishing at each unbaited location by total pooled fishing at all locations on each day (e.g. duration at hole 1/[duration at holes
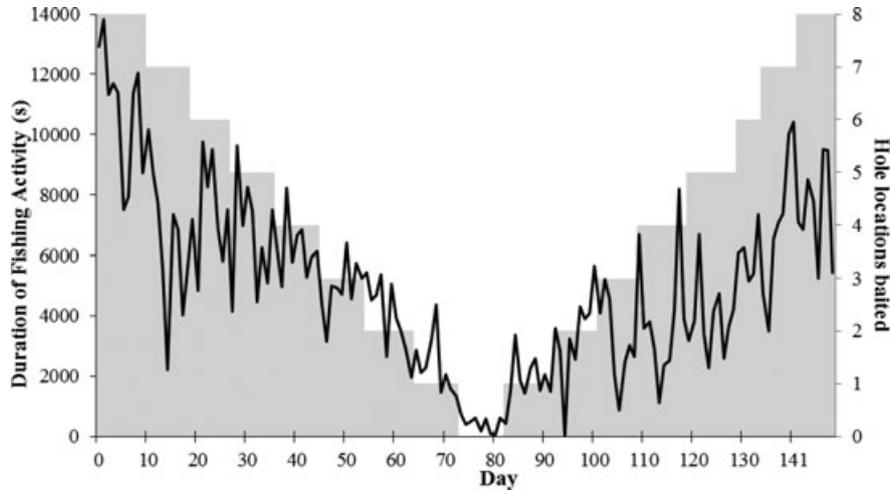
Fig. 2. Average (± SD) number of hole locations fished, **(A)** pooled for all subjects and **(B)** by each subject, by number of baited hole locations. The number of baited hole locations (gray bars) decreased by one approximately every 10 days between days 1 and 82 of testing. Beginning on day 83, the number of baited hole locations then increased by one approximately every 10 days through the end of the study.
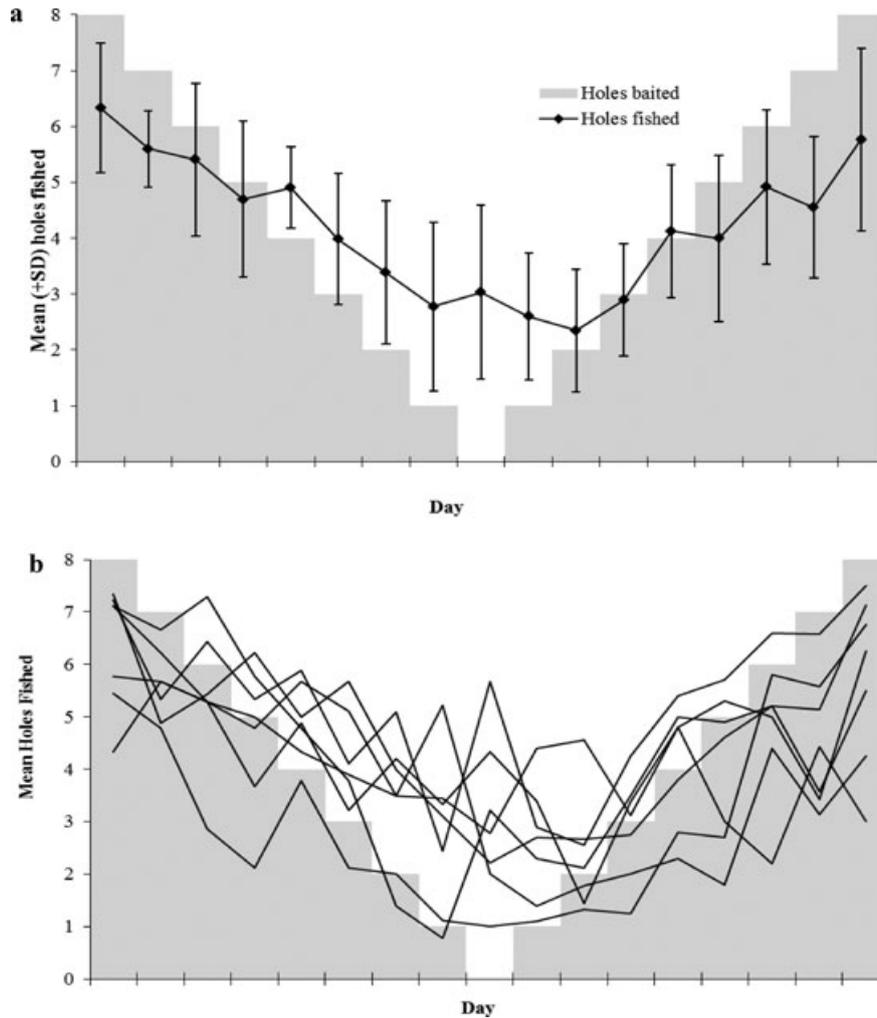

Fig. 3. Total duration of group fishing activity (line), pooled for all subjects (*N* = 7) on each day of observation. The number of baited hole locations (gray bars) decreased by one every 10 days between days 1 and 82 of testing. Beginning on day 83, the number of baited hole locations then increased by one approximately every 10 days through the end of the study.

$1 + 2 + 3 + 4 + 5 + 6 + 7 + 8$]). As a group (durations of fishing activities were pooled across subjects), subjects immediately decreased fishing activity at a location on the first day it was not baited with ketchup (Wilcoxon signed-rank, $N = 8$, $Z = 2.52$, $P = 0.012$) compared to the previous day. However, when individual fishing effort was examined this trend was not confirmed. Individually, only one of the seven chimpanzees in the study (S1) showed a significant change in fishing effort at a hole location on the first day it was not baited compared to the previous day. Instead of decreasing fishing activity at an unbaited hole location, the alpha male of the group (S1) fished significantly more at a hole location when it did not contain ketchup as compared to the previous day (Wilcoxon signed-rank, $N = 8$, $Z = 2.37$, $P < 0.05$). Finally, a significant change in the pooled effort allotted to a hole over the first 5 days after a hole location was unbaited was found (Friedmans, $N = 8$, df $= 4$, $\chi^2 = 10.99$, $P < 0.05$).

Fishing activity at each hole location was monitored throughout the study in order to determine whether chimpanzees would abandon fishing at a location that was no longer baited. Overall, fishing activity was related to the number of baited holes (Fig. 3). However, when less than half of the locations were baited, chimpanzees continued to fish at holes that did not, and had not for several days, contain food. This trend continued even when the mound provided no food at any location. Although there was some individual variability (Fig. 3B), chimpanzees, on average, were observed fishing at three holes when none of the eight holes were baited.

Finally, we predicted that chimpanzees would renew their fishing effort at a location when the hole again contained ketchup, and that fishing effort would increase as resource availability increased (Fig. 3, days 82–151). As a group (durations of fishing activities were pooled across subjects), subjects immediately increased fishing activity at a location on the first day it was again baited with ketchup compared to the previous day (Wilcoxon Signed-Rank, $N = 8$, $P < 0.05$). Individually, this finding was confirmed in two subjects. S2 and S6 each showed a significant increase in fishing effort at a hole location on the first day it was rebaited compared to the previous day (Wilcoxon Signed-Ranks, $N = 8$, $P < 0.05$). However, no significant change in the pooled effort allotted to a hole over the first 5 days after the hole was baited was found (Friedmans, $N = 8$, df $= 4$, $\chi^2 = 6.7$, $P = 0.153$).

DISCUSSION

In their natural environment, chimpanzees are often faced with fluctuations in resource availability, and must use personally acquired information and/or publicly available information to adapt to this variability. In nature, the availability of foods upon which chimpanzees have been observed to feed can be linked to seasonal changes in weather [Nishida & Uehara, 1983; Wrangham, 1977]. With respect to termite fishing, chimpanzees have been observed to fish more at the start of the wet season [Lonsdorf, 2005], and the availability of termites within a mound may also be affected by seasons [Deblauwe, 2009; Goodall, 1968; McGrew, 1979]. We simulated this natural environmental change using an artificial termite mound with a group of captive chimpanzees. As a group, chimpanzees changed their fishing efforts based on the number of baited holes—decreasing their overall fishing activity at the mound as the number of holes decreased, and again increasing their fishing activity as the number of holes later increased. Although repeated exposure to ketchup may have resulted in a decreased motivation to fish during the first half of the study, this decrease in fishing activity is most likely related to the changes in availability of food at the mound, and is predicted by learning and optimal foraging theories. As the number of baited hole locations decreased, the total amount of ketchup available also decreased, such that the decrease in fishing activity might simply be explained by the fact that chimpanzees exhausted the supply of food provided by the mound more quickly as the study progressed.

At the group level, the observed decrease in fishing effort was immediate, elimination of a hole resulted in a significant drop in fishing at that location on the first day the hole did not contain ketchup. However, individuals varied considerably in their fishing efforts. For example, the alpha male (S1) fished significantly more at a hole location when it did not contain ketchup as compared to the previous day.

In contrast to standard predictions surrounding extinction of behavior through individual learning and findings that chimpanzees typically have little difficulty with tasks involving reversal learning and transfer of training [Martin et al., 2011; Nissen et al., 1938; Schusterman, 1962], the chimpanzees in our study were observed fishing at unbaited hole locations even days and weeks after a hole had last contained ketchup (Fig. 3). This finding is similar to those reported by Bonnie [2007], Price et al. [2009], and Hrubesch et al. [2009], such that in all cases chimpanzees persisted in using a previously successful strategy to obtain food even though that strategy was unsuccessful or less successful than an observed alternative. Several possible explanations may account for the persistence of chimpanzees to fish at unbaited hole locations throughout the study. First, data gathered by Rumbaugh and colleagues on the transfer index indicate that previous experience with a particular stimulus-reward association can interfere with the acquisition of the reversed association [Rumbaugh, 1970; Rumbaugh & Gill, 1973]. Furthermore, according to prominent theories of

social learning, continued individual sampling of alternative behaviors within a variable environment is an adaptive strategy through which individuals can confirm the accuracy of social information received [Giraldeau et al., 2002]. Thus, individuals should utilize both individual and social information during foraging, particularly when resource availability varies.

Our findings are also consistent with those reported in the literature on metacognition in which individuals look to confirm the location of a reward even after observing the reward being placed, particularly when the cost of confirming the location of a reward is low [Call & Carpenter, 2001; Hampton et al., 2004; Paukner et al., 2005]. Finally, the chimpanzees in our study [as well as in Bonnie, 2007] are provided with ample and consistent food and therefore need not be concerned with whether or not they miss an opportunity to retrieve a relatively small amount of a low calorie, but preferred food such as ketchup. Likewise, there is little energetic or time cost to fishing at an empty hole. Chimpanzees may continue to fish at unbaited holes simply because the cost of doing so is incredibly low, simply because fishing is behaviorally or cognitively enriching [Maki et al., 1989]. The design of our study and limitations of the exhibit in which this research took place prevent us from determining whether chimpanzees relied on individual learning, social learning, or a combination of both to learn which hole locations were baited with ketchup. Previous research [Drea & Wallen, 1995; Menzel & Juno, 1982; Schusterman, 1962] showed that primates are able to learn in both individual and group settings that rewards associated with a specific choice can change. Furthermore, chimpanzees are known to be adept social learners and are highly tolerant of others in foraging situations, so we assume that social learning played at least some role in the fishing activity observed here. However, it is also important to note that group living may in some contexts impede learning or the expression of a learned behavior [e.g., Drea & Wallen, 1999; Lonsdorf et al., 2009; Lonsdorf & Bonnie, 2010]. Although we did not observe any agonistic behavior among chimpanzees around the mound, low-ranking individuals may have had limited access to the mound or to specific holes if a higher ranking chimpanzee was also fishing. As a result, some fishing behavior at unbaited hole locations may have been a result of the social context in which fishing was taking place [Coussi-Korbel & Fragaszy, 1995; Lonsdorf & Bonnie, 2010], and not a lack of learning. Future research should address the positive and negative impacts of the social group on individual fishing behaviors and strategies. It would also be interesting to investigate how chimpanzees and other social animals balance individual and social learning strategies, if they indeed use a mixed approach to learning in a variable environment. Although some research in this area has been reported [e.g. Kendal et al., 2009, 2005; Laland, 2004], continued investigations are necessary to develop a rich understanding of learning in a social and variable environment.

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