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Social Learning and Developmental Stages of Probe Tool-Use in Captive Bonobos

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Social Learning and Developmental Stages of Probe Tool-Use in Captive Bonobos

A thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Biology

by

Gloria Marie Brattich

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James Charles Nieh
Federico Rossano

2021

The thesis of Gloria Marie Brattich is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2021

This thesis is dedicated to Dr. Alexander Liberman, without whom it would assuredly not have been completed. His unwavering support, frequent encouragement, generous provisioning of delicious leftovers, and gracious acceptance that I did not always want his (generally prudent) advice are all emblematic of his strengths as a partner.

He is also a fantastic cat butler.

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ABSTRACT OF THE THESIS

Social Learning and Developmental Stages of Probe Tool-Use in Captive Bonobos

by

Gloria Marie Brattich

Master of Science in Biology

University of California San Diego, 2021

Professor Carolyn M. Kurle, Chair

Bonobos (*Pan paniscus*) are capable of diverse tool-use; however, research on the role of social learning on vertical tool-use transfer and the developmental stages of juveniles has been limited. Captive bonobo populations provide novel opportunities to study juvenile skill development in naturalistic social settings.

This study was conducted using film taken at the San Diego Zoo over four consecutive years. The bonobo enclosure included an artificial termite mound which was provisioned to provide enrichment. All bonobos demonstrated the proper application of probe tools required to extract bait during the study, and “fishing” was a common activity.

This bonobo group included two infants, a mother-raised female, and an effectively orphaned male. Both infants observed and interacted with older members as they fished. As they aged, their contacts with the artificial termite mound increased, and eventually both successfully used probe tools like their conspecific models. The skill development process involved five distinctive stages, the identification of which allowed for detailed evaluation of the social learning process of the young bonobos. The order and rate at which the juvenile bonobos acquired critical fishing skills paralleled the processes described for probe-fishing juvenile chimpanzees. Despite this inter-species concordance, the social learning environment the juvenile bonobos experienced involved a higher level of expert tolerance than that reported among probe-fishing chimpanzees. Two observed behaviors of primary models, active tool transfer to juveniles and repetitive dip exaggeration, are indicative of scaffolding, or parental modeling, in bonobos. Identified individual fishing technique preferences did not appear to be vertically transmitted.

Introduction

Once highly controversial, the occurrence of non-human tool-use throughout the animal kingdom now enjoys widespread academic and cultural acceptance (Seed & Byrne, 2010). The ability of all extant *Hominidae* (the “great apes”: Orangutans, Gorillas, Chimpanzees, Bonobos, and Humans) to fashion and use tools is well established (Mulcahy, Call, & Dumbar, 2005; Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Herrmann, Wobber, & Call, 2008). Current research has largely focused on understanding the cognitive processes and social mechanisms for skill transmission of novel tool-use between individuals and within populations (Whiten & van de Waal, 2018). Though several studies on great apes have provided evidence of imitation and other forms of social learning, most of these have been controlled experiments restricted to one-to-one learning, typically relying on a human model, rather than a more ecologically relevant, but experimentally thorny, conspecific dynamic (Tennie, Call, & Tomasello, 2010; Whiten, 2015). In addition, the vast majority of non-human great ape studies have focused on chimpanzees (*Pan troglodytes*), due to their comparatively abundant wild and captive populations (Subiaul, 2016; Whiten, 2015). Significantly fewer studies have been published on their close cousins, bonobos (*Pan paniscus*).

Pan paniscus was first described by western scientists in the early 20th century (Furuichi, 2019). Commonly referred to as “pygmy chimpanzees”, they were initially categorized as a subspecies of common chimpanzees (Kano, 1992). Their classification as a separate species was proposed in 1933 (Coolidge), and today bonobos are generally considered to be a separate species (Groves, 2018).

Bonobo extant populations are confined to rainforests south of the Congo River in the Democratic Republic of the Congo (Kano, 1984), an area that has been difficult for researchers to access due to the remote and isolated nature of their habitat as well as the political instability of the surrounding area. Their population, estimated at 50,000 in 1973 (Kano, 1992), is threatened by increasing habitat fragmentation and loss, poaching, and disease transmission (Idani, et al., 2008), and is now estimated to be as low as 15,000 individuals (Mallon, et al., 2015). Due to these constraints, *in situ* research of bonobos has been conducted at just three field sites, the first of which was established in 1973 (Kano, 1992). Few bonobos exist in captivity; an estimated 225 bonobos are in managed populations such as reserves and zoos (Stevens, 2020).

Bonobos are estimated to have diverged from central African chimpanzees 1-2 million years ago (Caswell, et al., 2008). Despite their recent common ancestry, the two species of *Pan* differ notably in several aspects, particularly in their social behavior. In contrast to the male-dominated society of chimpanzees, bonobos regularly engage in nonconceptive sexual behavior and juvenile levels of play into adulthood (Kano, 1992; Palagi, 2006). The cognitive and social underpinnings of this behavioral paedomorphism also facilitate higher levels of food sharing (Fruth & Hohmann, 2002; Fruth & Hohmann, 2018), social cooperation, and individual tolerance (Hare, Melis, Woods, Hastings, & Wrangham, 2017) than that seen in chimpanzees.

In the wild, bonobos have been known to use tools only occasionally, and rarely in foraging contexts (Ingmanson, 1996; Hohmann & Fruth, 2003). Chimpanzees, in contrast, are prolific and versatile natural tool-users, primarily involving the acquisition and processing of food (Seed & Byrne, 2010; Boesch & Boesch-Achermann, 2000; Goodall, 1986; Matsuzawa, 1994; McGrew, 1974; McGrew, 1992). There is little evidence, however, that this disparity is a result of lower bonobo intelligence or ability. In captivity, the proficiency and amount of tool-use by bonobos approaches that of the chimpanzees (Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993; Neufuss, Humle, Cremaschi, & Tracy, 2016; Gruber, Clay, & Zuberbühler, 2010; Roffman, et al., 2015) and they perform equivalently well in experiments requiring using tools to solve problems (Takeshita & Walraven, 1996; Mulcahy & Call, 2006; Visalberghi, Fragazy, & Savage-Rumbaugh, 1995).

Longitudinal studies of wild chimpanzees have explored the role of social learning on vertical tool-use transfer and associated developmental stages common to juveniles (Biro, Sousa, & Matsuzawa, 2006; Sanz & Morgan, 2007; Whiten, et al., 1999). Due to their smaller population, study site inaccessibility, and lower predilection for tool-usage, comparable research on wild bonobos has been difficult. Captive bonobo groups, therefore, provide an alternative avenue to study technically complex skill development in young bonobos in a naturalistic social context.

In this thesis I will explore the unstructured artificial termite mound fishing activities of a captive bonobo group at the San Diego Zoo, using film taken between October 2004 and June 2009. From an extensive video library provided by Dr. Christine Johnson (Department of Cognitive Sciences, University of California San Diego), I have isolated clips that include fishing-related activity among eight bonobo subjects. The clips have been temporally segmented into individual fishing bouts, dips, and tool modification sessions. Each segment was scored, using a constrained vocabulary, for multiple data tiers (Figure 35).

Of particular interest were the two youngest subjects, who were born shortly prior to the start of the study. To further understanding of the social learning environment and process, identifiable skill developmental stages of the two novices were compared with what has been reported for juvenile chimpanzees. Chimpanzee mothers serve as the primary models for their offspring, and it was expected that bonobo mothers would fill that role as well. By scoring juvenile proximity and attention to fishing activity, the relative likely influence of potential models was measurable. Evaluation of fishing-related interactions between novice and expert tool-users may provide further insight into whether scaffolding or other forms of teaching are evident in this population.

Personal observation of the group indicated that the bonobos each utilized distinct fishing styles. To verify this, each recorded dip was scored for identified technique variations, and the results were compared for each subject. These data were also used to investigate vertical transmission. By comparing the fishing styles of juveniles with that of their models, I evaluated the role of imitation vs emulation in the acquisition of tool-using skills among captive bonobos.

Methods

This longitudinal study focuses on the unstructured artificial termite mound fishing activities of the captive bonobo group at the San Diego Zoo (SDZ) which was possible thanks to a multi-year video library of this population provided by Dr. Christine Johnson (Department of Cognitive Science, University of California, San Diego). From approximately 560 hours of tape taken between October 2004 and June of 2009, I have isolated 475 clips (approximately 19 hours combined) which capture termite-mound related activity among eight resident bonobos. All eight subjects were present throughout the study.

Study Site

The San Diego Zoo bonobo habitat consists of an outdoor, open-air enclosure connected to a heated indoor (off-exhibit) space consisting of one large room (136m^2) and four smaller rooms (55m^2 each). Movement between the indoor and outdoor areas is keeper restricted. The outdoor space (560 m^2) is comprised of five main areas of different elevations, connected by hanging ropes and hammocks attached to bamboo sway poles and log structures which simulate an arboreal habitat. A large waterfall feeds two small streams that connect different areas. Several twisted palms grow in the enclosure, and the substrate is primarily grass, dirt, and rocky outcroppings. A wide concrete pathway for zoo visitors borders roughly half of the outdoor enclosure. Four large glass windows are situated at regular intervals along the pathway. Each offers a different vantage point, and combined the windows provide unobstructed visual access to most of the outdoor enclosure.

Area 2 of the outdoor enclosure includes an includes an artificial termite mound (Figure 1). The mound can be seen from two different angles from Windows 2 and 3 (Figure 2,

Figure 3). The mound is provisioned daily with liquid bait, typically human baby food or honey, which is accessible via multiple small openings spaced around the mound (Figure 4). The mound is large enough for multiple individuals to fish simultaneously. The food is minimally accessible without the implementation of slender probes; however, the bonobos do appear able to access small amounts near the openings of the baited holes using their fingers or mouths. Leafy browse provisioned throughout the enclosure provides plentiful raw material for fashioning appropriate probes.

The bonobo group is fed a varied diet several times daily, and other enrichment foods such as popcorn, apple slices, nuts, and seeds are commonly scattered throughout the enclosure. The artificial termite mound functions as an additional enrichment activity rather than a primary source of calories.

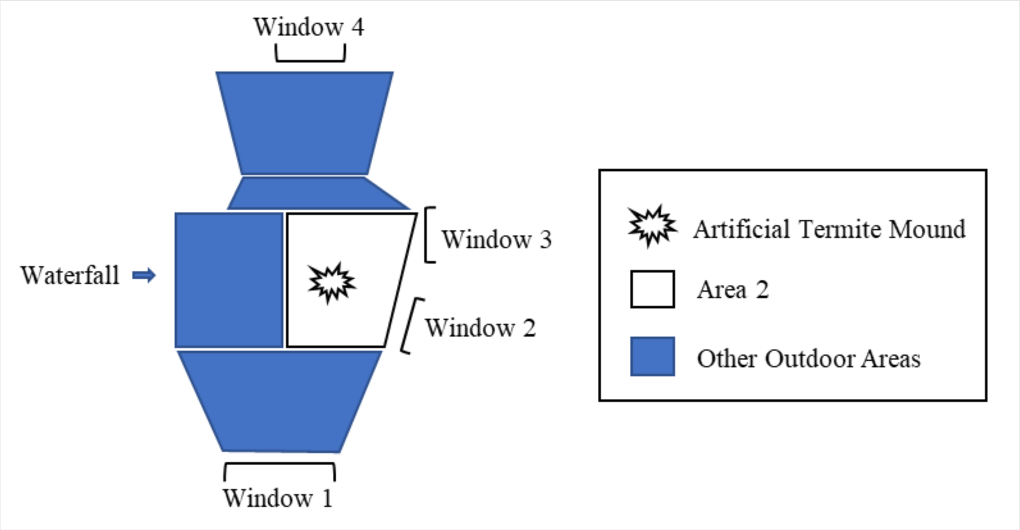

Figure 1: San Diego Zoo outdoor enclosure layout.

Figure 2: View of the artificial termite mound from Window 2

Figure 3: View of the artificial termite mound from Window 3

Figure 4: Bonobos fishing at the artificial termite mound at the San Diego Zoo

Group Composition

Bonobo social groups in the wild are matriarchal and patrilocal, with an approximately equal proportion of males and females in all age classes (Kano, 1992). Like common chimpanzees (*Pan troglodytes*), nulliparous females emigrate into other bonobo troops between 9-14 years of age. A bonobo troop occupies a set territory that may partially overlap with neighboring groups. Each troop divides into fission-fusion subgroups (parties), which forage and sleep separately from the other parties of the troop. Party sizes vary from 1-40 individuals, and on average consist of an equal number of sexually mature females and males, with a slightly lower proportion of immature offspring. When parties re-group, they may create new combinations upon separating.

The 2004-2009 San Diego Zoo bonobo group composition was managed to mimic, to the extent possible, the typical bonobo social structures observed in the wild. *In situ* party fluctuations are simulated at the SDZ by discretionary keeper management. The bonobos spent their nights in the indoor rooms, and during the day were released into the outdoor enclosure in two groups: the morning party (9:00 a.m. to approximately 12:30 p.m.) and the afternoon party (12:30 p.m. to 5:00 p.m.). The size of the morning and afternoon parties ranged from 3-6 individuals, with an average party size of 5. Party composition provided variability as well as reinforced positive social dynamics (e.g., mothers were always paired with their young), and were adjusted to avoid violent antagonism within a party.

Subjects

At the study onset in October of 2004, the SDZ bonobo group consisted of three adult females, one adult male, one adolescent male, one juvenile female, one infant male, and one infant female (Table 1). All eight original bonobos were present throughout the study period. In September and October of 2007, two additional infants (Mali (f) and Tutapende (m)) were born; however, neither was integrated into the group until early 2009. Due to their lack of representation in the selected video (0 and 2 appearances, respectively), both Mali and Tutapende were excluded from this study. With the exception of the two new infants, no other bonobos were introduced into the group during the study period. All bonobos in the group were born in captivity.

Lana, the matriarch and highest-ranking member, was born in 1979. The two lower-ranking adult females, Lolita and Ikela, were born in 1979 and 1981 respectively. All three adult females were born in San Diego, either at the Zoo or in a separate group housed at the San Diego Zoo Safari Park. All three females were nursery-raised.

Yenge, the adult male, was born in 1982 at the Frankfort Zoo. Lana's son, Junior, was born in 1995 and was raised by his mother. The juvenile female, Mchumba, was born in late 2000 and was raised by her mother, Lolita. The infant male, Makasi, was born in April of 2004 at the Safari Park, but was rejected by his mother and was nursery raised until he could be fully integrated into the Zoo group. Kesi, the youngest member, was born to Lana and Yenge in August of 2004. Lana raised Kesi, and her matriarch status conferred a much higher social status to Kesi compared to Makasi, who was an effective orphan. It is the two infants - Kesi and Makasi - that are the main focus of this developmental study.

Table 1**:** List of subjects observed at the San Diego Zoo over a period of 5 years. Age classes were based on Kano's (1992) classification and are listed by age class at study start (10/4/2004) and end (6/19/2009) if multiple age classes were recorded.

Subject	DOB	Lineage	Gender	Age Class (Start/End)
Lana (N)	13 April 79	Linda & Kakowet	Female	Adult
Yenge (G)	25 Dec. 82	Salonga & Mato, Frankfurt	Male	Adult
Lolita (O)	20 April 89	Louise & Vernon, (nursery)	Female	Adult
Ikela (I)	27 Nov. 91	Louise & Akili, (nursery)	Female	Adult
Junior (J)	14 Jan. 95	Lana & Maiko	Male	Adolescent/Adult
Mchumba (B)	22 Dec. 00	Lolita & Congo	Female	Juvenile/Adolescent
Makasi (M)	22 April 04	Loretta & Jumanji (nursery)	Male	Infant/Juvenile
Kesi (K)	15 Aug. 04	Lana & Yenge	Female	Infant/Juvenile

Data Collection

Nonintrusive video collection of the bonobos at the San Diego Zoo was directed by Dr. Christine Johnson and undertaken primarily by UCSD undergraduate interns (including myself) over the course of 5 academic years. The size and layout of the outdoor space allowed for individual bonobos to be out of each other's view, and it was not uncommon for pairs or trios to break off from the main social group for extended periods during the day. Each of the four public viewing windows provided a partial view of the enclosure. It was therefore common for only a subset of any given party to be in-view at the same window at any given time. Due to these limitations, the videographers were instructed to prioritize capturing certain activities/ individuals opportunistically in the following hierarchy:

1. All artificial termite mound-related activity.
2. Dyadic focal-level interactions between Lana and Kesi (the only mother-infant offspring dyad in the group).
3. Other social behaviors at the discretion of videographer.

In addition, videographers had discretion between capturing all in-view bonobos or zooming in on activities of interest to allow for a more detailed analysis. For this reason, termite mound-related video was often filmed with a tight focus on the active fishing activity, at the expense of capturing other individuals in the surrounding area.

From the video collected between October 2004 and June 2009, I isolated all clips containing mound-directed behavior. This was defined as any video in which the artificial termite mound was in frame and at least one individual was in contact with the mound and/or engaged in tool creation/modification. Video was clipped as broadly as possible, typically beginning from a subject's approach to the mound area and ending when either all individuals had left the mound area, or the mound area was no longer in frame. From the collected video, 475 mound clips were identified, constituting approximately 19 hours of total mound-related video over the study period. A complete catalog of tapes and isolated clips can be found in Appendix II: Video Inventory pp. 116-139. Video of mound activity was disproportionately collected in accordance with the school calendar and number of interns available each quarter. Both number of clips and total mound activity minutes captured are consistently lower in quarter 3 (July-September), which roughly corresponds with the UCSD summer break period.

Video analysis was conducted using ELAN, an audio and video annotation software developed by the Max Planck Institute for Psycholinguistics, The Language Archive, Nijmegen, The Netherlands. Video was temporally segmented into individual fishing bouts, specific juvenile interactions, individual dips, and tool modification sessions according to the criteria as defined in Table 15. Segments were individually annotated, with each segment type corresponding to an established set of sub-tiers (Figure 35). Each tier annotation was coded according to an ethogram developed for this study (Table 16). Terms with study-specific definitions have been capitalized for clarity (e.g., Bout, Dips, In-View).

Inter-coder reliability was monitored by periodically comparing percent segmentation overlap, as well as subsequent segment annotation agreement, from a subset of clips which were independently scored by myself and Jade Hookham, an undergraduate intern. A random subset of 9% of the scoring files were directly compared using the multiple-file processing features included in ELAN. Between the two coders, percent segmentation overlap was 80.3%. Inter-coder reliability for segments with at least 70% overlap was high (Cohen's κ=0.9707). Inter-coder reliability for all annotations was also high (Cohen's κ=0.9032).

Statistical Analyses

Exact binomial goodness of fit tests were used to compare frequency data with expected proportions. Differences within frequency data set categories were compared using Fisher's exact tests of independence where possible, while Chi-square tests of independence were reserved for frequency data with more than two values per nominal variable, or when the sample size was too large to run a Fisher's exact test (typically *n* >1000). A Bonferroni correction was applied to all post-hoc analyses of Chi-square tests.

Analysis of variance tests (ANOVA)s were used to test for significant differences in means; however, for data involving unequal and/or small samples sizes, or when the standard deviations within groups were heterogeneous, Welch's one-way ANOVA was used instead. Post-hoc analyses of ANOVAs were run using Tukey-Kramer tests.

Relationships between two measurement variables were evaluated using Pearson correlation tests. Paired *t*-tests were used to evaluate mean differences between pairs of measurements. When the distribution of the differences between pairs was non-normal, a Wilcoxon signed-rank test was substituted for a paired *t*-test.

Chapter 1 Skill Development of Probe Fishing in Juvenile Bonobos

1.1 Introduction

Longitudinal studies of wild chimpanzees (*Pan troglodytes*) have detailed how juvenile members learn to probe fish like the older members of their social groups (Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2005). Hirata and Celli (2003) have likewise documented the social learning process of captive juvenile chimpanzees in a honey-fishing task. Like captive adults, juvenile chimpanzees learn to probe fish primarily, though not purely, through a combination of trial-and-error learning and expert fisher observation. The juvenile learning period, however, is highly protracted compared to that of captive adults, who were often successful in a matter of days. This elongated learning period can be divided into stages that are distinct from the adult learning process. These periods involve varying levels of intense expert observation, tool manipulation, and unsuccessful attempts prior to successful fishing. The amount of time before immature chimpanzees successfully wielded probe tools varied by environment and task complexity. Captive subjects in a relatively simple experimental honey-fishing task were successful at <2 years of age (Hirata & Celli, 2003), while immature chimpanzees in Gabon were not successful in accessing honey from underground nests before 8.5 years (Estienne, Stephens, & Boesch, 2017). Comparing the probe-fishing skill acquisition process of captive juvenile bonobos to that observed for juvenile chimpanzees may help identify ontogenetic differences between the sister species.

1.2 Methods

Film used in this study was collected between 9/29/05-6/25/09 (with an additional hour taken in October of 2004). During this period, the San Diego Zoo bonobo group included two infants, Makasi (m, b. 4/22/2004), and Kesi (f, b. 8/15/2004). In >200 hours of video across approximately 4 years, Makasi and Kesi observed and interacted with older, expert members of the group as they fished on the artificial termite mound for provisioned liquid food. As they aged, the two novices' interactions with the termite mound increased, and eventually both gained the skill to successfully fish as well as their expert adult models. Their interactions with active fishers, the baited mound, and probe tools were coded and analyzed, and five distinct developmental stages were identified (Table 2). This section details the skill developmental stages observed for the novices, the analysis used to characterize these stages, and compares the results to what has been published regarding juvenile chimpanzee probe fishing skill development.

Exact binomial goodness of fit tests were used to compare frequency data with expected proportions. Differences within frequency data set categories were compared using Fisher's exact tests of independence where possible, while Chi-square tests of independence were reserved for frequency data with more than two values per nominal variable, or when the sample size was too large to run a Fisher's exact test (typically n >1000). A Bonferroni correction was applied to all post-hoc analyses of Chi-square tests.

Analysis of variance tests (ANOVA)s were used to test for significant differences in means; however, for data involving unequal and/or small samples sizes, or when the standard deviations within groups were heterogeneous, Welch's one-way ANOVA was used instead.

1.3 Results

1.3.a Observed Developmental Stage Progression

This study followed two young bonobos from infancy through the age of 5. By the end of the study, they had both acquired the knowledge and critical skills required to successfully fish at the artificial termite mound in ways similar to the adults in their group. These critical skills included identifying a baited hole, manipulating a probe tool, making a probe tool from leafy browse, and inserting a probe tool into a baited hole deep enough to successfully retrieve bait (Table 3). Although making a tool was not strictly necessary for successful fishing, as prepared tools were commonly left near the mound by previous fishers and frequently re-used by all group members, tool modification was an activity that all adults performed, and is therefore considered a critical element of the “adult” fishing skill set. Both infant bonobos followed a similar progression through the five distinct Developmental Stages (Table 2) and demonstrated all critical skill components as outlined in Table 3.

Young bonobos are constantly carried for several months after birth, and at six months their range is limited to being within reach of their mother (Kano, 1992). This period was reflected in Stages 1 and 2. Stage 1, in which infant mound interaction is limited to being carried by an active fisher, was observed for Kesi primarily before the age of 14 months. Makasi, likely due to his orphan status and dearth of film representation prior to 18 months, was not observed engaging in Stage 1 behavior.

Stage 2 mound interactions, also restricted to bodily contact with an adult fisher, incorporated the addition of more active mound-related interactions, primarily through manual contact with the mound and the solicitation of tolerated scrounging behaviors from active fishers. One such behavior, touching the tool of an active fisher, was the first critical skill exhibited by

Kesi at 14 months old, during her Stage 2 period. Unlike Stage 1, Makasi was observed engaging in Stage 2 behaviors, including being the recipient of limited tolerated scrounging. However, instances of Stage 2 mound interactions involving Makasi were scarce (*n*=2), and his record does not include a discrete Stage 2 period, as he was 18 months and already exhibiting Stage 3 "independent" behaviors at the time of his first recorded mound interaction.

The distance young bonobos will venture gradually increases over several years, and at 18 months both infants had begun to move about the exhibit more independently, a behavioral shift that signaled the onset of Developmental Stage 3. The age at which both juveniles were recorded identifying baited holes coincided with their being mobile enough to climb on the mound unassisted. Both infants identified the location of the baited tubes by probing at the holes with their fingers and placing their mouths directly at the openings. These investigations were rewarded, as the infants often appeared to obtain small amounts of the bait in the process. It was during this period that Makasi was first observed touching an active fisher's tool, at nearly 10 months older than Kesi had been when she first showed this behavior.

After identifying bait holes, the next critical skill that Kesi and Makasi demonstrated was manipulating a tool discarded by another individual, observed while both were in Stage 3 (Table 3). As with touching an active fisher's tool, Kesi reached this milestone earlier than Makasi, at 20 months old compared to his 32. Kesi also began contacting the mound with probe tools earlier than Makasi. Kesi first successfully Dipped with a probe at 2.2 years of age, nearly a year younger than Makasi was at his first recorded successful probe Dip. Kesi's apparent precocity, however, did not appear to translate into earlier fishing competence; her inexpert fishing period (Stage 4) was elongated compared to Makasi's (Figure 5). Kesi also exhibited a longer transition period between Stage 4 and Stage 5 level Bouts, while Makasi, once he had mastered fishing, was rarely observed to similarly regress in his technique (Figure 6). Both bonobos were observed making and modifying their own tools during or soon after their first fishing attempt (Stage 4), but not before.

Table 2: Identified Developmental Stages

Stage	Name	Characteristics
1	**Passive Interaction**	Infant (novice) is carried to/on the mound but does not interact directly with either the mound or active fishers beyond visual attention.
2	**Active Interaction**	Novice is carried to/on the mound and maintains physical contact with carrier while interacting with mound (touch, kiss, probe with finger), and/or with active fishers and their probe tool. Novice is not independent.
3	**Independent Exploration**	Novice climbs on the mound independently. Characterized by an increase in Dips (tool not yet utilized) (p. 22), increased attention to active fishers (p. 23), and may involve an increase in tolerated scrounging behavior (p. 24).
4	**Inexpert Fish**	Novice begins to use tool to fish, but still relies primarily on finger and mouth Dips (p. 24). Tool Dips tend to be shallow (p. 26) inefficient (p. 27), and are less likely to be completed compared to those in Stage 5 (p. 28).
5	**Expert Fish**	Novice primarily uses tool to fish (p.25). Dips usually involve tool being inserted more than 25% of tool length into hole (p. 26). Novice increases Tool Modifications (p. 29). Tool size or suitability does not appreciably change from Stage 4 (pp. 30-31).

Table 3: Ages, in years, at which the focal bonobos (Kesi and Makasi) were first recorded performing critical elements of probe fishing on the artificial mound. “Chimpanzee” age ranges refer to the earliest and latest appearance of the indicated behavior among a wild chimpanzee group (n=8) (Lonsdorf, 2005). *Makasi finger probed during his first filmed appearance at the mound, and so likely exhibited such behavior earlier than recorded.

Behavior	Definition	Kesi	Makasi	Chimpanzee
Touch Tool	Solo possession not necessary, but stick must have a known association with fishing.	1.2	2.0	NA
Identify Hole	Poke, sniff, or look into bait hole.	1.5	1.5*	0.5-1.5
Manipulate Tool	Solo possession of tool, manipulate previously used tool with hands.	1.7	2.7	1.5
Successful Dip	Full Dip with stick: insert tool into hole, remove tool from hole, and eat from stick. For Chimpanzee: extract termites.	2.2	3.1	2.5-5.5
Make Tool	Select and modify vegetation to use as a probe tool.	2.2	3.5	1.5-3.5

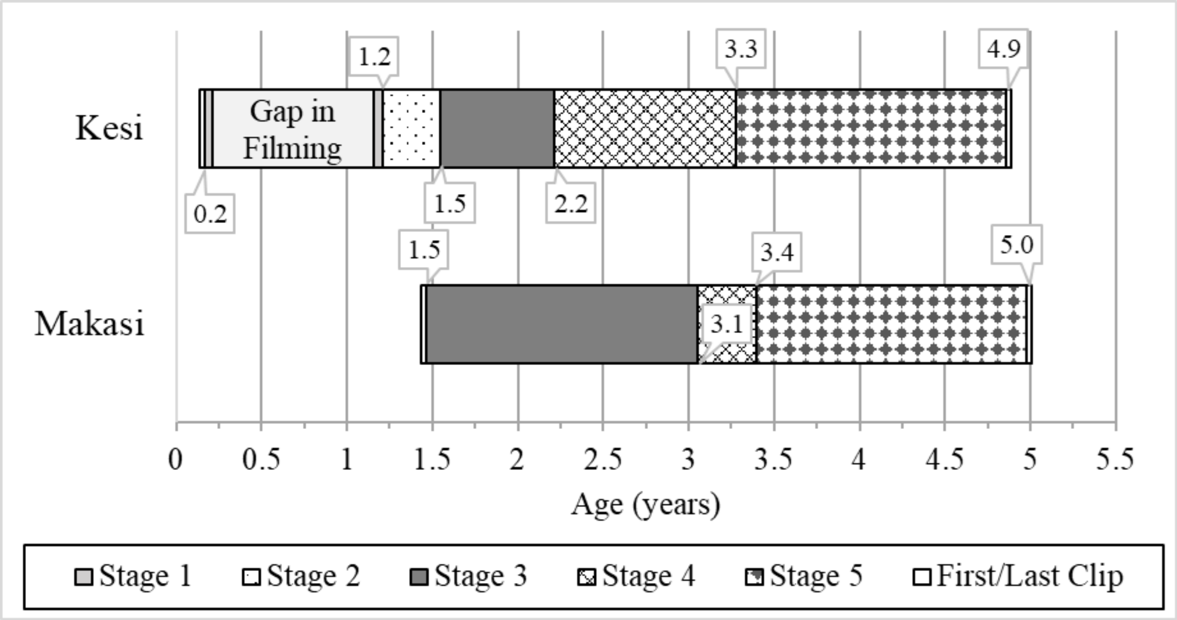

Figure 5: “Discrete” Developmental Stage boundaries for Makasi and Kesi, by age. The end of the previous stage is defined as the day before the first instance of the next stage behavior was first recorded. Makasi’s first mound appearance included both Stage 2 and Stage 3 Bouts. No Stage 1 behavior was recorded for Makasi during the study. Only the beginning and end of Kesi’s Stage 1 were recorded due to an 11-month pause in filming at the SDZ between 2004 and 2005.

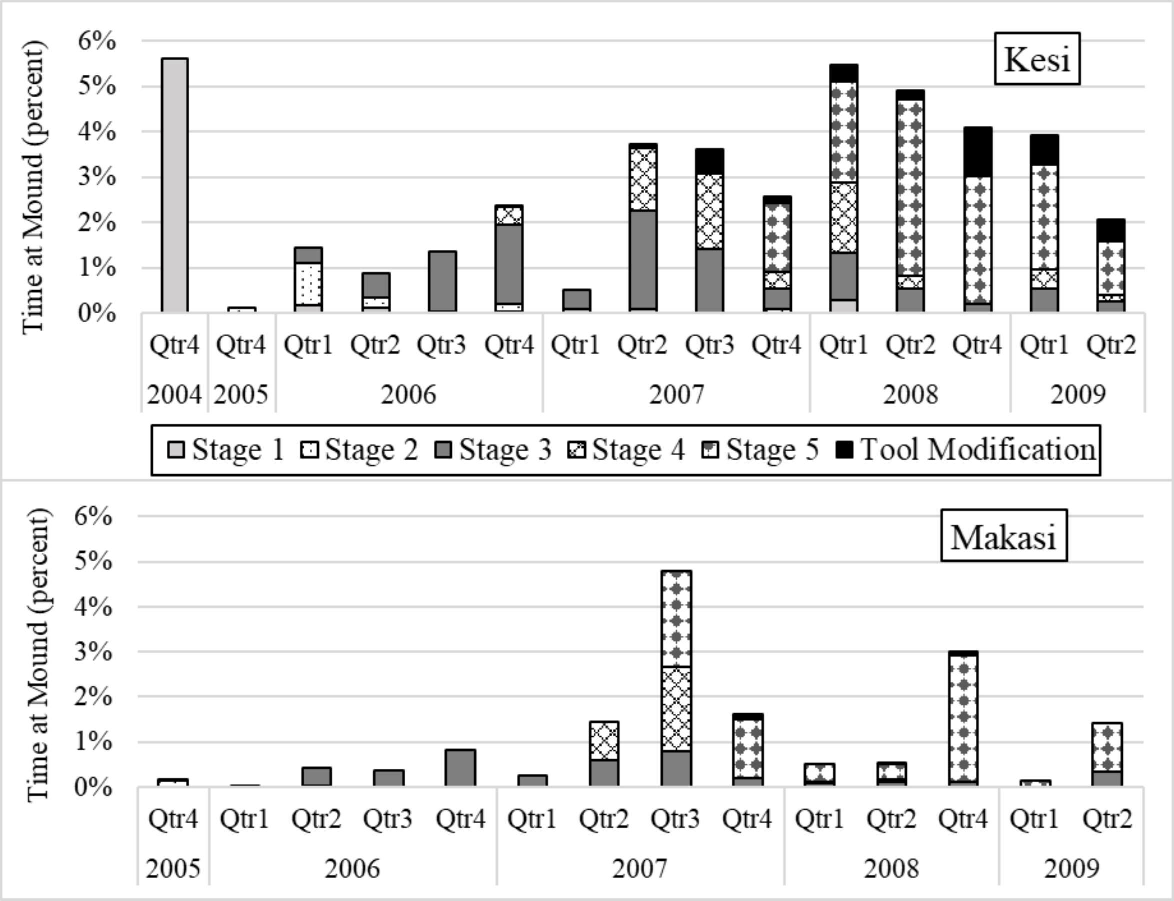

Figure 6: Artificial termite mound interactions over time, calculated as the time at the mound (Bout time of the accompanying adult (for Stages 1&2) or of the indicated novice (for Stages 3-5 & Tool Modification) divided by that novice's "In-Party" time, for each quarter of the study. Each mound visit was scored with the highest Developmental Stage behavior exhibited during the interaction.

1.3.b Developmental Stages Confirmation

The five Developmental Stages (outlined in Table 2) were first identified and characterized subjectively through video observation. The start of each stage was likewise selected as the date at which each stage's unique behavior was first observed. The observed characteristics of Stages 1 and 2 were the same as their gating criteria (e.g., being carried to the mound, but not interacting with the mound or fisher, was automatically categorized as Stage 1). Later stages were characterized by both gating criteria as well as observations that required confirmation. The hypothesized characteristics of each stage were tested via the following evaluations, and the associated definitions were adjusted accordingly where necessary. As the proposed Developmental Stages are based on the observations of n=2, they should be considered highly speculative pending future observational study of bonobo young.

- **Does Dip frequency increase from Stage 2 to Stage 3?**

Metric: Count of [*novice*]'s Dips recorded during Stage 2 and Stage 3 (Figure 5), weighted by [*novice*]'s In-Party combined Mound tape time for each Stage.

Result: **Yes.** A clear increase (1237.3%) in Dips/minute was demonstrated for Kesi (Table 4). Makasi did not have a discrete Stage 2 recorded to compare.

Table 4: Counts of Dips and In-Party Mound-tape time (minutes) for Kesi (K) and Makasi (M).

Discrete Stage	K Dips	K Party Mound Tape Time (min)	M Dips	M Party Mound Tape Time (min)	K Dips/min	M Dips/min
Stage 2	3	1711	NA	NA	0.002	NA
Stage 3	68	2900	94	6598	0.023	0.014

- **Is there an increase in novice attention to active fishers from Stage 2 to Stage 3?**

Metric: Total Dips w/ [*novice*] Attention (excludes Dips where [*novice*] Attention could not be determined), weighted by total Dips (excluding [*novice*]'s Dips) when [*novice*] was In-Party. Calculated separately for Stage 2 and Stage 3.

Result: **Yes.** The frequency of Kesi's gaze being directed toward another fisher's Dips doubled from Stage 2 to Stage 3 [X^2 (1, 2110)=16.59, *p* <.001]. Kesi was also more likely to be In-View of other fishers in Stage 3 as compared to Stage 2 [X^2 (1, 2110)=58.07, *p*<.001]. When considering only Dips for which Kesi was In-View, there was not a significant difference in Kesi's Attention rate between Stage 2 and Stage 3 [Fisher's exact test *p*=.142] (Figure 7). The increase in Attention was therefore attributable to increased exposure and proximity to active fishers during Stage 3, rather than an increase in Attention rate to In-View Dips generally. Makasi did not have a discrete Stage 2 recorded to compare Attention rates with Stage 3.

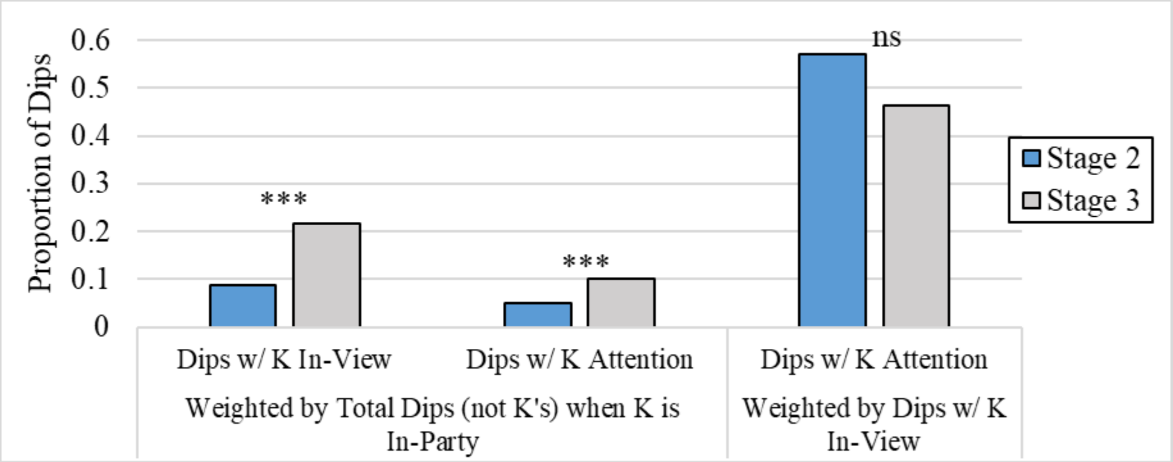

Figure 7: Kesi's (K) Attention rate to other fishers during discrete Stages 2 and 3. Dips for which Attention could not be determined were excluded. *** = *p*<.001. ns = *p*>.05

- **Does the frequency of tolerated scrounging increase from Stage 2 to Stage 3?**

Metric: Count of [*novice*]'s Directed Contacts weighted by total Bout time (excluding [*novice*]'s Bouts), when [*novice*] was In-Party. Calculated separately for Stage 2 and Stage 3.

Result: **Inconclusive**. Kesi's rate of Directed Contacts increased slightly from Stage 2 to Stage 3 (30.9% increase) (Table 5). Makasi did not have a discrete Stage 2 recorded to compare.

Table 5: Count of Directed Contacts for discrete Stages 2 and 3, for Kesi (K) and Makasi (M). [*Novice*]-Party Bout time includes all Bouts (except for those of the indicated novice) that were recorded while the indicated novice was on-exhibit.

Discrete Stage	K Directed Contacts	K-Party Bout Time (minute)	M Directed Contacts	M-Party Bout Time (minute)	K Dir. Cont./min	M Dir Cont./min
Stage 2	37	121	NA	NA	0.305	NA
Stage 3	87	218	16	576	0.399	0.028

- **Are <50% of Dips in Stage 4 performed with a probe tool?**

Metric: Count of [*novice*]'s Dips using probe tool during Stage 4, divided by all [*novice*]'s Dips in Stage 4.

Result: **Likely**. The proportion of tool Dips/all Dips in Stage 4 for was 37.5% (45/120) for Kesi, and 66.7% (10/15) for Makasi. Although Makasi's tool-use rate in Stage 4 was >50%, there was insufficient data to sufficiently power a statistical test. [Exact Binomial Goodness of Fit test, H_0: there is an equal likelihood of tool Dips and non-tool Dips in Stage 4, two-tailed: K: n=120, p=.008; M: n=15, p=.302].

- **Does the frequency of tool Dips increase from Stage 4 to Stage 5?**

Metric: Count of [*novice*]’s tool Dips weighted by [*novice*]’s total Dips. Calculated separately for Stage 4 and Stage 5.

Result: **Yes.** The proportion of Dips using a tool increased from Stage 4 to Stage 5 by 117.8% for Kesi and 29.9% for Makasi. A Fisher’s exact test found that this observed increase was significant for Kesi (*p*=<.001) but fell short of significance for Makasi (*p*=.058). A one-tailed Exact Binomial Goodness of Fit test found that in Stage 5, both Kesi (*n*=568, *p*<.001) and Makasi (*n*=134, *p*<.001) used tools when Dipping at a rate significantly higher than 50% (Figure 8).

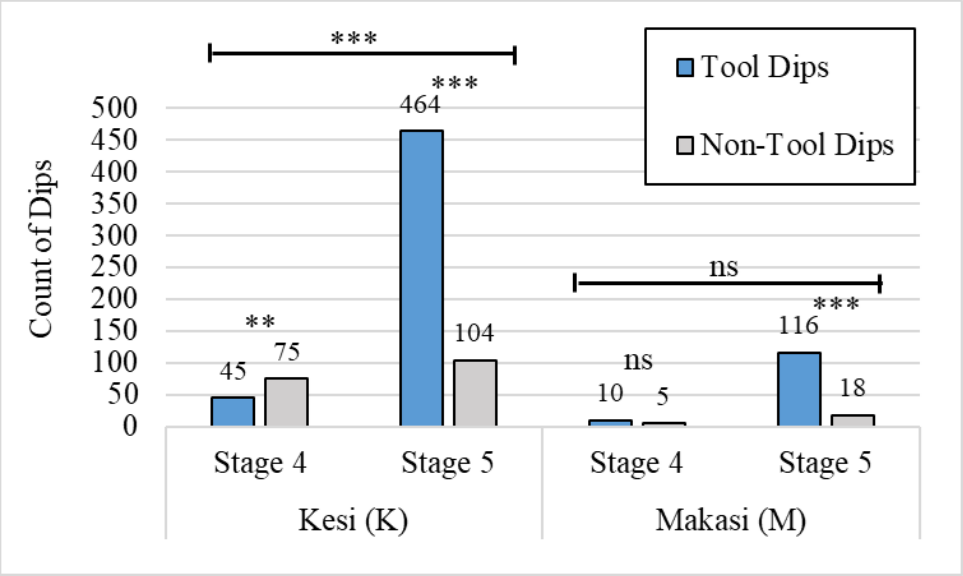

Figure 8: Comparison of tool Dips with non-tool Dips recorded during Stage 4 and Stage 5 for both novices. Numbers above columns indicate count (*n)* of Dips represented. ***=p<.001; **=p<0.01; *=p<.05; ns=Not Significant

- **Do novice probe tool Dips tend to be deeper in Stage 4 compared to Stage 5?**

Metric: Compare Shallow (≤25% of tool inserted during Dip) Dips, to Deep (>25% of tool inserted) Dips during Stage 4 and Stage 5.

Result: **Yes.** The proportion of Deep tool Dips increased from Stage 4 to Stage 5 for both Kesi (+55.7%) and Makasi (+563.6%). These increases were significant by Fisher's exact test for both Kesi (*p*=.002) and Makasi (*p*<.001) (Figure 9).

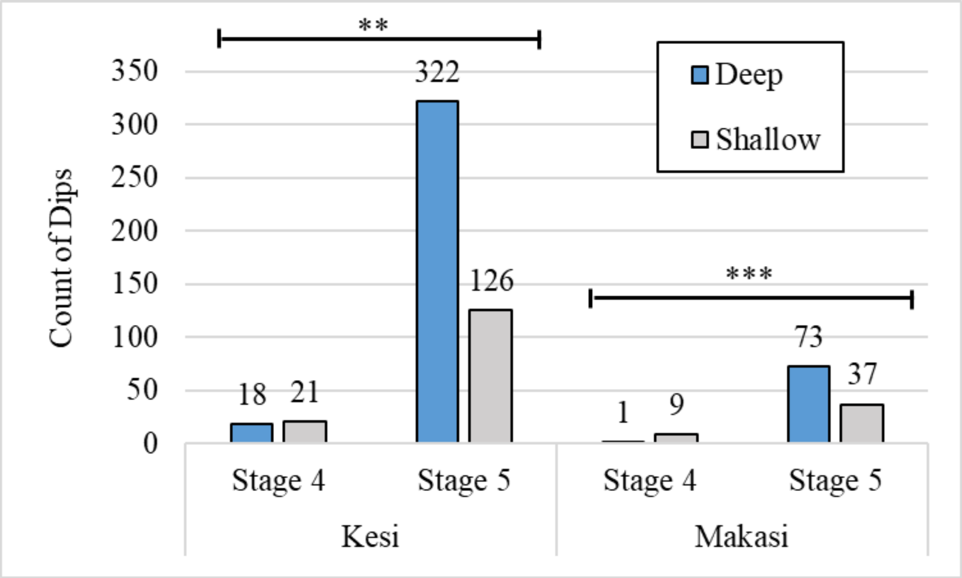

Figure 9: Count of Deep vs Shallow tool Dips Recorded during Stage 4 and Stage 5 for Kesi and Makasi. Numbers above columns indicate count (*n)* of Dips represented. ***=p<.001; ** =p<0.01; *=p<.05; ns=Not Significant

- **Are novice tool Dips more efficient in Stage 5 than in Stage 4?**

Metric: Compare mean duration of [*novice*]'s Full ("1_3") tool Dips in Stage 4 and Stage 5.

Result: **Yes**. Dip duration decreased from Stage 4 to Stage 5 for both Kesi (Stage 4: *M*=8.8 seconds, *SD*=6.4; Stage 5: *M*=5.4 seconds, *SD*=4.2) and Makasi (Stage 4: *M*=9.2 seconds, *SD*=10.4; Stage 5: *M*=6.8 seconds, *SD*=3.9). The decrease in average Dip duration, as compared by Welch's one-way ANOVA, was significant for Kesi [F(1, 34.15)=8.97, *p*=.005], but not for Makasi [F(1, 12.40)=0.64, *p*=.441] (Figure 10).

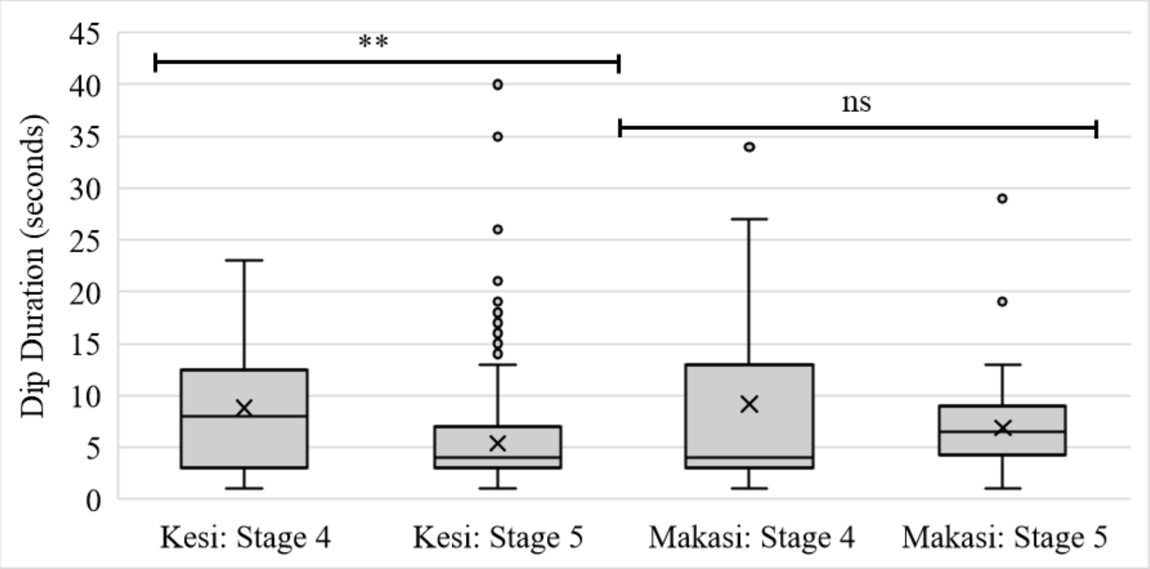

Figure 10: Mean Dip duration (seconds), by stage, for Kesi and Makasi. The boxplots show the median, the first and third quartiles, and the lower and upper extremes within the group. Only Full ("1_3") tool Dips were included. **=*p*<.01; ns = Not Significant

- **Does the Dip completion rate increase from Stage 4 to Stage 5?**

Metric: Count of Full tool Dips (coded as “1_3”, where “1”=Tool Insertion, “2”=Tool Removal, & “3”=Tool to Mouth) compared to Incomplete probe tool Dips (must include “1”: Insertion) for each novice in Stage 4 and Stage 5. Dips that did not include “1”: Insertion were not included.

Result: **Likely.** The percent of tool Dips that were completed increased for both Kesi and Makasi from Stage 4 to Stage 5. This increase was not significant for Kesi but was for Makasi [Fisher’s exact test: Kesi *(*p=.112); Makasi (*p*=.037)] (Figure 11).

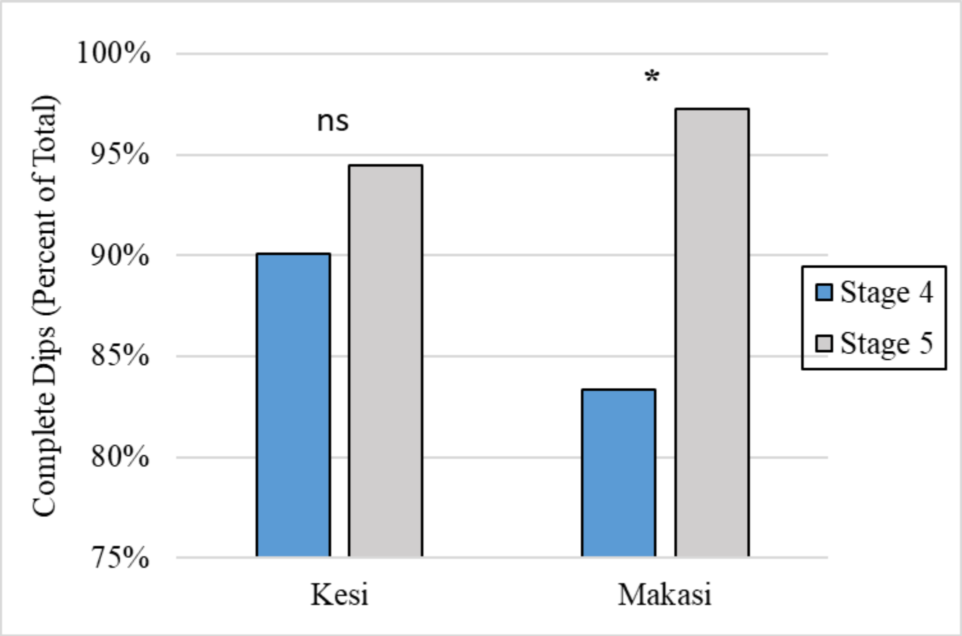

Figure 11: Percent of tool Dips completed, by stage, for Kesi and Makasi.
*=p<.05; ns=Not Significant

- **Does novice Tool Modification behavior change between Stage 4 and Stage 5?**

Metric: Count of Tool Modification sessions compared to active Bouts with probe tool and In-Party Mound-tape time in each stage.

Result: **Likely.** Relatively few Tool Modification sessions were recorded for the novices. Makasi was not recorded making or modifying tools in Stage 4 and had four Tool Modification sessions in Stage 5. Kesi's frequency of Tool Modification increased in Stage 5 relative to both her number of probe tool Bouts (+68.4%) and her In-Party Mound-tape time (+348.7%). More data is needed to confirm. (Figure 12).

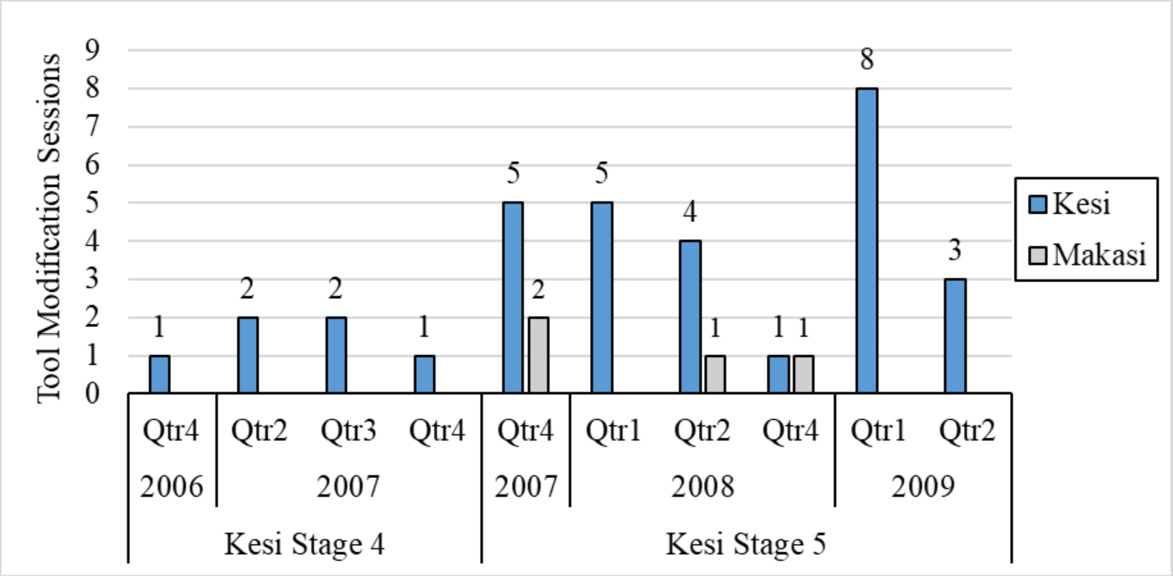

Figure 12: Count of Tool Modification sessions recorded, by date and Kesi's Developmental Stage. Neither novice was recorded making or modifying tools prior to reaching Stage 4. All of Makasi's Tool Modifications were recorded during his Stage 5.

- **Do novices choose Long tools more often in Stage 5 than in Stage 4?**

Metric: Count of [*novice*]’s Dips using a Short (<fisher’s arm length) tool, compared to Dips using a Long (≥fisher’s arm length) tool in Stages 4 and 5.

Result: **No.** Tool length did not significantly vary for either novice between Stage 4 and Stage 5 [Fisher’s exact test: Kesi (*p*=.415); Makasi (*p*=1.000)] (Figure 13).

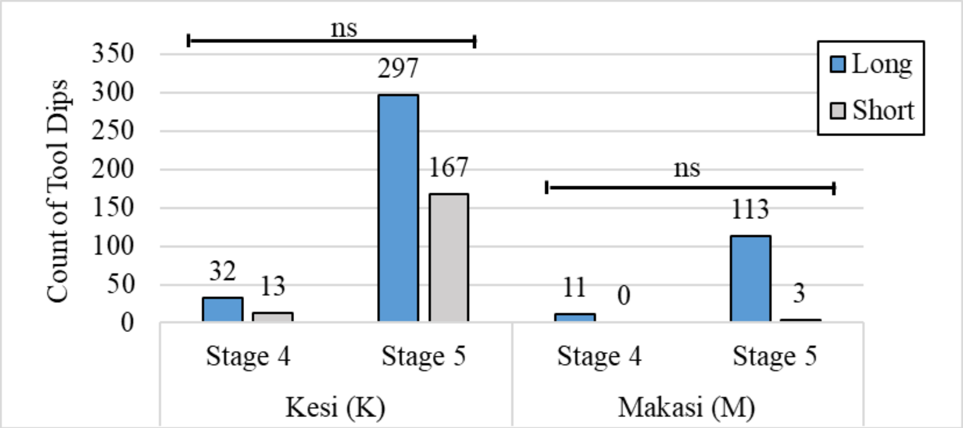

Figure 13: Count of tool Dips involving either a Long or Short tool for both novices during their respective Stage 4 and Stage 5 periods. ns=Not Significant

When fishing, the bonobos typically chose a probe tool and then used that same tool for multiple Dips performed in a series. The tool used in each Dip is therefore not independent of that used in previous Dips. To control for this “choice” amplification, I also compared Kesi and Makasi’s tool *choice* for Stage 4 and Stage 5 Bouts. “Chosen” tools were identified as any new tool used during clip (i.e. all Dips with a “Tool Origin” other than “Previous Dip, Same Individual”). The distribution of novice choice of Short or Long tools did not substantially differ from that for all Dips, and there was no significant difference between the lengths of probe tools *chosen* in Stage 4 vs. Stage 5 [Fisher’s exact test: Kesi (*p*=.765); Makasi (*p*=1.000)].

- **Do novices choose Suitable[1] tools more often in Stage 5 than in Stage 4?**

Metric: Count of Dips using a Suitable tool, compared to the count of Dips using a Poor tool in Stage 4 and Stage 5 for each novice.

Result: **No.** Tool suitability did not significantly vary between Stage 4 and Stage 5 by a Fisher's exact test for either Kesi (*p*=.519) or Makasi (*p*=.130) (Figure 14). The relative frequencies of "chosen" Suitable tools vs those used in Dips for each stage were also not significantly different by a Fisher's exact test (Kesi Stage 4: *p*=0.676; Stage 5: *p*=.166; Makasi Stage 4: *p*=1.000; Stage 5: *p*=1.000).

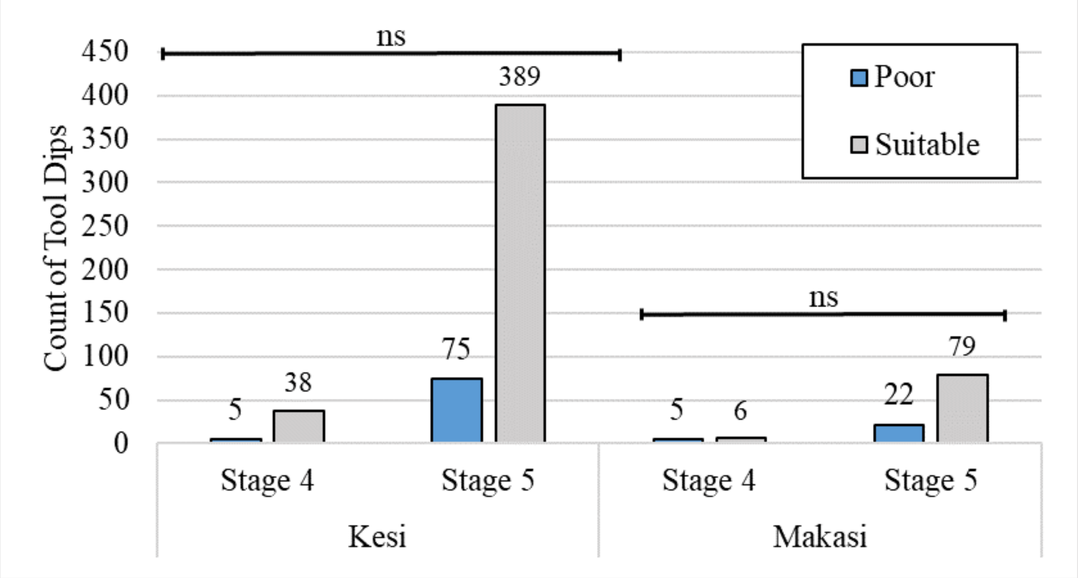

Figure 14: Count of Suitable tools compared to Poor tools used in Dips by each novice during their respective Stages 4 and 5.Numbers above the columns indicate the count (*n*) of Dips represented. ns=Not Significant.

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[1] A "Suitable" tool is defined as a stick or branch that is longer than subject's fingers, has had (most) leaves and side twigs stripped off, and is not so wide, crooked, or flexible so as to be difficult to insert into mound for a successful Dip, i.e., "Poor".

1.4 Discussion

The identified Developmental Stages (Table 2) provide a useful framework to explore the nuances of the developmental progression observed for the young bonobos. As the number of novice subjects followed in the study was unavoidably small, the conclusions drawn should not be considered universally applicable to young bonobos. This case study, possibly the first of its kind, should instead be considered a starting point on which to build future comparative research.

Although each progressive Stage involved the addition of new behaviors and a shift away from others, there was considerable behavioral fluidity throughout the study. This was particularly true for Kesi; after becoming a competent fisher herself (Stage 5), Kesi was observed being carried to the mound and merely observing her mother fish as she had in Stage 1 (Figure 6). Kesi also exhibited an extended transition period between inexpert (Stage 4) and expert (Stage 5) fishing, continuing to perform amateurish bouts through the end of the study despite contemporaneously demonstrating adult-level competency. This more nuanced picture of the progression of skill development provides unique insight into the cognitive, physical, and motor control changes that young bonobos undergo as they age.

Of particular interest was the comparative evaluation of juvenile bonobo and chimpanzee tool-use skill development in naturalistic social settings. The observed developmental progression observed for the two captive bonobos was similar in several respects to that documented for probe-fishing chimpanzees. The ages at which the two juvenile bonobos first performed identified critical fishing skill components were comparable to those of termite-fishing wild chimpanzees at Gombe, Tanzania, and both populations appeared to follow the same general order of acquisition (Lonsdorf, 2005). A separate study of chimpanzees in Bossou found that juveniles first successfully probe fish for ants between 2 and 3 years of age (Humle & Matsuzawa, 2002). This range, though skewed both younger and more compactly than that observed at Gombe, was also similar to what was observed for our two captive bonobos. Both the general developmental progression and age of skill attainment appear to be highly analogous for juveniles of both species.

Although both bonobos were within the range of that recorded for juvenile chimpanzee probe-fishers, Makasi often lagged behind Kesi in exhibiting these critical behaviors. These gaps may reflect the social discrepancies in access and opportunity between the juveniles; Makasi did not have the benefit of the close mother-offspring relationship that Kesi enjoyed[2], and therefore may not have been tolerated at a level that facilitated contacts with active fishers and their tools. It also may be a consequence of deficiency in the study data; the 11-month gap in filming coincided with the period when Makasi began locomoting on his own, and important milestones were likely missed. Both these factors likely contributed to the comparative paucity of Stage 1 and Stage 2-type activity recorded for Makasi, as illustrated in Figure 6.

The effect that increased access to fishing models has on the learning trajectory of juvenile *Pan troglodytes* has also been explored. Juvenile chimpanzees at Bossou who had less exposure to fishing adults (“low learning opportunity”) were approximately a year older (2.9-3.0 years) on average at their first fishing success than those with more exposure (2.1-2.3 years) (Humle, Snowden, & Matsuzawa, 2009). This closely accorded with the experience of the naive captive bonobos; Makasi, who had significantly less exposure to the termite mound and active fishers in his youth was first recorded successfully fishing at 3.1 years old, compared to the higher-exposure subject, Kesi, who first dipped at 2.2 years old.

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[2] For more details on the type and level of interactions between the focal juveniles and their fishing models, see Chapter 2: Novice-Model Interaction pp. 35-68.

Interestingly, despite spending less time interacting with the mound, observing active fishers, and manipulating probe tools than Kesi, Makasi exhibited fishing competence (Stage 5) at approximately the same age as Kesi. This phenomenon was also observed for captive honey-fishing chimpanzees; juveniles who did not spend as much time watching adults fish were successful at about the same age as young who had more exposure (Hirata & Celli, 2003). Both observations suggest that the timing of adult-level tool-use for *Pan* juveniles may also be contingent on physical, rather than purely social, development. Indeed, observations of chimpanzees that use probes to extract honey from the underground nests of stingless bees, a particularly complex task, found that juveniles attempted adult-like techniques prior to developing the strength and size to effectively execute them (Estienne, Stephens, & Boesch, 2017). Juveniles of both species may comprehend the methodology of the particular fishing task prior to developing the physical ability to properly, and consistently, manipulate probes. These observed similarities may indicate that both species, despite their myriad *in situ* behavioral variations, share a common ontogeny for behavioral patterns involved in tool-use.

Chapter 2 Novice-Model Interaction

2.1 Introduction

Studying the commonalities and divergences of tool-use between groups and species continues to provide new insight into the origins, cognitive implications, and evolution of tool-use in both humans and animals (Biro, Haslam, & Rutz, 2013). For highly social species such as chimpanzees (*Pan troglodytes)* and bonobos (*Pan paniscus)*, the interplay between individual and social learning is still being explored. Chimpanzees have been documented using tools in more contexts than any other animal, with a large variation of tools and associated behaviors across different genetic populations and geographical ranges (McGrew, 1992; Shumaker, Walkup, & Beck, 2011; Whiten, et al., 1999; Boesch & Boesch-Achermann, 2000; Sanz & Morgan, 2007). Fewer variations of tool-use have been reported from bonobo field sites (Hohmann & Fruth, 2003; Kano, 1982; Ingmanson, 1996) and tool-use repertoires between the two species are particularly disparate in feeding contexts in the wild (Furuichi, et al., 2015; White, Waller, Cobden, & Malone, 2008). Despite this distinction, bonobo tool-use in captivity is comparable to that of chimpanzees (Gruber, Clay, & Zuberbühler, 2010). Further comparative research of these two species is key to understanding how differences in social tolerance and group dynamics affect the type and impact of social learning (van Schaik, 2003; Coussi-Korbel & Fragazy, 1995).

Considerable research into the processes by which juvenile chimpanzees learn complex technical skills has been published. Nut-cracking by wild chimpanzees in Bossou, Guinea was observed to be transmitted via a process described as “education by master-apprenticeship"; a combination of the master's high tolerance for the close proximity of, scrounging by, and interference from a juvenile apprentice (Matsuzawa, et al., 2001). This process allows for close observation and exploration by the apprentice of the tools and techniques exhibited by the master. This level of access and reinforcement may be required for most young chimpanzees to become proficient in complex tool-usage. In an experiment that loosely replicated this environment, young chimpanzees that closely observed expert adults dip for honey later chose the more efficient tools favored by their models, and did so earlier in their own fishing attempts than the adults had (Hirata & Celli, 2003). A longitudinal study of termite fishing by wild chimpanzees at Gombe found that young females spent significantly more of their time watching adults fish than young males did (Lonsdorf, 2005). Those females became proficient fishers earlier than the males and exhibited fishing techniques (as measured by length of tool chosen) that mirrored their mothers'. The slower-to-learn males tended to use less effective, shorter tools regardless of their mother's preference, and their dip success was correspondingly lower. These observations were further reinforced by a 2009 study of ant-dipping by young chimpanzees at Bossou (Humle, Snowden, & Matsuzawa, 2009).

Due to their lower population size in both native habitats and captivity, fewer studies into the learning mechanisms for young bonobo novices has been possible, particularly in naturalistic social contexts (Gruber & Clay, 2016). One such study involved the introduction of a baited artificial termite mound to a captive bonobo group at the Columbus Zoo and Aquarium (CZA) (Boose, White, & Meinelt, 2013). The bonobos were observed as they explored the mound and developed fishing strategies unaided by their human caretakers. Although the bonobos ranged in age from 0.5-32 years, no particular attention was paid to the juveniles in the group; in fact, for many analyses, subjects younger than 5 were excluded altogether. The authors did note that one low-ranking adult male appeared to lean to fish primarily via observation of others, rather than the socially mediated trial-and-error process presumed for the other bonobos, but as the ontogenetic process was not the primary focus, more detailed information on individual learning process and attention to others was not included.

In this study I intend to build on the comparative analyses of Boose, White, & Meinelt (2013) using Lonsdorf's (2005) research in Gombe as a guide. To evaluate the effect of expert fisher activity on the novices'[3] skill acquisition, special attention was paid to novice proximity, attention, and interactions with active fishers. This additional data enabled identification of apparent models for each of the novices. It also provided a detailed record of fishing-related social behaviors among the juveniles, which appear to be strongly affected by social status and maternal relationships.

In addition, I will evaluate whether any observed behavior qualifies as teaching, according to the functionalist approach outlined by Caro and Hauser (1992), which lays out three criteria: 1) The behavior is performed in the presence of a novice learner, 2) the behavior has no added benefit or some cost to the teacher, and 3) the behavior facilitates learning. As functional teaching has rarely been identified in great-apes (Boesch, 1991), I will focus on tool-transfer, which recent studies have identified as suggesting teaching in chimpanzees (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016). This, along with the

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[3] Despite being a proficient fisher at the start of the study, the additional "novice" tiers were applied to Mchumba due to her status as a juvenile according to Kano's (1982) age class definitions (infant: 0–1; juvenile: 2–6; adolescent: 7–14; adult: 15). Select analyses for Mchumba are included to provide context and additional data. Evaluations of the two novices that include Mchumba will refer to all three subjects as "juveniles" rather than "novices".

identification of possible instances of stimulus and local enhancement, will be combined with the longitudinal study of the novices' skill development and granularity of individual techniques to provide a more complete understanding of the social learning of young bonobos.

2.3 Methods

Interactions between the three juveniles (novices Kesi (K) and Makasi (M), and expert juvenile Mchumba (B)) and all active fishers were primarily assessed by recording juvenile proximity and attention states for every recorded Dip. Uniform standards for identifying the start and end of each Dip were applied, and each juvenile's proximity was scored ordinally (only the closest observed proximity during the Dip was recorded). The four proximity zones were as follows, from furthest to closest: "Out-of-Frame", where the juvenile was not in frame at any point during the Dip; "Out-of-Easy-Reach", defined as when the juvenile was In-View, but was not within an arm or leg length of the active fisher during the Dip; "Close", defined as when juvenile *was* within easy reach but was not in indirect physical contact with the fisher; and "Indirect Touch", defined as being close enough to the fisher to make body contact, but excluding "Directed Contacts", or touching that resulted from one party intentional reaching out with a hand or foot towards the other. The most common "Indirect Touches" were offspring being ventrally or dorsally carried by fishing mothers.

Attention to Dips were similarly scored for each juvenile. Attention was achieved if the juvenile's gaze was directed towards an active fisher for any duration during a Dip.

In addition to proximity and Attention, physical interactions between juveniles and active fishers were also captured. These "Directed Contacts" were divided into two types, "Hand" and "Mouth". "Hand" contacts encompassed intentionally touching the active fisher or their probe tool, while "Mouth" contacts captured successful tolerated scrounging (getting food from another animal) by the juvenile. Each "Directed Contact" that was recorded during a Bout was annotated based on the specifics of the action performed. All Directed Contact annotations were ordinally ranked based on the estimated cost to the fisher/benefit to the juvenile. Touches were ranked based on the extent that the juvenile impeded fishing activity (e.g., touching the fisher was lowest, firmly gripping the fisher's probe, which often fully paused an in-progress Dip, was higher). Food or tools taken by a scrounging juvenile were considered to represent both a higher cost to the fisher and greater benefit to the juvenile scrounger than other touches. For continuous "Hand" contacts that could encompass several annotations (e.g., juvenile begins by co-touching a fishing probe but then takes possession of the probe) only the highest ranked action was annotated. Details on Directed Contact Segmentation and Annotations can be found in Appendix I: Scoring Tier Structure and Ethogram, pp. 110 & 114.

Some actions were analyzed in relation to the Developmental Stage of the juvenile in question. The Developmental Stages (as described above in Table 2) are Passive Interaction (Stage 1), Active Interaction (Stage 2), Independent Exploration (Stage 3), Inexpert Fish (Stage 4) and Expert Fish (Stage 5). Characteristics and individual ages for each Stage are detailed in pp. 14-20.

Differences within frequency data set categories were compared using Fisher's exact tests of independence where possible, while Chi-square tests of independence were reserved for frequency data with more than two values per nominal variable, or when the sample size was too large to run a Fisher's exact test (typically n>1000). Analysis of variance tests (ANOVA)s were used to test for significant differences in means. Post-hoc analyses of ANOVAs were run using Tukey-Kramer tests. Relationships between two measurement variables were evaluated using Pearson correlation tests.

2.4 Results

2.4.a Juvenile Party Composition

To understand the group dynamics that would affect access to skilled adults, party compositions for the recorded mound activity were compiled for each juvenile. Kesi and Makasi were included in most of the 310 filmed parties (K: 85.8%, M: 71.0%) and were on-exhibit for the majority of the approximately 200 “Mound tape” hours filmed (K: 91.6%, M: 80.2%[4]). Mchumba, who unlike the younger novices was not a primary film target, was included in 51.3% of the recorded parties and 50.2% of the total film time. Exposure to other group members varied for each juvenile (Figure 15). Kesi and Makasi were often on-exhibit together (76.7% of the parties that included either included both), and so largely had similar access to group members and fishing activities during the study.

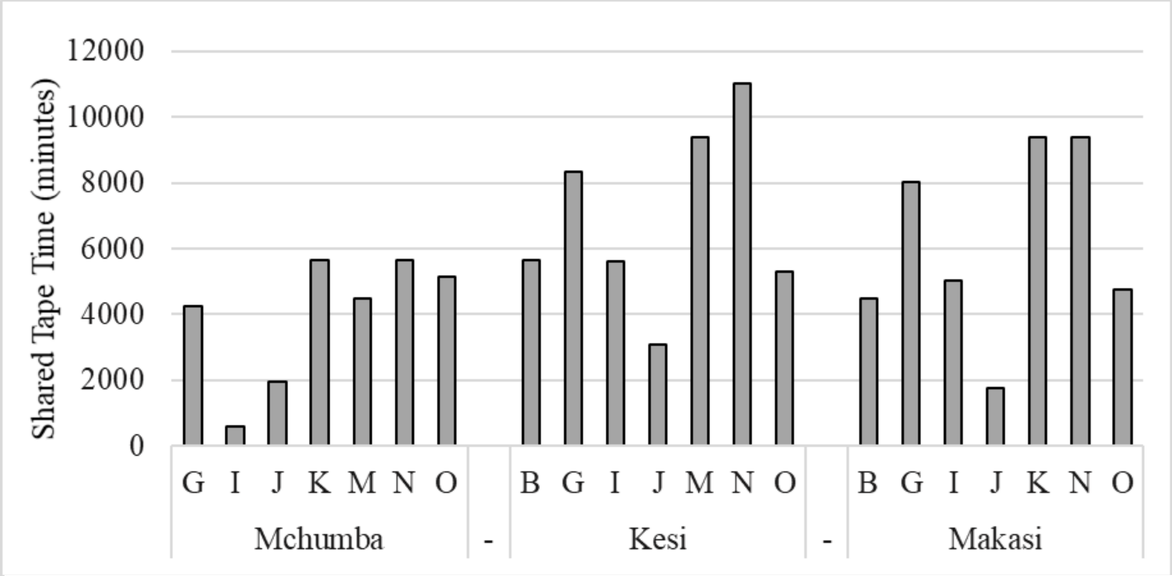

Figure 15: Amount each subject was In-Party with each juvenile, in “Mound tape” minutes. Total juvenile In-Party time: B: 6,041 min; K: 11,058 min; M: 9,687 min.

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[4] The actual time that Makasi was on-exhibit during filming may be less than recorded. Makasi was occasionally (verbally) noted as having joined the party after filming had begun but was recorded as being in the party for the entirety of the filmed period.

2.4.b Juvenile Proximity During Active Bouts

Party affiliation alone was not indicative of which subjects were most likely to serve as fishing models. Comparison of the proportion, by subject, of Dips recorded while a juvenile was on-exhibit with the proportion of those Dips for which the juvenile was In-View illustrates juvenile inclination to associate with specific fishers, irrespective of opportunity (Figure 16). For example, Lolita (O) performed 33.1% of the Dips recorded while Mchumba was on-exhibit but accounted for more than twice as many (69.2%) of the Dips for which Mchumba was In-View, a 2.09X increase over expected In-View Dips [X^2 (1, 1322)=341.00, $p<.001$]. Kesi was In-View for Lana's (N) Dips 2.59X more than expected [X^2 (1, 4910)=1037.45, $p<.001$] and was also more likely to be In-View of Junior's (J) Dips, albeit to a lesser extent (1.30X higher In-View than expected) [X^2 (1, 4910)=17.33, $p<.001$]. The subjects for whom Makasi was more likely to be In-View were Mchumba (1.48X over expected [X^2 (1, 4866)=60.84, $p<.001$]) and Lolita (1.83X over expected [X^2 (1, 4866)=39.84, $p<.001$]).

In addition to being In-View during a Bout, the amount of time juveniles spent within easy reach to an active fisher may indicate whether those fishers functioned as models. The only juvenile-expert pairs where the juvenile was both significantly more likely to be In-View and significantly more likely to be Close+ (either Close or Indirect Touch) during the expert's Dips were the two mother-daughter pairs; Lolita and Mchumba (1.17X more Close+ Dips than expected [X^2 (1, 403)=36.61, $p<.001$]) and Lana and Kesi (1.57X more Close+ Dips than expected [X^2 (1, 1465)=327.22, $p<.001$]). Overall, Mchumba was Close+ to 58.6% (236/403), Kesi was Close+ to 48.5% (710/1465), and the male Makasi was Close+ to 23.5% (146/620) of their respective In-View Dips (Figure 16).

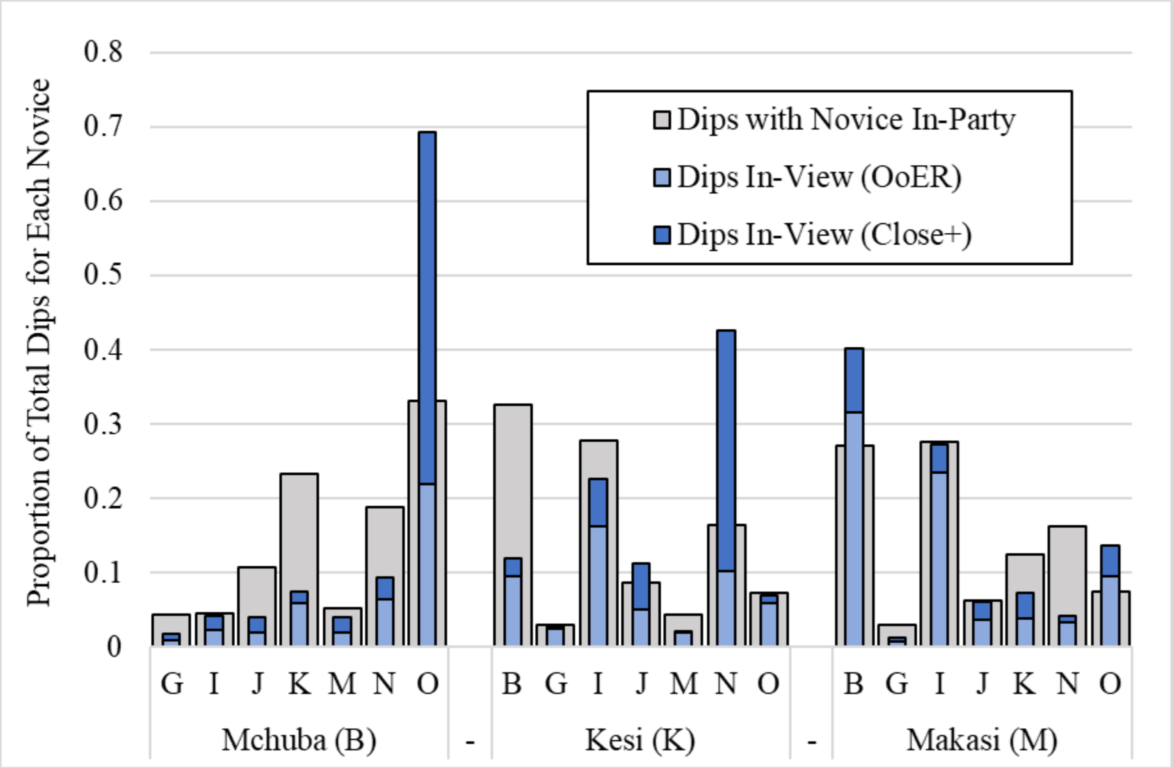

Figure 16: Proportional representation by subject of all Dips recorded when each juvenile (Mchumba (B), Kesi (K), or Makasi (M)) was In-Party (wide gray bars) contrasted with the relative proportion of all Dips for which each juvenile was In-View (narrow blue bars). In-View Dips were further broken down by closest juvenile proximity during each Dip; Out of Easy Reach (OoER; light blue) or Close+ (within easy reach, coded as either "Close" or "Indirect Contact"; dark blue).

Increased proximity to active fishing relative to opportunity identified that the likely primary models for each of the juveniles followed were Lolita (for Mchumba), Lana (for Kesi), and Mchumba as well as possibly Lolita (for Makasi).

2.4.d Novice Proximity to Models Over Time

The longitudinal nature of the study allowed for analysis of novice-model interaction during the different learning periods of the two youngest members (Figure 17). For Kesi, the breakdown by Developmental Stage confirmed Lana as her primary fishing model during all stages (Stage 1-3: 5.47X more In-View Dips than expected [X^2 (1, 2289)=855.34, *p*<.001]; Stage 4: 1.97X more than expected [X^2 (1, 1501)=234.53, *p*<.001]); Stage 5: 1.66X more than expected [X^2 (1, 1120)=141.38, *p*<.001]. Lana was the only significantly overrepresented subject during Kesi's primary learning period (Stages 1-4).

In Stage 5, after Kesi had acquired the skills to successfully fish at the mound, Lana's influence share decreased from ~50% of Kesi's In-View Dips to 32.6%. This relative decrease is partially attributed to Junior, who represented 20.4% of Kesi's Stage 5 In-View Dips, significantly above expected (1.13X more In-View Dips than expected [X^2 (1, 1120)=5.13, *p*=.023]). Lolita also represented a disproportionate, but smaller share, of Kesi's Stage 5 In-View Dips (5.9% (36/607) of Kesi's In-View Dips, 1.58X more In-View Dips than expected [X^2 (1, 1120)=17.46, *p*<.001]).

When comparing In-View Dips by Developmental Stage, the only subjects for whom Kesi was Close+ significantly more than expected were Lana, in each of Kesi's Developmental Stages (All *p*<.001, by Fisher's exact test), and Junior when Kesi was in Stage 5 (*p*=.002, by Fisher's exact test). The analysis of which fishers Kesi was most likely to be near over time, particularly in the period before Kesi was a proficient fisher, confirm that Lana likely served as her primary model.

In contrast to Kesi, Makasi's identified models were far less stable across Developmental Stages. In Stage 3, Makasi was more likely to be In-View of Dips by

Mchumba (1.53X more than expected [X^2 (1, 3241)=61.76, *p*<.001]) and Lolita (1.98X more than expected [X^2 (1, 3241)=42.08, *p*<.001]). This corresponded with Makasi's likely models being identified as Mchumba and Lolita as detailed on p. 43. During Stage 4, however, while Makasi was still more likely to be In-View of Dips by Mchumba (1.54X more than expected [X^2 (1, 202)=9.88, *p*=.002]), Mchumba made up a smaller share of both Makasi's In-Party Dips (Stage 3: 35.5%; Stage 4: 26.7%) and In-View Dips (Stage 3: 54.2%; Stage 4: 41.3%). Lolita was not recorded fishing while Makasi was on-exhibit during Stage 4 at all. Instead, Ikela accounted for a plurality (46.0%) of Makasi's Stage 4 In-View Dips (1.90X more than expected [X^2 (1, 202)=10.96, *p*<.001]).

In Stage 5, Ikela again made up nearly half (44.7%) of Makasi's In-View Dips (1.95X more than expected [X^2 (1, 1423)=43.07, *p*<.001]). Makasi was still disproportionately likely to be In-View of Dips by Mchumba (1.73X more than expected [X^2 (1, 1423)=10.88, *p*<.001]) and Lolita (2.41X more than expected [X^2 (1, 1423)=14.80, *p*=.001]), but Mchumba and Lolita combined accounted fewer (21.8%) of Makasi's Stage 5 In-View Dips than they had in Stages 3 (45.3%) and 4 (26.7%). Junior accounted for 11.4% of the Dips Makasi was In-View during Stage 5, but this was not significantly more than expected based on his amount of In-Party Dips during that period (1.18X more than expected [X^2 (1, 1423)=1.44, *p*=.230]).

When comparing the proportion of Out of Easy Reach Dips to Close+ Dips by Fisher's exact test, the only fishers for whom Makasi was Close+ more often than expected were Kesi (*p*<.001) and Junior (*p*=.004), both when Makasi was in Stage 5. Makasi was not significantly more likely to be Close+ to any particular fisher during his primary learning period (Stages 3 & 4).

The analysis of Makasi's proximity to active fishers over time indicates that Makasi had multiple models whose influence varied across his Developmental Stages. Although Makasi was preferentially close to Mchumba and Lolita in all Stages, his access to both decreased once he started attempting to use a probe tool to fish. Ikela became a comparatively more prominent model beginning in Stage 4, but Makasi became proficient fairly quickly and was exposed to relatively few Dips before he reached Stage 5. Overall, Mchumba accounted for the majority of Dips that Makasi was In-View of, and Close+ to, during his primary learning period and by that metric can likely be considered his primary model. Lolita and Ikela appear to be secondary influences based on Makasi's overall access and proximity to their fishing behavior.

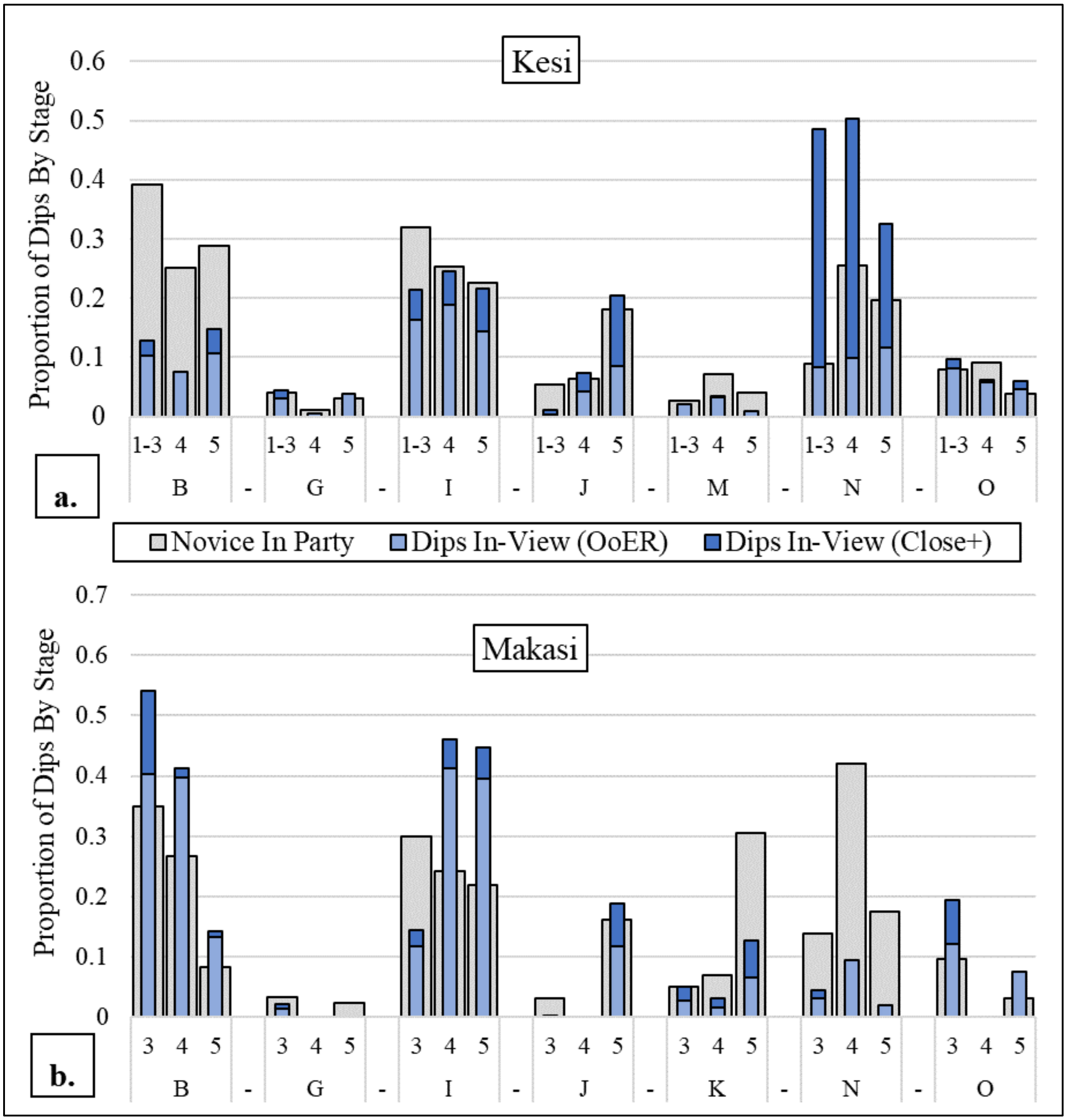

Figure 17: Proportional representation by subject and Developmental Stage for Dips when the novices were In-Party (wide gray bars), contrasted with the proportion of Dips for which the novice was In-View (narrow blue bars). In-View Dips were broken down by novice proximity to the subject; Out-of-Easy-Reach (OoER; light blue) or Close+ (within easy reach, coded as either "Close" or "Indirect Contact"; dark blue). Dip counts represented per Stage (# [*novice*] In-View/ # [*novice*] In-Party): a. Kesi [Stage 1-3:(369/2289); Stage 4: (489/1501); Stage 5: (607/1120)] and b. Makasi [Stage 3: (360/3241); Stage 4: (63/202); Stage 5: (197/1423).

2.4.e Juvenile Attention to Models

Proximity to active fishers can provide clues as to which subjects serve as models, but ultimately, attention is required for bonobos to learn about fishing via observation. Juvenile Attention, defined in this study as orienting the head toward an active fisher at any point during a Dip, was scored for each Dip for which a juvenile was In-View.

Kesi and Makasi displayed similar average Attention rates overall. Kesi Attended to 52.7% (682/1294) of her In-View Dips, and Makasi Attended to 53.9% (263/488). The older Mchumba Attended to only 46.6% (162/348) of the Dips she was present for, however the difference between the In-View Attention rates of the three juveniles was not significant [X^2 (2, 2130)=5.10, *p*=.078]. Attention rates to In-View Dips decreased with age, *r*(20)= -.71, *p*<.001 (Figure 18).

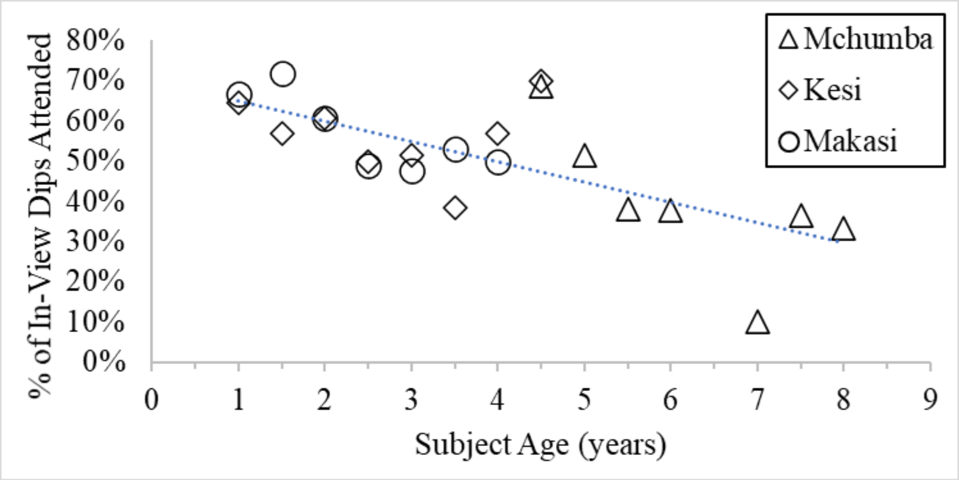

Figure 18: Attention rates, by age, of In-View Dips for all three juveniles. The dotted line represents the linear fit of all data points.

When only Close+ Dips were included, the Attention rate increased for all three juveniles. Kesi's Close+ Attention rate was 70.1% (442/630), Makasi's was 88.4% (114/129), and Mchumba's Attention rate increased to 57.7% (127/220). In contrast to all In-View Dips generally, the observed individual Attention rates for Close+ Dips did differ significantly, both among the three [X^2 (2, 979)=36.33, $p<.001$] and between each pair [Fisher's exact test (Bonferroni adjusted alpha level: $\alpha=0.017$); All pairs: $p<.001$].

For all three juveniles, the majority of the Dips they Attended to were performed by their respective models, as determined by the prior proximity evaluations (B: O; K: N; M: B, O and I) (Figure 19). When only Close+ Dips were evaluated, these identified models accounted for an even larger percentage of the Attended Dips[5].

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[5] The only outlier in this trend was between Ikela and Makasi; Ikela made up a smaller percentage of Makasi's Attended Close+ Dips than of his Attended In-View Dips. This aligns with the proximity results, as Ikela made up 27.3% of Makasi's In-View Dips, but only 15.7% of his Close+ Dips.

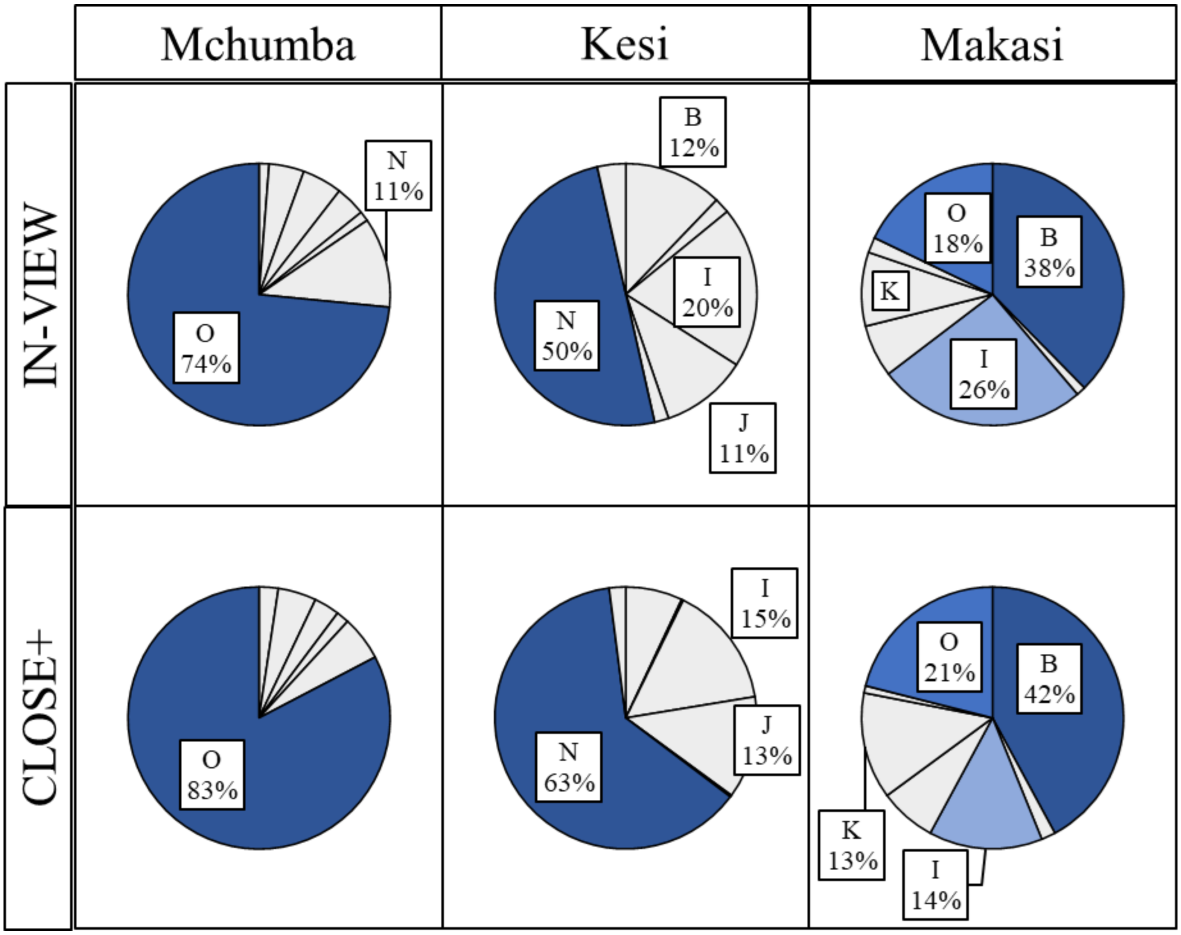

Figure 19: Proportional representation by subject of the Dips Attended to by each juvenile. Relative Attention is shown for both all In-View Dips and the subset for which the juvenile was Close+" (within easy reach, coded as either "Close" or "Indirect Contact"). Blue shading indicates identified models, with darker shading indicating more primary models. Labels were included for all subjects that represented >10% of indicated Dips.

2.4.f Directed Contacts

Physical interaction with active fishers and their tools may increase the salience of the benefits and nuances of probe dipping for juveniles. To understand the level of toleration exhibited by the San Diego Zoo bonobo group, all Directed Contacts by juveniles toward subjects during a Bout, including those resulting in tolerated scrounging, were recorded by contact type, specific action, and level of estimated relative cost to the fisher and/or benefit to the juvenile (Table 6).

The majority of the 358 Directed Contacts recorded occur between the two mother-daughter pairs, Lana-Kesi (*n*=238) and Lolita-Mchumba (*n*=76). Mchumba had only one non-mother Directed Contact, while Kesi was recorded Contacting all group members except for Lolita. Makasi, having no mother present, had far fewer Directed Contacts. Of his 17 recorded Directed Contacts, 15 were directed at his primary model Mchumba, and the remaining 2 were directed at Kesi in a play context.

The rate of Directed Contacts, calculated as the number of Directed Contacts divided by the total Bout time[6] of the Contacted fisher, varied individually and over time (Figure 20). Kesi's overall Contact rate was the highest (0.32 Contacts/minute), followed by Mchumba (0.27 Contacts/minute). Makasi had the lowest overall Directed Contact rate (0.02 contacts/minute). When excluding her Contacts with Lana, Kesi's Contact rate was closer to Makasi's, at 0.04 Contacts/min.

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[6] Only Bouts for which the juvenile in question was In-Party were included.

Table 6: Ethogram of the types of Directed Contacts performed by the three juveniles. "*n*"= total counts of each behavior recorded. "Rank" refers to the estimated relative cost to the fisher and/or benefit to the juvenile of each contact type, with "1" being the least costly.

Category	**Directed Contact**	**Description**	***n***	**Rank**
Hand	Touch Subject	Juvenile contacts fisher with a directed touch with hand or foot during Bout	108	1
	Touch Tool	Juvenile touches fisher's tool with hand or foot (fisher not in current possession of tool, but tool ownership is clear AND fisher's Bout is still on-going)	3	2
	Co-Touch Tool	Juvenile touches fisher's probe tool with hand or foot (fisher maintains possession, the touch is not a "grab")	81	3
	Co-Hold	Fisher and attendant juvenile grip probe tool simultaneously (juvenile "grabs" tool held by fisher)	44	4
	Take	Co-Hold that ends with juvenile taking possession of probe tool from the fisher	16	7
Mouth	Eat From Own Hand	Juvenile touches fisher or fisher's tool followed by the juvenile bringing that hand to their mouth	51	5
	Eat from Subject's Hand	Juvenile's mouth touches fisher's hand during (or soon after) a Dip	2	6
	Eat from Subject's Tool	Juvenile's mouth touches fisher's tool while the tool remains in the fisher's possession	53	6

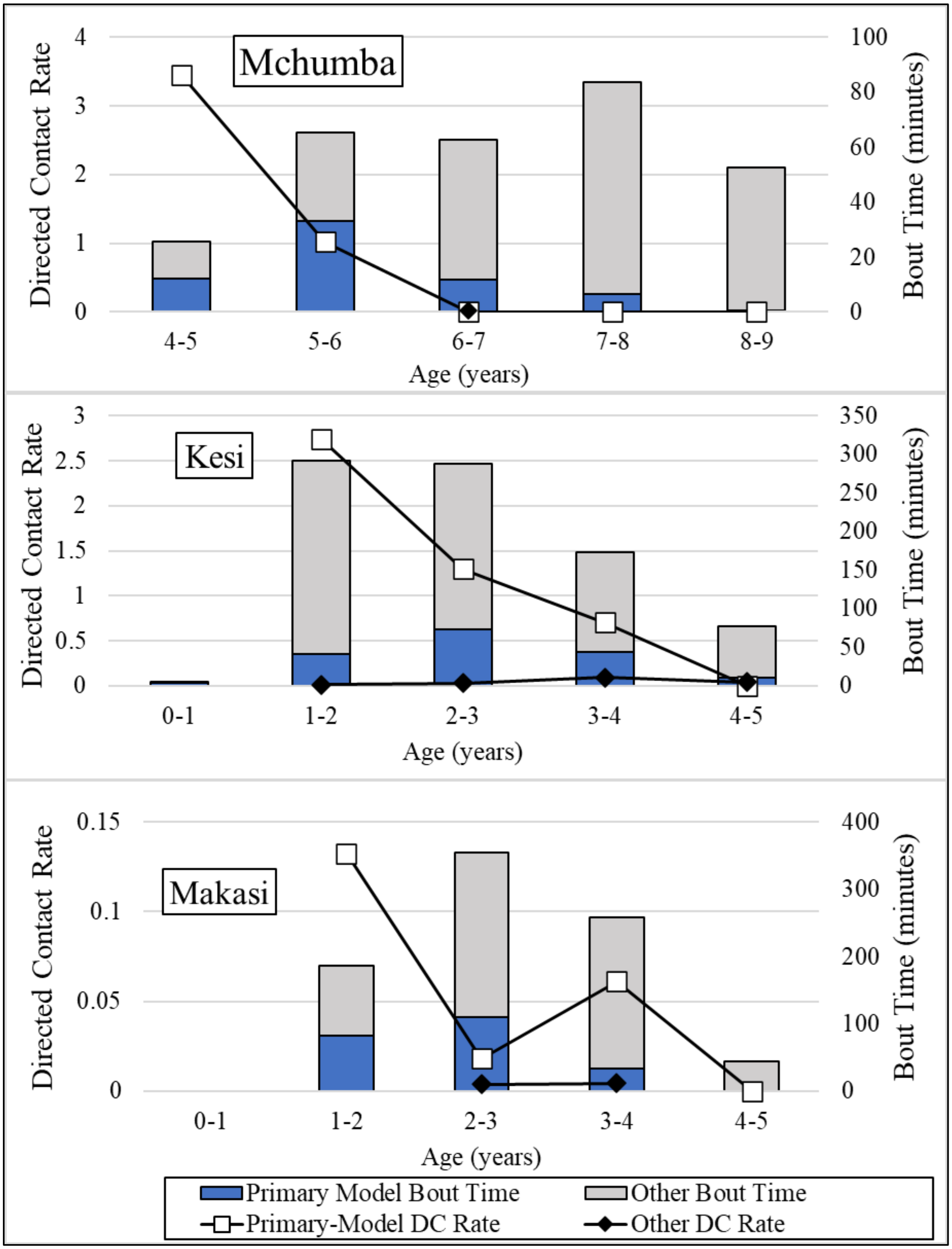

Figure 20: Directed Contact (DC) rates of the three juveniles, by age. Rates were calculated by dividing the total number of Directed Contacts recorded by the combined Bout time of the other fishers for which the juvenile was In-Party. Separate calculations were made for identified primary models (B:O, K:N, M:B) and all other fishers.

Directed Contact rates between the novices (Kesi and Makasi) and their primary models (Lana and Mchumba, respectively) decreased as each became more proficient fishers (Table 7).

Table 7: Directed Contact (DC) count (*n)*, potential opportunity time, represented by the primary model's Bout time (whole minutes) while [*novice*] was In-Party, and the resulting Directed Contact rate by Developmental Stage for each novice with their primary model.
—:Makasi did not have a discrete Stage 2.

	Kesi (K)→Lana (N)			**Makasi (M)→Mchumba (B)**		
Developmental Stage	***n***	**N Bout Time (min)**	**K→N DC Rate**	***n***	**B Bout Time (min)**	**M→B DC Rate**
2	37	9	4.06	—	—	—
3	77	35	2.20	15	199	0.08
4	94	79	1.20	0	7	0.00
5	30	46	0.65	0	21	0.00
Study Total	238	172	1.38	15	226	0.07

2.4.g Types of Directed Contact

The three juveniles, in addition to having disparate rates of Contact, also differed in Contact *type*. Contacts were classified broadly into categories as being either “Hand” or “Mouth” driven. “Hand” Contacts, encompassing any intentional contact with a fisher with a hand or foot, were more common than “Mouth” Contacts (i.e., being the recipient of tolerated scrounging). As with Directed Contact rates, the type of Kesi’s observed Directed Contacts more closely resembled Mchumba’s than Makasi’s (Figure 21). When compared by Fisher’s exact test, Mchumba and Kesi’s categorical distributions were not significantly different (p=.120) while Makasi had a significantly lower proportion of “Mouth” Contacts than both Mchumba (p=.010) and Kesi (p=.048). The ratio of “Mouth” to “Hand” Contacts was highest between the mother-offspring dyads. When only non-maternal Directed Contacts were compared, Kesi and Makasi’s Contacts did not differ significantly by category (p=.632).

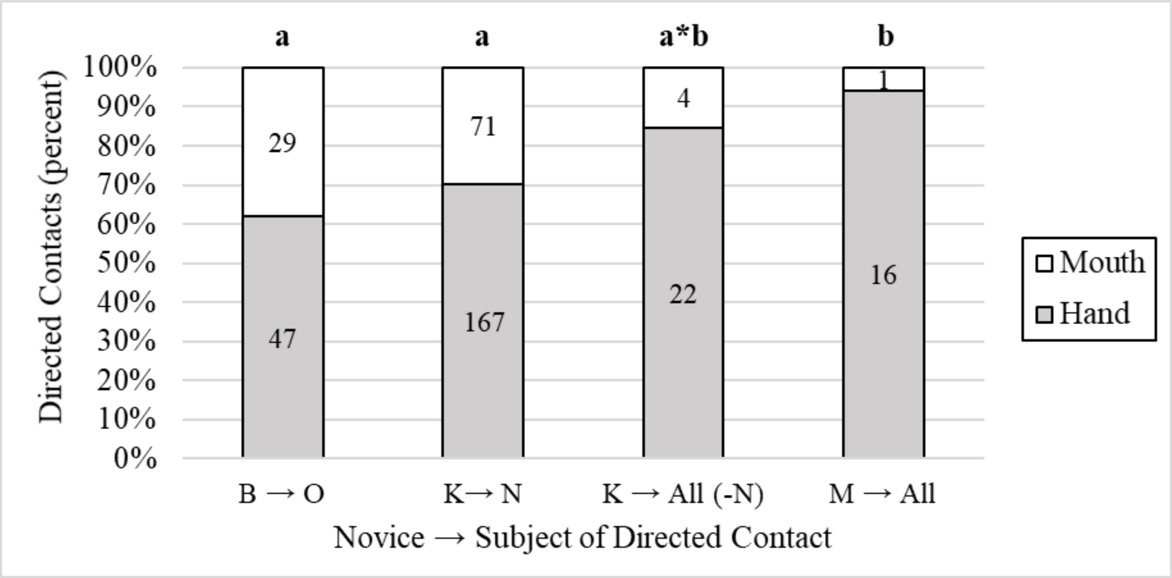

Figure 21: Ratio of "Hand" to "Mouth" Directed Contacts for different juvenile/fisher pairings. Each bar is labeled with the count (*n*) of Contacts referenced. Different lowercase letters in bold indicate significant differences in pairs’ ratios by a Fisher’s exact test at p<.05. *The difference between B→O and K→ All (-N) was just shy of significance (p=.050).

The eight identified specific Directed Contact actions were ranked according to level of interference or cost levied on the fisher, and/or the perceived level of benefit or access they afforded to the juvenile (Table 6). Under these criteria, “Touch Subject”, the least disruptive and apparently least beneficial action, was ranked 1st. The “Take” Contact, taking possession of the active fisher’s tool, had both the highest assumed cost & benefit of the Directed Contacts and was ranked 7th. The remaining five Directed Contact types were subjectively ranked between those two extremes. This ordinal ranking allowed for a comparison of the degree of tolerated interference afforded the three juveniles. All three had significantly different Directed Contact rank means (one-way ANOVA, $F(2,355)=15.07$, $p<.001$; all post-hoc Tukey-Kramer tests were significant at $\alpha=.05$). A comparison of the mother-daughter contacts showed that those between Mchumba and Lolita had a mean rank that was significantly higher than that between Kesi and Lana [one-way ANOVA, $F(1,312)=8.29$, $p=.004$]. Kesi’s ranked mean of non-maternally Directed Contacts was not significantly different than Makasi’s [one-way ANOVA, $F(1,42)=0.83$, $p=.368$] (Figure 22).

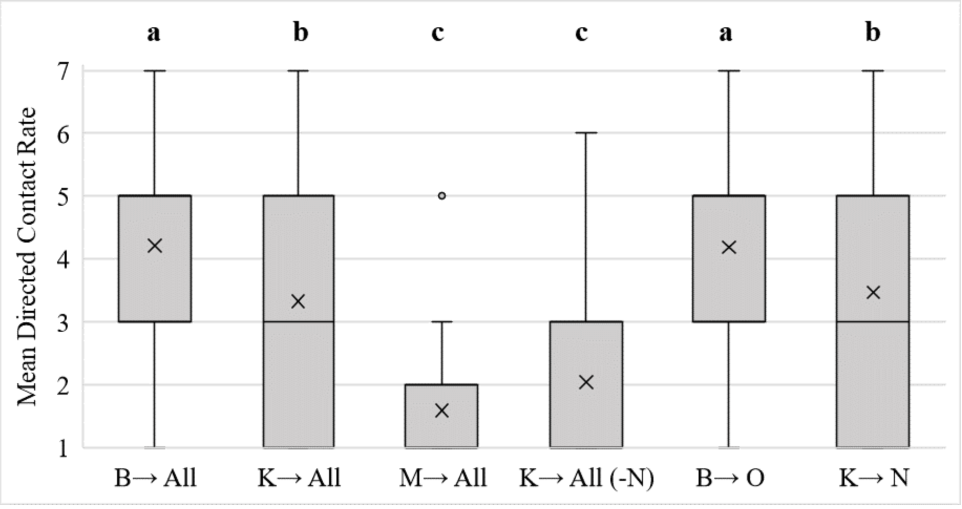

Figure 22: Distribution of Directed Contact ranks for different juvenile-fisher pairs. The boxplots show the median, the first and third quartiles, and the lower and upper extremes within the group. The means of all Directed Contact rank sets shown were compared by one-way ANOVA, F(5,692)=11.28, p<.001). The means for each pair were then compared with a post-hoc Tukey-Kramer test, and different lower-case letters in bold indicate significant differences at *p*<.05).

Directed Contacts were recorded as being directed towards many adults, but those between offspring and their mothers were more frequent and reflected a higher average level of toleration than actions directed at other fishers. Makasi, who did not have a mother present, had a much lower Directed Contact rate, and his Contacts tended to be of a less intrusive variety than that observed for Mchumba and Kesi. Although the majority or Makasi’s Contacts were directed towards Mchumba, his closest maternal surrogate and model, his rate and type distribution were more akin to the Directed Contacts Kesi performed towards non-maternal adults. Makasi was not afforded the heightened access and toleration mothers afford to their juvenile offspring.

Take Tool

Tool transference by chimpanzees has been identified as a possible form of teaching (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016). To better compare chimpanzee tool transfers to those recorded in this study, the 16 "Takes" were graded by possessor willingness to part with their tool. All Directed Contact Takes were between the mother-daughter dyads (Table 8).

An additional eight tool transfers that were noted by the scorer, but fell outside of the scoring protocol as the "Taker" was not one of the juveniles, were included in this analysis (Table 8, gray columns). Six of these eight "noted" tool transfers were uncontested "robbings" by a higher-ranked bonobo, where no request preceded the transfer. In the other two cases, Kesi lost possession of her tool after a co-fisher removed it from the mound and discarded it, seemingly because it impeded their own fishing. None of the noted tool transfers resulted in observed aggression, though in one instance quick mollification by the recipient may have forestalled a negative reaction[7].

The Directed Contact Takes appeared to differ from the additional noted tool transfers in that they were typically preceded by other Directed Contacts or gestural requests. 25.0% (4/16) of these Takes were "Active" transfers, where the tool was proffered to the recipient by the original possessor (Table 8, white columns). Active transfers were only recorded from mothers to juvenile offspring. Most Takes resulted in the donor mother leaving the mound area, but in 5 instances she continued to fish after the transfer: either by getting her probe back (n=1), retrieving a nearby prepared tool (n=3), or preparing a new probe tool altogether

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[7] Mchumba, who was fishing alone, robbed Kesi as she approached the mound with a prepared tool. Mchumba then quickly initiated a brief genital to genital (G-G) rubbing with Kesi. Kesi left the mound area and Mchumba resumed fishing alone.

(*n*=1). Following 12 of the Takes, the juvenile used the obtained tool to fish, and in the other 4 cases (all of which were between Kesi and Lana), Kesi ate from the transferred tool uninterrupted. Based on these observations, Takes, particularly those that were Active, may fulfill the functional criteria to qualify as teaching.

Table 8: Ethogram of tool transfer types, adapted from Musgrave, et al., 2020. Counts of observed types are grouped by original possessor and tool recipient. U = 16, P = 5, S = 3.

Transfer Type*	**Possessor:**	**N**	**O**	**J**	**K**	
	Definition **Recipient:**	**K^{δ}**	**B^{δ}**	**I,N**	**B**	**I,J,N**
Active	Possessor moves to facilitate transfer (U, P)	1	3			
Tolerated Take	Possessor allows recipient to take tool; possessor shows neither facilitation nor hesitation (U, P, S)	4**	5	2		4
Hesitant	Recipient grasps tool; possessor transfers tool only after delaying or resisting the transfer (U, P)	1	2			
Steal	Recipient takes tool from possessor, who reacts negatively (e.g., attempts to keep tool, gestures for its return, or threatens stealer) (U, P, S)	1			1	

***Transfer types were categorized according to whether the tool possessor facilitated or protested the transfer, and whether at the time of transfer the tool was in use (U), physical possession (P), or spatial possession (S).**
δ indicates the transfers that were captured as Directed Contacts. Shaded columns indicate tool transfers that were not actively scored but were noted by the scorer.
**** One Tolerated Take recorded between N and K was a tool-transfer that occurred outside of a Bout, and so was not counted as a Directed Contact “Take”.**

2.5 Discussion

Group dynamics and social context impact the opportunity for social learning and are an important part of understanding the propensity of group-living animals to adopt certain behaviors (Coussi-Korbel & Fragazy, 1995). Although the juvenile bonobos at the SDZ were exposed to the fishing behavior of all group members, the amount of exposure, attention given, and interactions with fishing adults varied widely.

As expected[8], the strongest associations were between the mother-offspring pairs (Lolita-Mchumba and Lana-Kesi). Both juveniles were nearby for a greater proportion of their mothers' fishing than that of other adults. They were also more likely to be Close or in Indirect Contact with their fishing mother. Attention to fishing activity tended to increase with proximity, and this was particularly true for the mother-daughter pairs. A majority of the Dips, and an even greater majority of the Close+ Dips, that Mchumba and Kesi attended to were performed by their respective mothers. These findings complement observations of ant-dipping chimpanzees in Bossou and termite-fishing chimpanzees in Gombe, where the mother was also the primary model and target of observation for the young novice fishers (Humle, Snowden, & Matsuzawa, 2009; Lonsdorf, 2006).

Makasi, who was nursery raised, exhibited a model preference for competent juvenile Mchumba. Unlike the familial pairs, Makasi's access to his preferred model was restricted; less than half of his recorded parties included Mchumba. Young chimpanzees who have less opportunity to observe their prime model have been observed to redirect their attention to more active adults (Hirata & Celli, 2003), and Makasi's behavior appeared to follow this

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[8] Also see Discussion of Churn Technique, p. 102

tendency. Adult female Ikela made up the largest share of Makasi's In-View Dips during Stages 4 and 5, and Makasi was recorded watching twice as many of Lolita's Dips in Stage 4 as he did Mchumba's. While Kesi did not spend more relative time near fishers other than her primary model until reaching competency, Mchumba represented fewer of both Makasi's In-Party and In-View Dips in each successive Developmental Stage. As a result, Makasi had a markedly more varied model distribution than both Kesi and Mchumba. Despite having multiple models, Makasi had less cumulative access to expert fishers than Kesi, particularly Close+ observation time.

Attending to conspecifics is an important feature of bonobo behavior regardless of age (Kret, Jaasma, Bionda, & Wijnen, 2016; Kano, Hirata, & Call, 2015; Kano, Shepherd, Hirata, & Call, 2018). Attention to expert fishing behavior, however, may be modulated by the age and skill of the observer. Juvenile chimpanzees, for example, show lower levels of attention to active termite-fishers as they age (Lonsdorf, 2005), a trend that was also observed for the juvenile bonobos in this study. Makasi and Kesi, who were very close in both age and skill progression, had similar average rates of Attentiveness to the Dips they were present for, while Mchumba, who was several years older and a proficient fisher throughout the study, paid comparatively less Attention to other fishers. Interestingly, Attention rates for the three juveniles were similar at overlapping ages, and a significant negative correlation of Attention with age was observed. These observations indicate that for young bonobos, attention rates towards expert conspecifics are likely a function of observer age and/or fishing competency. As the sample size was small, more longitudinal studies of juvenile bonobos, coupled with a comparison with adult attention, are necessary to confirm this trend.

In addition to allowing close observation, primary models also exhibited a high tolerance for active interaction and even interference by juveniles during fishing Bouts. Lolita remained highly tolerant of her daughter Mchumba for years after Mchumba attained fishing competency. Kesi, as the daughter of the matriarch, was highly tolerated generally[9]. Her interactions with her mother, however, were more frequent and tended to be more disruptive than those directed at others. The count and rate of Kesi's non-maternally Directed Contacts were higher, though not significantly so, than Makasi's, who was lowest in the group hierarchy and was half as likely to be within reach of an active fisher.

The frequent tolerated scrounging of juvenile bonobos from their mothers and, to a lesser extent, other group members, differ from the interactions among probe-fishing chimpanzees (Hirata & Celli, 2003; Lonsdorf, 2006; Estienne, Robira, Mundry, Deschner, & Boesch, 2019). Although highly tolerant of close observation, older chimpanzees only infrequently allow young to "steal" fished food in the wild (Lonsdorf, 2006; Estienne, Robira, Mundry, Deschner, & Boesch, 2019). They also rarely pause to allow young to eat directly from their tools, in stark contrast to the over 100 times this was observed for the SDZ bonobos. In an experimental setting, adult chimpanzees who were engaged in a honey-fishing task did allow naive juveniles to lick their fishing tool, but rejection rates were high, particularly when there was honey left on the tool (Hirata & Celli, 2003). Rejection rates were higher for their own offspring, and there was no change in tolerated scrounging rate over time or by juvenile tool-use stage.

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[9] Kesi performed Directed Contacts towards all group members except Lolita, including successfully scrounging bait from several non-maternal members.

While fisher tolerance towards bonobo young seen at the SDZ appears markedly different from that observed for chimpanzees, behavioral parallels have been recorded in other contexts. In Bossou, nut-cracking chimpanzees exhibit patterns of toleration towards novices that mirrors that of the SDZ bonobos (Biro, Sousa, & Matsuzawa, 2006). Bossou infants will hold their mothers' hand or arm during nut-cracking blows, touch her anvil, and are allowed to take freshly cracked nuts during her bout. Although most of these interactions occur between mothers and their offspring, adult chimpanzees were observed to tolerate a lower level of scrounging by non-related juveniles.

It has been posited that the technical complexity of nut cracking accounts for the higher tolerance chimpanzees exhibit towards novices beyond that shown in other tool-using contexts (Matsuzawa, 1996). Successful nut-cracking requires precise bimanual coordination of three separate objects, and there is an apparent critical learning period; chimpanzees who do not learn by the age of 7 are unlikely to acquire the skill (Matsuzawa, 1994). Greater access to tools, nuts, and active experts may provide a level of stimulus enhancement necessary for young to persevere through an extensive learning process; chimpanzee nut-crackers do not have their first success until between three and five years of age, and often do not attain adult-level mastery before the age of nine (Matsuzawa, 1994).

Technical complexity does not adequately explain why social tolerance should be higher among these probe-fishing bonobos than in chimpanzees. Firstly, the tool-use observed at the SDZ is comparatively simple, requiring the application of a single tool on the food source. Indeed, the probe fishing of wild chimpanzees, which does not engender tolerance of novice interference, is arguably more complex than what is encountered in captivity. Both ant-dipping and termite fishing often feature biting prey (Humle & Matsuzawa, 2002;

McGrew, 1974), and even honey-extraction from stingless bee nests involve the complexity of nest identification and careful excavation (Estienne, Stephens, & Boesch, 2017). Artificial mounds provided to captive apes, in contrast, contain nonanimated “prey” in reliably stocked and readily apparent openings. The objective difficulty of the task is therefore unlikely to be the determinative factor. It is also unlikely that bonobos find probe fishing to be subjectively more challenging than their relatives do. As was demonstrated at CZA, adult bonobos have little trouble learning to fish at a baited mound (Boose, White, & Meinelt, 2013). Although the age at which juvenile chimpanzees successfully use probes varies based on the conditions, both the SDZ novices managed their first successful dip between the ages of two and three (Table 3), within the range observed for chimpanzees (Hirata & Celli, 2003; Lonsdorf, 2005; Estienne, Robira, Mundry, Deschner, & Boesch, 2019). The observed disparity between bonobos and chimpanzees in their respective treatment of novice probe-fishers is therefore unlikely to be purely in response to task difficulty.

Rather than reflecting complexity, the different tolerance levels bonobo and chimpanzee fishers display towards juveniles appears to be reflective of fundamental socio-biological differences between the species. Bonobos generally have a higher affiliative disposition towards conspecifics, particularly in food-related contexts (Kuroda, 1984; Yamamoto, 2015; Kano, Hirata, & Call, 2015; Hare, Melis, Woods, Hastings, & Wrangham, 2017). Experiments comparing social behavior and cognition have found that while chimpanzees become less tolerant as they age, bonobos maintain juvenile levels of sharing, perhaps at the expense of cognitive skill development (Wobber, Wrangham, & Hare, 2010). Extensive observation of bonobo tool-use in the wild, however, led Ingmanson (1996) to conclude that bonobo intelligence is not lower than that of chimpanzees, but has simply been directed towards different, more prosocial aims. As the tolerance towards juveniles observed for the SDZ bonobos has also been observed with chimpanzees, and both species show comparable tool-use abilities in captivity, the primary behavioral distinction observed in this study is that bonobos do not appear to have the same high complexity threshold requirement that chimpanzees do before permitting juvenile interference during tool-use.

Higher general sociality among bonobos does not preclude an “education by master-apprenticeship” dynamic akin to that observed with chimpanzees. In fact, the specific hallmarks thought to indicate this learning model in chimpanzee groups were also present for the SDZ bonobos. The heightened tolerance observed was disproportionally bestowed on the most naive group members; close attention and scrounging at the SDZ fishing mound was predominately performed by naive juveniles towards their primary models. In addition, this tolerance often cost the expert fishers in both time and food. Directed contacts frequently lowered the efficiency of the fisher’s efforts, as young both interfere with Dips by grabbing at the in-use tool as well as remove food from the tool before it reaches the fisher. Close observation of experts has been found to lower the age of successful fishing in wild chimpanzees (Lonsdorf, 2005), and it stands to reason that the high tolerance bonobos exhibit may provide a level of stimulus and local enhancement that increases a juvenile’s propensity to fish at an earlier age. Indeed, Kesi, who observed and interacted with expert fishers significantly more than Makasi, started attempting to probe fish when she was nearly a year younger than Makasi. Kesi was also younger than Makasi, albeit by only 1.5 months, when she became a competent fisher. With so few subjects, Kesi’s earlier attempts and proficiency cannot be definitively attributed to her level of early exposure to conspecific fishing, but it does provide a basis for future skill development studies.

Tool transfer is one high-level form of tolerated scrounging observed among both the SDZ bonobos and probe-fishing chimpanzees. Captive chimpanzees occasionally gave their honey-dipping tools to observing infants (Hirata & Celli, 2003) and tool transfers were recorded among termite-fishing wild chimpanzees in the Goualougo Triangle (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016) and at Gombe (Lonsdorf, 2005). In prosociality experiments, adult bonobos, while more likely to share food, were less likely to share tools than chimpanzees (Krupenye, Tan, & Hare, 2018). The seven "noted" tool transfers between peers, or from younger to older bonobos at the SDZ, do not appear to conflict with this finding. The noted transfers are more accurately described as "robbing" than as voluntary "sharing", as they were neither preceded by requests nor were the noted transfers facilitated by the donor. "Takes", or tool transfers to juvenile fishers, however, appear to be substantially different than the "robbing" of tools by adults and can be classified as prosocial sharing.

The Directed Contact "Takes" observed in the SDZ bonobo group appear to meet the Caro and Hauser (1992) criteria for teaching; the transfers to juveniles are distinct from the robbing seen among adults, are undertaken at a cost to the adult donor, and appear to benefit the juvenile recipients. All sixteen Takes observed were between the mother-offspring pairs Lolita-Mchumba and Lana-Kesi; Makasi was never recorded being the recipient of a tool. Takes were often the culmination of a series of other Directed Contacts, which may reasonably be interpreted as a request by the donor. While half of the transfers were tolerated[10], involving neither resistance nor noticeable facilitation by the probe donor, three of the Takes between Lolita and Mchumba, and one between Lana and Kesi, involved active

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[10] The only negative reaction observed for a "Take" involved Kesi, who robbed Lana during a Bout. Lana successfully gestured for the return of her tool, but did not display or threaten vocally. Kesi was allowed to eat from the tool before it was voluntarily returned, and Lana resumed fishing.

facilitation, with the donor initiating the transfer by moving her probe towards the recipient in an "offering" motion. Most Take transfers were followed by the original possessor ending their fishing Bout. Other abandoned tools were often available nearby, however, and in four cases after transferring possession the donor immediately retrieved an alternate tool and continued fishing. The incidence of both tolerated and active tool transfers, despite the possessor's desire to continue fishing, indicates that tool transfer imparts a cost on the donor.

All Take transfers to Mchumba, and the Take transfers to Kesi after she reached Stage 4, were immediately followed by the recipient fishing with the transferred tool. In some cases, the transferred tool replaced the tool the juvenile had been fishing with previously, implying that the donated tool was preferable and potentially more effective than the original. Although precise tool effectiveness was not discernable from the videotape, the available evidence indicates that the donated tools induced and/or aided fishing by the recipient juveniles. Takes, in addition to being an example of prosocial sharing, appear to satisfy the same teaching criteria that have been claimed for chimpanzee tool transfers to juveniles (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016).

Despite the current study providing a detailed account of the social learning process of captive bonobos, many questions remain unanswered. More data on the interactions of adult fishers with their peers is needed to adequately contrast general bonobo social behaviors with that directed specifically towards juveniles. It is possible that additional expert attention may affect the propensity of individuals to fish as adults, and how that may relate to previous findings of female bias in tool-use in *Pan* is unclear (Boose, White, & Meinelt, 2013; Lonsdorf, 2005). Critically, this study was unable to determine whether, and to what extent, the "master-apprenticeship" dynamic observed accelerates the learning process of juvenile bonobos. More comprehensive longitudinal studies of both juvenile and adult bonobo tool-users are needed to better understand the potential benefits of early exposure to tolerant experts on the learning process.

Chapter 3 Individual Dip Technique

3.1 Introduction

The connection between increased cognition with the level of complexity and flexibility involved in habitual tool-use, and the role that tool-use may play in the evolution of intelligence, has inspired a large body of multi-disciplinary research (Biro, Haslam, & Rutz, 2013). Although clear correlations have been established between tool-use and brain size in primates (Reader & Laland, 2002), other analyses between tool-users and closely related non-tool-using species suggest that the situation is more complicated. (Teschke, et al., 2012). Certainly, the disparity between the prolific tool-use of wild chimpanzees and the paucity for wild bonobos is not reflected in their respective intelligence (Lee, 2007; Furuichi, et al., 2015). Understanding the cognitive, social, ecological, and evolutionary underpinnings of flexible tool-use will require more detailed surveys of tool applications and the techniques employed, both across species and within social groups.

The probe fishing performed by the bonobos at the San Diego Zoo (SDZ) provided an opportunity to create a detailed account of flexible tool-use within a social group. Although all members utilized the same basic action repertoire for successful extraction, there appeared to be individual stylistic differences that could not be explained by environmental differences. I sought to accurately characterize the substance and degree of this individuality. This assessment could then be used to compare the technique preferences of younger fishers with that of their models, and further elucidate the process and impacts of social learning in bonobos.

3.2 Methods

A fishing Bout was defined as starting when a bonobo came into contact with the mound, either bodily or with a probe tool, and ending when the subject was out of easy reach of the mound and was no longer in possession of the fishing tool used (if any) or left the mound area entirely[11]. As the video framing was dynamic, not all Bouts were fully captured; filming sometimes started after a Bout began or ended before the Bout did. A “Full” Bout was defined as one for which the subject was recorded continuously from the initial approach to the mound through their departure. Unless otherwise noted, Dips from both Full and Incomplete Bouts were included in the following evaluation.

To evaluate the individuality of fishing technique preferences within the group, each subjects’ recorded Dips were temporally segmented and annotated with the following technique elements:

1. Dip Components: Dips were comprised of three separate actions performed in sequence 1) Insertion of probe tool or finger into the mound; 2) Removal of Inserted tool or finger; 3) Tool (or finger) brought to the mouth. Dips are considered “Full” if they included all three actions in sequence (“1_3”). Dips not involving either a probe tool or finger, wherein the subject’s mouth was directly applied to the bait hole entrance, were considered to be “Full” by default.

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[11] For precise segmentation and annotation definitions, see Appendix I: Scoring Tier Structure and Ethogram, p. 106

2. Tool Used: Did the extraction attempt involve a probe tool, Finger, or Mouth (lips or tongue, applied directly to the mound).
3. Hand(s) Used: Left, Right, or Both (only applicable if a tool was used), NA (not applicable, i.e., if mouth Dip).
4. Regripping: Modified method of Insertion and/or Removal where the subject inserts/removes the probe partially, then re-adjusts their hand position by releasing and regripping the tool at a different point along the length of the probe before continuing Insertion/Removal.
5. Churning: Dip modification characterized by partial removal of the tool from bait hole, followed by a re-insertion of that tool before the Dip sequence is completed (can be any time after Insertion begins and before Removal is complete).
6. Mouth Used: During a tool Dip, the subject uses their mouth (teeth or lips) to aid in Insertion and/or Removal.

Each of these components were evaluated separately, and several were considered together to characterize a “typical” Dip. Uniform standards for identifying the start and end of each Dip were applied, and the duration of each Full Dip was recorded. Dips from the entirety of the study period were included for all bonobos, with the exception of the two youngest members. As Kesi (K) and Makasi (M) developed their fishing skills during the study and exhibited technique changes as their probe fishing proficiency increased, only Dips performed within their respective Stage 5 (Expert Fish) were evaluated in this chapter. For more information, see Dip Technique Changes Related to Skill Developmental Stage, p. 84.

Differences within frequency data set categories were compared using Fisher’s exact tests of independence where possible, while Chi-square tests of independence were reserved for frequency data with more than two values per nominal variable, or when the sample size was too large to run a Fisher’s exact test (typically n>1000). A Bonferroni correction was applied to all post-hoc analyses of Chi-square tests.

Analysis of variance tests (ANOVA)s were used to test for significant differences in means, however, for data involving unequal and/or small samples sizes, or when the standard deviations within groups were heterogeneous, Welch’s one-way ANOVA was used instead. Post-hoc analyses of ANOVAs were run using Tukey-Kramer tests.

Relationships between two measurement variables were evaluated using Pearson correlation tests. Paired t-tests were used to evaluate mean differences between pairs of measurements. When the distribution of the differences between pairs was non-normal, a Wilcoxon signed-rank test was substituted for a paired t-test.

3.3 Results

3.3.a Tool Utilization

Although most feeding behavior on the mound involved a probe tool (96.7% of Full Dips), subjects were also observed feeding by inserting their fingers into the mound ("Finger": 2.7%) and by placing their mouth directly in contact with the bait openings ("Mouth": 0.6%). Individual rates of tool-usage were not consistent within the group (subject range: 82.8%-99.9%), [X^2 (7, 6106)=483.13, *p*<.001], and the two youngest fishers (Kesi and Makasi) were the most likely to forgo tools for manual or oral probing (Figure 23).

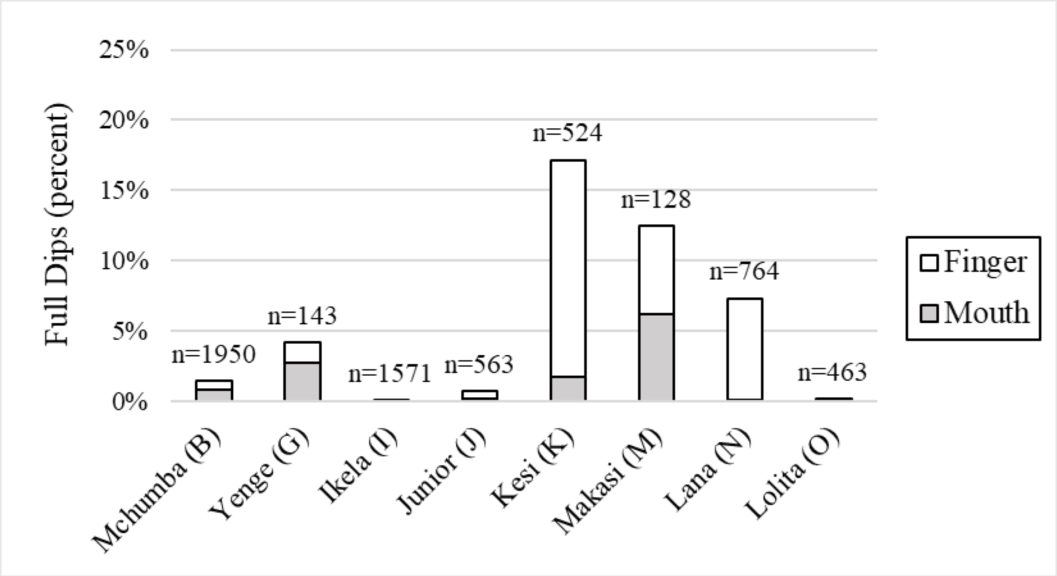

Figure 23: Percent of Full Dips that did not involve a probe tool, by subject and Dip type. *n*= individual subject count of Full Dips.

The mean Dip durations[12] of Mouth, Finger and tool Dips were significantly different as compared by Welch's one-way ANOVA [F(2, 11.27)=15.45, *p*<.001]. A post-hoc Tukey-

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[12] Subject Dip duration means were significantly heterogenous [one-way ANOVA, F(7, 5895=170.38, p<.001] and the number of Dips per subject was not equal (subject range: 112-1921 Dips). Therefore, to avoid over-weighting by individual, all group duration means were calculated and analyzed using the means of each subject, rather than that of each Dip.

Kramer test found that tool Dips (*M*=5.2 seconds, *SD*=1.6) took significantly longer on average than both Finger (*M*=2.3 seconds, *SD*=0.5) and Mouth Dips (*M*=1.6 sec, *SD*=0.6) at *p*<.05. The difference between Mouth and Finger mean Dip duration was not significant.

Only 11.1% of Full Bouts did not involve a probe tool, and these were unevenly distributed among the fishers (subject range: 0.0%-27.3%) (Table 9). Full Bouts involving a tool were significantly longer, (*M*=9.9 Dips per Bout, *SD*=13.5), than those without, (*M*=4.2 Dips per Bout, *SD*=6.8), as evaluated by a Welch's one-way ANOVA [F(1, 58.96)=13.85, *p*<.001]. This increase in Bout length, along with the group-wide preference to use probe tools to access the mound, despite the added cost in complexity and time associated with probe tool-use, indicates that probes are more effective for bait retrieval. Indeed, tool employment is likely necessary to access much of the provided food. Non-tool Dips, then, may have exploratory motivations. They may also reflect either lower comfort with probe tools (particularly for the youngest fishers) or temperamental/motivational differences between individuals.

Table 9: Count of Full Bouts by composition and subject. Count of all Bouts (both Full and Incomplete) in parenthesis. Bouts that did not include any Dips were excluded.

	B	**G**	**I**	**J**	**K**	**M**	**N**	**O**
Mouth Only	0 (1)	1 (1)	0 (0)	1 (1)	0 (1)	1 (1)	1 (1)	0 (0)
Finger Only	1 (2)	0 (0)	0 (1)	0 (0)	10 (12)	1 (2)	9 (11)	0 (1)
Mouth & Finger	0 (0)	0 (0)	0 (0)	0 (0)	3 (3)	1 (1)	0 (0)	0 (0)
Mouth & Probe	5 (8)	1 (2)	0 (0)	0 (0)	3 (3)	0 (2)	0 (0)	0 (0)
Finger & Probe	0 (2)	0 (1)	0 (0)	1 (2)	0 (1)	0 (0)	7 (9)	0 (0)
Probe Only	65 (155)	10 (21)	31 (96)	25 (53)	39 (50)	8 (20)	25 (56)	20 (47)
All 3 Types	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total	72 (170)	12 (25)	31 (97)	27 (56)	55 (70)	11 (26)	42 (77)	20 (48)

3.3.b Bilateral Hand Use

Most (92.9%) Full probe Dips scored were completed using a single hand. When using both hands, the subject typically would fully switch the hand used mid-Dip (e.g., subject Inserts the probe tool with their right hand, but Removes it with their left), rather than perform the entire Dip bimanually. As with tool utilization, the propensity to use both hands during a Dip varied significantly by individual (subject range: 0.6%-21.4%), [X^2 (7, 5903)=483.13, p<.001) (Figure 24), and tended to be higher among the juveniles (average percent of bilateral probe Dips: juveniles: 12.5%; adults: 4.1%) and the familial subgroup (JKN: 13.0%; Other subjects: 3.8%). The group mean duration of bilateral Dips (M=8.3 seconds, SD=1.9) was significantly longer than for single-handed Dips (M=4.9 seconds, SD=1.6), [paired t-test, $t(7)=6.72$, p<.001]. Like other modifications, switching hands exacts a cost on the fisher in the form of greater time investment per Dip.

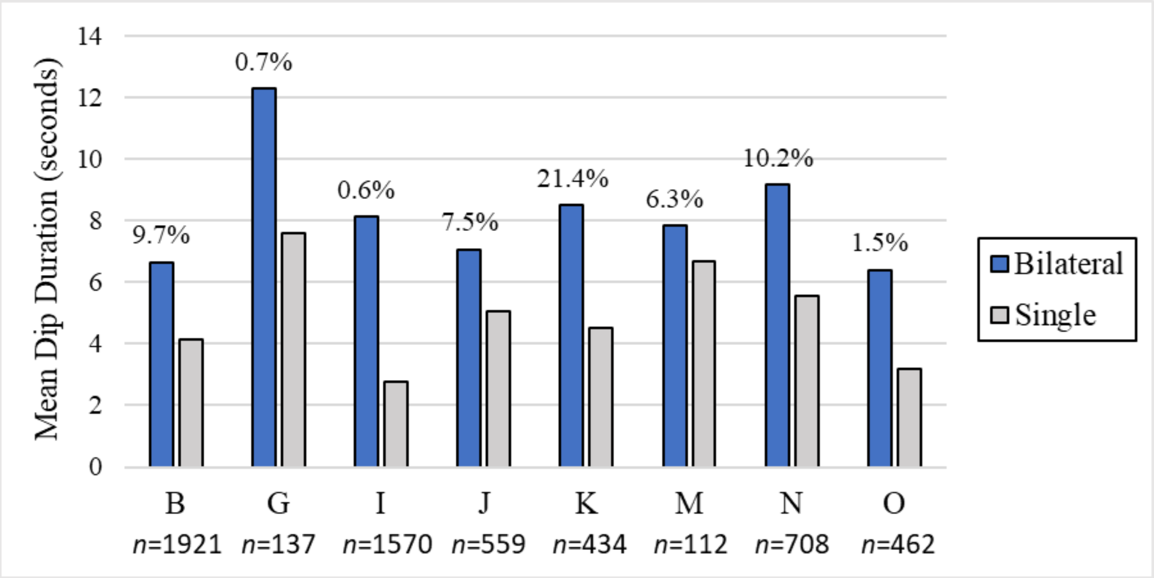

Figure 24: Comparison of mean Dip duration by hand use (single or bilateral) for each subject. Only Full tool Dips were included. Bilateral Dip columns are labeled with the percent of each subject's Dips that were bilateral. *n* indicates the number of Dips that were included in this analysis for each subject.

3.3.c Handedness

Bonobo laterality is task-specific (Hopkins, 2006), including for different types of tool-use. Previous research on tool-use among captive bonobos has found group-level bias towards using the right hand for nut cracking and food extraction tasks (Neufuss, Humle, Cremaschi, & Tracy, 2016; Bardo, Pouydebat, & Meunier, 2015). A study of artificial termite mound fishing by bonobos at the Columbus Zoo and Aquarium found strong individual laterality, but no group-wide hand bias (Brand, et al., 2017). At the SDZ, all bonobos also demonstrated significant laterality while probe fishing (excluding Dips where both hands were used); six subjects primarily used their left hand and two primarily used their right (Table 10). The group-level bias was towards left-handed probe Dipping, though this finding did not reach significance [Wilcoxon signed rank test (n=8, 0.05<p<0.10]. Finger Dip laterality (when discernable) tended to concord with tool Dip laterality; Lana was the only exception, showing a significant right-hand preference when Dipping with her fingers and a significant left-hand preference when using a tool.

Table 10: Individual Handedness Scores, for both probe tool Dips and Finger Dips. “Left” and “Right” columns refer to the number of Dips executed by that hand. Dips where both hands were used (probe tool only) were excluded. *p*-values are from two-tailed binomial tests. “HI” refers to the Handedness Index [HI=(R-L)/(R+L)] (Hopkins, et al., 2005). “—” Indicates insufficient data to determine preference.

Subject	Dip Type	Left	Right	Total	*p*	HI	Handedness
Mchumba (B)	Tool	1756	0	1756	0E+00	-1.000	Left
	Finger	13	3	16	0.021	-0.625	Left
Yenge (G)	Tool	38	102	140	6E-08	0.457	Right
	Finger	0	2	2	0.500	1.000	—
Ikela (I)	Tool	1565	12	1577	0.000	-0.985	Left
	Finger	6	0	6	0.031	-1.000	Left
Junior (J)	Tool	128	399	527	2E-33	0.514	Right
	Finger	2	1	6	1.000	-0.333	—
Kesi (K)	Tool	363	2	365	2E-105	-0.989	Left
	Finger	89	6	95	5E-20	-0.874	Left
Makasi (M)	Tool	108	0	108	6E-33	-1.000	Left
	Finger	4	6	10	0.754	0.200	Insignificant L. Bias
Lana (N)	Tool	450	207	657	1E-21	-0.370	Left
	Finger	22	52	74	0.001	0.405	Right
Lolita (O)	Tool	461	0	461	3E-139	-1.000	Left
	Finger	0	1	1	1.000	1.000	—

3.3.d Regripping

Regripping, the act of moving the tool-hand along the length of the probe during Insertion and/or Removal, was observed in 56.1% of the 5574 Full tool Dips for which Regripping data was available. Regrip behavior varied significantly by subject[13] [X^2 (14, 5566)=3942.86, *p*<.001] (Figure 25).

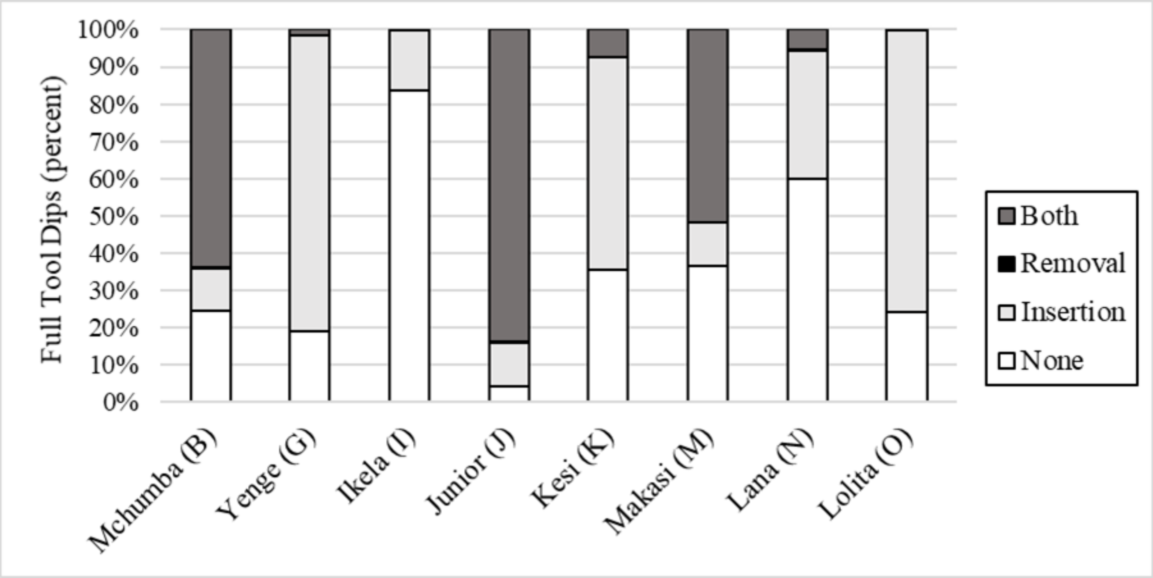

Figure 25: Percent of each subject's Dips that included each Regrip type. Only Full tool Dips with Regrip data were included.

Regripping during Removal alone was exceptionally rare (*n*=8; 0.1% of Dips) and was therefore excluded from the following statistical evaluations. Group mean Dip durations were significantly different among the different Regrip types [one-way ANOVA, F(2,21)=10.202, *p*<.001]. The group mean Dip duration was lowest for Dips without Regripping ("None") (*M*=3.6 seconds, *SD*=1.6), followed by Dips with Regripping on Insertion (*M*=5.8 seconds, *SD*=1.3). The highest mean group Dip duration was observed for Dips with Regripping during Insertion *and* Removal ("Both") (*M*=7.9 seconds, *SD*= 2.6).

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[13] Insertion Regrip and Removal Regrip Dips were binned together for this Chi-Square test.

A post-hoc Tukey-Kramer test showed that Both Regrip Dips were significantly longer than "None" Dips at *p*<.05, but that Insertion Regrip Dips did not significantly vary from either None or Both Regrip Dips. (Figure 26).

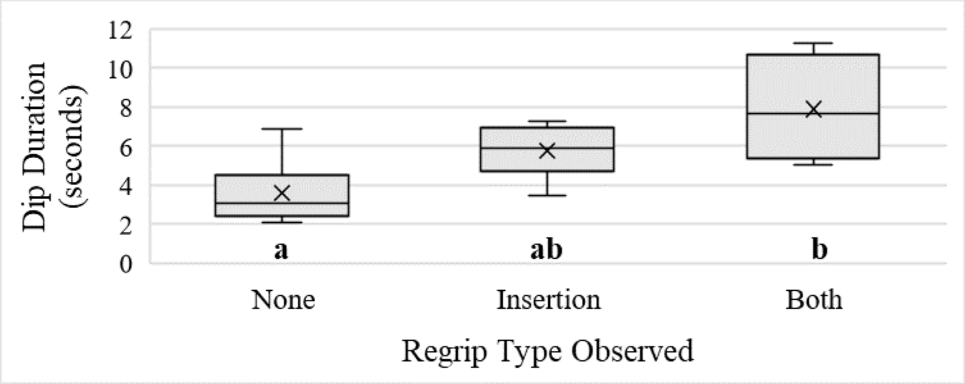

Figure 26: Group mean Dip duration by Regrip type. Only Full tool Dips with Regrip data were included. The boxplots show the median, the first and third quartiles, and the lower and upper extremes within the group. Different lowercase letters in bold indicate significant differences between means at *p*<.05.

3.3.e Churning

Churning, the act of partially removing and reinserting the probe one or more times during a Dip, had neither clear utility nor consistent presentation. It is examined in-depth in Chapter 4: Churn Technique; p. 91.

3.3.f Mouth Use and Incomplete Dips

Using the mouth, specifically the teeth, to assist in the Removal step was observed in 1.0% of tool Dips (57/5967). This modification was generally observed to accompany Dips for which the fisher appeared to have difficulty Removing the probe, either because the tool was wedged tightly into the bait hole or had been inserted too far, leaving not enough protruding length to firmly hand-grip. It is not surprising, therefore, that Mouth Use was more common in Incomplete probe Dips (Incomplete: 3.3% (4/116); Complete: 0.9% (58/5851)), [Fisher's exact test, p=.027]. As with other techniques, Mouth Use varied by individual (subject range: 0.0%-5.1% of tool Dips). There was a significant negative correlation in Mouth Use by age (r(6)= -.77, p=.026) that was not seen for Incomplete Dips (r(6)= -.33, p=.420).

3.3.g Typical Probe Dip

Each of the probe-tool specific technique modifications (Bilateral Hand Use, Regripping, Churning, and Mouth Use) were employed together during each Dip. The combination of the separate techniques used (Dip Technique Combination, abbreviated as "DTC") varied by individual, and did not appear to be random. As Mouth Use was rare, and primarily used by the youngest subset of the group, it was not included for the purposes of evaluating Dip Technique Combinations. Sixteen possible unique Dip Technique Combinations were identified and their observed incidence, both in total Dips and average subject utilization, were evaluated (Table 11).

Of the sixteen possible Dip Technique Combinations, only four represented ≥10.0% of any one subject's tool Dips. Typical Dip profiles varied significantly among the subjects [X^2 (28, 5496)=3944.54, *p*<.001] (Figure 27).

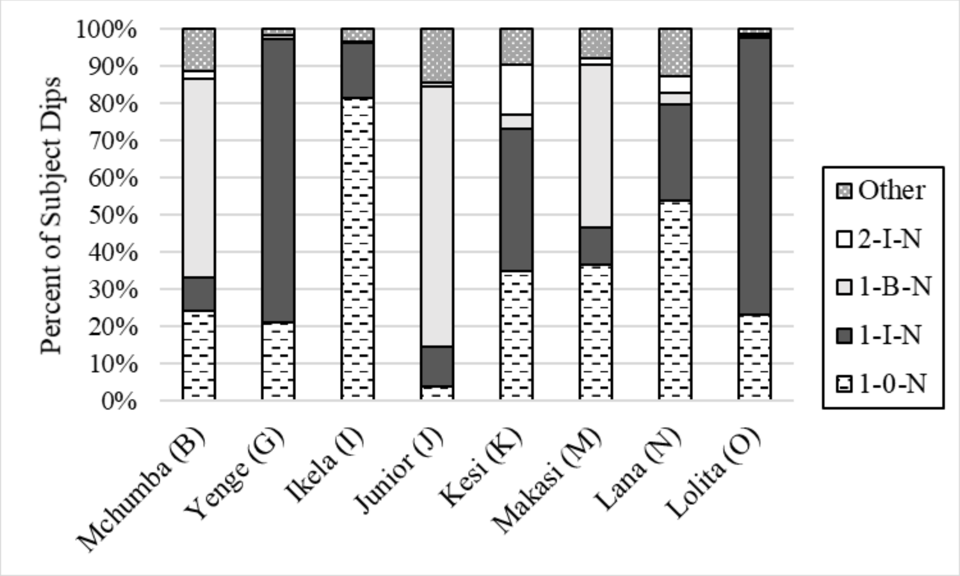

Figure 27: Typical Dip Technique Combination (DTC) profiles by subject. Only Full tool Dips with data for all included technique modifications were included. All DTCs that did not reach 10% of at least one subject's tool Dips were consolidated into "Other".

Table 11: Possible Dip Technique Combinations (DTCs) and their recorded frequency. Only Full Tool Dips for which all technique modifications were observable were included. Bolded rows indicate a DTC profile that made up ≥10% of at least one subject's tool Dips.

Rank	Hand(s) Used	Regrip	Churn	Code	Total Dips Recorded	Average % of Subject Dips
1	**One**	**None**	**No**	**1-0-0**	**2333**	**34.85%**
2	**One**	**Insertion**	**No**	**1-I-0**	**1161**	**32.31%**
3	**One**	**Both**	**No**	**1-B-0**	**1392**	**21.84%**
4	**Both**	**Insertion**	**No**	**2-I-0**	**139**	**3.09%**
5	Both	Both	No	2-B-0	177	2.69%
6	One	Both	Yes	1-B-C	101	1.83%
7	One	Insertion	Yes	1-I-C	45	0.89%
8	One	None	Yes	1-0-C	69	0.87%
9	Both	None	No	2-0-0	35	0.67%
10	Both	Insertion	Yes	2-I-C	22	0.53%
11	Both	Both	Yes	2-B-C	13	0.31%
12	One	Removal	No	1-R-0	6	0.09%
13	Both	None	Yes	2-0-C	1	0.02%
14	Both	Removal	No	2-R-0	2	0.01%
15	Both	Removal	Yes	2-R-C	0	0.00%
16	One	Removal	Yes	1-R-C	0	0.00%

Post-hoc comparisons of the 28 subject pairs[14] found that only Mchumba-Makasi [X^2 (3, 1928)=8.08, *p*=.018] and Yenge-Lolita [X^2 (3, 532)=0.21, *p*=.902] were not significantly different using the Bonferroni adjusted α of 0.0018. All other tested pairs were significantly different at *p*<1E-10 (Table 12).

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[14] To minimize expected frequencies falling below the thresholds (<1, or >20% of values at <5), pairwise comparisons were adjusted by consolidating DTC counts that were <10% for both subjects into the "Other" category prior to running pairwise Chi-square post-hoc tests. One pair (I-M) still failed to meet the test requirements post-consolidation and was excluded.

Table 12: Typical Dip Technique Combination (DTC) post-hoc analysis results for all subject pairs.

Subject Pair	**chi-square:**	**d.f.:**	***p*-value:**	***n***
B-G	421.24	3	5.55E-91	1931
B-I	1457.64	3	0.000	3334
B-J	98.00	3	4.19E-21	2307
B-K	498.35	4	1.5E-106	2221
B-M	8.08	2	0.01756	1928
B-N	543.07	3	2.2E-117	2482
B-O	965.15	3	6.5E-209	2255
G-I	241.03	2	4.58E-53	1611
G-J	282.48	3	6.14E-61	584
G-K	52.19	3	2.72E-11	498
G-M	103.71	3	2.48E-22	205
G-N	103.83	2	2.84E-23	759
G-O	0.21	2	0.902027	532
I-J	1480.00	3	0.000	1987
I-K	420.04	3	1.01E-90	1901
I-N	223.09	2	3.6E-49	2162
I-O	590.62	2	5.6E-129	1935
J-K	480.37	4	1.2E-102	874
J-M	103.14	3	3.28E-22	581
J-N	634.29	3	3.7E-137	1135
J-O	628.23	3	7.6E-136	908
K-M	139.91	4	2.95E-29	495
K-N	58.27	3	1.37E-12	1049
K-O	141.85	3	1.51E-30	822
M-N	183.02	3	1.96E-39	756
M-O	253.18	3	1.34E-54	529
N-O	255.68	2	3.03E-56	1083

3.3.i Dip Technique Changes Related to Skill Developmental Stage

Researchers of wild chimpanzees have found that tool-usage among young chimpanzees tends to involve less stereotyped behavior than that seen for older members (Inoue-Nakamura & Matsuzawa, 1997; Biro, Sousa, & Matsuzawa, 2006). To determine whether captive juvenile bonobos' fishing techniques remain static, the tool Dips recorded for Kesi and Makasi when they first started to probe fish (Stage 4) were compared with those after they became competent fishers (Stage 5).The specific variations assessed are Hand(s) used, Regripping, Using Mouth, and Churning. Any Dips for which the technique variation being evaluated could not be determined (coded as ND) were excluded from this evaluation. The technique frequency data for the two stages were compared by Fisher's exact test. Although robust comparison between Stage 4 and Stage 5 was not feasible for Makasi, as only 9 qualifying Dips were recorded during his Stage 4 period, all available data is included for context.

Both Kesi and Makasi exhibited technique changes as their probe fishing proficiency increased. Kesi's tendency to Dip single-handedly, as opposed to using both hands during a Dip, significantly increased from 61.1% (22/36) of her Dips in Stage 4 to 78.8% (350/444) in Stage 5 (p=.021). Makasi's tendency to Dip single-handedly also increased from 88.9% (8/9) in Stage 4 to 93.0% (107/115) in Stage 5, though this change was not significant (p=.504).

Kesi's Regrip utilization significantly increased from 24.2% (8/31) of Dips in Stage 4 to 63.3% (260/411) in Stage 5 (p<.001). Kesi Regripped either during Insertion or both Insertion *and* Removal ("Both"), but never on Removal alone. The proportion of Kesi's Regrip Dips that involved Insertion-only significantly increased from 25.0% (2/8) in Stage 4 to 88.5% (230/260) in Stage 5 (p<.001).

Makasi's Regrip utilization also increased, from 25.0% (2/8) in Stage 4 to 62.6% (67/107) in Stage 5, though this shift fell short of significance (*p*=.058). Too few Regrip Dips were recorded for Makasi during Stage 4 to compare his Regrip-subtype proportions to those in Stage 5.

Neither Kesi nor Makasi showed a significant difference between Stages 4 and 5 in their rates of Churning (K: *p*=1.000; M: *p*=1.000) or Using their Mouth during a tool Dip (K: *p*=1.000; M: *p*=.239).

Based on the above evaluation, it appears likely that individual fishing technique changes as young bonobos become proficient. Dips that occurred prior to each novice reaching competency (Stage 5) were therefore excluded from the preceding general Technique analysis (pp. 73-83) to minimize skewing the individual results for those subjects.

3.4 Discussion

3.4.a Individual Technique

Detailed evaluation of fishing techniques among the SDZ bonobo group confirmed that individuals diverged in their fishing action sequences in ways that imply individual idiosyncratic preference and/or reflect individual variations in manual dexterity required to fish with a probe.

The moderate use of Finger and Mouth Dips by all subjects imply it is possible to extract bait without a probe. However, both the low percentage of active Bouts that did not involve a probe and the significantly shorter length of tool-less Bouts indicate that probe tool Dips are more effective. The extra labor involved, in fashioning or procuring a suitable tool accompanied by >55% increase in average Dip duration, further supports the likelihood of increased reward of tool-mediated extraction. It is notable that the two subjects most likely to rely on Finger and Mouth Dips are the two newest fishers, who may still find probe-fishing to be challenging. Other studies have considered Finger and Mouth Dips to be an investigatory behavior, rather than a concerted feeding effort, and the patterns seen in this bonobo group, particularly among the adults, appear to support this interpretation (Boose, White, & Meinelt, 2013).

Dip duration, however, is not a direct proxy for Dip efficiency (yield/time), as shown by the significantly shorter time required for Finger or Mouth Dips as compared to those using a probe. The greater accessible depth combined with a greater surface area imply that probe use would indeed be more effective, however, as yield estimation was not possible from the video, the utility of Dip alterations cannot be fully evaluated. Despite this limitation, the available data on the frequency, individual variation, and time-cost offers a basis for understanding the underpinnings of the observed stylistic variation.

The most commonly performed Dip technique combination (DTC) was also the simplest: a single-handed Insertion and Removal with no Regripping or Churning (coded as 1-0-0). However, this DTC was not the most popular at the individual level; only Ikela and Lana used it for >50% of their Dips. Instead, 1-0-0 was the secondary method for most subjects (B, G, K, M, & O), and one subject, Junior, executed <5% of his Dips using this DTC. Most subjects' preferred DTC incorporated Regripping either during Insertion (1-I-0; G, K, O) or both Insertion and Removal (1-B-0; B, J, M).

As each deviation from the basic sequence increased both the complexity and the Dip duration, it is incongruous that the 1-0-0 DTC was both commonly utilized but not necessarily preferred. Although it is possible that Regripping or Hand Switching increases a Dip's average yield, it does not seem probable. Visual survey of such Dips did not indicate a change in Dip depth nor angle which could have affected yield, although admittedly this was not specifically evaluated. It also remains possible that tool-choice impacts individual DTC preference, but this was also not within the scope of this study.

Regripping appears to aid in fishing by lowering the dexterity and control needed to properly insert and smoothly remove the probe from the bait hole. This is supported by the scarcity of Removal Regrips; if there was no need to Regrip on Insertion then there is unlikely to be difficulty in Removal. Regripping's time cost is likely balanced by the extra control and resultant ease in Dipping, both in inserting the tool properly and in easily bringing the probe up to the mouth. A preference to Regrip, then, could be reflective of either lower individual dexterity, a preference for ease over speed, or some combination of both.

Other studies on probe extraction in apes have found ecological or cultural factors that account for individual differences in technique. Humle and Matsuzawa (2002) documented two different techniques among ant-dipping chimpanzees at Bossou, for example, that were attributed to specific prey attributes and fishing context. Similar differences noted at other chimpanzee sites at Gombe and Taï may reflect cultural differences (McGrew, 1992; Whiten, et al., 1999; Yamakoshi, 2001). As all SDZ fishing took place at the same site and within the same social group, ecological and cultural differences cannot explain the individual differences.

A more analogous situation was encountered at Loango NP, Gabon, where the focal chimpanzee community utilized several different grip types during their extraction of honey from underground nests (Estienne, Stephens, & Boesch, 2017). Although some aspects of extraction behavior did appear to be primarily driven by nest-specific challenges, individual grip type preferences were not significantly affected by environmental conditions. This "individual idiosyncrasy" explanation for technique variation within a social group fits the diversity of Dip Technique Combination preferences seen at the SDZ.

3.4.c Technique Comparison: Prime Models and Juveniles

Having established through proximity, attention, and physical interaction that young bonobos receive enhanced exposure to particular models (See Chapter 2: Novice-Model Interaction pp. 35-59), the question remains whether those models affect the adoption of particular fishing techniques by the juveniles. To evaluate whether new fishers imitate their models, the techniques of the juveniles (Mchumba (B), Kesi (K), and Makasi (M)) were compared with that of their respective primary models (Lolita (O), Lana (N), and Mchumba (B)).

As all techniques were employed by all subjects, albeit at varying rates, it was difficult to definitively connect a juvenile's fishing strategy to that of their primary model. Despite this inherent ambiguity, Lolita and Mchumba appeared to employ distinctly different fishing styles. Within the group (*n*=8), Lolita was the least likely to Churn, and the 2nd least likely to Dip bimanually, whereas Mchumba was closer to the middle of the group for both (4th and 3rd highest rate, respectively). "Both" Regrip Dips (Regripping on both Insertion and Removal) made up majority of Mchumba's fishing, while Lolita "Both" Regripped only once during the study. These technique differences were reflected in their respective typical DTC profiles (see Figure 27), which differed significantly.

In contrast, Lana and Kesi, the other mother-daughter pair, exhibited some notable similarities. They had the two highest rates of finger Dipping and were the two most likely subjects in the group to Dip bilaterally. As noted in Churn Technique (p. 92), the JKN familial subgroup were significantly more likely to Churn than the other bonobos in the group. Despite these apparent similarities, Kesi and Lana's DTC profiles (Figure 27) were also significantly different from one another.

Makasi, who had the least access and attentional fidelity to his primary model, nonetheless showed the highest level of stylistic similarity with his primary model, Mchumba. Makasi and Mchumba were one of only two pairs that had individual DTC profiles that were not significantly different, although it should be noted that this comparison is based on relatively few Makasi Dips (B: 1827 Dips; M: 101 Dips).

It is interesting that the two newest fishers, whose fishing technique may still be developing, showed more similarities with their primary models, while Mchumba, who was already an avid and successful fisher at the beginning of the study, did not. It is possible that young bonobos' fishing more closely resembles their primary model when they first begin to use tools, only to differentiate over the next few years. Junior, who would likely also have had Lana as his primary model, shares a high Churn rate with Lana, but otherwise employs a fishing style as different from his mother's as that seen between Mchumba and Lolita. It is also possible that any observed similarities are coincidental: there was significant individual variation in all techniques and the group size was not especially large, making it difficult to reach firm conclusions. More longitudinal studies of bonobos in naturalistic settings, particularly of infants and juveniles, are needed to clarify these results.

Chapter 4 Churn Technique

4.1 Introduction

A “Churn” is defined as follows:

> *Dip modification characterized by the partial Removal of the tool from the baited mound hole, followed by a re-insertion of that tool before the Dip sequence is completed (can be any time after Insertion (“1”) begins but before Removal (“2) is complete* (Table 16).

Although Churning during a Dip was a technique practiced by all subjects, the rarity of use, as compared to more common Dip variations such as Regripping or hand switching, implied that it may be categorically different, both in what prompts subjects to adopt this variation and how they may benefit by doing so. The following analysis explores the presentation of this technique and the possible motivations.

4.2 Methods

This chapter relies on data and analyses that have been previously outlined in the methods sections of Chapter 2 (pp. 39-40) and Chapter 3 (pp. 70-72).

4.3 Results

4.3.a Overall Churning Rates

Churn Dips were observed in 4.5% of all probe Dips[15] (subject range: 0.9%-8.3%). The observed Churn rate was not significantly different between males and females [Fisher's exact test; *p*=.591]. The highest individual Churn rates belonged to Lana, followed by her two offspring, Junior and Kesi. This familial subgroup collectively had a significantly higher Churn rate than the rest of the group (*p*=.002) (Figure 28). Dips with Churning took longer to be completed[16] (*M*=6.9 seconds, *SD*=5.0), than Dips without Churning (*M*=4.1 seconds, *SD*=2.9), [Welch's one-way ANOVA, F(1, 265.23)=77.05, *p*<.001].

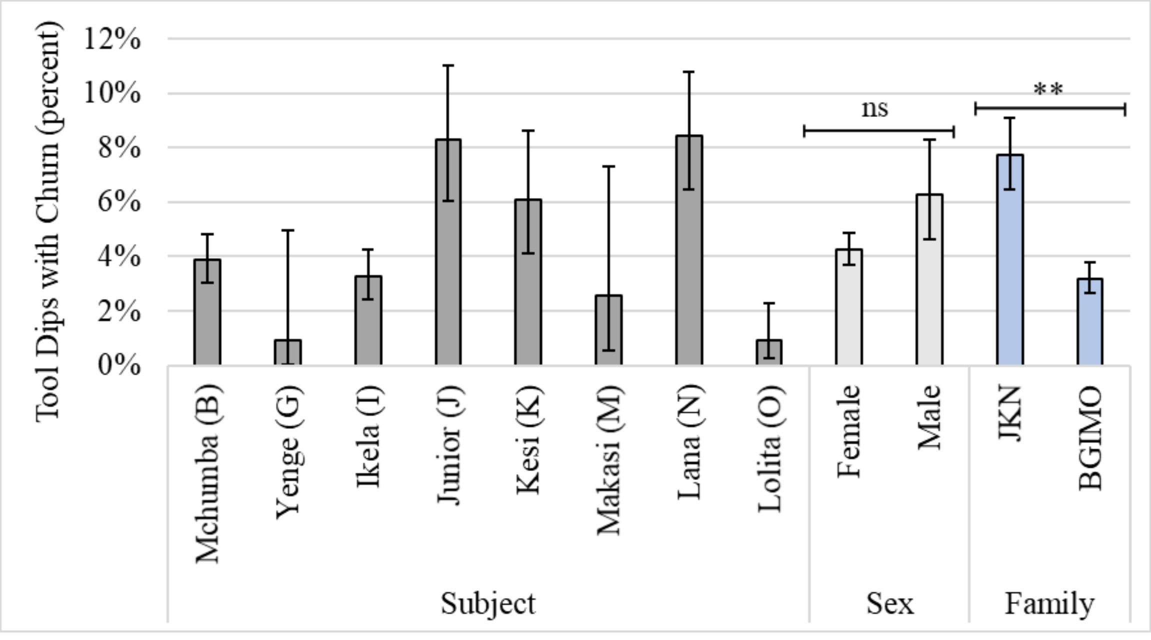

Figure 28: Percent of probe tool Dips that incorporate Churning (all counts exclude Dips where Churning could not be verified). The error bars represent the 95% Exact Binomial Confidence Interval. "Sex" & "Family" groupings were calculated by weighting individual counts to *n*=100 prior to combination.

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[15] Dips using "Mouth" or "Fingers" rather than a probe tool were not observed to include Churning, and so were excluded from all Churn analyses.

[16] For Dip duration calculations, only Full Dips were considered.

4.3.b Churning over Time

Overall Churn rates were stable between 2005-2007, but increased in both 2008 and 2009 (Table 13). This trend is still apparent, if somewhat weaker, when Kesi and Makasi were excluded from this analysis (neither novice used a tool to fish prior to November of 2006)) (Figure 29).

Table 13: Annual counts of Churn Dips with total probe Dips recorded in parenthesis, separated by year and subject. Dips without Churn data were excluded.

	B	**G**	**I**	**J**	**K**	**M**	**N**	**O**	**Total**
2004	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (7)	0 (0)	1 (7)
2005	6 (277)	0 (2)	4 (143)	13 (171)	0 (0)	0 (0)	0 (2)	1 (77)	24 (672)
2006	48 (971)	1 (64)	25 (819)	2 (54)	0 (10)	0 (0)	13 (221)	1 (243)	90 (2382)
2007	3 (271)	0 (16)	7 (324)	0 (97)	2 (95)	1 (50)	27 (279)	2 (78)	42 (1210)
2008	4 (98)	0 (28)	3 (184)	26 (174)	4 (273)	2 (48)	11 (162)	0 (44)	50 (1011)
2009	11 (246)	0 (0)	11 (67)	1 (11)	23 (98)	0 (19)	6 (17)	0 (1)	52 (459)
Total	72 (1835)	1 (106)	50 (1521)	42 (498)	29 (437)	3 (111)	57 (666)	4 (437)	258 (5611)

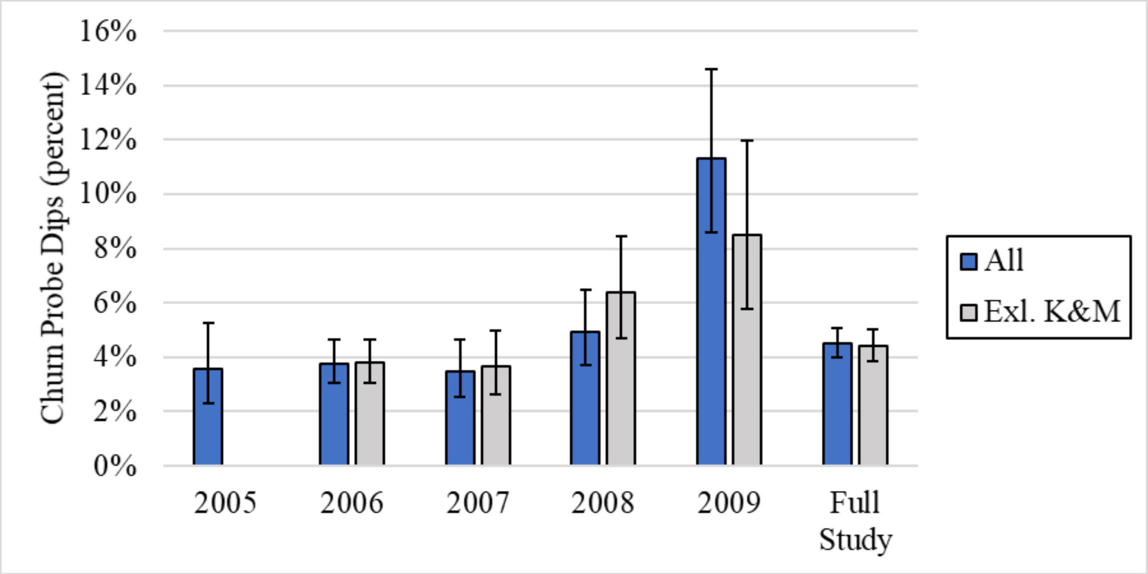

Figure 29: Proportion of probe Dips that incorporate Churning, by study year. 2004 (*n*=7) was excluded from figure. Neither Kesi (K) nor Makasi (M) had recorded probe Dips in 2005. Dips without Churn data were excluded. The error bars represent the 95% Exact Binomial Confidence Interval.

4.3.c Fishing Behavioral Context of Churn Dips

To determine whether Churn Dips were clustered on specific days, which could indicate that Churning was employed in response to an environmental change, the frequency and distribution of Churn Dips per study day were evaluated. The distribution of Churn Dips was heavily skewed toward few Churn Dips per day; 72.4% of probe fishing days involved either no Churn Dips (55.1%, 102/185) or a single observed Churn Dip (17.3%, 32/185). There was little evidence of Churns being clustered on specific days. The daily Churn rate (proportion of all tool Dips that included Churning) was lower than 0.25 on 95.0% (115/121) of fishing days, and Churn Dips never exceeded 46% of observed daily probe Dips (Figure 30).

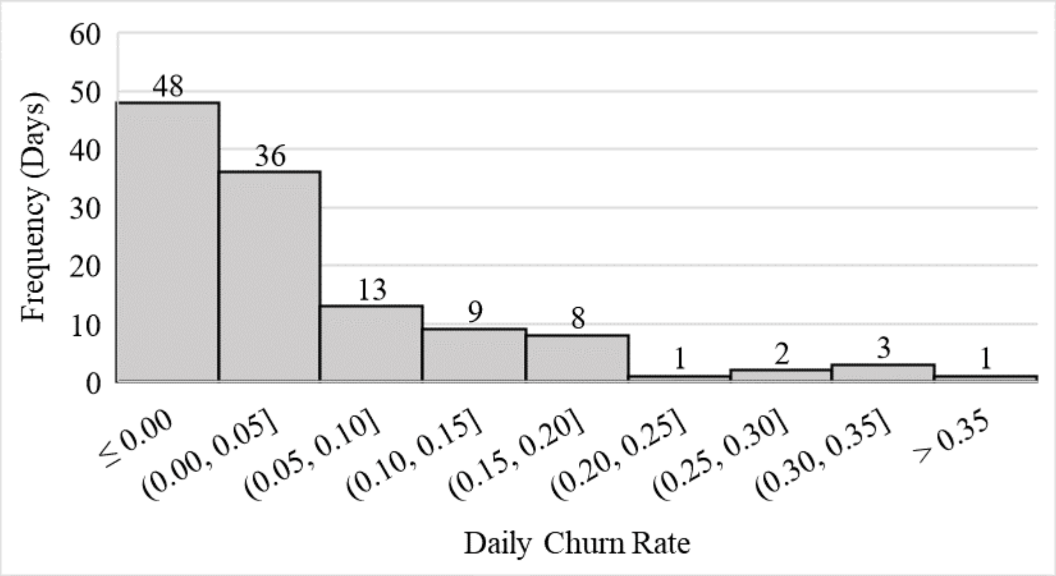

Figure 30: Histogram of daily Churn rate (Churn Dips as a proportion of all probe tool Dips recorded, by day). Dips for which Churning could not be determined we excluded from analysis. To avoid small sample size effects, only days with ≥10 Dips were included.

To understand the relationship of Churning to overall fishing behavior, days with ≥1 observed Churn Dips (Churn days) were compared to probe fishing days without observed

Churn Dips. Churn days included, on average, significantly more probe Dips (*M*=50.7 Dips, *SD*=39.5) than days for which no Churning was observed (*M*=15.0 Dips, *SD*=17.6) [Welch's one-way ANOVA, F(1, 108.29)=58.53, *p*<.001]. When controlling for the number of active probe fishers on a given day, Churn days were still characterized by significantly more probe Dips on average per fisher (*M*=24.2 Dips/fisher, *SD*=18.4) than were seen on non-Churn days (*M*=9.8, *SD*=10.5) [Welch's one-way ANOVA; F(1, 124.29)=39.96, *p*<.001]. Churn days were also significantly more likely to involve multiple probe fishers (61.4%, 62/101) than non-Churn days (25%, 21/84) [Fisher's exact test, *p* <.001]. The incidence of Churning increased with the amount of fishing activity (Figure 31).

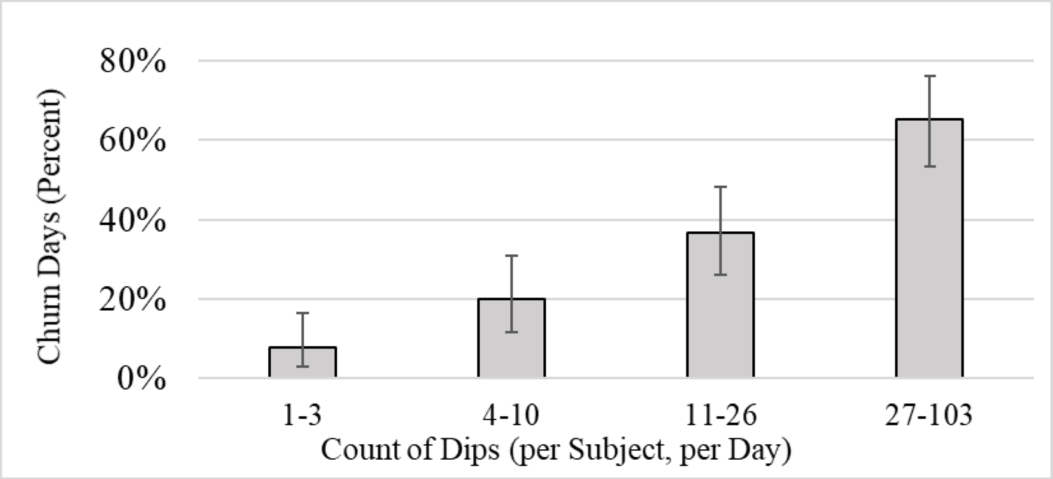

Figure 31: Percent of individual fishing days with ≥1 recorded Churn Dip, by number of tool Dips recorded on that day. Each unique Subject x Day was binned into approximate quartiles by Dip count. Tool Dips without Churn data were excluded. The error bars represent the 95% Exact Binomial Confidence Interval.

Having established that Churn days were characterized by increased fishing activity, I next evaluated how these factors related to the Churn rates of individual Bouts. Although Bout length (as measured by the number of tool Dips with Churn data per Bout) was positively correlated with the number of Churn Dips recorded for that Bout (*r*(537)=.36, *p*<.001), Bout Churn *rates* were not affected by Bout length (*r*(537)=.01, *p*=.837. The distribution of

Churning in individual Bouts appeared to be similar to what was observed for aggregate Churning by day; Churning increases in proportion to fishing activity.

As Churning was more likely on days with multiple active fishers, I hypothesized that Churning may be influenced by the presence of other group members. However, the average Churn rate for video clips[17] in which a single subject was scored as having a Bout (*M*=0.05, *SD*=0.17) did not differ significantly from the rate for clips in which multiple subjects engaged in a Bout (*M*=0.04, *SD*=0.11) [Welch's one-way ANOVA, F(1, 356.30)=0.204, *p*=.651]. This trend was conserved even in the JKN subgroup, whose Churn rates in solo-bout clips (M=0.05, SD=0.15) were not significantly different than in clips in which >1 subject engaged in a Bout (*M*=0.06, *SD*=0.14) [Welch's one-way ANOVA, F(1, 130.63)=0.29, *p*=.590]. Social proximity data to active fishers was not collected for the adult subjects, which precluded further evaluation of this hypothesis.

To examine whether juvenile proximity influenced the Churning behavior of the juveniles' primary models, counts of tool Dips with and without Churning were compared when the juvenile was either In-View or Out-of-Frame. None of the juvenile–primary-model pairs showed a significant correlation between juvenile proximity and expert Churning [Fisher's exact test; Mchumba-Lolita: *p*=.306 , Kesi-Lana: *p*=.050, Makasi-Mchumba: *p*=.718]. Juvenile Attention also did not appear to affect Churn rates; when considering all juvenile In-View Dips, the likelihood of any of the subjects Churning during a Dip did not vary related to juvenile attention [X^2 (1, 5492)=0.04, *p*=.841].

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[17] Evaluating individual clips, rather than study days, allowed for a more accurate measure of how many subjects were in the mound area around the same time. This comparison does not account for nearby subjects who do not directly contact the mound during the clip.

4.3.d Exaggerated Churning

Although Churning did not correlate with the proximity of juveniles, the observation of several aberrantly prolonged Churn Dips raises the possibility that there may be different *types* of Churning, with different motivations. More granular analysis indicated that 78.0% of Churn Dips involved a single additional partial insertion (API) per Dip and 12.0% involved 2 APIs per Dip. Only 10.0% of Churn Dips consisted of more than 2 APIs per Dip.

For the purposes of this analysis, I designated Churn Dips with single or double APIs as "Regular" and those with three or more as "Exaggerated". 4.5% (233/5741) of tool Dips involved Regular Churning while only 0.5% (26/5741) involved Exaggerated Churning. Of the 26 Exaggerated Churn Dips recorded, Lana accounted for 19 (73.1%) and was the only subject significantly more likely to Exaggerate Churn Dips when compared to the rest of the group, (Fisher's exact test, *p*<.0001, using a Bonferroni adjusted α level of .00625 per test (.05/8)) (Figure 32).

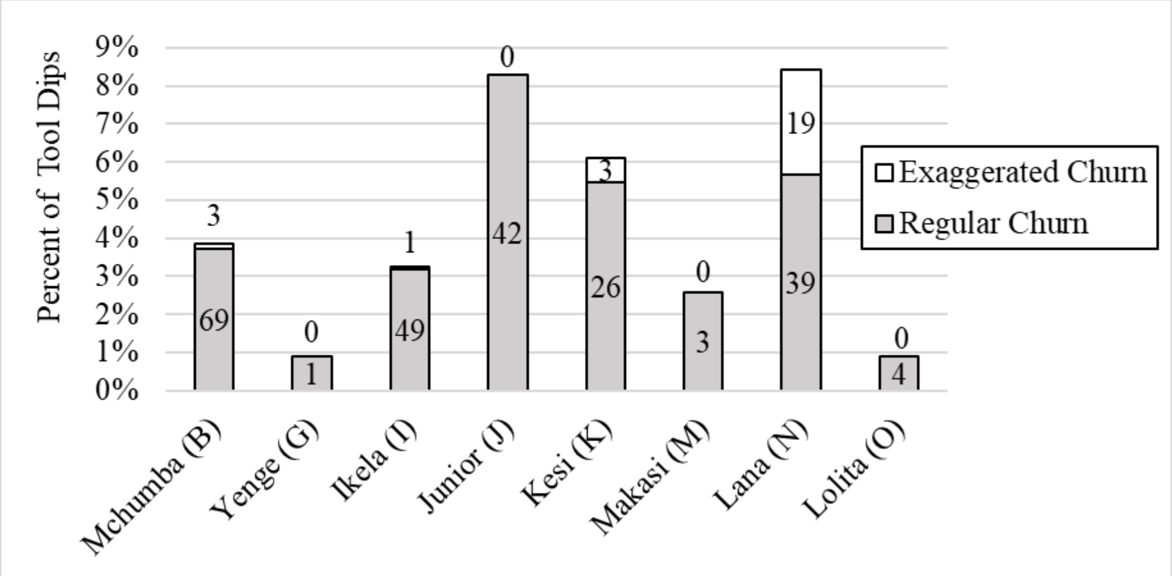


Figure 32: Percent of each subject's tool Dips that include Churning, broken down by Churn type. Each bar is labeled with the count of Dips represented.

4.3.e Effect of Novice Proximity & Attention on Exaggerated Churning Behavior

Although Churning, in general, was not positively correlated with novice proximity or Attention, it was plausible that the Exaggerated Churn subset might show such a relationship. Separate evaluation showed that Makasi was not In-View for any of the recorded Exaggerated Churn Dips. Kesi, however, was In-View for 52.6% of Lana's recorded Exaggerated Churn Dips, which though higher than the other juvenile-primary model dyads, was significantly lower than Kesi's In-View rate for Lana's non-Exaggerated Churn tool Dips of 77.3% [Fisher's exact test, *p*=.023]. Kesi's gaze was directed at Lana for 60.0% of the Exaggerated Churn Dips that she was In-View of (Table 14).

Table 14: Counts of Exaggerated Churn Dips recorded during the study period, by fisher.
* All "Novice Attention" associated with Exaggerated Churn Dips were coded either "Subject" or "None", none were scored as "ND".

Fishing Subject	Exaggerated Churn Dips	Novice In-View		Novice Attention *
		Kesi	Makasi	Kesi
Mchumba	3	0	0	0
Ikela	1	0	0	0
Kesi	3	NA	0	NA
Lana	19	10	0	6

4.3.f Effect of Kesi's Developmental Stage on Lana's Exaggerated Churning Behavior

To evaluate whether Lana's Exaggerated Churning was related to Kesi's fishing skill development, Lana's Churn Dips were binned by Kesi's Developmental Stage. As the number of recorded Exaggerated Churn Dips were low, these analyses should be considered preliminary. Stages 1-3 (before Kesi used a tool to fish) were pooled.

Lana's propensity to Exaggerate Churning increased from 22.2% of her Churn Dips while Kesi was in Stages 1-3 to 51.8% during Stage 4, but dropped back to 13.6% of her Churn Dips after Kesi was in Stage 5. For Dips when Kesi was verified as being In-View, Lana's Exaggerated Churn rate increased while Kesi was in Stage 4, despite Lana's Regular Churn rate decreasing during that same period (Figure 33).

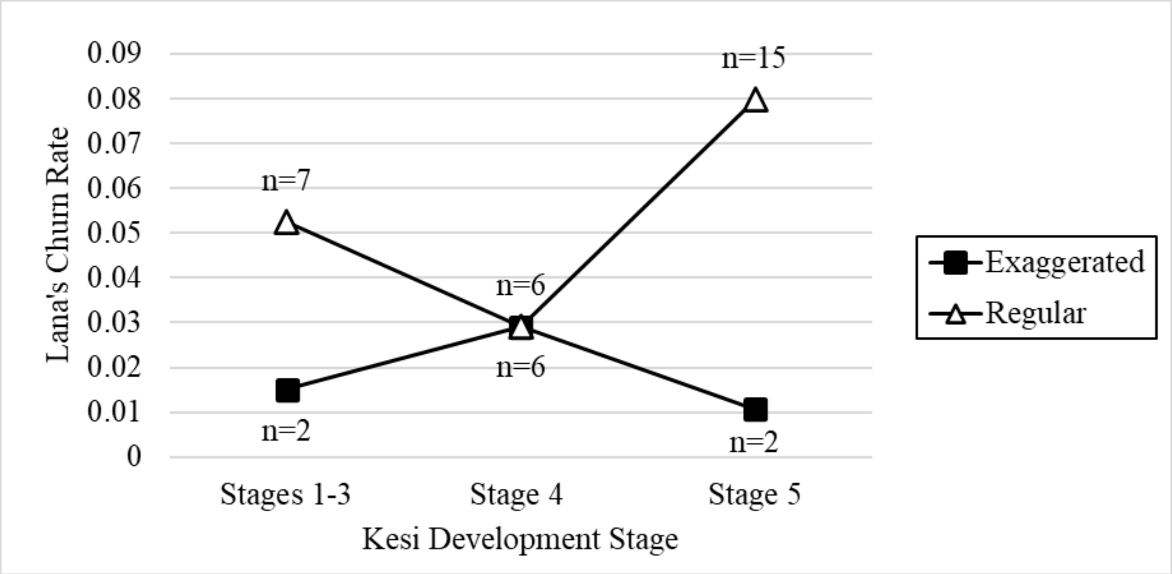


Figure 33: Lana's Exaggerated and Regular Churn Dips, as a proportion of all Lana's tool Dips recorded when Kesi was In-View, during each of Kesi's Developmental Stages. Each data point is labeled with the number of Lana's Respective Churn Dip Types Recorded. The total number of Kesi-In-View Dips recorded for Lana during each of Kesi's Developmental Stages is as follows: Stages 1-3: 133 Dips; Stage 4: 206 Dips; Stage 5: 188 Dips. Dips for which Churning could not be evaluated (coded "ND") were excluded.

Lana’s mean API per Exaggerated Churn Dip also increased while Kesi was in Developmental Stage 4, but only for Dips when Kesi was In-View. No similar increase was observed in either Stage 1-3 or Stage 5 (Figure 34).

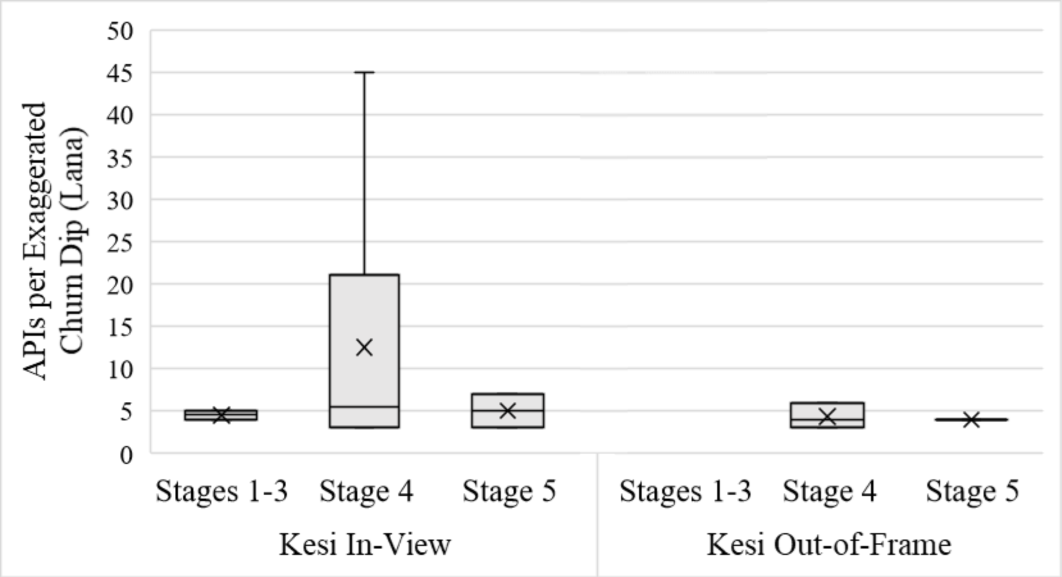


Figure 34: API distribution of Lana’s Exaggerated Churn Dips, by Kesi’s fishing Developmental Stage, for Dips when Kesi was either In-View or Out-of-Frame. The boxplots show the median, the first and third quartiles, and the lower and upper extremes within the group. No Churn Dips were recorded for Lana when Kesi was Out-of-Frame during Stages 1-3.

4.4 Discussion

Despite extensive analysis, the motivations for Churning during a Dip remain ambiguous. The observation that Lana, who was raising Kesi during the study, had the highest Churn rate within the group prompted the evaluation of Churning-as-demonstration directed at novice fishers, a potential form of teaching. Standards for characterizing nonhuman social behavior as teaching are understandably rigorous, and in 1992 Caro and Houser advanced an operational definition that allows for such evaluation:

> An individual actor **A** can be said to teach if it modifies its behavior only in the presence of a naïve observer, **B**, at some cost or at least without obtaining an immediate benefit for itself. **A**'s behavior thereby encourages or punishes **B**'s behavior, or provides **B** with experience, or sets an example for **B**. As a result, **B** acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all.(p. 153)

A number of behaviors by nonhuman subjects have been documented which may satisfy these requirements (Thornton & McAuliffe, 2006; Hoppitt, et al., 2008; Kline, 2015). Many of these feature scaffolding, wherein the expert creates opportunities for the novice to practice or complete tasks by controlling the aspects that are beyond the skill level of the novice (Meinertzhagen, 1954; Caro, 1992; Guinet & Bouvier, 1995; Thornton & McAuliffe, 2006). Other examples involve transmitting information via local enhancement, observational conditioning, or coaching (Nicol & Pope, 1996; Riley, Greggers, Reynold, & Menzel, 2005; Franks & Richardson, 2006). Examples of nonhuman demonstrative teaching are scarce, although both Atlantic spotted dolphins (*Stenella frontalis*) (Bender, Herzing, & Bjorklund, 2008) and wild chimpanzees (*Pan troglodytes*) (Boesch, 1991) have been observed doing so.

Although a binary (Churn versus no Churn) evaluation did not support a Churning-as-demonstration theory, Lana was observed in several instances to exaggerate Churning, in one case incorporating 45 Additional Partial Insertions (APIs) into a single Dip while Kesi was present. I hypothesized that although Churning in general did not appear to be novice-related, this "Exaggerated" Churning (defined as >2 APIs per Dip) might be a distinct behavior, and therefore may serve a different function than the more common and less costly "Regular" Churning. Further evaluation of all Churning Dips confirmed that Lana was both more likely to Exaggerate Churn Dips and had a significantly higher API per Churn Dip rate than the other subjects. Few Exaggerated Churns were recorded, however, and so all deeper analyses are necessarily provisional.

Kesi was confirmed as being In-View for just over half of Lana's Exaggerated Churn Dips, and so Exaggerated Churning may not meet the first of Caro and Hauser's "teaching" requirements. It should be noted, however, that one of the limitations of the video analysis was a bias toward a narrower frame on active fishers, and it is probable that Kesi was near and/or watching Lana during some of the Dips for which she was recorded as being Out-of-Frame. With that caveat in mind, it is still true that Kesi did not Attend as closely as might be expected if Lana was Exaggerating Churning for her benefit. This may not have directly affected Lana's behavior; novice Attention rates to active fishers were high (See Chapter 2.5.e: Juvenile Attention to Models p. 48), and so Lana may have expected that her actions were being noted by Kesi generally.

Unlike her propensity for Regular Churning, Lana's rate of Exaggerated Churning increased during Kesi's Stage 4, the period in which Kesi was beginning to use a probe tool to fish but was not yet competent. Once Kesi displayed fishing proficiency (Stage 5), Lana's

Exaggerated Churn rate returned to the lower level recorded prior to Kesi's fishing probe use. Lana's mean Churn API was also noticeably higher during Kesi's Stage 4, but only when Kesi was In-View. This increase in Exaggerated Churning dependent on novice Developmental Stage and proximity, if confirmed by additional studies and shown to correspond with faster acquisition of fishing competency by the attendant novice, could signify that this Exaggerated Churning behavior is a form of scaffolding.

As Regular (≤2 APIs per Dip) Churning is performed by all adults regardless of novice proximity, it does not qualify as a teaching. Further, the absence of *any* positive correlation between general Churning behavior (aggregate of Regular and Exaggerated Churning) and novice proximity within the group indicates that most of the observed Churning behavior is likely unrelated to the proximity, or attention, of novice fishers, regardless of relationship or Developmental Stage. The purpose of general Churning, therefore, remains unclear. While it is possible that Churning is a response to stimuli that are not easily detectable from the video (e.g., qualities of the probe, insertion resistance, obstructions in the bait holes), the increased likelihood of observing Churn Dips with increased fishing activity, along with the low frequency of Churn Dips (both overall and daily) indicates that Churning may be an idiosyncratic behavior.

Despite this apparent randomness, it remains possible that Churning is a strategic technical adjustment. Churn Dips may yield more food than non-Churn Dips, if not generally, then under certain circumstances. In this case, the low incidence of Churning may be a product of subjects' occasionally testing the technique during a Bout and generally determining that the return is not commensurate with the added cost in time per Dip. Churning may provide an unequal benefit depending on the bait type or the amount of bait remaining in the mound at the time of fishing; if there is less bait available at the time of the Dip, the reinsertion may result in higher probe capture than when bait is well stocked. The increase in Churning seen in 2008 and 2009 may be reflective of an unrecorded environmental change. Direct evaluation of yield-related hypotheses was not within the scope of the study, however, as neither identification of daily mound contents nor individual Dip yields were available.

In addition to potential Dip-efficacy motives, the observed increase in Churning behavior on days with multiple fishers may indicate that social factors are at play. Social relationships strongly influence bonobo foraging behavior; the typical year-round access to abundant food sources for bonobos in their natural forested habitat results in relatively low levels of feeding competition and infrequent monopolization of food sources (White & Wrangham, 1988; Inogwabini & Matungila, 2009). Bonobos will frequently share food that is easily obtainable (Kuroda, 1984; Yamamoto, 2015). Even consumption of highly prized, less abundant foods such as prey species often involves passive sharing and peaceful co-eating (Wakefield, et al., 2019). In fact, bonobos exhibit a preference to co-feed even when it diminishes their own food access (Tan & Hare, 2013). Thus, since foraging and feeding are important social activities, such associations should be considered when evaluating causes of food-related behavior.

As was the case for technique efficacy explanations for Churning, social causation was difficult to confirm from this study. One possibility is that Churning may be a form of display, an intentional exaggeration or elongation of the Dip intended to catch the attention of nearby individuals. Though there was no significant difference in Churning between subjects fishing alone vs. those with a confirmed audience, the observed increase in individual Churn rates on days with multiple active fishers could indicate a display motivation. If Churn Dips are intended as a display, an increase in Churn rates might be expected when other members of the group were nearby. However, as adult vicinity to active fishers was not evaluated for this study, the extent to which the presence of other adults influences fishing behavior could not be directly evaluated. Even for the JKN subgroup (which includes focal juvenile Kesi and her mother), Churning occurred at similar rates regardless of whether the Churner was the sole fisher during a clip or not. These findings imply that a display explanation is unlikely, and the "social" increase noted is connected to the increase in fishing activity seen on days with multiple active fishers.

Alternatively, Churning may be tangentially social, a "neutral" continuation of the Dip that occurs while the fisher temporarily redirects their attention to track nearby individuals. Rather than pause the Dip motion while attention is momentarily elsewhere, the repetitive nature of the partial re-insertion of the fishing probe may allow for a sort of mindless movement, the Dip concluding only after the fisher's attention returns to the mound. As with the previous "display" possibility, verification of was not possible, as fisher attention was not recorded for this study. While it was observed that fishers frequently direct their gaze away from the mound during Dips, without more detailed analysis on when precisely attention shifts this hypothesis remains largely untested.

The significantly elevated Churn rates seen in the familial JKN subgroup, while unexpected, fits within known bonobo socio-biology. Bonobo mothers typically assume the majority of parental care (de Waal, 1997) and are known to be indulgent and protective of their offspring for the length of their relationship (Kano, 1992). Young bonobos are not weaned until 4-5 years of age and are largely carried by their mother during this time; even when moving independently young bonobos stay close enough to quickly return to their mother for support, protection, and carries (Kuroda, 1989). Lana, who raised both Junior and Kesi, would have served as the primary model for both during critical learning periods when tool-use behaviors were acquired (van Schaik, Fox, & Fechtman, 2003). The higher propensity to Churn in this kin subgroup, particularly if Churning is not, in and of itself, a more functional method, may reflect a greater social learning influence over that of individual learning (Hirata & Morimura, 2000; Shorland, Genty, & Zuberbühler, 2015).

It was not possible to robustly compare the Churn rate of Makasi, the other novice fisher who became proficient during the study, to that of his primary models due to Makasi's low Churn rate over comparatively fewer Dips. Mchumba and Lolita, the other mother-offspring dyad present in the group, did not exhibit the same similarity of Kesi and Lana in their respective Churn frequencies; Lolita had the group's lowest Churn rate (<1% of probe Dips), while Mchumba had a Churn rate closer to the group average of 3.8%. It is possible that Mchumba, a proficient juvenile at the start of this study, may have previously had more opportunity to observe higher-Churning individuals, or that Lolita Churned at a higher rate during Mchumba's primary learning period. It is equally possible that the high Churn rates seen among JKN are coincidental. More longitudinal data, particularly of mother-offspring dyads, are needed to better understand the extent to which Churning propensity may be influenced by early observation of expert fishers.

Overall, evidence for the motivations and benefits of Churning during a Dip were not conclusive from this study. Although Churning as an idiosyncratic and non-beneficial Dip variation remains the most likely explanation, several alternate hypotheses remain largely untested. The special case of Exaggerated Churning, particularly that exhibited by Lana in the presence of novice-fisher Kesi, may indicate demonstrative scaffolding behavior contingent on novice skill-level in bonobos. More research is necessary to corroborate this finding.

Appendix I: Scoring Tier Structure and Ethogram

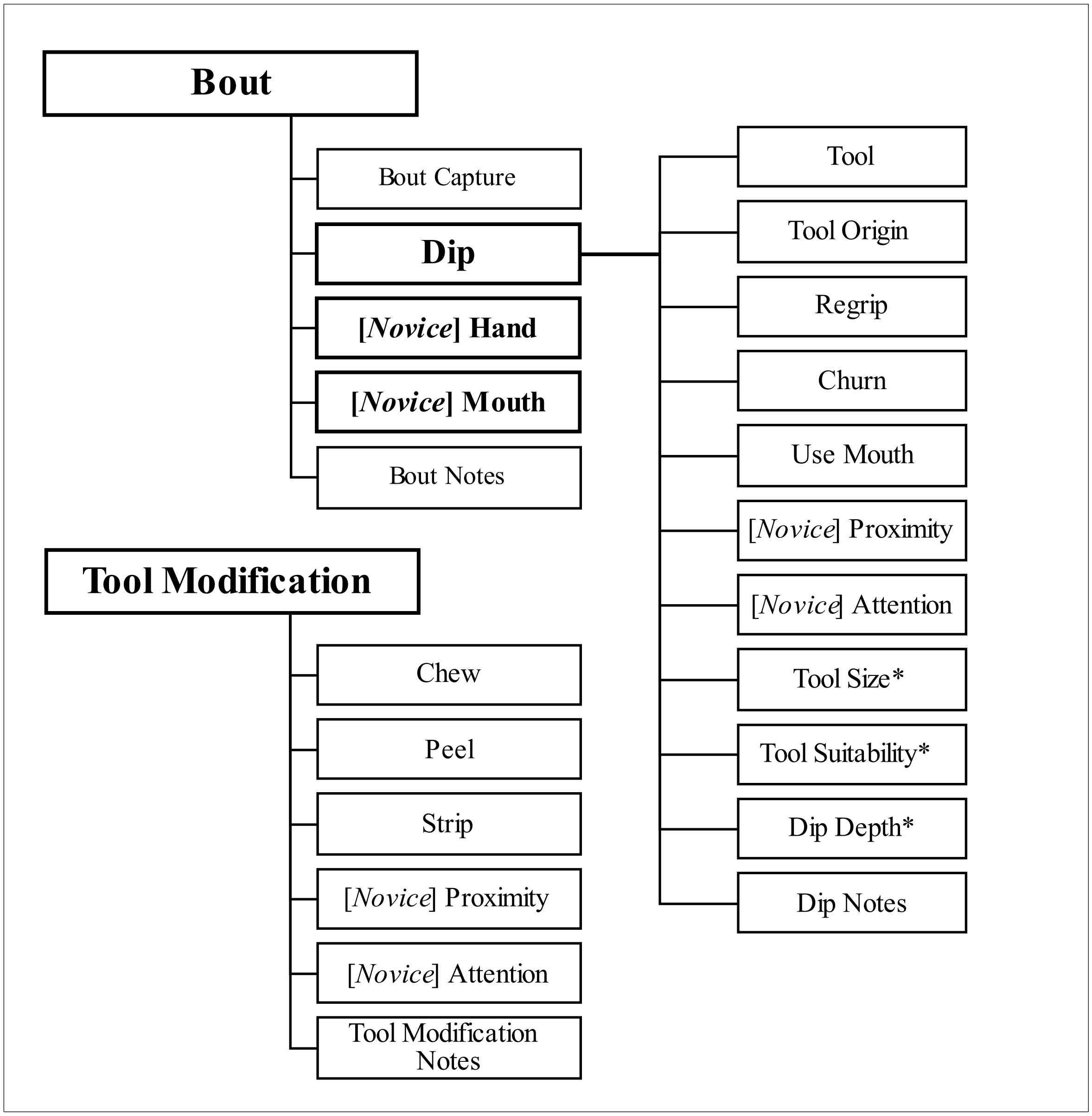
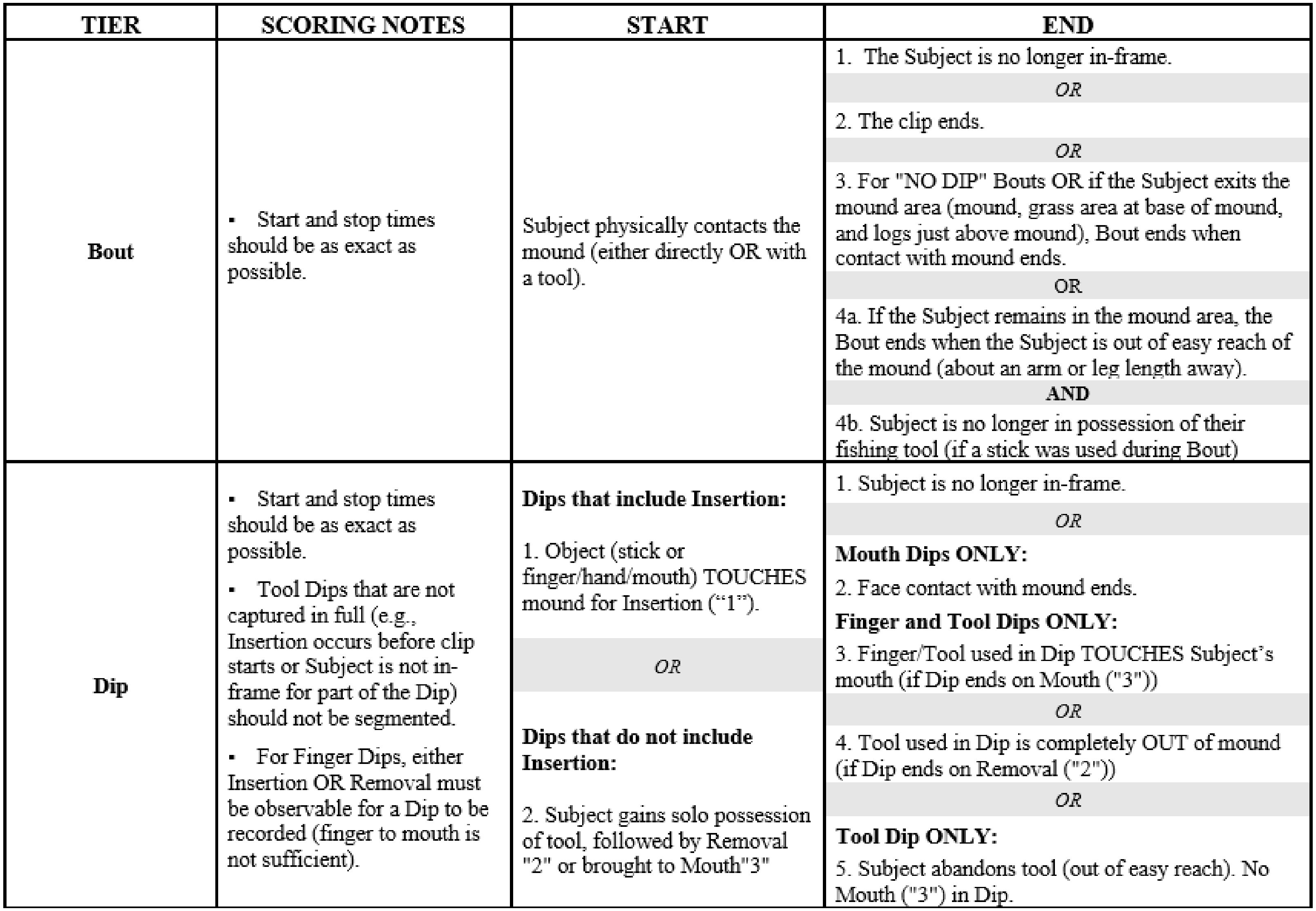


Figure 35: Scoring Tier Structure. Tiers in Bold indicate segmented (time-dependent) tiers. [*Novice*] indicate tiers that had separate entries for each juvenile (Mchumba, Kesi, and Makasi). * indicates tiers that were only applied to Dips by novices Kesi and Makasi. All other tiers were applied separately to each subject.

Table 15: Segmentation guidelines for segmented tiers



TIER	SCORING NOTES	START	END
Bout	▪ Start and stop times should be as exact as possible.	Subject physically contacts the mound (either directly OR with a tool).	1. The Subject is no longer in-frame. *OR* 2. The clip ends. *OR* 3. For "NO DIP" Bouts OR if the Subject exits the mound area (mound, grass area at base of mound, and logs just above mound), Bout ends when contact with mound ends. OR 4a. If the Subject remains in the mound area, the Bout ends when the Subject is out of easy reach of the mound (about an arm or leg length away). **AND** 4b. Subject is no longer in possession of their fishing tool (if a stick was used during Bout)
Dip	▪ Start and stop times should be as exact as possible. ▪ Tool Dips that are not captured in full (e.g., Insertion occurs before clip starts or Subject is not in-frame for part of the Dip) should not be segmented. ▪ For Finger Dips, either Insertion OR Removal must be observable for a Dip to be recorded (finger to mouth is not sufficient).	**Dips that include Insertion:** 1. Object (stick or finger/hand/mouth) TOUCHES mound for Insertion ("1"). *OR* **Dips that do not include Insertion:** 2. Subject gains solo possession of tool, followed by Removal "2" or brought to Mouth"3"	1. Subject is no longer in-frame. *OR* **Mouth Dips ONLY:** 2. Face contact with mound ends. **Finger and Tool Dips ONLY:** 3. Finger/Tool used in Dip TOUCHES Subject's mouth (if Dip ends on Mouth ("3")) *OR* 4. Tool used in Dip is completely OUT of mound (if Dip ends on Removal ("2")) *OR* **Tool Dip ONLY:** 5. Subject abandons tool (out of easy reach). No Mouth ("3") in Dip.

Table 15: Segmentation guidelines for segmented tiers, continued

TIER	SCORING NOTES	START	END
[*Novice*] Hand	▪ Accurately capture the NUMBER of directed actions on Subject. ▪ Exact segment timing is not important.	New segment for EACH distinct instance of a juvenile intentionally touching a Subject or their Tool while that Subject is in a Bout. Can be with either a hand or foot.	1 Second (Use 1 keystroke/ annotation, 1000 ms)
[*Novice*] Mouth	▪ Accurately capture the NUMBER of directed actions on Subject. ▪ Exact segment timing is not important.	New segment for EACH distinct instance of a juvenile eating after touching a Subject or their Tool while that Subject is in a Bout.	1 Second (Use 1 keystroke/ annotation, 1000 ms)
Tool Modification	▪ Start and stop times should be as exact as possible	1. First contact with tool (Subject takes possession of a stick and subsequently performs a Tool Modification (Chew, Strip, or Peel) with continuous tool possession or contact)	1. Subject begins a Dip with the modified tool (no temporal overlaps between Dip and Tool Modification)
		OR	*OR*
		2.When Previous Dip ends (tool touches mouth) (e.g., If between Dips, Subject completes a Dip and subsequently performs a Tool Modification (peel or strip))	2. Subject loses contact with the modified tool
		OR	*OR*
		3. When Tool is completely free of mound hole (for "1_2" or "2" Dips only) and Subject subsequently performs a Tool Modification	3. Subject is no longer in-frame.

Table 16: Ethogram for tier annotations

Tier	Annotation	Definition
Bout Capture	Full	Entire Bout captured (i.e., clip includes Subject's approach to mound, first Dip through last Dip, and departure)
	Abbreviated	End of Bout not captured (first Dip captured, last Dip likely not captured or not fully captured)
	Truncated	Beginning of Bout not captured (first Dip likely not captured (or not fully captured), last Dip and departure captured)
	Partial	Neither beginning (first Dip) nor end of Bout (last Dip) captured
	NO DIPS	Bout does not include any Dips
Dip	1_3	Insertion, Removal, and tool or finger to Mouth
	1_2	Insertion and Removal only, tool/finger is fully removed from mound
	2_3	Removal and Mouth only
	1	Tool Insertion only (tool stays in mound)
	2	Tool Removed from Mound. No Insertion or to Mouth
	3	Tool used in previous Dip (that ended on "2") touches Subject's mouth
Tool	Tool_R	Tool used in Dip, held in right hand
	Tool_L	Tool used in Dip, held in left hand
	Tool_B	Tool used in Dip, both hands used during Dip
	Mouth	Subject's mouth (including lips or tongue) directly contacts a bait hole
	Finger_R	Right Hand/ Fingers ONLY used during Dip (no tool)
	Finger_L	Left Hand/ Fingers ONLY used during Dip (no tool)

Table 16: Ethogram for tier annotations, continued

Tier	Annotation	Definitions
Tool Origin	PDS	Tool last used in a previous Dip by same Subject
	PDOI	Tool last used in a Dip by other individual (not Subject)
	Mound	Tool was at mound before the Subject gained possession, not known if PDS or PDOI (at mound=on or within easy reach of mound when Subject gained possession)
	Off_Mound	Tool was brought from off-mound (out of easy reach), not known if PDSI or PDOI
	N/A	Tool not used in Dip
	ND	No determination possible (i.e., clip starts when Bout is already in-progress
Regrip	Insertion	Modified method of tool Insertion (“1”) where the Subject inserts the tool partially, then adjusts their hand position by releasing and re-gripping further up the tool (away from the mound) before continuing Insertion
	Removal	Modified method of tool Removal (“2”), where, after beginning Removal, the Subject adjusts their hand position on the fishing tool by releasing the tool and re-gripping lower down (closer to the mound) before continuing Removal
	Both	Regrip occurs on both Insertion ("1") AND Removal ("2") of tool from mound
	None	Subject does not Regrip the tool during Insertion or Removal portions of Dip OR Tool not used in Dip
	ND	Scorer unable to make a clear determination. Applies if EITHER Regrip on Insertion or Removal cannot be ascertained
Churn	Yes	Dip modification characterized by the partial Removal of the tool from the baited mound hole, followed by a re-insertion of that tool before the Dip sequence is completed (can be any time after Insertion (“1”) begins but before Removal (“2) is complete
	No	No Churn during Dip OR tool not used in Dip
	ND	No determination possible

Table 16: Ethogram for tier annotations, continued

Tier	Annotation	Definitions
Use Mouth	Yes	During Dip, Subject uses mouth to aid in Insertion or Removal of tool from a bait hole
	No	Mouth not used to aid in Insertion or Removal of tool OR tool not used in Dip
	ND	No determination possible
Tool Size	Short	Tool used in Dip is shorter than the Subject's arm
	Long	Tool used in Dip is either about the same length or longer than the Subject's arm
	ND	Unable to make a clear determination
Tool Suitable	Yes	Tool is able to be used for successful fishing. Can be easily inserted, removed. Is not too flimsy to control. Leaves have been removed.
	No	Stick used as tool is too wide, or bent, floppy, leafy etc. (length not considered)
	ND	Unable to make a clear determination
Dip Depth	0.25	Less than 1/4 of tool Inserted during Dip
	0.5	Between 1/4 to about half of tool Inserted
	0.9	More than half to nearly all of tool Inserted
	1	Entire tool Inserted into mound (tool completely out-of-view)
	ND	Unable to make a clear determination
	NA	Dip does not include Insertion (no "1")
Dip Notes	Free text	Free space for scorer notes related to Dip.

Table 16: Ethogram for tier annotations, continued

Tier	Annotation	Definitions
[*Novice*]_Proximity	Indirect Touch	Juvenile is being (ventrally or dorsally) carried by Subject, or other non-directed contact with Subject at any point during Subject's Dip or Tool Modification session
	Close	Juvenile is within easy reach (arm or leg length) of Subject at any point during Subject's Dip or Tool Modification session
	Out-of-Easy-Reach	Juvenile is out of easy reach (arm or leg length) of Subject during entire Dip or Tool Modification session but is In-Frame (in-view) at any point
	Out-of-Frame	Juvenile is not in frame at any point during Dip or Tool Modification session
[*Novice*] Hand	Touch Subject	Juvenile intentionally touches (with hand or foot) Subject during a Bout or Tool Modification session (e.g., being carried does not count but touching to initiate a carry does)
	Touch Tool	Juvenile intentionally touches Subject's tool (with hand or foot) when Subject is not in current possession of tool, tool ownership is clear AND Subject's Bout is still on-going).
	Co-Touch Tool	Juvenile intentionally touches Subject's tool (with hand or foot) while Subject is in possession of tool. Juvenile's touch does not control tool, i.e., is not a "grab")
	Co-Hold	Juvenile firmly grips Subject's tool while Subject is in possession of tool
	Take	Co-Hold that ends with Juvenile taking possession of tool from Subject (single action can either be a Co-Hold or a Take, but NOT BOTH)
[*Novice*] Mouth	Eat From Own Hand	Juvenile brings their hand to their mouth immediately following a [*novice*] Hand action
	Eat From S's Tool	Juvenile's mouth touches Subject's tool while it is in Subject's possession
	Eat From S's Hand	Juvenile's mouth touches Subject's hand while/soon after Subject Dips.
Bout Notes	Free text	Free space for scorer notes related to Bout.

Table 16: Ethogram for tier annotations, continued

Tier	Annotation	Definitions
Tool Modification	Before 1st Dip	First Dip in Bout occurs after modification WITH modified tool, within same clip
	Between Dips	Tool is used during Dip, is modified, and then used again in subsequent Dip
	During Dip	Dip has begun and Tool Modification begins before Dip ends.
	No Dips	No Dips with modified tool follow tool modification (within same clip)
Chew	Yes	Insert the end of the stick into mouth, as if to modify end into brush-tip PRIOR to first Dip with that tool
	No	No Chew during Tool Modification. NOTE: Chew is not scored between or after Dips with the same tool
	ND	Unable to make a clear determination
Strip	Yes_Hands_Only	Subject removes leaves and smaller branches from stick sides, or shortens tool. May be before OR in-between Dips. DOES NOT USE MOUTH.
	Yes_With_Mouth	Subject removes leaves and smaller branches from stick sides, or shortens tool. May be before OR in-between Dips. MOUTH USED IN ACTION
	No	No stripping during Tool Modification
	ND	Unable to make a clear determination
Peel	Yes_Hands_Only	Subject removes bark or wood from the stick sides, resulting in a thinner tool. May be before OR in-between Dips. DOES NOT USE MOUTH
	Yes_With_Mouth	Subject removes bark or pieces of wood from the stick sides, resulting in a thinner tool. May be before OR in-between Dips. MOUTH USED IN ACTION
	No	No Peeling during Tool Modification
	ND	Unable to make a clear determination
Tool Modification Notes	Free text	Free space for scorer notes related to Tool Modification.

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Appendix II: Video Inventory

Table 17: Tapes of the San Diego Zoo bonobo exhibit. Each tape represents approximately one hour of film taken.

Date	Tapes
Aug-04	1
Sep-04	4
Oct-04	3
Nov-04	2
Jul-05	1
Sep-05	1
Oct-05	30
Nov-05	36
Dec-05	0
Jan-06	16
Feb-06	28
Mar-06	13
Apr-06	20
May-06	27
Jun-06	10
Jul-06	7
Aug-06	5
Sep-06	0
Oct-06	24
Nov-06	23
Dec-06	1
Jan-07	13
Feb-07	22
Mar-07	8
Apr-07	19
May-07	22
Jun-07	6
Jul-07	2
Aug-07	2
Sep-07	1
Oct-07	18
Nov-07	17
Dec-07	6
Jan-08	12
Feb-08	27
Mar-08	11
Apr-08	11
May-08	8
Jun-08	4
Jul-08	0
Aug-08	0
Sep-08	1
Oct-08	10
Nov-08	13
Dec-08	6
Jan-09	13
Feb-09	14
Mar-09	11
Apr-09	9
May-09	9
Jun-09	10
Jul-09	0
Aug-09	0
Sep-09	0
Oct-09	9
Total:	566

Table 18: Inventory of video that included interactions with the artificial termite mound.
— indicates party membership was not noted.

Tape ID	Date	Party	Length (min)
cindy2	10/16/2004	JKN	14
cl4	10/31/2004	GIKN	46
ac0	9/29/2005	—	60
af0	10/10/2005	BGKMNO	55
cd0	10/10/2005	GIJKMN	20
cd0	10/13/2005	GIJ	20
cd0	10/14/2005	—	20
cs1	10/15/2005	BGJKNO	30
av0	10/15/2005	—	16
cs1	10/16/2005	BGKMNO	30
bm0	10/16/2005	GIJ	60
jt1	10/18/2005	BGJO	60
av0	10/20/2005	BGJO	15
jt2	10/20/2005	GIJKMN	40
bm1	10/24/2005	IJKN	60
hr1	10/25/2005	BGKMNO	60
jt2	10/25/2005	BGKMNO	20
jt3	10/25/2005	GIJ	40
av0	10/25/2005	GIJ	8
jt3	10/27/2005	BGKMNO	20
cd2	10/29/2005	BGKMNO	60
ez2	10/31/2005	BGJKMN	53
av1	11/1/2005	BGKNO	20
hr2	11/1/2005	GIJKMN	60
cd3	11/2/2005	GIJ	40
av1	11/3/2005	BGJO	20
af1	11/5/2005	GIJKNM	43
ez3	11/7/2005	BGKMNO	60
af2	11/7/2005	GIJ	30
js6	11/8/2005	GIJKMN	60
av1	11/8/2005	BGJO	20
js7	11/9/2005	BGKMNO	50
cd3	11/11/2005	BGKMNO	20
bm5	11/13/2005	IJKN	60
Colin4	11/13/2005	BGKMNO	45

Table 18: Inventory of video that included interactions with the artificial termite mound. — indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
af2	11/14/2005	BGJO	20
ez4	11/14/2005	GIJKN	60
af2	11/14/2005	GIJKMN	10
hassan5	11/15/2005	BGKMNO	60
jt7	11/15/2005	GIJ	15
jt7	11/15/2005	BGKMNO	45
jt8	11/17/2005	GIJKN	40
jt8	11/17/2005	BGKMNO	20
cd5	11/19/2005	BGKMNO	60
cd6	11/19/2005	BGKMNO	60
cs5	11/19/2005	GIJ	10
cs5	11/20/2005	BJO	5
ku0	1/19/2006	BGJO	22
lw0	1/19/2006	BGJO	30
av2	1/19/2006	GIKMN	10
lw0	1/19/2006	GIKMN	10
em6	1/20/2006	GIJ	3
lw0	1/20/2006	BGKMNO	20
lk0	1/21/2006	BGKMNO	50
em6	1/23/2006	BGKMNO	55
bp0	1/24/2006	BGKMNO	35
bp0	1/26/2006	BGKMNO	25
bp1	1/26/2006	BGKMNO	40
lk0	1/27/2006	GIKMN	10
ku1	1/29/2006	BGJO	13
ku1	1/29/2006	GIKMN	10
bp1	1/31/2006	BGKMNO	10
ku2	1/31/2006	GIJ	20
bp2	2/2/2006	BGKMNO	60
af4s1	2/2/2006	BGKMNO	5
ez7	2/3/2006	BGKMNO	60
af4	2/5/2006	BGKMNO	55
ku2	2/6/2006	BGJO	40
lw4	2/6/2006	GIKMN	55
ku2	2/6/2006	GIKMN	3

Table 18: Inventory of video that included interactions with the artificial termite mound.
— indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
ku3	2/7/2006	GIJ	1
ku3	2/7/2006	BGKMNO	58
bp3	2/9/2006	BGKMNO	60
jt9	2/9/2006	BGKMNO	54
av2	2/9/2006	BGKMNO	50
af6	2/12/2006	GIKMN	60
af7	2/12/2006	GIKMN	10
af7	2/16/2006	BJO	30
ku3	2/19/2006	GIJ	1
lw6	2/22/2006	GIKMN	40
cs5	2/24/2006	BGJO	30
ku3	2/26/2006	BGJO	15
af7	2/26/2006	GIKMN	20
lw6	2/27/2006	BGKMNO	20
af9	3/2/2006	GIKMN	50
bp8	3/2/2006	GIKMN	60
bp9	3/2/2006	GIKMN	50
ez12	3/3/2006	BGKMNO	60
lw8	3/7/2006	BGKMNO	60
ku5	3/7/2006	GIJ	24
ku5	3/7/2006	BGKMNO	12
cs5	3/8/2006	BGJO	30
lw10	3/15/2006	GIKMN	60
ku6	3/16/2006	GIJ	2
bp12	4/6/2006	GIKMN	50
ku6	4/8/2006	GIJKMN	40
bp13	4/12/2006	BGKMNO	60
bp14	4/12/2006	BGKMNO	55
lw11	4/17/2006	GIKMN	40
lw11	4/19/2006	BGKMNO	20
bp15	4/20/2006	GIKMNO	60
kl1	4/23/2006	BGKMNO	59
bp16	4/27/2006	BGKMNO	57
kl3	4/30/2006	GIKMN	60
sy1	5/3/2006	BGKMNO	60

Table 18: Inventory of video that included interactions with the artificial termite mound. — indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
kl5	5/7/2006	BGKMNO	55
lw15	5/10/2006	IKMN	25
ku8	5/12/2006	BGKMNO	60
lu7	5/13/2006	BGKMNO	60
kl6	5/14/2006	GIKMN	58
sy3	5/15/2006	BGKLMN	30
lw15	5/16/2006	GIKMN	35
bp19	5/18/2006	GIKMN	60
bp20	5/18/2006	GIKMN	60
kl8	5/21/2006	BKMNO	52
lw17	5/23/2006	BGKMNO	30
sy5	5/24/2006	GIKMN	52
lw17	5/30/2006	GIKMN	30
lw18	5/31/2006	BGKMNO	60
bp22	6/1/2006	GIKMN	60
kh9	6/2/2006	BGKMNO	50
sy7	6/7/2006	GIKMN	60
ku11	6/11/2006	GIKMN	60
lw20	6/14/2006	BGKMNO	55
ku13	6/15/2006	GIKMN	50
lw21	7/17/2006	GIKMN	60
lw22	7/18/2006	BGKMNO	60
ku16	7/18/2006	BGKMNO	20
lw24	7/21/2006	GIKMN	60
ku16	7/25/2006	GIKMNO	40
ku17	7/25/2006	GIKMN	14
bp25	8/11/2006	BGKMNO	51
ku17	8/18/2006	GIKMN	45
sy8	8/24/2006	GIKMN	60
sy10	8/30/2006	GIKMN	60
kh0	10/5/2006	GIKMN	61
as2	10/9/2006	BGJO	7
ck0	10/10/2006	BIKMN	30
ck0e	10/12/2006	GIJ	3
ck0e	10/13/2006	GIKN	25

Table 18: Inventory of video that included interactions with the artificial termite mound. — indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
as2	10/16/2006	GIJ	40
kh12	10/18/2006	BGKMNO	50
kl10	10/22/2006	BGKMNO	51
kh13	10/23/2006	GIKMN	50
kh2	10/24/2006	BGKMNO	50
ck3	10/24/2006	GIJ	12
kh3	10/24/2006	—	35
ck3	10/26/2006	BGKMNO	15
as3	10/27/2006	BGJO	10
as3	10/27/2006	GIKMN	5
ck3	10/27/2006	GIKMN	30
kh3	10/31/2006	GIKMNO	25
kh4	10/31/2006	GIKMN	20
as3	10/31/2006	GIKMN	45
ck5	11/1/2006	BGKMNO	58
bp28	11/2/2006	GIKMN	47
kl13	11/5/2006	GIKMN	53
kh4	11/7/2006	GIKMN	40
as6	11/9/2006	GIKMN	55
kh17	11/11/2006	BGKMNO	22
kl15	11/12/2006	BGKMNO	50
kh6	11/14/2006	BKMNO	60
kh17	11/15/2006	GIKMN	35
bp30	11/16/2006	BKMNO	60
kh7	11/21/2006	GIKMN	60
bp31	11/25/2006	GIKMN	51
bp32	11/30/2006	BKMNO	60
kh8	12/12/2006	BGKMNO	60
bp33	1/4/2007	GIKMN	54
kh9	1/9/2007	BGKMNO	60
kh10	1/15/2007	BGKMNO	60
kh11	1/21/2007	BGKMNO	53
ck9	1/22/2007	GIKMN	15
ck9	1/24/2007	GIKMN	45
kr38	1/26/2007	GIKMN	60

Table 18: Inventory of video that included interactions with the artificial termite mound. — indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
kr39	2/2/2007	BGKMNO	55
khl8	2/6/2007	BGKMNO	50
ck13	2/7/2007	GIKMN	58
kmh13	2/8/2007	BGKMNO	56
jf1	2/10/2007	BGKMNO	50
ma6	2/23/2007	BGJMO	1
kmh16	3/1/2007	GIKMN	57
ma6	3/1/2007	GIKMN	45
jf5	3/3/2007	GIKMNO	53
jf6	3/3/2007	GIKMNO	20
jf7	3/9/2007	BGKMNO	15
jf7	3/10/2007	GIKMN	35
jf6	3/18/2007	BGKMNO	35
kmh17	4/7/2007	BGKMNO	53
kmh19	4/14/2007	GIKMN	55
rh1	4/20/2007	GKMNO	55
kmh20	4/21/2007	BGKMNO	54
rh2	4/22/2007	BJKMNO	35
kmh21	4/28/2007	BJKMNO	53
kmh22	5/5/2007	IJKMN	52
kmh23	5/12/2007	GIKMN	52
kmh24	5/12/2007	GIKMN	51
ma14	5/26/2007	BGKMNO	35
rh6	5/26/2007	BGKMNO	40
ma14	6/1/2007	BGKMNO	20
jf15	6/3/2007	BJKMNO	54
kmh	8/24/2007	GIKMN	51
kmh30	9/16/2007	IJKMN	60
rh9	10/1/2007	BJKMNO	50
kd2	10/27/2007	IJKMN	60
dn2	10/27/2007	IJKMN	52
dn3	10/28/2007	BGKMNO	60
kd5	11/3/2007	GIKMN	54
dn4	11/5/2007	BGKMN	54
ab5	11/11/2007	GIKMN	61

Table 18: Inventory of video that included interactions with the artificial termite mound. — indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
kd6	11/17/2007	IJKMN	52
cb3	11/20/2007	BGKMN	34
ab7	11/25/2007	IJKMN	51
cb3	11/27/2007	IJKMN	20
dn8	12/2/2007	GIKMN	54
cb6	12/11/2007	GIKMN	54
rh13	1/2/2008	BIJKMN	48
cy7	1/12/2008	BIJKN	3
cb7	1/14/2008	BJKMNO	50
rt0	1/20/2008	BGKMNO	30
ee1	1/22/2008	BGKMNO	55
cb8	1/25/2008	GIKMN	50
rt1	1/31/2008	IJKMN	60
ab8	2/5/2008	BGKMNO	50
du11	2/9/2008	IJKMN	54
ab10	2/10/2008	BGKMNO	51
rt0	2/10/2008	BGKMNO	27
cm2	2/11/2008	GIKN	16
cb9	2/11/2008	IJKMN	25
cm2	2/13/2008	IJKMN	40
ab11	2/16/2008	BGKMNO	52
rt2	2/17/2008	IJKMN	52
cm3	2/18/2008	BJKMNO	55
rt5	2/21/2008	IJKMN	60
cb9	2/25/2008	GIKMN	35
ee8	3/4/2008	IGKMN	55
cb12	3/10/2008	IJKMN	50
rt7	4/7/2008	IJKMN	52
np0	4/11/2008	BGKMNO	30
ee9	4/12/2008	GKMNO	60
ee11	4/13/2008	BJKMNO	60
np0	4/16/2008	IJKMN	27
ee13	4/27/2008	IJKMN	55
ee14	5/17/2008	GIJKMN	60
np6	6/4/2008	GJKMNO	52

Table 18: Inventory of video that included interactions with the artificial termite mound. — indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
rt13	6/8/2008	GIJKMN	55
cy0	10/12/2008	BJKNO	25
mw0	10/13/2008	IMOTY	30
jb0	10/13/2008	BJKN	28
cy0	10/14/2008	IMOTY	23
mw0	10/14/2008	—	10
jb0	10/19/2008	BGJKN	35
cy1	10/19/2008	BGJKN	35
mw1	10/20/2008	GIMTY	30
cy1	10/21/2008	BGJKN	24
mw1	10/22/2008	IMOTY	30
mw2	10/27/2008	GIMTY	60
bk2	11/2/2008	BJKNO	30
mw3	11/5/2008	GITY	40
bk2	11/9/2008	BJKNO	30
mw3	11/10/2008	GIMTY	20
bk3	11/11/2008	BJKNO	30
mw4	11/12/2008	GIMTY	31
bk3	11/16/2008	BJKNO	20
mw4	11/17/2008	GIMTY	30
bk4	11/22/2008	BIJKN	20
cy5	11/23/2008	BJKNO	25
bk4	11/23/2008	BJKNO	30
cy5	11/24/2008	GKMNOTY	26
cy6	12/2/2008	BJKNO	22
cy6	12/14/2008	BJKNO	28
jo0	1/17/2009	BIJKN	33
hg0	1/19/2009	GIKMNTY	30
jo0	1/20/2009	BIJKN	20
hg0	1/22/2009	BJKNO	30
jo1	1/26/2009	BIJKN	35
ab15	1/28/2009	GIKMN	60
cy7	2/1/2009	BIJKMN	47
jo1	2/3/2009	BIJKN	20
hg3	2/10/2009	BJKNO	30

Table 18: Inventory of video that included interactions with the artificial termite mound. — indicates party membership was not noted, continued.

Tape ID	Date	Party	Length (min)
ab16	2/15/2009	BJKNO	50
hg3	2/17/2009	BIJKN	25
hg3	2/17/2009	GIKMN	5
ab17	2/18/2009	BIJKN	12
ab17	2/18/2009	—	39
jo2	2/20/2009	BJKNO	38
jb9	2/24/2009	BIJKN	25
ab19	2/25/2009	GIKN	35
jb9	2/26/2009	BJKNO	25
cy9	3/1/2009	GKNO	50
jo2	3/2/2009	BIJKN	22
jo3	3/6/2009	BIKN	32
jo3	3/9/2009	BIKNTY	28
hg5	3/10/2009	BJKNO	30
ab20	3/11/2009	GIKN	52
ab19	3/11/2009	GIKN	20
hg5	3/17/2009	GKMNOTY	30
th0	4/8/2009	BJKNO	15
th0	4/12/2009	BJKNO	25
sm0	4/12/2009	GIKMNTY	30
th0	4/12/2009	GIKMNTY	15
sm0	4/15/2009	BIJKN	30
pr5	4/16/2009	GIKMNTY	60
th1	4/17/2009	BIJ	20
th1	4/20/2009	GIKMNTY	40
th2	5/1/2009	BIJKN	25
hg7	5/2/2009	BJKNO	40
hg7	5/10/2009	GIKMNTY	20
th2	5/11/2009	BIJKN	30
pr7	6/6/2009	BIJKN	30
pr7	6/9/2009	GIKMNTY	30
jo7	6/17/2009	BIJKN	30
jo7	6/19/2009	GKMNOTY	30
jo	6/23/2009	BIJKN	30
jo	6/24/2009	GKMNOTY	10
jo	6/24/2009	BJKNO	10

Table 19: Clip Inventory

Tape Date	File Name	Length (minutes)
10/16/2004	KNmound16Oct04cindy2s1	0.20
10/16/2004	KNmound16Oct04cindy2s2	2.88
10/31/2004	GKNmound31Oct04GIKNcl4s1	1.12
9/29/2005	I29Sep05ac0e1	1.37
9/29/2005	I29Sep05ac0e2	0.55
10/10/2005	BMmound10Oct05BGKMNOaf0s1	1.30
10/10/2005	BMmound10Oct05BGKMNOaf0s2	2.05
10/13/2005	Jmound13Oct05cd0s1	4.05
10/15/2005	BJ(IorO)mound15Oct05cs1s1	17.17
10/15/2005	Jmound15Oct05BGJOcs1s3 (duplicate)	2.35
10/15/2005	Bmound15Oct05BGJOcs1s4 (duplicate)	1.27
10/16/2005	Imound16Oct05bm0s1	9.47
10/16/2005	Imound16Oct05bm0s2	3.87
10/16/2005	Imound16Oct05bm0s3	2.17
10/16/2005	Imound16Oct05bm0s4	3.08
10/16/2005	Bmound16Oct05BGKMNOcs1s1	3.52
10/16/2005	Bmound16Oct05cs1s1 (duplicate)	3.48
10/18/2005	Jmound18Oct05BGJOjt1s1	1.23
10/18/2005	Bmound18Oct05BGJOjt1s2	0.97
10/20/2005	Bmound20Oct05s1	1.72
10/20/2005	Bmound20Oct05s2	1.50
10/20/2005	Imound20Oct05GIJKMNjt2s1	0.58
10/24/2005	Jmound24Oct05IJKNbm1s1	0.65
10/25/2005	Imound25Oct05av0s1	0.78
10/25/2005	BOmound25Oct05BGKMNOhr1s1	1.52
10/25/2005	BOmound25Oct05BGKMNOjt2s1	1.37
10/25/2005	IJmound25Oct05BGKMNOjt3s1	6.20
10/29/2005	BOmound29Oct05BGKMNOcd2s1	4.32
10/29/2005	Gmound29Oct05BGKMNOcd2s2	0.42
10/31/2005	Bmound31Oct05BGJKMNez2s1	4.27
10/31/2005	KNmound31Oct05BGJKMNez2s2	1.23
11/1/2005	Bmound01Nov05BGKNOav1s1	0.28
11/1/2005	Jmound01Nov05hr2s1	2.32
11/2/2005	Imound02Nov05BGKMNOcd3s1	0.52
11/2/2005	Imound02Nov05BGKMNOcd3s2	0.48
11/3/2005	Omound03Nov05BGJOav1s1	2.00
11/3/2005	BGmound03Nov05BGJOav1s2	2.02

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
11/5/2005	KN(check)mound05Nov05GIJKNMaf1s1	1.93
11/7/2005	Jmound07Nov05GIJaf2s1	3.85
11/7/2005	Imound07Nov05GIJaf2s2	0.85
11/7/2005	BOmound07Nov05BGKMNOez3s1	3.52
11/8/2005	Omound08Nov05BGJOav1s1	0.40
11/8/2005	Omound08Nov05BGJOav1s2	1.00
11/8/2005	Jmound08Nov05GIJKMNjs6s1	3.40
11/9/2005	Bmound9Nov05BGKMNOjs7s1	1.38
11/11/2005	Bmound11Nov05BGKMNOcd3s1	1.25
11/13/2005	Jmound13Nov05IJKNbm5s1	3.13
11/13/2005	Imound13Nov05IJKNbm5s2	1.10
11/14/2005	Omound14Nov05BGJOaf2s1	0.48
11/14/2005	Bmound14Nov05BGJOaf2s2	1.02
11/14/2005	IJmound14Nov05GIJKNez4s1	7.85
11/14/2005	Jmound14Nov05GIJKNez4s2	3.55
11/15/2005	B15Nov05BGKMNOhassan5s1e1	8.82
11/15/2005	B15Nov05BGKMNOhassan5s5e1	1.23
11/15/2005	Jmound15Nov05GIJjt7s1	0.33
11/15/2005	Jmound15Nov05GIJjt7s2	0.55
11/15/2005	Jmound15Nov05GIJjt7s3	1.85
11/17/2005	Jmound17Nov05GIJjt8s1	1.22
11/19/2005	B19Nov05BGKMNOcd5s1e1	2.27
11/19/2005	BKN19Nov05BGKMNOcd5s1e2	0.67
11/19/2005	BO19Nov05BGKMNOcd6s7e1	1.15
11/19/2005	Jmound19Nov05GIJcs5s1	3.47
11/20/2005	BOmound20Nov05BJOcs5s1	0.58
1/19/2006	Imound19Jan06GIKMNav2s1	4.83
1/19/2006	Bmound19Jan06BGJOku0s1	4.12
1/19/2006	Bmound19Jan06BGJOlw0s1	3.32
1/20/2006	Jmound20Jan06GIJem6s1	3.77
1/20/2006	Mmound20Jan06BGKMNOlw0s1	0.27
1/21/2006	Bmound21Jan06BGKMNOlk0s1	0.65
1/24/2006	BOmound24Jan06BGKMNObp0s1	1.37
1/26/2006	BOmound26Jan06BGKMNObp0s1	0.00
1/26/2006	Bmound26Jan06BGKMNObp0s1	2.53
1/29/2006	OBmound29Jan06BGJOku1s1	2.72
1/29/2006	BJmound29Jan06BGJOku1s2	9.47

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
1/31/2006	KNmound31Jan06BGKMNObp1s1	0.27
1/31/2006	Bmound31Jan06BGKMNObp1s1	4.25
1/31/2006	Jmound31Jan06GIJku2s1	4.23
2/2/2006	Bmound2Feb06BGKMNObp2s1	1.28
2/2/2006	Omound2Feb06BGKMNObp2s2	0.62
2/2/2006	BOmound2Feb06BGKMNOez7s1	0.42
2/3/2006	GO3Feb06BGKMNOez7s6e1	0.60
2/5/2006	BO5Feb06BGKMNOaf4s1e1	12.58
2/5/2006	B5Feb06BGKMNOaf4s3e1	0.25
2/5/2006	BO5Feb06BGKMNOaf4s6e1	1.97
2/6/2006	BOmound06Feb06BGJOku2s1	1.12
2/6/2006	BOmound06Feb06BGJOku2s2	1.48
2/6/2006	BOmound06Feb06BGJOku2s3	2.73
2/6/2006	Bmound06Feb06BGJOku2s4	1.48
2/6/2006	Bmound06Feb06BGJOku2s5	1.82
2/6/2006	Bmound06Feb06BGJOku2s6	3.47
2/6/2006	Imound6Feb06GIKMNlw4s2	5.33
2/6/2006	Imound6Feb06GIKMNlw4s1	2.75
2/6/2006	KNmound6Feb06GIKMNlw4s1	7.52
2/7/2006	Jmound07Feb06GIJku3s1	0.98
2/9/2006	BOmound9Feb06BGKMNObp3s1	4.25
2/9/2006	Bmound9Feb06BGKMNObp3s2	3.38
2/9/2006	Bmound9Feb06BGKMNOjt9s1	0.50
2/12/2006	Imound12Feb06GIKMNaf6s1	6.03
2/16/2006	Omound16Feb06BJOaf7s2	0.38
2/16/2006	Omound16Feb06BJOaf7s3	0.67
2/16/2006	Omound16Feb06BJOaf7s1	0.43
2/16/2006	Bmound16Feb06BJOaf7s1	1.32
2/16/2006	BOmound16Feb06BJOaf7s1	1.92
2/19/2006	Jmound19Feb06GIJku3s1	0.83
2/24/2006	Bmound24Feb06BGJOcs5s1	0.28
2/26/2006	Imound26Feb06GIKMNaf7s1	4.72
2/26/2006	BOmound26Feb06BGJOku3s1	1.42
2/26/2006	Bmound26Feb06BGJOku3s2	0.45
2/26/2006	Jmound26Feb06BGJOku3s3	0.42
2/26/2006	BJOmound26Feb06BGJOku3s4	11.77
2/26/2006	Omound26Feb06BGJOku3s5	4.05

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
2/27/2006	BKNmound27Feb06BGKMNOlw6s1	2.85
3/2/2006	I2Mar06GIKMNaf9e1	0.45
3/2/2006	I2Mar06GIKMNaf9e2	0.70
3/2/2006	Imound2Mar06GIKMNbp8s2	0.58
3/2/2006	Kmound2Mar06GIKMNbp8s1	1.83
3/2/2006	IKmound2Mar06GIKMNbp8s1	5.20
3/2/2006	Imound2Mar06GIKMNbp8s1	0.53
3/2/2006	KNmound2Mar06GIKMNbp8s1	1.48
3/2/2006	Kmound2Mar06GIKMNbp9s1	0.58
3/2/2006	IKNmound2Mar06GIKMNbp9s1	2.08
3/3/2006	KNmound3Mar06BGKMNOez12s1	0.95
3/3/2006	KNmound3Mar06BGKMNOez12s2	3.20
3/7/2006	Jmound7Mar06GIJku5s1	2.30
3/7/2006	BKNOmound7Mar06BGKMNOlw8s1	3.08
3/7/2006	Omound7Mar06BGKMNOlw8s2	0.80
3/7/2006	KNmound7Mar06BGKMNOlw8s3	0.50
3/7/2006	Bmound7Mar06BGKMNOlw8s4	0.33
3/7/2006	BKNmound7Mar06BGKMNOlw8s1	1.28
3/7/2006	Gmound7Mar06BGKMNOlw8s1	0.90
3/7/2006	Bmound7Mar06BGKMNOlw8s1	0.00
3/7/2006	KNmound7Mar06BGKMNOlw8s1	0.00
3/7/2006	BKOmound7Mar06BGKMNOlw8s1	0.00
3/8/2006	Omound8Mar06BGJOcs5s1	1.48
3/15/2006	Imound15Mar06GIKMNlw10s1	0.40
3/15/2006	Imound15Mar06GIKMNlw10s2	4.05
3/15/2006	Imound15Mar06GIKMNlw10s3	0.27
3/15/2006	KNmound15Mar06GIKMNlw10s4	3.23
4/6/2006	IKNmound6Apr06GIKMNbp12s1	2.88
4/8/2006	KNmound8Apr06GIJKMNku6s1	0.45
4/8/2006	Imound8Apr06GIJKMNku6s2	0.85
4/8/2006	Jmound8Apr06GIJKMNku6s3	0.37
4/12/2006	BMOmound12Apr06BGKMNObp13s1	11.75
4/12/2006	KNmound12Apr06BGKMNObp14s1	1.47
4/17/2006	KNmound17Apr06GIKMNlw11s1	3.38
4/20/2006	KNmound20Apr06GIKMNObp15	0.25
4/23/2006	Bmound23Apr06BGKMNOkl1s1	11.48
4/27/2006	BMmound27Apr06BGKMNObp16s1	0.73

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
4/27/2006	Bmound27Apr06BGKMNObp16s1	0.82
4/30/2006	Imound30Apr06GIKMNkl3s2	1.93
4/30/2006	Imound30Apr06GIKMNkl3s3	3.53
4/30/2006	Gmound30Apr06GIKMNkl3s1	0.40
4/30/2006	KNmound30Apr06GIKMNkl3s1	0.25
4/30/2006	GKNmound30Apr06GIKMNkl3s1	3.77
4/30/2006	Imound30Apr06GIKMNkl3s1	1.22
5/3/2006	Bmound3May06BGKMNOsy1s1	0.55
5/7/2006	Bmound7May06BGKMNOkl5s1	4.82
5/12/2006	Bmound12May06BGKMNOku8s1	1.15
5/13/2006	Bmound13May06BGKMNOlu7s1	2.53
5/14/2006	Nmound14May06GIKMNkl6s1	0.20
5/14/2006	Kmound14May06GIKMNkl6s1	1.60
5/14/2006	GKmound14May06GIKMNkl6s1	0.62
5/14/2006	Mmound14May06GIKMNkl6s1	1.07
5/14/2006	Imound14May06GIKMNkl6s1	4.07
5/15/2006	Bmound15May06BGKLMNsy3s1	2.38
5/16/2006	Imound16May06GIKMNlw15s1	2.97
5/18/2006	Kmound18May06GIKMNbp19s1	1.77
5/18/2006	Mmound18May06GIKMNbp20s1	0.45
5/21/2006	BMmound21May06BKMNOkl8s1	1.05
5/21/2006	Bmound21May06BKMNOkl8s1	4.90
5/21/2006	KNmound21May06BKMNOkl8s1	0.60
5/21/2006	Bmound21May06BKMNOkl8s2	3.43
5/21/2006	BMmound21May06BKMNOkl8s2	0.20
5/24/2006	M24May06GIKMNsy5e1	0.70
5/30/2006	Nmound30May06GIKMNlw17s1	1.48
5/30/2006	Mmound30May06GIKMNlw17s2	0.33
5/31/2006	KMmound31May06BGKMNOlw18s1	1.08
6/1/2006	Mmound1Jun06GIKMNbp22s1	0.22
6/2/2006	BMmound2Jun06BGKMNOkh9s1	3.52
6/7/2006	I7Jun06GIKMNsy7e1	4.20
6/11/2006	IMNmound11Jun06GIKMNku11s1	1.05
6/11/2006	KMNmound11Jun06GIKMNku11s1	1.78
6/11/2006	Mmound11Jun06GIKMNku11s1	0.10
6/11/2006	KMmound11Jun06GIKMNku11s1	0.27
6/11/2006	Mmound11Jun06GIKMNku11s2	0.08

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
6/11/2006	KMNmound11Jun06GIKMNku11s2	4.65
6/14/2006	G14Jun06BGKMNOlw20e1	0.53
6/15/2006	Mmound15Jun06GIKMNku13s1	0.50
6/15/2006	Mmound15Jun06GIKMNku13s2	0.15
6/15/2006	Kmound15Jun06GIKMNku13s3	0.27
6/15/2006	Imound15Jun06GIKMNku13s4	1.17
7/11/2006	B11Jul06BGKMNOku15e1	1.15
7/17/2006	Mmound17Jul06lw21s1	0.17
7/17/2006	GIKmound17Jul06lw21s1	3.27
7/18/2006	BMmound18Jul06BGKMNOlw22s1	2.27
7/18/2006	GMmound18Jul06BGKMNOlw22s2	0.43
7/18/2006	Bmound18Jul06BGKMNOlw22s3	0.97
7/18/2006	Mmound18Jul06BGKMNOlw22s4	0.25
7/21/2006	Gmound21Jul06GIKMNlw24s2	0.68
7/21/2006	Kmound21Jul06GIKMNlw24s5	8.37
7/21/2006	Gmound21Jul06GIKMNlw24s1	0.18
7/21/2006	IGmound21Jul06GIKMNlw24s1	1.60
7/21/2006	KNmound21Jul06GIKMNlw24s1	0.43
7/21/2006	Kmound21Jul06GIKMNlw24s1	0.40
7/25/2006	Kmound25Jul06GIKMNOku16s1	0.15
8/11/2006	KNmound11Aug06BGKMNObp25s1a	4.38
8/18/2006	Kmound18Aug06GIKMNku17s1	2.22
8/24/2006	KMmound24Aug06GIKMNsy8s1	0.75
8/30/2006	Mmound30Aug06GIKMNsy10s1	0.50
8/30/2006	Mmound30Aug06GIKMNsy10s2	0.28
8/30/2006	Mmound30Aug06GIKMNsy10s3	0.15
10/5/2006	KN5Oct06GIKMNkh0e1	0.20
10/5/2006	K5Oct06GIKMNkh0e2	0.12
10/5/2006	IKM5Oct06GIKMNkh0e3	3.95
10/5/2006	G5Oct06GIKMNkh0e4	1.07
10/9/2006	B9Oct06BGJOas2e1	0.78
10/10/2006	BM10Oct06BIKMNck0e1a	8.00
10/10/2006	BM10Oct06BIKMNck0e1b	5.22
10/16/2006	J16Oct09GIJas2e1	0.25
10/16/2006	IJ16Oct09GIJas2e2	0.63
10/16/2006	J16Oct09GIJas2e3	5.98
10/18/2006	KNmound18Oct06BGKMNOkh12s1	0.73

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
10/22/2006	BIKNmound22Oct06BGIKMNkl10s1	9.82
10/22/2006	Bmound22Oct06BGIKMNkl10s2	0.50
10/22/2006	IKNmound22Oct06BGIKMNkl10s1	1.67
10/22/2006	Bmound22Oct06BGIKMNkl10s1	7.20
10/22/2006	Gmound22Oct06BGIKMNkl10s1	0.48
10/23/2006	Mmound23Oct06GIKMNkh13s1	0.18
10/23/2006	IKmound23Oct06GIKMNkh13s1	0.62
10/23/2006	IMmound23Oct06GIKMNkh13s1	2.33
10/23/2006	IKMmound23Oct06GIKMNkh13s1	0.55
10/23/2006	IKmound23Oct06GIKMNkh13s2	0.37
10/23/2006	IKMmound23Oct06GIKMNkh13s2	3.70
10/24/2006	J24Oct06GIJck3e1	1.22
10/24/2006	B24Oct06BGKMNOkh2e1	1.03
10/24/2006	B24Oct06BGKMNOkh2e2	3.45
10/24/2006	B24Oct06BGKMNOkh2e3	3.85
10/24/2006	B24Oct06BGKMNOkh2e4	1.13
10/24/2006	M24Oct06BGKMNOkh3e1	1.13
10/27/2006	B27Oct06BGJOas3e1	1.88
10/27/2006	B27Oct06BGJOas3e2	0.28
10/31/2006	O31Oct06GIKMNOkh3e1	6.38
10/31/2006	G31Oct06GIKMNOkh3e2	16.45
10/31/2006	Imound31Oct06GIKMNkh4s1	4.18
10/31/2006	Mmound31Oct06GIKMNkh4s2	0.90
11/1/2006	BKNmound1Nov06BGKMNOck5s1	1.62
11/1/2006	Kmound1Nov06BGKMNOck5s1	0.50
11/2/2006	Kmound2Nov06GIKMNbp28s1	0.22
11/2/2006	GIKMNmound2Nov06GIKMNbp28s1	9.85
11/2/2006	INmound2Nov06GIKMNbp28s1	2.65
11/5/2006	IKNmound5Nov06GIKMNkl13s1	9.45
11/5/2006	IKNmound5Nov06GIKMNkl13s2	6.35
11/9/2006	KNmound9Nov06GIKMNas6s1	0.58
11/9/2006	KMound9Nov06GIKMNas6s1	0.52
11/12/2006	BO12Nov06BGKMNOkl15e1	3.37
11/14/2006	BKMNO14nov06BKMNOkh6e1	4.47
11/14/2006	BMO14nov06BKMNOkh6e2	2.07
11/14/2006	BM14nov06BKMNOkh6e3	0.40
11/14/2006	BM14nov06BKMNOkh6e4	0.38

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
11/15/2006	Kmound15Nov06GIKMNkh17s1	1.13
11/15/2006	Kmound15Nov06GIKMNkh17s2	2.38
11/16/2006	B16nov06BKMNObp30e1	0.97
11/21/2006	KNmound21Nov06GIKMNkh7s1	1.73
11/21/2006	Kmound21Nov06GIKMNkh7s1	0.33
11/21/2006	Mmound21Nov06GIKMNkh7s1	0.63
11/21/2006	Imound21Nov06GIKMNkh7s1	2.83
11/25/2006	KNmound25Nov06GIKMNbp31s1	3.15
11/25/2006	Mmound25Nov06GIKMNbp31s2	0.35
11/25/2006	KNmound25Nov06GIKMNbp31s3	0.38
11/30/2006	Bmound30Nov06BKMNObp32s1	0.53
11/30/2006	Bmound30Nov06BKMNObp32s2	0.52
11/30/2006	Mmound30Nov06BKMNObp32s3	0.62
11/30/2006	KNmound30Nov06BKMNObp32s4	0.98
12/12/2006	Mmound12Dec06BGKMNOkh8s1	0.87
1/4/2007	KNmound4Jan07GIKMNbp33s1	1.95
1/4/2007	Imound4Jan07GIKMNbp33s2	0.05
1/9/2007	B9jan07BGKMNOkh9e1	0.68
1/9/2007	B9jan07BGKMNOkh9e2	0.87
1/9/2007	BM9jan07BGKMNOkh9e3	1.93
1/15/2007	B15jan07BGKMNOkh10e1	0.18
1/15/2007	M15jan07BGKMNOkh10e2	0.13
1/15/2007	B15jan07BGKMNOkh10e3	0.25
1/15/2007	BMO15jan07BGKMNOkh10e4	10.98
1/15/2007	B15jan07BGKMNOkh10e5	0.32
1/21/2007	BM21Jan07BGKMNOkh11e1	0.97
1/22/2007	Kmound22Jan07GIKMNck9	0.60
1/26/2007	KNmound26Jan07GIKMNkr38s1	0.42
2/2/2007	KNmound2Feb07BGKMNOkr39s1	0.38
2/6/2007	BM6Feb07BGKMNOkhl8e1	0.33
2/7/2007	IM7Feb07GIKMNck13e1	0.62
2/8/2007	BOmound8Feb07BGKMNOkmh13s1	1.18
2/8/2007	Bmound8Feb07BGKMNOkmh13s2	0.35
2/8/2007	KNmound8Feb07BGKMNOkmh13s3	2.17
2/10/2007	BMOmound10Feb07BGKMNOjf1s1	2.77
2/23/2007	BM23Feb07BGJMOma6e1	0.50
3/1/2007	IKNmound1Mar07GIKMNkmh16s1	3.30

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
3/3/2007	KO3Mar07GIKMNOjf5e1	1.35
3/3/2007	KO3Mar07GIKMNOjf5e2	1.55
3/3/2007	KNO3Mar07GIKMNOjf5e3	0.62
3/3/2007	KO3Mar07GIKMNOjf6e1	0.82
3/10/2007	IKM10Mar07GIKMNjf7e1	6.20
3/10/2007	M10Mar07GIKMNjf7e2	0.65
4/7/2007	BG7Apr07BGKMNOkmh17e1	1.25
4/7/2007	GN7Apr07BGKMNOkmh17e2	5.42
4/7/2007	B7Apr07BGKMNOkmh17e3	2.58
4/14/2007	KN14Apr07GIKMNkmh19e2	15.43
4/14/2007	KN14Apr07GIKMNkmh19e2b	6.45
4/20/2007	Mmound20Apr07GKMNOrh1s6	0.63
4/21/2007	BGM21Apr07BGKMNOkmh20e1	2.80
4/21/2007	BG21Apr07BGKMNOkmh20e2	2.18
4/21/2007	BGKMNO21Apr07BGKMNOkmh20e3	4.37
4/21/2007	B21Apr07BGKMNOkmh20e4	0.82
4/21/2007	BM21Apr07BGKMNOkmh20e5	0.43
4/22/2007	GM22Apr07BGKMNOrh2e1	2.88
4/28/2007	O28Apr07BJKMNOkmh21e1	0.82
4/28/2007	BM28Apr07BJKMNOkmh21e2	0.88
4/28/2007	BM28Apr07BJKMNOkmh21e4	3.83
4/28/2007	GK28Apr07BJKMNOkmh21e5	3.80
4/28/2007	KNO28Apr07BJKMNOkmh21e3a	9.45
4/28/2007	KNO28Apr07BJKMNOkmh21e3b	3.25
5/5/2007	N5May07IJKMNkmh22e1	0.25
5/5/2007	K5May07IJKMNkmh22e2	0.63
5/5/2007	IJ5May07IJKMNkmh22e3	1.95
5/12/2007	K12May07GIKMNkmh23e1	0.43
5/12/2007	K12May07GIKMNkmh23e2	0.42
5/12/2007	N12May07GIKMNkmh23e3	0.27
5/12/2007	I12May07GIKMNkmh23e4	0.97
5/12/2007	KN12May07GIKMNkmh23e5	1.92
5/12/2007	IKN12May07GIKMNkmh24e1	9.85
5/12/2007	IM12May07GIKMNkmh24e2	5.85
5/12/2007	KN12May07GIKMNkmh24e3	1.52
5/26/2007	B26May07BGKMNOma14e1	0.65
5/26/2007	B26May07BGKMNOma14e2	1.82
5/26/2007	M26May07BGKMNOma14e3	0.55

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
5/26/2007	B26May07BGKMNOrh6e1	4.52
6/3/2007	B3Jun07BIJKMNjf15e1	0.45
6/3/2007	B3Jun07BIJKMNjf15e2	0.47
6/3/2007	K3Jun07BIJKMNjf15e3	0.55
8/24/2007	M24Aug07GIKMNkmhe1	0.92
8/24/2007	KN24Aug07GIKMNkmhe2	1.05
9/16/2007	IJM16Sep07IJKMNkmh30e1	1.20
9/16/2007	I16Sep07IJKMNkmh30e2	0.40
9/16/2007	K16Sep07IJKMNkmh30e3	1.17
9/16/2007	M16Sep07IJKMNkmh30e4	0.12
9/16/2007	N16Sep07IJKMNkmh30e5	7.37
9/16/2007	K16Sep07IJKMNkmh30e6	0.20
9/16/2007	K16Sep07IJKMNkmh30e7	0.40
9/16/2007	M16Sep07IJKMNkmh30e8	1.25
9/16/2007	M16Sep07IJKMNkmh30e9	0.32
9/16/2007	K16Sep07IJKMNkmh30e10	0.28
9/16/2007	M16Sep07IJKMNkmh30e11	2.40
9/16/2007	K16Sep07IJKMNkmh30e12	0.48
10/1/2007	B1Oct07BJKMNOrh9e1	0.33
10/27/2007	J27Oct07IJKMNdn2e1	2.95
10/27/2007	JK27Oct07IJKMNkd2e1	3.92
10/27/2007	IKN27Oct07IJKMNkd2e2	0.92
10/28/2007	G28Oct07BGKMNOdn3e1	2.73
10/28/2007	B28Oct07BGKMNOdn3e2	0.18
10/28/2007	M28Oct07BGKMNOdn3e3	0.55
10/28/2007	G28Oct07BGKMNOdn3e4	0.42
10/28/2007	B28Oct07BGKMNOdn3e5	2.12
10/28/2007	M28Oct07BGKMNOdn3e6	2.05
11/3/2007	K3nov07GIKMNkd5e1	1.08
11/5/2007	B5nov07BGKMNdn4e1	3.02
11/5/2007	M5nov07BGKMNdn4e2	1.28
11/11/2007	I11nov07GIKMNab5e1	3.30
11/11/2007	IM11nov07GIKMNab5e2	4.33
11/11/2007	M11nov07GIKMNab5e3	2.02
11/17/2007	IN17nov07IJKMNkd6e1	0.00
11/17/2007	J17nov07IJKMNkd6e2	1.25
11/25/2007	K25Nov07IJKMNab7e1	1.27
11/25/2007	N25Nov07IJKMNab7e2	0.67

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
11/27/2007	KN27Nov07IJKMNcb3e1	0.82
11/27/2007	IK27Nov07IJKMNcb3e2	6.57
11/27/2007	JK27Nov07IJKMNcb3e3	0.88
11/27/2007	JK27Nov07IJKMNcb3e4	1.02
12/2/2007	I2Dec07GIKMNdn8e1	3.40
12/2/2007	K2Dec07GIKMNdn8e2	1.97
12/11/2007	IN11Dec07GIKMNcb6e1	1.05
12/11/2007	KN11Dec07GIKMNcb6e2	2.65
12/11/2007	IK11Dec07GIKMNcb6e3	2.77
1/2/2008	JM2Jan08BIJKMNrh13e1	5.80
1/14/2008	KNO14Jan08BJKMNOcb7e1	1.97
1/14/2008	KN14Jan08BJKMNOcb7e2	1.93
1/22/2008	BN22Jan08BGKMNOee1e1	2.68
1/22/2008	B22Jan08BGKMNOee1e2	0.78
1/22/2008	B22Jan08BGKMNOee1e3	3.12
1/25/2008	IK25Jan08GIKMNcb8e1	0.73
1/25/2008	K25Jan08GIKMNcb8e2	0.48
1/31/2008	K31Jan08IJKMNrt1e2	0.22
1/31/2008	N31Jan08IJKMNrt1e3	0.25
2/5/2008	G5Feb08BGKMNOab8e1	0.28
2/5/2008	G5Feb08BGKMNOab8e2	0.63
2/5/2008	GKN5Feb08BGKMNOab8e3	10.10
2/5/2008	KN5Feb08BGKMNOab8e4	4.13
2/5/2008	B5Feb08BGKMNOab8e5	3.40
2/9/2008	K9Feb08IJKMNdu11e1	0.85
2/9/2008	K9Feb08IJKMNdu11e2	0.48
2/9/2008	J9Feb08IJKMNdu11e3	3.38
2/10/2008	B10Feb08BGKMNOab10e1	2.72
2/10/2008	K10Feb08BGKMNOrt0e1	3.12
2/11/2008	IJ11feb08IJKNcm2e1	1.57
2/11/2008	J11feb08IJKNcm2e2	0.23
2/11/2008	K11feb08IJKNcm2e3	0.40
2/11/2008	I11feb08IJKNcm2e4	1.85
2/16/2008	K16feb08BGKMNOab11e1	0.40
2/17/2008	J17feb08IJKMNrt2e1	0.35
2/17/2008	IJ17feb08IJKMNrt2e2	3.53
2/17/2008	K17feb08IJKMNrt2e3	1.12
2/17/2008	JK17feb08IJKMNrt2e4	8.23

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
2/18/2008	JK18Feb08BGKMNOcm3	12.83
2/21/2008	K21Feb08IJKMNrt5e1	0.47
2/21/2008	JK21Feb08IJKMNrt5e2	6.83
2/25/2008	IK25Feb08IJKMNcb9e1	2.93
2/25/2008	K25Feb08IJKMNcb9e2	1.85
2/25/2008	K25Feb08IJKMNcb9e3	1.03
3/4/2008	N4Mar08IGKMNee8e1	0.33
3/4/2008	K4Mar08IGKMNee8e2	4.42
3/10/2008	I10Mar08IJKMNcb12e1	0.42
3/10/2008	N10Mar08IJKMNcb12e2	0.75
4/7/2008	N7Apr08IJKMNrt7e1	0.63
4/12/2008	GI12Apr08GIKMNee9e1	2.98
4/13/2008	N13Apr08GKMNOee11e1	0.27
4/13/2008	GI13Apr08GKMN0ee11e2	1.43
4/16/2008	JKN16Apr08IJKMNnp0e1	4.95
4/16/2008	K16Apr08IJKMNnp0e2	1.62
4/16/2008	N16Apr08IJKMNnp0e3	0.90
4/16/2008	IJ16Apr08IJKMNnp0e4	0.88
4/16/2008	I16Apr08IJKMNnp0e5	4.55
4/27/2008	K27Apr08IJKMNee13e1	6.22
5/17/2008	KN17May08GIJKMNee14e1	8.38
5/17/2008	IN17May08GIJKMNee14e2	2.00
6/4/2008	JK4Jun08GJKMNOnp6e1	11.00
6/8/2008	J8Jun08GIJKMNrt13e1	2.42
6/8/2008	M8Jun08GIJKMNrt13e2	0.70
10/13/2008	O13Oct08IMOTYmw0e1	0.42
10/14/2008	M14Oct08IMOTYcy0e1	0.63
10/14/2008	M14Oct08IMOTYcy0e2	2.40
10/19/2008	K19Oct08BGJKNcy1e1	1.03
10/19/2008	B19Oct08BGJKNjb0e1	0.97
10/20/2008	I20Oct08GIMTYmw1e1	4.83
10/27/2008	M27Oct08GIMTYmw2e1	0.53
11/5/2008	I5Nov08GITYmw3e1	1.60
11/9/2008	BJN9Nov08BJKNObk2e1	3.52
11/16/2008	K16Nov08BJKNObk3e1	1.93
11/17/2008	M17Nov08GIMTYmw4e1	5.00
11/23/2008	K23Nov08BJKNObk4e1	7.67
11/23/2008	B23Nov08BJKNOcy5e1	3.23

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
11/24/2008	K24Nov08GKMNOTYcy5e1	1.23
12/14/2008	B14Dec08BJKNOcy6e1	0.88
12/14/2008	K14Dec08BJKNOcy6e2	1.87
1/17/2009	BKN17Jan09BIJKNjo0e1	0.70
1/17/2009	KN17Jan09BIJKNjo0e2	1.80
1/17/2009	KN17Jan09BIJKNjo0e3	2.82
1/22/2009	B22Jan09BJKNOhg0e1	1.22
1/22/2009	JK22Jan09BJKNOhg0e2	0.82
1/28/2009	M28Jan09GIKMNab15e2	0.23
1/28/2009	N28Jan09GIKMNab15e1	2.68
2/1/2009	I1Feb09BIJKNcy7e2	0.18
2/1/2009	I1Feb09BIJKNcy7e4	1.40
2/1/2009	IK1Feb09BIJKNcy7e3	0.83
2/1/2009	KN1Feb09BIJKNcy7e1	1.73
2/3/2009	B3Feb09BIJKNjo1e1	1.70
2/10/2009	B10Feb09BJKNOhg3e1	4.38
2/15/2009	BKN15Feb09BJKNOab16e2	8.87
2/15/2009	J15Feb09BJKNOab16e1	1.73
2/17/2009	B17Feb09BJKNOhg3e1	9.42
2/17/2009	K17Feb09BJKNOhg3e2	3.65
2/18/2009	B18Feb09BJKNOab17e2	1.67
2/18/2009	K18Feb09BJKNOab17e1	0.93
2/18/2009	K18Feb09BJKNOab17e4	9.33
2/18/2009	N18Feb09BJKNOab17e3	0.37
2/20/2009	K20Feb09BIJKNjo2e2	0.83
2/20/2009	K20Feb09BIJKNjo2e3	0.48
2/24/2009	BK24Feb09BIJKNjb9e2	1.28
2/24/2009	K24Feb09BIJKNjb9e1	0.67
2/25/2009	IKN25Feb09GIKNab19e1	2.03
3/1/2009	G1Mar09GKNOcy9e2	0.20
3/1/2009	K1Mar09GKNOcy9e1	0.25
3/2/2009	B2Mar09BIJKNjo2e1	0.38
3/2/2009	BI2Mar09BIJKNjo2e2	0.90
3/6/2009	K6Mar09BIKNjo3e1	1.65
3/10/2009	B10Mar09BJKNOhg5e2	2.07
3/10/2009	J10Mar09BJKNOhg5e1	0.37
3/10/2009	K10Mar09BJKNOhg5e3	3.25
3/11/2009	K11Mar09GIKNab20e1	1.68

Table 19: Clip Inventory, continued.

Tape Date	File Name	Length (minutes)
4/12/2009	B12Apr09BJKNOth0e1	0.83
4/15/2009	BK15Apr09BIJKNsm0e1	6.98
4/16/2009	MY16Apr09GIKMNTYpr5e1	5.37
4/17/2009	BJO17Apr09BJOth1e1	7.88
5/2/2009	BK2May09BJKNOhg7e1	5.72
5/11/2009	B11May09BIJKNth2e1	0.58
6/6/2009	K6Jun09BIJKNpr7e1	1.13
6/17/2009	BK17Jun09BIJKNjo7e1	6.88
6/23/2009	B23Jun09BIJKNjoe1	5.77

This thesis, in part, is being prepared for submission for publication of the material. Brattich, Gloria; Johnson, Christine M., Hookham, Jade E. The thesis author was the primary investigator and author of this material.

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