Behavioral processes and social influences on the development of stone-tool use in long-tailed macaques

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**BEHAVIORAL PROCESSES AND SOCIAL INFLUENCES ON THE
DEVELOPMENT OF STONE-TOOL USE IN LONG-TAILED MACAQUES**

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Abstract

Coastal populations of macaques maintain rare stone-tool-use traditions for exploiting shellfish. I provide the first examination of macaque tool-use development on Koram Island ($N = 69$), Khao Sam Roi Yot National Park, Thailand. Macaques perform simple exploratory manipulations from 1-2 months. Around 1.5 years, combinatorial manipulations, including ineffective percussion and object-action sequences predominate until competence is achieved between 2.5-3.5 years. Mastering percussion and relating objects, particularly in three-item combinations (stone-shellfish-anvil vs. stone-sessile oyster), are challenging for macaques. Young macaques engage in tool-related interactions with tool users (e.g. scrounging, observing) preferentially according to tool-users' skill in addition to social relationships. Their interactions, and social learning opportunities influenced by maternal behaviour and sociality, affected developmental speeds, and social relationships related to similarity in tool users' hammering patterns and food choices. Understanding how macaques interact with their physical and social environments to develop tool-use skills, contributes to broader discussions of cultural evolution.

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TABLE OF CONTENTS

SUMMARY	1
LIST OF TABLES	3
LIST OF FIGURES	4
CHAPTERS	
1 INTRODUCTION	5
2 THE DEVELOPMENT OF STONE-TOOL USE IN LONG-TAILED MACAQUES	15
3 PATTERNS OF SOCIAL LEARNING INTERACTIONS WITH TOOL-USING GROUP MEMBERS OVER DEVELOPMENT	99
4 THE EFFECTS OF SOCIAL LEARNING OPPORTUNITIES ON DEVELOPMENT	135
5 SOCIAL RELATIONSHIPS AND CONFORMITY IN TOOL-USE BEHAVIORAL PATTERNS	160
6 GENERAL DISCUSSION AND FUTURE DIRECTIONS	184
REFERENCES	190
APPENDICES	
1 CURRENT KNOWLEDGE OF LONG-TAILED MACAQUE STONE-TOOL USE	213
2 DATA MATRICES (CHAPTER 3)	225
3 DATA MATRICES (CHAPTER 5)	256

SUMMARY

Long-tailed macaques are one of only three nonhuman primates, in addition to robust capuchins and West African chimpanzees, in which habitual stone-tool use under free-living conditions has been documented in some populations. Macaque stone-tool use is distinctively carried out in coastal environments, on primarily animal prey consisting of a variety of hard-shelled marine invertebrates. Macaques therefore provide a unique opportunity for broadening scientific knowledge regarding the environmental and social influences on skill development and behavioral patterns in rare primate lithic traditions, ultimately contributing to conceptual discourse in evolutionary biology and cultural evolution. Macaques use specialized axe-hammering techniques to crack open sessile rock oysters and pound-hammering to process motile shellfish with a variety of action patterns, with considerable individual variation in the expression of tool-use behaviour. How macaques develop these tool-use behavioral patterns has not been examined. In Chapter 2, I examined the developmental trajectory of stone-tool use in macaques, from object manipulation, to competency, and improvements in proficiency. I found that infants began simple manipulation of stones and shells at 1-2 months. These are replaced by combinatorial manipulations, including ineffective percussive actions, and object-action sequences, most prevalent around 1.5 years of age, and persisting until tool use is achieved at 2.5-3.5 years of age. New tool users continue to refine their skills particularly in terms of strike accuracy and efficiency. General patterns highlight mastering effective percussion, and producing spatial relations between objects particularly when three items are involved (stone-shellfish-anvil vs. stone-sessile oyster), as relatively challenging aspects of tool use for macaques. Considerable individual variation in manipulative

activity and tool-use expression suggests additional biological and social influences on tool-use acquisition. In Chapter 3, I examined scrounging, observation, and other tool-related interactions by tool-use naïve macaques with tool-using conspecifics. I found that interaction behaviour changed with age and skill, and immatures displayed more observation and interest in users' tools and actions compared to the purely scrounging behaviours of mature non-tool users. Furthermore, non-tool users directed their interactions preferentially not only towards closer social affiliates, but to more productive and proficient tool users. These suggest active information-seeking behaviour by developing individuals. In Chapter 4, I studied the effects of opportunities for learning derived from maternal behaviour, individuals' sociality, and interactions with skilled individuals, on tool-skill development. I found that maternal influences on development were strongest during infancy, after which the number and strength of immatures' social relationships and their interactions with tool users were predominant influences on the frequency and complexity of object manipulation behaviour. Finally, in Chapter 5, I found that patterns of social affiliation and kinship related to inter-individual behavioral similarity in terms of how much individuals used tools, and tool users' preferences for hammering patterns and food types. These studies provide the first examination of the behavioral and social processes involved in the ontogeny and expression of macaque stone-tool use. Overall, macaques develop stone-tool use through extensive exploratory manipulation and practice. This process is socially influenced, as evidenced by the ways in which unskilled macaques interact with tool-using group members, as well as the observed effects of social interactions and relationships on development and tool-use behavioral patterns.

LIST OF TABLES

Table 2.1	27
Table 2.2	33
Table 2.3	37
Table 2.4	39
Table 2.5	42
Table 2.6	47
Table 2.7	49
Table 2.8	55
Table 2.9	57
Table 2.10	63
Table 2.11	74
Table 2.12	81
Table 2.13	82
Table 2.14	83
Table 3.1	108
Table 4.1	147
Table 4.2	149
Table 4.3	150
Table 4.4	151
Table 4.5	151
Table 4.6	152
Table 4.7	153
Table 5.1	171
Table 5.2	172
Table A1.1.....	222
Table A1.2.....	223

LIST OF FIGURES

Figure 2.1	51
Figure 2.2	59
Figure 2.3	62
Figure 2.4	68
Figure 2.5	73
Figure 2.6	76
Figure 2.7	79
Figure 2.8	84
Figure 3.1	115
Figure 3.2	117
Figure 3.3	119
Figure 3.4	124
Figure 3.5	125
Figure 3.6	126
Figure 3.7	127
Figure 5.1	173
Figure 5.2	174
Figure 6.1	188

CHAPTER 1

INTRODUCTION

The Ontogeny of Tool Use

Tool use by nonhuman primates has been of scientific interest to understanding both the cognitive and cultural underpinnings of a behaviour that has evolved to an unequalled level of complexity and pervasiveness in our own human species. Animal tool use is rare, but recorded in a broad spread of animal taxa (Shumaker, Walkup, & Beck, 2011). The nature of tool use however, differs across animal species and have been classified into two types (Biro, Haslam, & Rutz, 2013; Call, 2013; Hunt, Gray, & Taylor, 2013; Meulman, Seed, & Mann, 2013). The first are those that appear to be genetically hard-wired species universals, which generally emerge according to an inflexible ontogenetic pattern not requiring social influence, and are performed as stereotyped fixed-action patterns. The second are those that must be developed via a suite of individual and/or social learning processes, and therefore are often variable across individuals and groups, and executed with a degree of adaptability according to changes in task or environmental demands.

Tool use by nonhuman primates is generally considered to fall into the latter category, being referred to as “flexible” or “creative” tool use (Call, 2013; Hunt et al., 2013). Much scientific effort has been devoted to examining the behavioral processes involved in the development of these skills, in order to better understand the cognitive and motor capacities that underlie these complex and dexterous tasks. In addition, when complex tool-use is reliably performed by several members of the population, or habitual

(McGrew, 1992), there is great interest in examining the role of cultural processes in behavioral development and transmission of these complex foraging tasks. Several approaches have been used to examine this process, ranging from carefully controlled experiments on captive animals, to broad comparisons between wild populations across wide geographic distributions. Within these approaches, there is an important role for detailed observational study of the ontogeny of tool use in the wild, to reveal the many potential effects of ecology, social structure, and other group and individual factors on tool use expression under natural conditions.

Understanding patterns of tool-use development

Observational field studies have been instrumental in identifying and describing the behavioral processes that take place during the long periods before young individuals are able to use tools competently (Meulman et al., 2013). These have been carried out across various modes of tool use in nonhuman primates, such as termite fishing (Lonsdorf, 2005), ant dipping (Humle, Snowdon, & Matsuzawa, 2009), and leaf-sponging (Biro, Sousa, & Matsuzawa, 2006) in chimpanzees, and nut-cracking in both chimpanzees (Inoue-Nakamura & Matsuzawa, 1997) and capuchins (Resende, Nagy-Reis, Lacerda, Pagnotta, & Savalli, 2014; Resende, Ottoni, & Fragaszy, 2008). Findings from these studies have revealed that tool-use competence is achieved through extensive manipulation of objects, typically progressing from simple to more complex manipulations before tool use, then continuing with a period of skill refinement before mature levels of proficiency are achieved. Additionally, within these global patterns of development, there are species-typical differences in the order in which the components of tool-use emerge, even for the same mode of tool use, for example, in the development of

nut cracking by capuchins and chimpanzees. Capuchins readily percuss items on surfaces but have difficulty mastering the requisite behaviour of placing food items on anvils (Resende et al., 2008), chimpanzees on the other hand readily placed items on other items, but found percussion most challenging (Resende et al., 2008; Inoue-Nakamura & Matsuzawa, 1997).

Apart from species-level differences in developmental patterns, detailed observations of known individuals in wild populations have also revealed that there is considerable variation in how quickly or well each young individual develops various aspects of tool skills, and differences in mature individuals' tool-use frequencies and proficiency (Resende et al., 2008; Lonsdorf, 2006; van Schaik, Fox, & Fechtman, 2003). These inter-individual differences are also commonly found in experimental studies on cognitive abilities including those involved in tool use. These experimental studies however, rarely attempted to examine the possible causes of such variation (Thornton & Lukas, 2012). Furthermore, in the interest of ruling out confounding effects of social influence on subjects' abilities to learn and solve problems, some experimental research specifically examine skill development in isolation from social input (Tennie & Hedwig, 2009). This further negates a candidate cause of individual differences, and cannot accurately reflect how behaviour is learnt and developed under natural conditions, where young animals are inevitably exposed to the behaviour of conspecifics. Developmental studies in free-living populations thus provide a way to identify individual differences in learning and behavioural expression across a larger sample of individuals within natural social settings, and examine the contribution of various social influences to these patterns of variation.

Social transmission and cultural processes

Cultural behaviour, commonly termed ‘behavioral traditions’ when applied to animals, are those that are spread and maintained in a population at least in part by social transmission processes (Fragaszy & Perry, 2003; Laland & Janik, 2006; Whiten et al., 1999). Early efforts to classify behaviour as traditional relied heavily on the ethnographic method (Wrangham, de Waal, & McGrew, 1994). This approach entailed documenting the presence and absence of habitual behaviour or behavioral variants across geographically separate populations of a species, then excluding genetic and ecological explanations to deduce that the behaviour was propagated socially. Perhaps the most well-known example is Whiten et al.’s (1999) examination of 65 types of behaviour across seven chimpanzee populations. The comparison revealed that the prevalence of 39 behavioural variants, including several forms of tool use, varied across sites despite an absence of ecological differences preventing or promoting the behaviours. The ethnographic approach has since been applied towards identifying behavioral traditions in orangutans (van Schaik, Ancrenaz, et al., 2003), capuchins (Panger et al., 2002; Perry et al., 2003), and Japanese macaques, as well as non-primate animals such as cetaceans (Rendell & Whitehead, 2001).

Although the ethnographic approach has been instrumental towards establishing cultural capacities in nonhuman animals, its reliance on excluding genetic and ecological explanations is inherently problematic, and can only provide indirect evidence of social transmission mechanisms (Laland & Janik, 2006; Meulman et al., 2013). In reality, a multitude of ecological factors can influence behaviour, and only a small subset of these factors might be considered and examined during ethnographic study. For example, an

ethnographic study may focus on the availability of food species and tool materials between study sites, but fail to consider differences in terrain, weather patterns, predation risks, or a host of other factors that could also influence animals' access to these resources. Furthermore, interactions between environmental variables and behaviour are expected under natural conditions, and should be understood instead of excluded. This is especially true when attempting to understand tool-use behaviour, since tool use is a foraging adaptation precisely for exploiting environmental resources. In view of these limitations, ontogenetic studies of tool use in free-living populations are therefore more productive and a necessary complement (Meulman et al., 2013), as direct evidence for social learning of tool skills can be identified within the context of ecological influences.

Studies of ontogeny afford several opportunities for identifying direct evidence for social learning in the development of tool-use and other foraging skills under natural conditions. One approach has been to document how young naïve individuals interact with group members carrying out tool use and other skilled foraging behaviours either directly, or indirectly via the products of their activities (Coussi-Korbel & Frigaszy, 1995; Frigaszy et al., 2013; Heyes, 1994). In tool-using capuchin and chimpanzee populations, naïve young actively observe skilled tool users from close proximity, obtain tool-processed food by scrounging or begging, and explore tools and materials used by skilled group members (Biro et al., 2003; Biro et al., 2006; Boesch & Boesch-Achermann, 2000; Coelho et al., 2015; Lonsdorf, 2005; Matsuzawa et al., 2001; Ottoni, Resende, & Izar, 2005). These findings demonstrate a direct link between young individuals' early experiences with the food items, materials, and actions involved in tool use, with the

behaviour of older experienced group members, a basic requirement for social transmission.

Further examining the characteristics of these interactions in terms of how they relate to learners' age or skill level, and the identities of skilled individuals that learners interact preferentially with, can provide stronger evidence that these interactions facilitate learning. Capuchin (Coelho et al., 2015) and chimpanzee (Biro et al., 2003) young preferably observe same aged or older tool users, suggesting attention to group members' skill levels which can enhance learning opportunities. Further examinations of strategies in directing social learning to different group members have been carried out with capuchins (Coelho et al., 2015; Ottoni et al., 2005), revealing that naïve individuals more often scrounged from and observed more proficient and productive nut-crackers. The identities or demographics of skilled individuals that are preferentially learnt from also provides insight into likely pathways of social transmission within animal groups (Coussi-Korbel & Frigaszy, 1995). For example, strong biases towards mothers or kin as documented in chimpanzees (Biro et al., 2006; Lonsdorf, 2006), could mean that vertical transmission from parent to offspring predominates, while learning interactions that are common between unrelated individuals, for example in capuchins (Fragaszy, Visalberghi, & Fedigan, 2004), could indicate a greater role for horizontal transmission of behaviour.

Evidence and descriptions of behavioural patterns that indicate a more definitive role for social learning provide starting points from which the effects of social factors and relationships on individuals' development and expression of tool use behaviour can be examined. One avenue of research in this regard has been in examining how differences in opportunities for social learning affect tool-use development (van Schaik, Fox, et al.,

2003; van Schaik & Pradhan, 2003). Ontogenetic studies have afforded direct examinations of these effects by correlating measures of opportunity with the development of behaviour. For example, opportunities for learning provided by maternal behaviour have been found to relate to various measures of offspring's behavioral acquisition in the ant-dipping (Humle et al., 2009) and termite fishing behaviours of chimpanzees (Lonsdorf, 2006), and the non-tool-use stone-handling behaviour of Japanese macaques (Nahallage & Huffman, 2007). These findings thus reveal a way in which social factors could contribute to individual differences in behaviour, and also complement population level findings that species or groups with tolerant or gregarious social structures better support social learning opportunities, and thus exhibit more frequent or complex tool-use behaviour (Meulman et al., 2013; van Schaik, Deaner, & Merrill, 1999).

Another effect that social dynamics can have on behaviour is in influencing behavioral similarity between individuals in a social group (Coussi-Korbel & Frigaszy, 1995). Currently, the strongest evidence for these influences comes from studies on populations of white-faced capuchins that exhibit several non-tool-aided foraging behaviours that vary between group members (Matthews, 2009; O' Malley & Fedigan, 2005; Panger et al., 2002; Perry & Ordonez-Jimenez, 2006). These studies found that for foods with rare or multiple processing techniques, dyads that tended to share the same techniques were also those that spent more time in close proximity, suggesting social relationships influenced behavioral similarity. A longitudinal study of one population provided further evidence that young individuals eventually developed behavioral patterns similar to those of individuals whom they observed most during early stages of

development (Perry, 2009). The transfer of similar behaviour amongst individuals in a group is what ultimately generates behavioural traditions. Therefore, how behaviour is successfully transferred, and the social learning processes behind transfer, are critical aspects in the study of cultural phenomena (Whiten & Claidière, 2012; Whiten, Hinde, Laland, & Stringer, 2011).

Scope and Aims

In this dissertation, I present examinations of the behavioural and social processes involved in the ontogeny of stone-tool use in a population of free-living long-tailed macaques on Koram Island, in Khao Sam Roi Yot National Park, Prachuap Khiri Khan, Thailand. Long-tailed macaques are the most recently studied primate species to exhibit habitual stone-tool use under natural conditions (Gumert, Kluck, & Malaivijitnond, 2009; Malaivijitnond et al., 2007). Prior to this research, the stone-tool using behaviour of long-tailed macaques had only been studied in detail at one other geographic location, on Piak Nam Yai in Laem Son National Park, in Ranong province. So far, these studies have revealed the skilled and varied nature of long-tailed macaque stone-tool use (Appendix 1). Macaques process a wide variety of hard-shelled marine invertebrates and a few species of hard plant fruit and seeds (Gumert & Malaivijitnond, 2012), selecting and handling tools differently according to the types of foods being processed (Gumert et al., 2009; Gumert & Malaivijitnond, 2013; Tan, Tan, Vyas, Malaivijitnond, & Gumert, 2015). In general, macaques crack open oysters that are sessile upon rock or other substrate with the points of smaller hand-held tools, and place other unattached shellfish and plant parts on anvils before hammering them, usually with the larger surface areas of stones, and with tool size further dependent on the food species. Within these general patterns, there is

wide variety of action patterns that differ in prevalence between groups and individuals on Piak Nam Yai (Gumert, Hamada, & Malaivijitnond, 2013; Gumert, Low, & Malaivijitnond, 2011; Gumert & Malaivijitnond, 2012; Tan et al., 2015). During the course of the current work, it has also become apparent that the stone-tool use of the Koram Island population differs from the Piak Nam Yai population in terms of the prevalence of overall tool use and tool-use hammering types and action patterns on each island, the variety of foods available and processed (Gumert et al. in prep), and possibly the age at which young macaques in each population appear to acquire tool competency.

The skills and techniques involved in long-tailed macaque stone-tool use, as well as the patterns of variation between individuals, groups, and populations, is indicative of a learning process that interacts with ecological and social influences. I focus here on understanding the ontogeny of stone-tool skills in macaques, and examining direct evidence for the involvement of social transmission on these behavioral processes. I begin in Chapter 2 by using longitudinal and cross-sectional analyses to examine the general developmental trajectory of stone-tool use in macaques, from object manipulation, to competency, and improvements in proficiency after tool-use is achieved. From these findings, I identify and describe the challenges that macaques face in developing tool skills, and individual variation in the ontogenetic process. In Chapter 3, I examine the social influences on macaque stone-tool use by identifying and characterizing the interactions that take place between naïve and skilled group members. I further explore differences in how naïve individuals of different ages and at different stages of skill development interact with skilled tool users, as well as how demographic and skill-related characteristics of tool users influenced naïve individuals' partner choices for these

interactions. In Chapter 4, I explore other possible sources of social learning opportunities, such as those related to the tool-use and social behaviour of young macaques' mothers, and individual macaques' own social relationships. I examine how differences in these social relationships and interactions influence individual differences in young macaques' rates of skill development and the prevalence and proficiency of tool-use behaviour in mature macaques. Finally, in Chapter 5, I move beyond individual differences, to explore how social relationships and transmission processes may contribute towards behavioral similarity between more closely associated individuals. The overarching aim of this dissertational research is to gain insight into the behavioral and social processes that underlie the individual, group, and population level behavioral patterns within the long-tailed macaque account of rare stone-tool-use traditions.

CHAPTER 2

THE DEVELOPMENT OF STONE-TOOL-USE IN LONG-TAILED MACAQUES

Introduction

Tool use tasks are developmental challenges as they require recognizing object properties, and then producing and managing actions and spatial relations between objects to accomplish a goal (Visalberghi & Fragaszy, 2006). Tool use is the employment of an external object to change the properties of another object, and requires that the user directly and effectively manipulates and orientates the tool (Shumaker, Walkup, & Beck, 2011). Matsuzawa (1996) distinguished between “levels” of tool use based on the number of objects involved. “Level 1” tool use entails relating one object to another, while the more complex ‘level 2’ tool use entails relating a total of three objects in a specific sequential and spatial configuration. Visalberghi & Fragaszy (2006) referred to level 1 tool use as “first order”, and level 2 tool use as “second order” spatial relational tasks. They further distinguished between static relations, where the object acted upon is in a fixed position, and dynamic relations, which are more challenging as the object acted upon is movable and therefore requires that the relation be constantly monitored to be maintained. They also distinguished between spatial relations that are produced sequentially, or if multiple relations must be produced and maintained simultaneously. Tool use tasks that require greater “specificity”, or greater precision in the actions required to produce the effective spatial relation, are also more challenging as maintaining precise relations requires greater attentional resources and finer motor control (Fragaszy & Cummins-Sebree, 2005). Directly studying the process by which tool skills emerge and

develop is critical to understanding how both ontogenetic and social processes influence how different organisms develop the requisite skills to handle different challenges of various tool use tasks (Meulman, Seed, & Mann, 2013).

Burmese long-tailed macaques (*Macaca fascicularis aurea*) are one of only three nonhuman primates that exhibit habitual stone-tool use behaviour under natural conditions, in addition to the West African chimpanzee (*Pan troglodytes verus*) (Boesch & Boesch, 1981) and the robust capuchins [*Sapajus libidinosus* (Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004); *Cebus xanthosternos* (Canale, Guidorizzi, Kierulff, & Gatto, 2009)]. Stone-tool using macaques offer a unique opportunity to further understand the ontogeny of percussive tool-use skills and the factors that influence the development and form of this rare behaviour across species. Capuchins and chimpanzees carry out stone-tool use in forest environments, primarily on various species of nuts and fruit (Boesch & Boesch, 1983; Canale et al., 2009; Spagnoletti et al., 2012; Sugiyama & Koman, 1979; Visalberghi et al., 2008). Both first place these food items onto anvils, then strike them with a tool stone to crack them. Chimpanzees primarily do so with hand-sized hammers from a seated posture, and capuchins usually crack with relatively large tools for their body size, holding the tools with both hands and sometimes rising bipedal before striking (Whiten, Schick, & Toth, 2009). In contrast, long-tailed macaque stone-tool use is uniquely a coastal foraging adaptation, carried out to crack primarily animal prey in the form of a wide variety of shelled marine invertebrates (Gumert & Malaivijitnond, 2012). Macaques appear distinctive in the variety of action patterns with which they carry out stone-tool use, with 20 different variants documented across two populations so far (Tan, Tan, Vyas, Malaivijitnond, & Gumert, 2015; Appendix 1). Some of these action patterns

are used by only a few individuals, and others are further limited to only idiosyncratic use by single individuals in the population. Overall, macaque tool use can be categorized into two types. Macaques crack motile organisms in the same ways that capuchins and chimpanzees crack nuts, collectively known as pound hammering (Gumert, Kluck, & Malaivijitnond, 2009; Tan et al., 2015). The most widely cracked food by long-tailed macaques however, are sessile rock oysters (*Saccostrea cucullata*) that grow with one valve cemented onto rock or other substrate surfaces (Gumert & Malaivijitnond, 2012), thus presenting a stone-tool-use task not encountered by other species. Since sessile oysters cannot and need not be placed on anvils, the macaques crack them by striking them mostly using the points of small tools with precision, in a form of tool use that is unique to their species, which has been referred to as axe hammering (Malaivijitnond et al., 2007; Gumert et al., 2009; Tan et al., 2015).

Processing motile organisms and sessile oysters differ in the challenges they entail. Cracking motile organisms on anvils is a form of level 2 tool use (Matsuzawa, 1996) or second-order relational task (Visalberghi & Fragaszy, 2006), where three objects and two spatial relations between objects must be related in a specific way. A food item must be stably placed on a suitable anvil stone, and then the tool stone is used to strike with adequate force and accuracy to crack the food item. Processing motile organisms on anvils also involves managing dynamic spatial relations simultaneously (Fragaszy & Cummins-Sebree, 2005; Visalberghi & Fragaszy, 2006). Since the food item is not fixed to the anvil and can shift while struck, the macaque must constantly monitor and maintain the spatial relation between the food item and anvil, sometimes at the same time as producing the spatial relation between the tool and the food item (e.g. holding the food

item in place on the anvil while striking with the stone). On the other hand, cracking sessile oysters is a form of level 1 tool use or first-order relational task involving managing only a static relation between the tool and oyster, as the sessile oyster is struck directly with the tool stone and does not move from its locus on the substrate. In terms of objects and action sequences involved axe hammering entails fewer degrees of freedom, and may therefore be less challenging to produce. Cracking sessile oysters however, likely requires greater specificity (Fragaszy & Cummins-Sebree, 2005) than pound hammering. Sessile oysters are small targets (~2cm in diameter), and macaques typically strike them with the points and protuberances of small tools, requiring greater precision than striking with the faces and edges of larger tools typically used for pound hammering. In addition, sessile oysters can grow at any orientation on the substrate, and macaques have to manage precision striking towards differently angled planes, for example, striking overhead when the oyster is located on the underside of an overhanging boulder. Cracking open these two categories of food items are therefore likely to pose different problems for macaques developing tool use skills.

The ontogeny of stone-tool use in long-tailed macaques has not been studied, and so little is known about how macaques develop different techniques, or why there is so much variation within the population. So far, it is reported that immature macaques use tools less than adults, and when using tools, strike sessile oysters at faster rates but unattached food items at slower rates than adults, using smaller tools like adult females as compared to adult males. These suggest a period of skill refinement following basic competency that is influenced by maturation in strength and motor control (Gumert, Low, & Malaivijitnond, 2011). The study also reported observations that infant macaques

handled stones in non-functional patterns similar to Japanese macaque stone handling (Huffman, 1984; Huffman, 1996; Leca, Gunst, & Huffman, 2007a, 2007b), and that tool use was observed in macaques as young as one-year old (Gumert et al., 2011). These results however, were obtained from just two weeks of observation on non-individually-identifiable subjects, and does not examine the detailed developmental trajectory of tool-use skills, particularly in terms of how object manipulation changes until tool use is achieved, and the normative trajectory from object manipulation, to tool competency, to refined proficiency, and how these processes may differ for pounding and axing techniques.

For an idea of how tool-skill development might proceed in macaques, we can compare observational studies of tool-use development in other habitual tool users. A comparison across 34 species including habitual tool users, non-habitual routine tool users, and species that exhibit routine complex but non-tool-assisted foraging skills, revealed that habitual tool use is acquired relatively late during development compared to non-habitual tool use and other foraging skills (Meulman et al., 2013). The period of development towards achieving regular success in habitual tool users may almost span the period of immaturity (Schuppli, Isler, & van Schaik, 2012), even though independent foraging is acquired within months after birth (Meulman et al., 2013). In chimpanzees for example, basic competence in various modes of habitual tool use takes years to develop. At Bossou, Guinea, it takes young chimpanzees two to three years to ant dip with manufactured stick tools (Humble, Snowdon, & Matsuzawa, 2009), while the use of leaf tools for drinking water, and stone tools to crack nuts, takes up to three and a half years to develop (Biro, Sousa, & Matsuzawa, 2006; Inoue-Nakamura & Matsuzawa, 1997; Sousa,

Biro, & Matsuzawa, 2009). At Gombe, termite fishing abilities take even longer to master, likely because it also involves tool manufacture, with up to five and a half years before juveniles achieve competence (Lonsdorf, 2006). In capuchins that use stone tools to crack nuts, competence emerges only between two to four years of age (Resende, Ottoni, & Fragaszy, 2008; Ottoni & Izar, 2008). Orangutans at Suaq Balimbing, Sumatra, develop competence in using sticks to probe tree holes between four to six years of age, while extracting *Neesia* fruits using stick tools develops even later at around 7 years (van Noordwijk & van Schaik, 2005). Amongst non-primate habitual tool users, bottlenose dolphins take over a year and a half to learn to forage with sponges (Sargeant & Mann, 2009). New Caledonian crows require between two to 12 months learn to manufacture and use stick and *Pandanus* probing tools (Holzhaidner, Hunt, & Gray, 2010; Hunt & Gray, 2004; Kenward, Rutz, Weir, & Kacelnik, 2006), coinciding with weaning (Schuppli et al., 2012). One exception to the pattern of late emergence of habitual tool-use competency is the ontogeny of stone-tool use by sea otters, which is acquired relatively early between 3 to 4.5 months of age, given that they only reach sexual maturity at 4 years of age (Reidman & Estes, 1990).

After the extended process of acquiring basic competency, young tool users continue to develop proficiency in tool-use skills, improving in efficiency and effectiveness specific to the tasks. In bottlenose dolphins, spongers improve efficiency by reducing the time spent looking for appropriate sponge tools and using single tools for longer times, thus allowing more time for obtaining food (Patterson, 2012). Higher tool fidelity has also been observed in adult chimpanzees' use of stone tools for nut cracking, while younger tool users often switch between suboptimal tools repeatedly during bouts,

and in addition, also often switch hands while striking, and require more strikes to crack food items until they improve on the strength and accuracy of their strikes (Biro et al., 2006). A similar pattern is observed in nut-cracking capuchins. Adults used optimal sequences that contained fewer actions that were not directly involved in nut cracking (e.g. rolling nuts), struck nuts accurately more often, and required fewer strikes to crack nuts, although improvements in juveniles' strike accuracy and efficiency were seen within the months following their first tool use (Resende, Nagy-Reis, Lacerda, Pagnotta, & Savalli, 2014). In the ant-dipping behaviour of chimpanzees, adults dipped for longer durations, obtaining more ants (Humble et al., 2009). As for termite fishing, older tool users were more flexible in adapting their tool use behaviour to atypical conditions, and also utilized techniques requiring greater coordination, like sweeping termites off tools with hands versus direct mouthing (Sanz & Morgan, 2011).

The long latency before competent tool use is achieved is typically characterized by developing individuals manipulatively interacting with tool and food materials (Biro et al., 2006; Resende et al., 2008; Frigaszy et al., 2013; Holzhaider et al., 2010; Inoue-Nakamura & Matsuzawa, 1997). In general, these manipulative behaviours consist initially of simple and seemingly random actions, then of incorrect expressions of the eventual tool-use behaviour, which generally diminish as immature individuals develop their skills and achieve competency. Developing individuals may perform inept forms of the actions required to carry out tool use, incomplete or wrongly-ordered action sequences, and incorrect or incomplete combinations of objects. For example, during the development of termite-fishing skills, young chimpanzees at Gombe progress from tactilely and visually exploring termite mounds and holes separately from manipulating

discarded tools, before bringing tools in contact with termite mounds by pressing or swiping tools against the mounds (3.5 years), and finally, they learn to make their own tools and insert tools into termite holes (4.5 years). However, they first perform insertions that are too rapid and shallow to catch termites, and are only successful after a further year of inept tool use (Lonsdorf, 2005). A similar pattern is observed in the development of *Pandanus* probing-tool use in New Caledonian crows (Kenward et al., 2006). Young crows first carry out “precursor actions” such as rubbing tools and performing probing motions without actually inserting tools into crevices, before these actions are gradually replaced by proper insertion actions that allow the crows to achieve access to food targets.

This general pattern of the canalization of a wide variety of ineffective exploratory behaviours towards the expression of successful tool use has been found to differ between species, particularly in terms of the order in which the components of tool use are mastered, even when considering the same mode of tool use. For example, both chimpanzees (Inoue-Nakamura & Matsuzawa, 1997) and capuchins (Resende et al., 2008) carry out stone-tool use for nut cracking, where developing individuals must learn to place nuts on anvils, then hit the nuts accurately and with sufficient force to crack them. Developing individuals of both species generally carry out simple manipulative actions such as touching or picking up single objects, before combining objects in various configurations, until the correct object-action sequences are achieved to produce first ineffective, then successful tool use. For young capuchins however, the component of placing nuts on anvils appears the hardest to master, although they readily carry out percussive actions (Resende et al., 2008). Young chimpanzees on the other hand predominantly placed objects on surfaces in their early combinatory manipulations, and

tended to combine objects by stacking them, rather than percussing (Hirata, Morimura, & Houki, 2009; Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, 1996; Matsuzawa et al., 2001; Takeshita et al., 2005). It is suggested that this difference in the developmental trajectories of the two species relates to their feeding ecology (Resende et al., 2008). Capuchins commonly consume encased plant matter that require percussive extraction even without tools, however, they are arboreal and therefore hesitant to release and risk dropping food, which prevents them from readily letting go of food items to place them on anvils. Chimpanzees are more terrestrial and do not risk losing food items by placing them on ground surfaces, however, they feed predominantly on fleshy fruit that although may require manipulative handling e.g. (Corp & Byrne, 2002), do not require percussion.

More recently, studies on the kinematics of object banging by human infants and toddlers have provided further insight into the challenges and developmental changes involved in effective percussion (Fragaszy, Simpson, Cummins-Sebree, & Brakke, 2016; Kahrs, Jung, & Lockman, 2012; 2013). Over development, young infants' banging actions during object play changed from varying widely in velocity, object displacement, strike angles, and strike trajectories that often involved lateral rather than up-down motions, to more consistently straighter strike trajectories, and perpendicular strike angles, that would enable greater accuracy and efficient force delivery should these exploratory percussive actions develop into tool use (Kahrs, Jung, & Lockman, 2013; 2013). When tasked to hammer pegs into boards, infants often failed to orient the effective striking surface of the hammer to the peg, indicating a further developmental challenge to effectively employing percussive actions for tool use (Fragaszy, Simpson, & Brakke, 2016).

Perception-action theory (Lockman, 2000) has been applied towards

understanding the adaptation of inefficient exploratory actions into tool use (Kahrs, Jung, & Lockman, 2013), and explaining species-specific variations in patterns of development (Resende et al., 2008; Takeshita et al., 2005). According to the perception-action perspective, complex tool use abilities originate and develop from innate motor routines that animals use to explore their environments, which allow animals to eventually produce biologically relevant activities (Gibson, 1966; Lockman, 2000). For example, the motor changes in infant banging into forms suitable for tool use occur in exploratory contexts, pre-adapting infants for percussive goal-directed actions (Kahrs, Jung, & Lockman, 2012). Over development, young individuals begin to incorporate objects into their perception-action routines, creating opportunities to experience and learn the consequences of combining different objects and surfaces (Takeshita et al., 2005).

With regards to learning how to relate objects and surfaces, a key component of tool use, the perception-action theory therefore predicts that: 1) simple actions performed on single objects at a time will emerge before routines in which objects and surfaces are combined, 2) earlier combinatory manipulations will first be carried out with apparent ignorance towards the physical properties of different objects and surfaces, specific spatial orientations between objects, and sequences of actions, and 3) the combinatory actions of immatures will increasingly resemble the adult form (which is effective tool use in this case), as young individuals learn to first distinguish between object properties and affordances, and then, learn to produce appropriate spatial relations between relevant objects in effective sequences (Resende et al., 2008; Kahrs & Lockman, 2014; Lockman, 2000; Takeshita et al., 2005). In addition, since advanced actions have their origins in the early perception-actions routines that are unique for different animals, between-species

differences in the specific trajectories of manipulative development are to be expected. This has indeed been found in the development of stone-tool use in capuchins and chimpanzees as described in the preceding paragraph. How do macaques fit into this comparison?

In this chapter, I report an analysis of developmental patterns in the ontogeny of stone-tool use from object manipulation to proficiency, in the long-tailed macaques on Koram Island, in Khao Sam Roi Yot National Park, Thailand. The goals are to provide the first detailed description of the ontogeny of stone tool use in macaques, using both qualitative descriptions and quantitative analyses of behavioral observations, and to examine this process within the perception-action framework, in order to contribute to comparisons with stone-tool using capuchins and chimpanzees. Applying perception-action theory, and considering the observed patterns of tool-use development across habitual tool-using species, I make several predictions about the ontogeny of stone-tool use in long-tailed macaques. Overall, I predict that macaque stone-tool use follows same general trajectory as capuchins and chimpanzees, where ability to use tools will develop over the first two to three years of life, during which developing individuals will carry out exploratory object manipulation until successful tool use is achieved. Exploratory object manipulation should proceed from a wide variety of simple actions, to various combinatorial manipulations, and action sequences should be carried out in improper configurations, until the correct sequence of actions for successful tool use is produced. Specific to macaques, I examine the order in which the cracking of sessile oysters versus unattached foods on anvils emerge. In addition, I examine the changes to various aspects of tool-use proficiency (e.g. efficiency, accuracy) that continue to occur after the initial

tool-use competence is achieved, to further understand the process of skill refinement in macaques.

Methods

Observation Periods

I collected data from 17 October 2013 to 2 December 2014, visiting Koram Island (see Appendix 1 for site description) daily, unless weather and tidal conditions did not permit, for a total of 227 days. During the months of November to January, the area experiences annual monsoon conditions that often prevented access to the island, therefore, less data could be collected during these months (monsoon: 5 – 13 days/month, non-monsoon: 20 – 25 days/month). I spent an average of 4 hours on the island each day, corresponding to the daily low tide hours when the monkeys would forage and use tools on the island's shores.

Subjects

I collected data on the largest group of macaques on Koram Island. The group receives provisioning from tourists that visit the island up to several times a day. As a result, the macaques are highly habituated to human presence, and can be observed at close range. The study group ranged between 65 to 72 individuals during the study, owing to immigrations, emigrations, presumed deaths of some individuals, and the birth of new infants. I was able to distinguish each subject according to their physical appearance. In total, sufficient data was collected on 69 individuals for inclusion in developmental analyses (Table 2.1).

Table 2.1

Age group classification and total number of focal samples, manipulative bouts, and tool-use bouts obtained for 69 study subjects. Number of tool-use bouts are marked “not applicable (n.a.) for non-tool users.

ID	Sex	Age Group	Focals	Manipulative bouts	Tool-Use Bouts		
					Ses.	Una.	Total.
Asg	M	>5.5	72	162	153	7	160
Chl	M	>5.5	66	182	176	6	182
Jsl	M	>5.5	62	0	n.a.	n.a.	n.a.
Krg	M	>5.5	60	1	153	0	153
Krb	M	>5.5	23	1	7	0	7
Mgp	M	>5.5	64	0	n.a.	n.a.	n.a.
Yak	M	>5.5	61	0	n.a.	n.a.	n.a.
Fhn	F	>5.5	151	0	n.a.	n.a.	n.a.
Hep	F	>5.5	144	303	301	2	303
Jan	F	>5.5	71	284	216	66	282
Kmk	F	>5.5	85	294	255	35	290
Kwg	F	>5.5	166	572	498	69	567
Lhm	F	>5.5	69	240	216	17	233
Mrk	F	>5.5	136	527	449	40	489
Ngr	F	>5.5	124	490	463	27	490
Nee	F	>5.5	67	12	n.a.	n.a.	n.a.
Ngk	F	>5.5	72	0	n.a.	n.a.	n.a.
Noi	F	>5.5	67	481	474	7	481
Nms	F	>5.5	75	122	9	52	61
Pet	F	>5.5	72	309	291	15	306
Pla	F	>5.5	94	34	n.a.	n.a.	n.a.
Poo	F	>5.5	89	2	n.a.	n.a.	n.a.
Suy	F	>5.5	67	31	n.a.	n.a.	n.a.
Yng	F	>5.5	87	21	n.a.	n.a.	n.a.
Grb	M	4.5-5.5	49	158	157	0	157
Kmy	M	4.5-5.5	59	91	91	0	91
Kwn	M	4.5-5.5	45	93	91	0	91
Plw	M	4.5-5.5	62	330	325	5	330
Nhk	F	4.5-5.5	187	652	537	107	644
Chg	M	3.5-4.5	70	243	203	39	242
Dto	M	3.5-4.5	69	218	160	55	215
Hee	M	3.5-4.5	79	304	294	10	304
Hgp	M	3.5-4.5	68	255	205	47	252
Cht	F	3.5-4.5	61	228	206	15	221
Htk	F	3.5-4.5	65	209	137	71	208
Chk	M	2.5-3.5	75	131	70	37	107
Moo	M	2.5-3.5	73	266	205	45	250
Nak	M	2.5-3.5	73	291	232	52	284
Som	M	2.5-3.5	67	1	n.a.	n.a.	n.a.
Hkr	F	2.5-3.5	66	0	n.a.	n.a.	n.a.
Fgn	M	1.5-2.5	70	29	No individuals in age classes 1.5-2.5 and younger observed		
Jgr	M	1.5-2.5	73	13			

ID	Sex	Age Group	Focals	Manipulative bouts	Tool-Use Bouts		
					Ses.	Una.	Total.
Knq	M	1.5-2.5	65	2	to use tools.		
Pri	M	1.5-2.5	71	0			
Dam	F	1.5-2.5	71	3			
Hmp	F	1.5-2.5	65	36			
Mty	F	1.5-2.5	67	1			
Nrk	F	1.5-2.5	73	37			
Pld	F	1.5-2.5	73	29			
Kgk	M	0.5-1.5	65	2			
Mnm	M	0.5-1.5	59	4			
Nmk	M	0.5-1.5	68	11			
Nmt	M	0.5-1.5	66	5			
Otn	M	0.5-1.5	67	10			
Pkr	M	0.5-1.5	66	3			
Tng	M	0.5-1.5	72	15			
Jrk	F	0.5-1.5	64	2			
Pyn	F	0.5-1.5	66	6			
Cha	M	0-0.5	203	40			
Dat	M	0-0.5	240	35			
Dwg	M	0-0.5	111	30			
Gbi	M	0-0.5	159	39			
Mpr	M	0-0.5	121	9			
Sai	M	0-0.5	187	41			
Sfa	M	0-0.5	128	7			
Tup	F	0-0.5	87	30			
Mek	F	0-0.5	154	41			
Tpt	F	0-0.5	138	42			
Waw	F	0-0.5	280	59			

I divided subjects into 7 age groups, and from youngest to oldest, these were, Group 1: 0 – 0.5 years (n = 11; 4 ♀, 6 ♂), Group 2: 0.5-1.5 years (n = 9; 2 ♀, 7 ♂), Group 3: 1.5-2.5 years (n = 9; 5 ♀, 4 ♂), Group 4: 2.5 – 3.5 years (n = 5; 1 ♀, 4 ♂), Group 5: 3.5-4.5 years (n = 6; 2 ♀, 4 ♂), Group 6: 4.5-5.5 years (n = 5; 1 ♀, 4 ♂), and Group 7: older than 5 years (n = 24; 17 ♀, 7 ♂). Exact ages are only known for individuals in Group 1, as these infants were born into the group during the data collection period. Group 2 juveniles were the existing infants in the group when I began study, and were estimated to be approximately 0.5 years of age based on the size and hair colouration. Three months into the study, in late December 2014, when these Group 2

infants were about 9 months of age, a birth peak began, during which, Group 1 infants were born over the several months, with most infants being born in March 2015 (Dec: 1, Jan: 2, Feb: 1, Mar: 4, Apr: 2, Jun: 1). I could therefore estimate that Group 2 juveniles were on average, one year older than Group 1 infants. Using this method, I determined which individuals belonged to the same generation based on physical characteristics, and estimate that each generation was a year older than the previous one. Individuals in Group 6 were adolescents that developed adult physical characteristics during the study (first birth and elongated nipples for females, adult muscularity for males). According to communications with staff from a captive primate facility (Singapore Institute for Clinical Sciences) these physical changes occur between 4 to 5 years of age, which matches with my age estimations. Individuals in Group 7 were already mature adults when I began the study, and I classified them as all being older than 5.5 years of age following from the estimated ages of younger age groups.

Data Collection

I collected behavioral data on object manipulation and tool-use behaviour via focal and ad libitum sampling (Altmann, 1974). All observations were either recorded on video or narrated into an audio recorder, and later transcribed and scored. In focal sampling, I sampled all individuals in random order on continuous rotation, for a 5-minute duration each time. During focal sampling, I recorded when focal individuals 1) started and ended foraging, resting, locomotive, and social behaviour, 2) picked up and dropped tools, 3) started and ended tool-use bouts, and 4) started and ended object manipulation bouts. Other data on social interactions were also collected, but will be elaborated on in the relevant chapters of this dissertation. Since object manipulation and tool use behaviour are

rare for some individuals, and may not be observed during focal sampling, I also recorded all instances of object manipulation that I observed outside of focal sampling, and recorded tool-use behaviour if an individual utilized an action pattern or processed a food type that had not previously been observed during focal sampling.

Data Scoring

Manipulative Behaviour

From focal samples, I scored manipulative bouts, which consisted of both object-manipulation bouts and tool-use bouts. Object-manipulation bouts are manipulative bouts in which the monkeys manipulated the objects associated with tool use, i.e. stones and shell items, in ways that do not constitute tool use. An object-manipulation bout began when the focal individual first contacts a stone or shelled item, and includes all items and actions until the focal individual ceases contact with all items for 10 seconds or more. Tool-use bouts began when the focal individual began striking the food item, and ended after the last strike, which is marked either by the individual consuming the food item, moving on to a different food item, or ceasing interaction with the food item for more than 10 seconds. Tool users sometimes walked with tools in hand while moving along the shore from one food item to another, particularly when cracking sessile oysters. These periods of walking with tools were not included in the durations of manipulative bouts, but were recorded to measure the amounts of time that individuals foraged with tools.

For each manipulative bout, I recorded the objects involved, and the manipulative actions carried out on objects. I considered only manipulative bouts in which stones, shell items, and anvils were involved. Anvil stones were distinguished from other stones either

by being non-movable stones that are embedded in the ground, or stones that showed signs of use as an anvil (i.e. having food debris or a tool stone placed on it). I distinguished two types of shell items, shelled food items (henceforth referred to as “food”) including unattached foods and sessile oysters, as well as old or empty shells that no longer contained edible contents (henceforth referred to as “shells”). I did not score a manipulative bout where only items that were not stones or shell items, such as pieces of trash, leaves, or twigs, were manipulated, but recorded these items as involved in manipulative bouts if stones and/or shell items were also involved.

I created an ethogram of actions performed on stones, food, shells, and anvils as I scored manipulative behaviour, recording and describing each new action (Table 2.2). At any one time, the macaques may manipulate single stones, food items, shells, and anvils, or manipulate several items simultaneously in various combinations.

I classified some actions as Critical Actions, and divided these actions into either Critical-A or Critical-B Actions (Table 2.3). Critical-A actions were actions directly involved in an optimal sequence of tool use. For tool use on sessile oysters, these were “pick up stone”, identify oyster (either by “pick at” or “mouth”), and “hit stone on oyster”. For tool use on unattached food items, these were “pick up stone”, “pick up food”, “place food on anvil”, and “hit stone on food”. Therefore, there were a total of 6 Critical-A actions across both food types. Critical-B Actions were inaccurate forms of Critical-A Actions that may still represent steps towards mastering the Critical-A Actions for an optimal tool-use sequence. For the Critical-A action “hit stone on oyster”, Critical-B actions were any actions in which the macaques brought stones in contact with oysters, and these were “rub stone on oyster”, and “swipe stone on oyster”. For “place food on

anvil”, Critical-B actions were any actions where the macaques brought foods in contact with anvils, or placed any item on an anvil. For these, I recorded “rub food on anvil”, “swipe food on anvil”, “direct percussion on anvil”, “place stone on anvil”, and “place shell on anvil”. For “hit stone on food”, Critical-B Actions were any actions where the macaques brought stones in contact with unattached foods, and these were “combine food under tool”, “combine food above tool”, and “combine food with two stones”. All other hitting actions were also scored as Critical-B actions, as hitting is a key action required for cracking foods. The macaques percussed various items and item combinations. I recorded a total of 21 Critical-B Actions.

Table 2.2

Object-manipulation actions on stones, unattached food items, sessile oysters, empty shells, and combinations of these items. Manipulations that are classified as Critical Actions are indicated by (A) for Critical-A actions and (B) for Critical B actions.

Item	Action	Description
<u>Single-Item Manipulations</u>		
Stone	Pick up (A)	Lift item off the ground, releasing the item within 2 seconds
	Hold	Lift item off the ground, continuing to hold item for >2 seconds
	Carry	Pick up and move item from one location to another
	Manipulate	Move item around in the hands
	Touch	Makes contact with item using the hand, does not proceed with picking up or manipulating the item
	Mouth	Makes contact with item using the mouth, includes biting but not ingesting item
	Sniff	Puts nose close to item
	<u>Rub on</u> ground	Holds item down on the surface and pushes it around, keeping item in contact with the surface
	Push off anvil	Nudges an item that is on an anvil with the hands, such that the item falls off the anvil
	Carry in mouth	Moves item from one location to another by holding it in the mouth
	Examine	Holds an item in the hand and looks at it intently. May involve some manipulation of the item.
	Hug	Holds item against the body
	Pick at	Plucks at item usually using either the index finger
	<u>Hit on</u> ground	Lifts item off the surface and brings it back down onto the surface with some force.
Unattached Food	Pick up (A)	
	Carry	
	Mouth	

Item	Action	Description
Sessile Oysters	Hold	Brings hand down onto item with some force
	Manipulate	
	Carry in mouth	
	Rub on ground	
	Rub on body	
	Hit with hand	
	Examine	
Empty Shells	Pick at (A)	
	Mouth (A)	
Anvil	Pick up	
	Mouth	
	Manipulate	
	Touch	
	Examine	
	Hold	
	Carry	
Anvil	Carry in mouth	
	Mouth	
Anvil	Pick at	
	<u>Two-Item Combinations</u>	
Stone / Anvil	<u>Place</u> stone on anvil (B)	Takes item from another location (e.g. on the ground), and releases it onto an anvil.
	Rub stone on anvil	
	<u>Swipe</u> stone <u>on anvil</u>	Holds item in one hand, lifting it off and bringing it back onto the anvil surface repeatedly, with a side-to-side U-shaped motion. The item makes contact with the anvil at the bottom of the U-shaped trajectory.
Unattached Food / Anvil	Hit stone on anvil (B)	
	Place food on anvil (A)	
	Rub food on anvil (B)	
	Swipe food on anvil (B)	

Item	Action	Description
Empty Shell / Anvil	Hit food on anvil (direct percussion) (B)	Hold items in adjacent contact with each other. In “combine with”, items are simultaneously brought together, whereas for “combine above/under” (see below), there appears to be a deliberate order of placing one item in contact with a specific surface of the other item.
	Place shell on anvil (B)	
	Rub shell on anvil	
Stone / Sessile Oyster	Hit shell on anvil (B)	
	Rub stone on oysters (B)	
	Swipe stone on oysters (B)	
Unattached Food / Sessile Oyster	Hit stone on oysters (A – Tool Use)	
	Rub unattached food on oysters	
	Hit unattached food on oysters (B)	
Two Stones	<u>Combine</u> stone <u>with</u> stone	
Stone / Other	Combine stone with other	Holds a stone in one hand and an unattached food item in the other hand, then puts and holds the food item in contact with the underside of the stone.
Stone / Unattached Food	Combine unattached food under stone (B)	
	Combine unattached food above stone (B)	
Unattached Food / Other	Combine unattached food with other	Holds a stone in one hand and an unattached food item in the other hand, then puts and holds the food item in contact with the top surface of the stone.
Two Unattached Foods	Combine food with food	
Unattached Food / Empty Shell	Combine unattached food with shell	
<u>Three-Item Combinations</u>		

Item	Action	Description
Unattached Food / Two Stones	Combine unattached food with two stones (B)	
Two Unattached Foods / Anvil	Hit unattached food on unattached food placed on anvil (B)	
Two Stones / Anvil	Hit stone on stone placed on anvil (B)	
Unattached Food / Shell / Anvil	Combine unattached food with shell and hit on anvil (B)	
Stone / Unattached Food / Anvil	Combine food above stone and place combination on anvil (B) Combine food above stone and hit combination on anvil (B) Combine food under stone and hit combination on anvil (B) Hit food on stone placed on anvil (B) Hit stone on food placed on anvil (A – Tool Use)	
<u>Four-Item Combinations</u>		
Unattached Food / Two Stones / Anvil	Combine food under stone and hit combination on another stone placed on anvil (B)	

Table 2.3

Critical-A Actions that are directly involved in an optimal sequence of tool use, and their inaccurate forms (Critical-B Actions).

Tool-Use Type	Critical-A Actions	Critical-B Forms
Sessile Oyster	Pick up stone	-
	Identify sessile oyster (Pick At/Mouth)	-
	Hit stone on sessile oyster	Rub stone on sessile oyster Swipe stone on sessile oyster Hit food on sessile oyster
Unattached Food	Pick up stone	-
	Pick up food	-
	Place food on anvil	Place stone on anvil Place shell on anvil Rub food on anvil Swipe food on anvil Hit shell on anvil Hit food on anvil
	Hit food (placed on anvil) with stone	Combine food under stone Combine food above stone Combine food with two stones Hit stone on anvil Hit food on another food placed on anvil Hit stone on another stone placed on anvil Hit food on stone placed on anvil Combine food with shell and hit combination on anvil Combine food above stone and place combination on anvil Combine food above stone and hit combination on anvil Combine food under stone and hit combination on anvil Combine food under stone and hit combination on another stone placed on anvil

I coded manipulative bouts according to a mutually exclusive and exhaustive hierarchical classification adapted from Inoue-Nakamura and Matsuzawa's (1997) study on the development of stone-tool use in young chimpanzees, altered to accommodate the cracking of sessile oysters that are unique to macaques (Table 2.4). The classification progresses according to the number of objects involved, the number of actions involved, and the relations between objects when multiple objects were manipulated. Manipulative bouts were first split into two classes depending on the number of objects manipulated simultaneously, single object (Class A), or multiple objects (Class B). Class A manipulative bouts were further divided into two classes depending on how many objects were manipulated in total; a single object (Class A-1), or multiple objects (Class A-2). Then, Class A-1 was again divided into two classes, this time based on how many actions were performed on the single object; a single action (Class-A-1-i), or multiple actions (Class A-1-ii). Class B manipulative bouts were subdivided according to whether the multiple items being manipulated simultaneously were brought in contact with each other; not combined (Class B-1), and combined (Class B-2). Lastly, manipulative bouts in which macaques carried out the correct object and action sequences involved in tool use were categorized as Class C. I split Class C manipulations into Class C-S, where macaques produced the tool-use sequence for sessile oysters, and Class C-U, where they produced the tool-use sequence for unattached food items. For Class C manipulations, it did not matter whether the individual was successful in cracking open the food item, as long as the correct object combinations and action sequences were produced.

Table 2.4

Definitions and examples of each hierarchical class of manipulative bouts.

Class	Definition
A-1-i: Single action on single object	Subject performed only one action on one object. (Example: touching a stone; mouthing a food item)
A-1-ii: Successive actions on a single object	Subject performed two or more actions, one after another on a single object. (Example: picking at a food item, then mouthing the same food item)
A-2-ii: Successive actions on multiple objects	Subject performed two or more actions, one after another, on two or more objects, but only one object at a time. (Example: picking up a stone, hitting the stone on the ground, then picking at a food item)
B-1: Simultaneous actions on multiple objects while not combining objects	Subject performed two or more actions on two or more objects simultaneously, while not bringing the objects into physical contact. (Example: handling a stone in one hand while picking at a food item with the other.)
B-2: Simultaneous actions on multiple objects while combining objects	Subject performed two or more actions on two or more objects either simultaneously, bringing the objects into physical contact. (Example: handling a food item in one hand and a stone in the other, and rubbing the two together.)
C-S: Tool-use on sessile oyster	Subject performed the correct sequence of tool use on sessile oyster (i.e. hitting a sessile oyster with a stone)
C-U: Tool-use on unattached foods	Subject performed the correct sequence of tool use on unattached food (i.e. hitting an unattached food that is placed on an anvil surface with a stone)

Tool Use

When manipulative bouts were tool use, I further scored the characteristics of tool-use bouts which were:

- a) *Duration*. The time taken to crack open a food item, measured by the time between the first and last strikes.
- b) *Tool Size*. Estimated tool size relative to the macaque's hand size.

c) *Hand Use*. For each strike, left, right, or both.

d) *Food Type*. Sessile oysters or unattached foods. For unattached food, the food species was noted (see Appendix 1 for list of food species on Koram Island)

e) *Strike Frequency*. The number of strikes used to crack open the food item.

f) *Strike Accuracy*. Accurate strikes were those in which the focal individual managed to make contact with the food item using the tool, and additionally in the case of tool use on unattached foods, the food item did not ricochet from its placement on the anvil. In inaccurate strikes, the tool user misses the food item, or causes the food item to ricochet when struck.

g) *Tool-Switching Frequency*. The number of times the focal individual switched to a different tool during each bout of tool use,

h) *Success*. Marked by whether the subject was able to crack and consume the food item.

i) *Hammering Class and Action Pattern*. According to an ethogram that was previously developed from the tool-use repertoire of a different population of macaques on Piak Nam Yai and Thao Islands in Laem Son National Park (Tan et al., 2015). If a new pattern was observed, I added it to the ethogram, thus creating an ethogram of tool-use action patterns for Koram Island (See Appendix 1 for ethogram of tool-use action patterns on Koram Island).

Analyses

I examined the development of manipulative and tool use behaviour using both

longitudinal and cross-sectional analyses. For manipulative behaviour, I carried out longitudinal analyses of object-manipulation bouts by infants born during the study over their first 6 months of development, and cross-sectional analyses of the differences in manipulative behaviour between individuals in different age groups. For tool use, I carried out a longitudinal examination of the tool-use characteristics of one juvenile male subject that began to use tools during the study period, over the first 10 months of his first tool use. I also carried out cross-sectional analyses of the differences in tool-use characteristics between individuals in different age groups.

Examining Changes in Manipulative Behaviour

Longitudinal Analyses of Infants' Object Manipulation Bouts. I examined changes in the proportions of time spent on object-manipulation bouts, and the rates at which infants performed object-manipulation bouts over the first 6 months of development. I included only infants with 6 full months of data ($n=7$). Two infants disappeared at three months of age (Dwg, Sfa), and the latest-born infant (Tup) only had 5 months of data by the end of the data-collection period, and these subjects were excluded from this analysis. I used Friedman tests to test for differences between months, and post-hoc tests with Bonferroni corrections to identify months that differed at the $p < 0.05$ level.

To examine changes in the characteristics of object manipulation bouts that occur after infants first start manipulating objects, I analyzed changes in the proportions of infants' object manipulation bouts in which different characteristics were recorded, over the six months following infants' first observed object-manipulation bouts. I required that each infant had at least 10 bouts of object-manipulation from which to calculate proportional data in each time period being compared. Eventually, I divided the first 6

months of each infant's object manipulation behaviour into two Time Periods – Time Period 1: 0-3 months, and Time Period 2: 4-6 months, to obtain a sample size of $n = 5$. Since some individuals were not observed to carry out object manipulation until their second month of development, these time periods corresponded to months 2-5, and 6-8 after birth. I included observations from focal samples and ad libitum observations of all infants to document the emergence of different manipulative actions. Table 2.5 shows which infants participated in each analysis.

Table 2.5

The number of object-manipulation bouts recorded for each infant in its first three months (Time Period 1) and fourth to sixth months (Time Period 2) of manipulative activity. X indicates which infants were involved in each analysis.

ID	No. of Bouts			Analysis	
	Time 1	Time 2	Total	Prop. Time / Rate	Bout Characteristics
Dwg¹	30	-	30		
Sfa¹	7	-	7		
Waw	39	24	70	X	X
Dat	19	29	52	X	X
Cha	35	5	43	X	
Sai	31	11	45	X	X
Mpr²	6	3	9		
Mek	14	27	43	X	X
Gbi	21	8	29	X	
Tpt	31	11	42	X	X
Tup³	30	-	30		

¹ Dwg and Sfa both went missing after their third month, before any object manipulation bouts were observed in Time 2.

² Mpr went missing in his fifth month, and therefore did not have a complete and usable dataset for Time 2.

³ Tup was only five months old at the end of the data collection period, and therefore did not provide a complete and usable dataset for Time 2.

I examined changes in:

- Objects infants manipulated, by calculating a) the proportions of object manipulation bouts in which each infant manipulated only stones, only shell items, both stones and shell items, and stones and/or shell items and anvils, as well as b) the average number of objects involved in object-manipulation bouts in the two time periods.
- Actions performed on objects, by a) documenting the emergence of different actions across the months of object manipulation, b) calculating the average numbers of actions each infant carried out during object-manipulation bouts, and c) the proportions of each infant's object-manipulation bouts in which Critical Actions were performed, in the two time periods.
- Complexity of object-manipulation bouts, by calculating the proportions of each infant's object manipulation bouts that fell into each Hierarchical Class, in the two time periods.

I used Wilcoxon signed-rank tests to test for differences ($p < 0.05$) between the two time periods.

Cross-Sectional Analyses of Manipulative Behaviour. To examine the prevalence of manipulative behaviour in each age group, I determined the proportion of individuals in each age group that engaged in manipulative bouts during focal sampling. I then calculated the proportion of total focal time that individuals in each age group spent in manipulative bouts, and the rate at which individuals carried out manipulative bouts per hour of focal time, and tested for differences between individuals in different age groups.

To examine changes in the two types of “correctness” of manipulative behaviour tending towards correct tool use across age classes, “object correctness” and “action correctness”, I examined differences in the objects and Critical Actions that individuals involved in manipulation bouts. For object correctness, I calculated the proportion of bouts in which a) only stones were manipulated, b) only shell items were manipulated, c) both stones and shell items were manipulated, and d) all items necessary for tool use was involved. For tool use on sessile oysters, these items were a stone and a sessile oyster, while for unattached foods, these items were a stone, a food item, and an anvil. For action correctness, I calculated the proportion of bouts in which Critical-A and Critical-B actions were carried out for each individual.

To examine changes in the complexity of manipulative behaviour across age classes, I calculated the proportion of bouts in which each Hierarchical Class was scored for each individual. I tested for differences between age groups using Kruskal-Wallis H tests, as the data could not be transformed to fit a normal distribution. I used Dunn post-hoc tests to identify which age classes differed. The level of significance was $p < 0.05$ for all tests.

Examining Changes in Tool-Use Behaviour

I examined changes in how much each individual used tools, and changes in tool-use proficiency. The tool-use characteristics I used to examine these changes were:

- a) proportion of foraging time spent carrying tools
- b) rate of tool use bouts per hour of focal time
- c) strike rate, which is the average number of strikes per second during tool-use

bouts

d) strike efficiency, measured by the average number of strikes needed to crack food items, with a higher average strike frequency indicating poorer strike efficiency

e) strike accuracy, measured by the average proportion of accurate strikes in tool-use bouts

f) tool fidelity, measured by the average number of times an individual switched tools during a bout, with more switches being lower fidelity

g) tool-use efficiency, measured by the average time taken to crack food items, less time being more efficient

h) tool-use effectiveness, measured by the proportion of successful bouts

Characteristics a) and b) measured how much each individual used tools, and characteristics c) to h) served as measures of proficiency. Strike rate was used as a measure of proficiency as previous research found that immature individuals struck sessile foods faster, but unattached foods slower, than mature individuals (Gumert et al., 2011). These differences may therefore reflect immature motor control or physical strength, and I wanted to examine changes in strike rate with more detailed age grouping. Measures d) to h) have not been previously examined in long-tailed macaque stone-tool use, and therefore, these analyses will also explore their usefulness as proficiency measures. I examined changes in tool-use characteristics separately across three food categories, all foods, sessile oysters only and unattached food items only.

Longitudinal Analyses of Tool-Use Behaviour Following First Tool Use. I calculated tool-use characteristics for the months following first tool use for the single subject that started using tools during the study period. The subject was a juvenile male, Chk, in Age Group 4 (2.5-3.5 years). I calculated each tool-use characteristic for bouts in each one-month period following Chk's first tool use, up to 10 months when our data collection period ended. Data from months 8 to 10 were pooled because less data was collected during this period due to monsoon weather conditions. Since this was a single-subject analysis, I could not use statistical tests, but used 95% confidence intervals and visual analyses of graphs to identify probably significant changes between months. This method is commonly used to assess single-subject data (Morgan & Morgan, 2009).

Cross-Sectional Analyses of Tool-Use Characteristics. In cross-sectional analyses, I included only individuals with more than 10 bouts of tool use in each food category. These analyses involved only individuals from Age Group 4 or older. Two individuals in Age Group 3 were observed to carry out the correct sequence of tool use on sessile oysters, but did not have more than 10 bouts of these correct sequences, furthermore, none of these sequences produced successful tool use. The number of individuals analyzed in each age class for each food category is listed in Table 2.6. For analyses of tool-use characteristics on unattached foods, I could not include Age Group 6, as only one individual from that Age Group was observed to use tools on unattached food, and post-hoc tests could not be run.

Table 2.6

Number of individuals in each age group with more than 10 bouts of tool use in each food category

Age Group	All Food	Sessile Oysters	Unattached Food
4 (2.5-3.5 years)	3	3	3
5 (3.5 – 4.5 years)	6	6	6
6 (4.5 – 5.5 years)	5	5	-
7 (>5.5 years)	13	13	8

To determine what statistical tests to use, I first examined if the data for each characteristic was normally distributed using a Shapiro-Wilks test. Then, I applied a square root transformation on characteristics that were found to deviate from a normal distribution, and tested for normality again. I used one-way between subjects ANOVA with Tukey post-hoc tests for data that was normally distributed, or could be transformed to fit a normal distribution. I used Kruskal-Wallis H tests with Dunn post-hoc tests for data that could not be transformed to fit normality. For f) strike accuracy, g) tool fidelity, and h) tool-use effectiveness, I used square root transformed data regardless of whether ANOVA or Kruskal-Wallis H tests were used, since the raw data was heavily skewed. The skews were because the macaques were overall very accurate in their strikes, seldom switched tools during bouts, and almost always successful in cracking open food items. In the end, one-way between subjects ANOVAs were used to test for differences in bout durations across all food items, strike efficiency for sessile oysters and unattached food, strike rate for all food categories, tool-selection effectiveness across all food categories, and strike accuracy and tool-use effectiveness for unattached foods. Kruskal-Wallis H tests were used for all other comparisons.

Tests of Coding Reliability

Ideally, coding reliability should be assessed by inter-rater reliability between two independent coders. However, I was unable to obtain a second coder, and instead assessed intra-rater reliability between my original coding of video-recorded data that I carried out directly after collection in the field, and a re-coding of a portion of video-recorded data carried out several months later. To confirm the coding reliability of behavioral variables used in analyses, I recoded and rescored video-taped object-manipulation and tool-use bouts, then examined concordance by calculating Interclass Correlation Coefficients (ICC) for continuous variables and kappa coefficients (Martin & Bateson, 1993) for categorical variables, and the percentage of agreement between the two coding events for all variables. For object manipulation, 43 object-manipulation bouts were video-taped during data collection, and I rescored all bouts. I first recoded the objects and manipulative actions involved in each manipulative bout as described in “Scoring Object Manipulation”, then recoded the variables used in analyses which were total number of actions, total number of objects, object category (stones only, shells only, stones and shells, stones/shells and anvils, stone and sessile oyster, and, stone, unattached food and anvil), Hierarchical Class, and whether Critical-A actions and Critical-B were performed. To select tool-use bouts for recoding, I selected 100 focal samples by assigning each focal sample a random sorting number with the RAND function in Microsoft Excel, and selecting the first 100 focal samples. I then recoded all tool-use bouts within these 100 focal samples, which was a total of 339 bouts. Variables of each bout that were analyzed for concordance were number of strikes, accuracy index, number of tool changes, and bout success. For both object manipulation and tool use bouts, I did not recode bout

durations as these were based on time stamps from the videos, and not on rater judgment. Consequently, I did not analyze concordance of strike rates in tool-use bouts, as these were calculated by dividing total strikes by bout duration, and would yield the same results as total strikes. ICCs and kappa coefficients indicated perfect or almost perfect concordance between the original and recoded scores for all tool use and object manipulation variables analyzed (cf. Martin & Bateson, 1993) (Table 2.7).

Table 2.7

Interclass Correlation Coefficients and kappa coefficients indicating coding reliability

	Variable	% Agreement	Reliability Statistic
Object Manipulation	Total Actions	97.56	ICC = 0.99
	Total Objects	100	ICC = 1.00
	Object Category	100	k = 1.00
	Hierarchical Class	100	k = 1.00
	Presence of Critical-A	100	k = 1.00
	Presence of Critical-B	97.56	k = 0.95
Tool Use	Number of Strikes	93.81	ICC = 0.99
	Accuracy Index	97.35	ICC = 0.98
	Number of Tool Changes	100	ICC = 1.00
	Success	100	k = 1.00

Results

Changes in Manipulative Behaviour

Longitudinal Changes in Infants' Object Manipulation Behaviour

Prevalence of Object Manipulation. I obtained 150 hours of total focal time, and recorded a total of 400 object manipulation bouts for all 11 infants across the study period. Infants were first observed to manipulate stones and/or shells in their first ($n = 3$), second ($n = 7$), or third ($n = 1$) months of age. Seven infants were included in statistical

analyses, contributing 93 hours of focal time across their first six months of development, during which I recorded and analyzed 324 object-manipulation bouts. Across all six months, the infants spent on average 0.02 of their focal time engaged in object-manipulation bouts, at an average rate of 0.04 bouts per minute. Friedman tests found significant differences in both the proportion of time that infants spent on object manipulation ($\chi^2_{(5)} = 20.31, p = 0.001$) and their rates of object manipulation ($\chi^2_{(5)} = 16.07, p = 0.01$) over the six months (Figure 2.1). Wilcoxon signed-rank post-hoc tests revealed that the median proportion of time spent in object manipulation increased significantly from the first month of development (Median = 0.00) to the fourth (Median = 0.02), $z = -3.57, p = 0.01$; fifth (Median = 0.03), $z = -3.71, p = 0.003$; and sixth (Median = 0.03), $z = -3.29, p = 0.02$, months of development. Post-hoc tests also revealed that the median rates of object-manipulation bouts increased significantly from the first month of development (Median = 0.00 bouts/min) to the third (Median = 0.08 bouts/min), $z = -3.29, p = 0.02$; and fourth (Median = 0.09), $z = -3.36, p = 0.01$, months of development.

Figure 2.1 Data showed that the prevalence of infants' ($n = 7$) object manipulation behavior increased over their first 6 months of age. The proportion of focal time that infants spent on object manipulation (o) increased significantly from the first to the fourth, fifth, and sixth months, while their rates of carrying out object manipulation bouts (♦) increased from the first, to the third and fourth months of development. Letters (proportion: lower case; rate: UPPER CASE) are used to denote statistical significance, such that significantly different months do not share letters.

Actions and Objects. I observed a total of 34 different actions in object manipulation activity recorded during focal sampling and ad libitum observations in the 6 months following infants' ($n = 11$) first recorded object manipulation bouts (Table 2.8). Infants with the full 6 months for analyses ($n = 7$) had developed 12 to 19 different actions each (Median = 16). Different actions emerged in different months for each infant, and there were general patterns in the emergence of different types of actions.

There were changes in the types of objects manipulated by infants over the two three-month time periods following their first object manipulation. All 11 infants were observed to interact with stones before shell items, with the exception of one infant, Cha, who interacted with a shell first. Within shell items, infants interacted with shells before they were observed to interact with food. For infants with more than 10 bouts of object manipulation in each time period for analysis ($n = 5$), there was a decrease in the proportion of bouts in which only shells were manipulated. A Wilcoxon signed-rank test revealed that the median proportion of bouts in which only shell items were manipulated showed a significant decrease from the Time Period 1 (Median = 0.32) to the Time Period 2 (Median = 0.18), $z = -2.02$, $p = 0.04$. I did not find significant differences in the proportions of bouts in which only stones, both stones and shell items, and stones and/or shell items with anvils were manipulated, or in the average number of objects manipulated in each bout for the two Time Periods. Only one infant, Dat, was observed to carry out an object manipulation bout in which all the objects necessary for tool use on sessile oysters were present (i.e. stone and sessile oyster) in the fourth month following his first object manipulation, but he did not continue to regularly do so. None of the infants performed object manipulation bouts in which all objects necessary for tool use on unattached foods (i.e. stone, food, and anvil) were involved.

There were changes in the numbers of actions performed in object manipulation bouts and the types of actions performed across the months of object manipulation. All five infants showed an increase in the number of actions performed in each object-manipulation bout over the two time periods. A Wilcoxon signed-rank test revealed that the median number of actions infants carried out during object-manipulation bouts

increased significantly from the Time Period 1 (Median = 2.00), to Time Period 2 (Median = 2.18), $z = 2.02$, $p = 0.04$.

The proportions of bouts in which infants carried out Critical Actions on objects also increased for all five infants. The median proportion of bouts in which infants carried out Critical Actions increased significantly from Time Period 1 (Median = 0.42), to Time Period 2 (Median = 0.64), $z = 2.02$, $p = 0.04$. Critical-A actions performed by infants were “pick up stone” ($n = 10$), “pick up food” ($n = 8$), and “pick at oyster” or “mouth oyster” ($n = 11$). Critical-B actions carried out by infants were “place shell” ($n = 1$), “place stone” ($n = 2$), “rub food on anvil” ($n = 1$), “rub stone on oyster” ($n = 1$), “hit food on anvil” ($n = 1$), and “hit stone on anvil” ($n = 1$). The Critical Actions involving “pick up” were the earliest to emerge, followed by those involving “place”, then those involving “rub”, and lastly, those involving percussive actions.

Lastly, there were changes in the complexity of object-manipulation bouts. All five infants showed an increase in the proportion of bouts that were Hierarchical Class B-2 object-manipulation bouts, i.e. object-manipulation bouts in which multiple objects were combined. A Wilcoxon signed-rank test revealed that the median proportion of bouts that were Hierarchical Class B-2 increased from Time Period 1 (Median = 0.00), and Time Period 2 (Median = 0.09), $z = 2.02$, $p = 0.04$. The first combinatory actions to emerge during the first six months of manipulative development were placing objects on anvils, which was carried out by four of the 11 infants (Dat, Sai, Tpt, Tup) and emerged between the first and fourth months following infants’ first object manipulations. The next combinatory actions to emerge were rubbing objects on sand substrate and anvils, carried out by five of the 11 infants (Waw, Dat, Sai, Mek, Tpt) and emerging between the third

and fifth months of object manipulation. One infant (Dat) rubbed a stone on a sessile oyster in his fourth month of object manipulation. Percussive actions were the last to emerge, and only observed in two infants. One infant (Sai) interspersed rubbing a *Planaxis sulcatus* snail on an anvil surface with several instances of directly percussing the snail on the surface in his fifth month of manipulative development. Another infant (Dat), hit a stone onto an anvil surface in his sixth month of manipulative development. None of the infants were observed to carry out combinatory manipulations involving more than two objects.

Table 2.8

Actions recorded in infants' object manipulation bouts, and the month in which each action was first recorded for each infant.

Item	Action	Dwg	Sfa	Waw ¹	Dat ¹	Cha ¹	Sai ¹	Mpr	Gbi ¹	Mek ¹	Tpt ¹	Tup	Total Ind.
Single-Item Manipulations													
Stone	Pick up (A)	2	1	1	2	2	2		2	1	1	1	10
	Hold	2		4	3	3	2		4		1	2	8
	Carry			4	3		3						3
	Manipulate	1	1	1	1	2	2	1	1		1	1	10
	Touch	1	1	1		1	1	2	2		1	1	9
	Mouth	2	1	1		1		2	1	1	1	1	9
	Sniff			2		2	1					1	4
	Rub on ground											2	1
	Push off anvil	2									2		2
	Carry in mouth					2							1
Unattached Food	Pick up (A)	2		4		5	2	4	5	1			7
	Carry					5			5	4			3
	Mouth			4		5	2	4	5	1			6
	Manipulate						3	4		4			3
	Carry in mouth	2											1
	Rub on ground									4			1
Sessile	Pick at (A)	2		2	4	2							4
Oysters	Mouth (A)	2		2	4	1							4
Empty Shells	Pick up			2	1	1	1	5	2	1	1	1	9
	Mouth			2	1	1	1		2	3	1	1	8
	Manipulate			1		2	2			1	3	1	6
	Touch			3									1

Item	Action	Dwg	Sfa	Waw ¹	Dat ¹	Cha ¹	Sai ¹	Mpr	Gbi ¹	Mek ¹	Tpt ¹	Tup	Total Ind.
	Examine			1				5					2
	Hold			3	3		2		2				4
	Carry			3	2	2			2	5	2		6
Anvil	Mouth	1						1	1				3
Two-Item Combinations													
Stone / Anvil	Place stone on anvil (B)			7	2		2				4		4
	Rub stone on anvil			5	3								2
	Hit stone on anvil (B)				6								1
Unattached Food / Anvil	Rub food on Anvil (B)						3			5			2
	Direct percussion on anvil (B)						5						1
Empty Shell / Anvil	Place shell on anvil (B)											1	1
	Rub shell on anvil										5		1
Stone / Sessile Oyster	Rub stone on oysters (B)				4								1
Total different actions:		11	4	19²	14	16	16	9	13	12	12	11	

¹ Data from these infants were used in statistical analyses on the longitudinal changes in object manipulation behavior.

² This count of actions developed at 6 months of object manipulation excludes the action “Place stone on anvil”, which was only recorded in Waw’s 7th month of object manipulation.

Differences in Manipulative Behaviour between Age Groups

Prevalence of Manipulative Behaviour. I obtained 8266 manipulative bouts consisting of 866 object-manipulation bouts, and 7400 tool-use bouts from 5990 focal samples on 69 macaques. This was a total time of about 181 hours of activity with stones and shells, consisting of approximately 72 hours of object manipulation, and 109 hours of tool use from 499 hours of focal sampling.

Altogether, 62 of the 69 macaques, or 90% of individuals were observed to carry out manipulative bouts, during their focal samples. This was 11 individuals (100%) in Age Group 1 (0-0.5 years), 9 individuals (100%) in Age Group 2 (0.5-1.5 years), 8 individuals (89%) in Age Group 3 (1.5-2.5 years), 4 individuals (80%) in Age Group 4 (2.5-3.5 years), 6 individuals (100%) in Age Group 5 (3.5-4.5 years), 5 individuals (100%) in Age Group 6 (4.5-5.5 years), and 19 individuals (79%) in Age Group 7 (>5.5 years). The total numbers of bouts, proportions of focal time spent on, and rates of manipulative bouts for each age group is given in Table 2.9.

Table 2.9

Number and % of individuals that carried out manipulative bouts, and the total hours and numbers of manipulative bouts analyzed in each age group

Age Group	Total N	n	Hours	Number of Manipulative Bouts (Object manipulation, Tool Use)
1	11	11 (100%)	18.98	363 (363, 0)
2	9	9 (100%)	2.61	46 (46, 0)
3	9	8 (89%)	20.06	150 (150, 0)
4	5	4 (80%)	21.41	689 (48, 641)
5	6	6 (100%)	23.52	1465 (23, 1442)
6	5	5 (100%)	22.17	1324 (11, 1313)
7	24	19 (79%)	72.46	4229 (225, 4004)
Total	69	62 (90%)	181.21	8266 (866, 7400)

Overall, individuals spent an average of 0.04 ($SD = 0.04$) of their total focal time engaged in manipulative bouts, and the proportions of focal time spent in manipulative behaviour differed significantly across age groups [$H_{(6, N=69)} = 18.44, p = 0.01$] (Figure 2.2). There was an overall upward trend in the proportion of time that individuals spent in manipulative bouts, but decreasing in the oldest age group. There were significant differences between Age Groups 2 (Median = 0.003) and 5 (Median = 0.07), $t = -35.89, p = 0.01$; and Age Groups 2 and 6 (Median = 0.07), $t = -34.96, p = 0.04$.

There were also differences between age groups in the rates of carrying out manipulative bouts [$H_{(6, N=69)} = 22.76, p = 0.001$] (Figure 2.2). On average, individuals carried out manipulative bouts at a rate of 1.71 bouts/hr ($SD = 2.09$ bouts/hr). The median rate generally increased from younger to older age groups, until the decrease in the oldest age group, with significant differences between Age Groups 2 (Median = 0.08 bouts/hr) and 5 (Median = 4.34 bouts/hr), $t = -39.72, p = 0.004$; 2 and 6 (Median = 3.87 bouts/hr), $t = -35.79, p = 0.03$; and 3 (Median = 0.34 bouts/hr) and 5, $t = -32.56, p = 0.04$.

Figure 2.2 Macaques in different age groups differed in the proportions of focal time spent in manipulative activity (o) and rates at which manipulative bouts were carried out (♦). These differences were between macaques in age groups 2 (0.5-1.5 years), and age groups 5 (3.5-4.5 years) and 6 (4.5-5.5 years) for both proportion of time spent and rate of manipulative activity, and additionally between age group 3 (1.5-2.5) and age group 5 for rate of manipulative activity. Letters (proportion: lower case; rate: UPPER CASE) are used to denote statistical significance, such that significantly different months do not share letters.

Correctness of Manipulative Behaviour.

Object Correctness. Overall, 0.32 ($SD = 0.38$) of all bouts involved only stones, 0.22 ($SD = 0.30$) involved only shell items, and 0.46 ($SD = 0.47$) involved both stones and shell items. Bouts corresponding to each object category composed a different proportion of the total bouts for each age group (Figure 2.3a). I found significant differences in the proportions of manipulative bouts in which individuals in each age group involved only stones [$H_{(6, N=62)} = 41.53, p < 0.001$], and both stones and shell items [$H_{(6, N=62)} = 34.43, p < 0.001$], but no significant differences in the proportions of manipulative bouts involving

only shell items. In all age groups, there was a lower proportion of manipulative bouts in which individuals handled only shell items as compared to the other two object categories, suggesting that the manipulation of shell items alone was less common in general.

Overall, manipulative bouts involving only stones decreased from younger to older age groups. Differences in the proportions of manipulative bouts involving only stones were significant when comparing between Age Groups 1 (Median = 0.72) and 5 (Median = 0.00), $t = 33.68$, $p = 0.002$; 1 and 6 (Median = 0.00), $t = 33.68$, $p = 0.004$; and 1 and 7 (Median = 0.00), $t = 30.42$, $p < 0.001$, and well as Age Groups 2 (Median = 0.60) and 5, $t = 31.94$, $p = 0.01$; 2 and 6, $t = 31.94$, $p = 0.01$; and 2 and 7, $t = 28.61$, $p = 0.001$ (Figure 2.3b).

Conversely, manipulative bouts involving both stones and shell items increased from younger to older age groups. Differences in the proportions of manipulative bouts involving both stones and shell items, were significant between Age Groups 1 (Median = 0.02) and 5 (Median = 0.99), $t = 31.88$, $p = 0.01$; 1 and 6 (Median = 0.99), $t = -34.05$, $p = 0.01$; and 1 and 7 (Median = 0.99), $t = -21.52$, $p = 0.03$, as well as Age Groups 2 (Median = 0.00) and 5, $t = -37.06$, $p = 0.002$; 2 and 6, $t = 39.22$, $p = 0.002$; and 2 and 7, $t = -26.70$, $p = 0.004$ (Figure 2.3b).

The proportions of bouts in which all objects needed for correct tool use also differed for individuals in different age classes [Sessile Oysters: $H_{(6, N=62)} = 36.71$, $p < 0.001$; Unattached Food: $H_{(6, N=62)} = 26.07$, $p < 0.001$]. Recall from the results of the longitudinal analysis on infants, objects needed for correct axe hammering on sessile oysters (i.e. stone and oysters) was first observed on one occasion in one infant (Dat) in his fourth month of manipulative development. However, bouts involving complete

objects for axe hammering remained rare, especially in Age Groups 1 and 2. The median proportions of bouts in which stones and sessile oysters were present increased across age classes, and was significantly higher in Age Groups 5 (Median = 0.81), 6 (Median = 0.98) and 7 (Median = 0.87), as compared to Age Group 1 (Median = 0.00); [$t_{(1 \times 5)} = -29.75, p = 0.02$; $t_{(1 \times 6)} = -40.55, p < 0.01$; $t_{(1 \times 7)} = -25.76, p = 0.002$], and Age Group 2 (Median = 0.00); [$t_{(2 \times 5)} = -29.94, p < 0.03$; $t_{(2 \times 6)} = -40.94, p = 0.001$; $t_{(2 \times 7)} = -26.16, p = 0.01$] (Figure 2.3b). Bouts in which all objects needed for pound hammering of unattached foods (i.e. food, stone, anvil), emerged later, and was only first observed in 1 juvenile (Pld) in Age Group 3 (1.5-2.5 years). The median proportions of bouts in which stones, unattached foods, and anvils were present was significantly higher in Age Group 5 (Median = 0.17), than Age Groups 1, 2, and 3 (Medians = 0.00); [$t_{(1 \times 5)} = -31.92, p = 0.002$; $t_{(2 \times 5)} = -30.50, p = 0.01$; $t_{(3 \times 5)} = -29.96, p = 0.01$] (Figure 2.3b).

Action Correctness. I documented 14 different actions on stones, 10 actions on unattached food items, 2 actions on sessile oysters, 8 actions on shells, and 2 actions on anvils. I also documented 23 two-item, 9 three-item, and 1 four-item combinatory manipulations (Table 2.2). The numbers of individuals observed to perform each action and the number of actions observed for each age group varied across age groups (Table 2.10). Some actions, i.e. picking up, holding, and carrying stones, picking up unattached foods, and picking at and mouthing sessile oysters were ubiquitous across all age groups. Three and four item combinations were not observed in age groups 0-0.5 years, and 0.5-1.5 years. The number of different actions performed was highest in Age Group 3, and was higher in younger age groups (Age Groups 1, 2, 3, and 4), than older age groups.

Figure 2.3 With regards to the types of objects manipulated and object correctness, a) data showed that different compositions of each age group's total manipulative bouts in which only stones, only shell items, or both stones and shells were involved. Kruskal-Wallis H tests found differences in the average proportions of bouts in which b) only stones, both stones and shell items, all objects involved in tool use on sessile oysters, i.e. a stone and sessile oyster, and all objects involved in tool use on unattached food, i.e. stone, anvil, unattached food was involved. Letters are used to denote statistical significance, and thus significantly different age groups do not share letters.

Table 2.10

Numbers of individuals in each age group observed to carry out each manipulative action, as well as the total number of individuals observed to carry out each action, and the total number of different actions observed for each age group

Item	Action	Number of Individuals / Age Group (N)							
		1 (11)	2 (9)	3 (9)	4 (5)	5 (6)	6 (5)	7 (24)	All (69)
<u>Single-Item Manipulations</u>									
Stone	Pick up (A)	9	8	7	4	6	5	15	54
	Hold	6	4	5	3	6	5	15	44
	Carry	5	2	3	3	6	5	13	37
	Manipulate	11	6	4					21
	Touch	10	4	1					15
	Mouth	11	3	2					16
	Sniff	6	1	1					8
	Rub on ground	1	3						4
	Push off anvil	1	1						2
	Carry in mouth	3							3
	Examine			2					2
	Hug		1						1
	Pick at			1					1
	Hit on ground			1					1
	Unattached Food	Pick up (A)	8	3	5	3	6	5	24
Carry		4	1	1	1	6	5	24	42
Mouth		8	4	4		6	5	24	51
Hold		8	4			6	5	24	47
Manipulate		6	4	2	1				13

Item	Action	Number of Individuals / Age Group (N)							
		1 (11)	2 (9)	3 (9)	4 (5)	5 (6)	6 (5)	7 (24)	All (69)
Sessile Oysters	Carry in mouth	2	3	2					7
	Rub on ground	2	2						4
	Rub on body			1					1
	Hit with hand				1				1
	Examine			1	1				2
	Pick at (A)	4	9	3	2	6	5	24	53
Empty Shells	Mouth	4	9	3	2	6	5	24	53
	Pick up	10	3	1					14
	Mouth	10	1	1					12
	Manipulate	7		1					8
	Touch	1							1
	Examine	2							2
Anvil	Hold	2							2
	Carry	5							5
	Carry in mouth	3							3
	Mouth	3							3
	Pick at			1					1
<u>Two-Item Combinations</u>									
Stone / Anvil	Place stone on anvil (B)	5	2	4	1	1			13
	Rub stone on anvil	2	3	7					12
	Swipe stone on anvil		1	1					2
	Hit stone on anvil (B)			3	3				6
	Place food on anvil (A)			1	2	6	1	11	21
	Rub food on Anvil (B)	3	2	5	1	1		1	13
Unattached Food / Anvil	Swipe food on anvil (B)			2	1				3
	Direct percussion on anvil (B)	1		2	3		3	14	23
	Place shell on anvil (B)	1							1
	Rub shell on anvil	1							1

Item	Action	Number of Individuals / Age Group (N)							
		1 (11)	2 (9)	3 (9)	4 (5)	5 (6)	6 (5)	7 (24)	All (69)
Stone / Sessile Oyster	Hit shell on anvil (B)			1					1
	Rub stone on oysters (B)	1		2					3
	Swipe stone on oysters (B)			2					2
Unattached Food / Sessile Oyster	Hit stone on oysters (A – Tool Use)			2	3	6	5	13	29
	Rub unattached food on oysters			1					1
	Hit unattached food on oysters (B)			1	1				2
Two Stones	Combine stone with stone		1						1
Stone / Other	Combine stone with other		1						1
Stone / Unattached Food	Combine unattached food under stone (B)			1					1
	Combine unattached food above stone (B)				1				1
Unattached Food / Other	Combine unattached food with other			1	1	1			3
Two Unattached Foods	Combine food with food			1					1
Unattached Food / Empty Shell	Combine unattached food with shell			1					1
<u>Three-Item Combinations</u>									
Unattached Food / Two Stones	Combine unattached food with two stones (B)				1				1
Two Unattached Foods / Anvil	Hit unattached food on unattached food placed on anvil (B)							1	1
Two Stones / Anvil	Hit stone on stone placed on anvil (B)				1				1
Unattached Food / Shell / Anvil	Combine unattached food with shell and hit on anvil (B)			1					1
Stone / Unattached Food / Anvil	Combine food above stone and place combination on anvil (B)				1				1
	Combine food above stone and hit				1				1

Item	Action	Number of Individuals / Age Group (N)							
		1 (11)	2 (9)	3 (9)	4 (5)	5 (6)	6 (5)	7 (24)	All (69)
	combination on anvil (B)								
	Combine food under stone and hit combination on anvil (B)				1				1
	Hit food on stone placed on anvil (B)			1	1				2
	Hit stone on food placed on anvil (A – Tool Use)				3	6	1	9	19
<u>Four-Item Combinations</u>									
Unattached Food / Two Stones / Anvil	Combine food under stone and hit combination on another stone placed on anvil (A)				1				1
Total Actions in Age Class:		35	27	44	28	15	13	15	

The proportions of manipulative bouts in which Critical-A Actions [$H_{(6, N=62)} = 54.98, p < 0.001$], and Critical-B Actions [$H_{(6, N=62)} = 17.27, p = 0.01$] were performed differed across individuals in different age groups (Figure 2.4). The proportion of manipulative bouts in which Critical-A Actions were performed increased from Age Group 1 (Median = 0.40) to Age Group 3 (Median = 1.00), and by Age Groups 4 to 7 Critical-A actions were performed in all bouts. The increase was significant between Age Groups 1 and 3 ($t = -25.49, p = 0.01$), 1 and 4 ($t = -33.36, p = 0.01$), 1 and 5 ($t = -33.36, p = 0.001$), 1 and 6 ($t = -33.36, p = 0.002$), and 1 and 7 ($t = -33.36, p < 0.001$). The increase in Critical-A actions was also significant between Age Groups 2 (Median = 0.67) and 3 ($t = -23.60, p = 0.04$), 2 and 4 ($t = -31.44, p = 0.02$), 2 and 5 ($t = -31.44, p = 0.003$), 2 and 6 ($t = -31.44, p = 0.01$) and 2 and 7 ($t = -31.44, p < 0.001$).

Since the Critical Actions “pick up stone”, “pick up unattached food” and “pick at sessile oyster” were carried out by all individuals, I also examined differences in the proportion of manipulative bouts in which Critical-A Actions were performed between age groups when these actions were excluded. There continued to be significant differences across age groups in the proportion of bouts in which Critical-A Actions were performed when “pick up stone”, “pick up unattached food”, and “pick at sessile oyster” were excluded [$H_{(6, N=62)} = 38.62, p < 0.001$]. After this exclusion, the proportions of individuals’ bouts in which Critical-A actions were performed fell to zero in Age Groups 1 and 2, and then increased from Age Groups 3 onwards. Increases were significant between Age Groups 1 (Median = 0.00) and 5 (Median = 0.99), $t = -33.83, p = 0.002$; 1 and 6 (Median = 0.99), $t = -36.00, p = 0.002$; and 1 and 7 (Median = 0.99), $t = -24.00, p = 0.004$, as well as between Age Groups 2 (Median = 0.00) and 5, $t = -33.83, p = 0.01$; 2

and 6, $t = -36.00$, $p = 0.003$; 2 and 7, $t = -24.00$, $p = 0.01$.

Unlike Critical-A Actions, the proportion of manipulative bouts in which Critical-B Actions were performed did not increase linearly across age groups. Instead, Critical-B Actions were performed in the highest proportion of bouts of individuals in Age Group 3, and this difference was significant between Age Groups 3 (Median = 0.61) and 1 (Median = 0.03), $t = -26.84$, $p = 0.03$; 3 and 2 (Median = 0.00), $t = -26.56$, $p = 0.047$; and 3 and 6 (Median = 0.01), $t = -35.36$, $p = 0.01$.

Figure 2.4 With regards to action correctness, Kruskal-Wallis H tests found significant differences in the average proportions of bouts in which Critical-A actions were performed, including when the more ubiquitous actions of “pick up stone” and “pick up food” were excluded, as well as in the proportion of bouts in which Critical-B actions were performed. Letters are used to denote statistical significance, and thus significantly different age groups do not share letters.

Complexity of Manipulative Behaviour. The composition of total manipulative bouts that fell into each hierarchical class differed for each age group (Figure 2.5). I found significant differences in the proportion of bouts in which individuals carried out manipulations of all Hierarchical Classes, except Class B1, which was not observed in any age group except Age Group 1 (Table 2.11), meaning that macaques did not often manipulate multiple objects simultaneously without combining them.

Class A-1-i manipulative bouts, single actions on single objects, decreased from Age Groups 1 to 4, and were not recorded for individuals from Age Groups 5 to 7. The median proportions of manipulative bouts that were Class A-1-i differed across age groups [$H_{(6, N=62)} = 42.76; p < 0.001$]. The median proportion of manipulative bouts for individuals in Age Groups 1 (Median = 0.38) that were Class A-1-i manipulative bouts was significantly higher than in Age Groups 5 (Median = 0.00), $t = 31.18, p = 0.001$; 6 (Median = 0.00), Dunn $t = 31.18, p = 0.003$; and 7 (Median = 0.00), $t = 31.18, p < 0.001$. The median proportion of bouts for individuals in Age Group 2 (Median = 0.36) that were =Class A-1-i was significantly higher than in Age Groups 5, $t = 26.16, p = 0.03$; and 7, $t = 26.17, p = 0.001$.

Class A-1-ii manipulative bouts, multiple actions on single objects, decreased from Age Groups 1 to 3, and were not recorded during focal samples for individuals from Age Groups 4 to 7, except for 1 individual in Age Group 7. There were significant differences in the proportions of manipulative bouts that were Class A-1-ii [$H_{(6, N=62)} = 42.71, p < 0.001$]. The proportion of bouts in which individuals in Age Group 1 (Median = 0.53) carried out Class A-1-ii manipulative bouts was higher than that of individuals in Age Groups 4 (Median = 0.00), $t = 34.46, p = 0.004$; 5 (Median = 0.00), $t = 34.46, p <$

0.001); 6 (Median = 0.00), $t = 34.46$, $p = 0.001$; and 7 (Median = 0.00), $t = 32.69$, $p < 0.001$.

Class A-2 manipulative bouts were carried out in the highest proportion of bouts by individuals in Age Group 1; only single individuals in Age Groups 2 and 3, and no individuals in Age Groups 4 to 7 carried out Class A-2 manipulative bouts. There were significant differences between age groups in the proportion of manipulative bouts that were Class A-2. The difference was significant between Age Group 1 (Median = 0.05) and all other age groups (Medians = 0.00), [$t_{(1 \times 2)} = 21.67$, $p = 0.001$; $t_{(1 \times 3)} = 22.08$, $p = 0.002$; $t_{(1 \times 4)} = 25.45$, $p = 0.01$; $t_{(1 \times 5)} = 25.46$, $p = 0.001$; $t_{(1 \times 6)} = 25.46$; $t_{(1 \times 7)} = 25.45$, $p = 0.002$].

Class B-2 manipulative bouts were carried out in the highest proportion of bouts by individuals in Age Group 3. There were differences between age groups in the median proportions of manipulative bouts that were Class B-2 [$H_{(6, N=62)} = 24.10$, $p < 0.001$] and the differences were significant between Age Groups 3 (Median = 0.80) and 1 (Median = 0.35), $t = 31.19$, $p = 0.004$; 3 and 5 (Median = 0.01), $p = 0.01$, $t = 34.10$; and 3 and 6 (Median = 0.01), $t = 37.09$, $p = 0.01$. In addition, the types of actions in B-2 manipulative bouts were different in different age groups. In Age Groups 1 to 4, individuals carried out a variety of B-2 manipulative actions, such as rubbing or swiping stones, shells, and shelled food items on anvils or other items. For one individual in Age Group 3 (Pld), two B-2 manipulative bouts featured all the actions required for cracking unattached foods, but carried out in erroneous sequence interspersed with other non-critical actions. In one of these bouts, she placed an unattached oyster on top of a stone, and hit both items down onto an anvil. In another bout involving a clam, an empty shell, a stone, and an anvil, she

again placed the clam onto the stone and hit both items down onto an anvil, amidst other inept actions that were hitting the stone on to the anvil, placing the clam on top of an empty shell and hitting both items onto the anvil, rubbing the clam on the anvil, directly percussing the clam on the anvil, and attempting to bite open the clam. In Age Groups 5 to 7 however, B-2 manipulative actions consisted only of direct percussion of unattached food items onto anvils, with the exceptions of one individual in Age Group 7 that rubs stones on anvils, and another individual in Age Group 7 that rubbed a clam on an anvil.

Opposite to Class A manipulative bouts, Class C-S and Class C-U manipulative bouts, which were those involving the correct action sequences for tool use on sessile oysters and unattached food respectively, increased from younger to older age groups. There were significant differences between age classes in the proportion of manipulative bouts that were Class C-S [$H_{(6, N=62)} = 38.43, p < 0.001$] and Class C-U [$H_{(6, N=62)} = 34.79, p < 0.001$]. Class C-S manipulations were only recorded in individuals from Age Group 3 and older. Two individuals in Age Group 3 (Pld, Fgn) hit sessile oysters with stones, but were not successful on any occasion. Proportions of bouts that were Class C-S were higher in Age Groups 5 (Median = 0.81), 6 (Median = 0.98), and 7 (Median = 0.87), than in Age Group 1 (Median = 0.00); [$t_{(5 \times 1)} = 28.67, p = 0.02$; $t_{(6 \times 1)} = 40.30, p < 0.001$; $t_{(7 \times 1)} = 25.21, p = 0.002$], and Age Group 2 (Median = 0.00); [$t_{(5 \times 2)} = 28.68, p = 0.03$; $t_{(6 \times 2)} = 40.30, p < 0.001$; $t_{(7 \times 2)} = 25.21, p = 0.01$], and also higher in Age Group 6 than in Age Group 3 (Median = 0.01); $t = 31.68, p = 0.02$. Class C-U manipulations emerged later than Class C-S, and were only recorded in individuals in Age Group 4 and older. The proportion of bouts that were Class C-U was higher in Age Group 5 (Median = 0.17) than in Age Groups 3, 2, and 1 (Medians = 0.00); [$t_{(5 \times 3)} = 33.50, p = 0.002$; $t_{(5 \times 2)} = 33.50, p =$

0.001; $t_{(5 \times 1)} = 33.50, p = 0.001$]. The proportion of bouts that were Class C-U were also higher in Age Groups 4 (Median = 0.18) and 7 (Median = 0.03) than in Age Group 1 [$t_{(4 \times 1)} = 27.50, p = 0.05$; $t_{(7 \times 1)} = 18.16, p = 0.046$].

In Age Group 4, two individuals that carried out Class-C manipulation bouts sometimes also carried out Class B-2 manipulations, amidst the correct tool use sequences. One individual (Chk), carried out erroneous object combinations and action sequences, in several bouts where he also produced the correct object-action sequences to crack a *Planaxis sulcatus* snail. These erroneous sequences were placing the snail either on top of the tool or under the tool and hitting both items on the anvil simultaneously, placing the tool on the anvil and hitting it with the snail, manipulating the tool and snail while holding them in contact with each other but not relating them to the anvil, and placing the snail on the anvil but striking at another location on the anvil with the tool. Another individual (Moo) picked up a stone and hit it on a blank rock surface (without sessile oyster coverage), before carrying the stone a short distance and using it to strike oysters. These superfluous action sequences were not observed in the Class C manipulations, i.e. tool use, of individuals in Age Group 5 and older.

Figure 2.5 With regards to the complexity of manipulative behaviour across age groups, data showed different compositions of each age group's total manipulative bouts that fell into each hierarchical class.

Table 2.11

Means and standard deviations of the average proportions of individuals' manipulative bouts in each Hierarchical Class and in each age group

Age Group	A-1-i	A-1-ii	A-2	B-1	B-2	C-S	C-U
1	0.36 ± 0.12	0.53 ± 0.10	0.07 ± 0.06	<0.01 ± 0.01	0.04 ± 0.05	0	0
2	0.37 ± 0.33	0.31 ± 0.26	0.01 ± 0.03	0	0.31 ± 0.28	0	0
3	0.03 ± 0.04	0.16 ± 0.18	<0.01 ± 0.01	0	0.78 ± 0.16	0.04 ± 0.05	0
4	0.25 ± 0.33	0	0	0	0.06 ± 0.07	0.53 ± 0.37	0.16 ± 0.13
5	0	0	0	0	0.01 ± 0.02	0.81 ± 0.11	0.17 ± 0.12
6	0	0	0	0	0.01 ± 0.01	0.96 ± 0.07	0.04 ± 0.07
7	0	0.03 ± 0.11	0	0	0.28 ± 0.41	0.63 ± 0.44	0.07 ± 0.11

Changes in Tool-Use Characteristics

Longitudinal Changes Following First Successful Tool Use. I observed one juvenile male, Chk, carry out his first successful tool use on an unattached food item (*Planaxis sulcatus*) on 5th February 2015, and observed him successfully cracking sessile oysters on 22nd February, 2015. In all food categories, Chk's average bout duration, strike frequency, and rate of tool changes decreased (i.e. tool fidelity increased) over the months following first tool use, while strike rate, strike accuracy index, and proportion of successful bouts increased (Figure 2.6a, b, c). Some changes appeared gradual with no significant change between months, however, by the third month of his first tool use, Chk's overall proportion of successful tool use bouts across sessile oysters and unattached foods increased beyond the 95% confidence limits of his first two months of tool use (Figure 2.6a vi, b vi, c vi). Strike accuracy also saw significant increases, with the strike accuracy index of the third month higher than the 95% confidence limit of the first two months for tool use on sessile oysters (Figure 2.6b iv). Strike accuracy took longer to improve for tool use on unattached food, with the difference only apparent from the fifth month. For tool use on sessile food, strike rate was significantly higher from the second month of tool use (Figure 2.6b iii), but this change was not observed for tool use on unattached food.

a) Tool-use characteristics across all food types

i) Duration

ii) Strike Frequency

iii) Strike Rate

iv) Strike Accuracy

v) Tool Fidelity

vi) Proportion of Successful Bouts

b) Tool-use characteristics on sessile oysters

i) Duration

ii) Strike Frequency

iii) Strike Rate

iv) Strike Accuracy

v) Tool Fidelity

vi) Proportion of Successful Bouts

c) Tool-use characteristics on unattached food

i) Duration

ii) Strike Frequency

iii) Strike Rate

iv) Tool Fidelity

v) Strike Accuracy

c vi) Proportion of Successful Bouts

Figure 2.6 Chk's average bout duration, strike frequency, strike rate, strike accuracy index, rate of tool change, and proportion of successful bouts showed changes over the months following first tool use on a) all food types, b) sessile oysters, and c) unattached food. Error bars represent the 95% confidence limits of each month's data, and red dotted lines indicate significant changes.

Differences in Tool-Use Characteristics between Age Groups

Prevalence of Tool Use. Overall, tool users spent 57% of their foraging time with a tool in hand, and carried out 1.30 bouts of tool use per minute of foraging time. These values increase from juvenile tool users (Age Group 4: $M_{\text{prop}} = 0.49$, $SD = 0.08$; $M_{\text{rate}} = 1.18$ bouts/min, $SD = 0.26$) into adolescence (Age Group 5: $M_{\text{prop}} = 0.55$, $SD = 0.07$; $M_{\text{rate}} = 1.26$ bouts/min, $SD = 0.19$) and early adulthood (Age Group 6: $M_{\text{prop}} = 0.61$, $SD = 0.13$; $M_{\text{rate}} = 1.45$ bouts/min, $SD = 0.56$), and fall slightly in mature adulthood (Age Group 7: $M_{\text{prop}} = 0.58$, $SD = 0.17$; $M_{\text{rate}} = 1.28$ bouts/min, $SD = 0.53$), but these differences did not reach statistical significance in ANOVA tests (Figure 2.7)

Figure 2.7 The proportion of their time that individuals in each age group spent using tools (o), and the rates (♦) at which they carried out tool use increased from 2.5 years to 5.5 years and fell slightly in the >5.5 years age group, but these differences were not significant. Error bars represent one standard error of the mean.

Changes in Proficiency Measures. The means and standard deviations of proficiency measures in different age classes are listed in Table 2.12. I found significant differences between age classes for some proficiency measures of tool use analyzed across all foods and on sessile oysters only, but no significant differences between age classes for tool use on unattached foods only. Results are described below, and test statistics provided in Tables 2.13 (ANOVA or Kruskal-Wallis H tests) and Table 2.14 (post-hoc tests).

There were significant differences between age groups in strike efficiency when tool use was analyzed across both food types (Figure 2.8ai), and sessile oysters only (Figure 2.8b). Strike efficiency increased (i.e. average strike frequency decreased) from younger to older age groups and differences were significant between Age Groups 4 and 7.

There were also significant differences between age groups in strike accuracy analyzed across both food types. Strike accuracy increased from younger to older age groups (Figure 2.8aaii). Macaques in Age Groups 6 and 7 had significantly higher median strike accuracy than those in Age Group 4 and Age Group 5.

Tool fidelity also differed between age groups when analyzed across all foods. Tool fidelity increased, i.e. the number of times the macaques changed tools per bout decreased, from younger to older age groups (2.8aiii). Tool fidelity was significantly higher in Age Groups 6 and 7 than in Age Group 4.

Lastly, tool-use effectiveness differed between age groups when analyzed across all foods Tool-use effectiveness, measured by the proportion of successful bouts,

increased across age groups (Figure 2.8aiv) however, these differences did not reach statistical significance in pairwise comparisons between groups.

Table 2.12

Means and standard deviations of each individuals' tool-use characteristics across age groups

Characteristic	Age Group	<i>M</i> ± <i>SD</i>		
		All Food	Sessile	Unattached
Duration	2.5-3.5 years	7.59 ± 2.58	7.21 ± 2.38	9.33 ± 5.13
	3.5-4.5 years	5.58 ± 1.18	5.30 ± 1.40	3.00 ± 10.38
	4.5-5.5 years	5.73 ± 1.57	5.41 ± 1.54	4.00 ± n.a.
	> 5.5 years	5.12 ± 1.38	4.93 ± 1.26	5.00 ± 2.16
	Total	5.59 ± 1.61	5.72 ± 1.88	8.63 ± 6.64
Strike Frequency	2.5-3.5 years	12.95 ± 3.50	5.74 ± 3.57	8.73 ± 3.15
	3.5-4.5 years	9.38 ± 2.14	13.88 ± 1.80	6.92 ± 4.12
	4.5-5.5 years	11.38 ± 2.89	10.09 ± 2.70	4.27 ± n.a.
	> 5.5 years	8.78 ± 1.89	9.28 ± 1.53	6.42 ± 2.76
	Total	9.86 ± 2.63	10.31 ± 2.58	685 ± 3.23
Strike Rate	2.5-3.5 years	2.13 ± 0.23	3.70 ± 0.50	3.23 ± 1.24
	3.5-4.5 years	2.16 ± 0.59	3.17 ± 0.29	0.93 ± 0.21
	4.5-5.5 years	2.51 ± 0.54	3.37 ± 0.41	1.08 ± n.a.
	> 5.5 years	2.11 ± 0.55	3.08 ± 0.29	1.26 ± 0.27
	Total	2.20 ± 0.54	3.22 ± 0.37	1.14 ± 0.27
Accuracy Index	2.5-3.5 years	0.93 ± 0.06	0.96 ± 0.05	0.74 ± 0.14
	3.5-4.5 years	0.96 ± 0.03	0.97 ± 0.02	0.71 ± 0.23
	4.5-5.5 years	1.00 ± 0.01	1.00 ± 0.01	0.89 ± 0.11
	> 5.5 years	0.97 ± 0.05	0.99 ± 0.01	0.81 ± 0.18
	Total	0.97 ± 0.04	0.99 ± 0.02	0.81 ± 0.29
Tool Change Rate	2.5-3.5 years	0.05 ± 0.04	0.03 ± 0.03	0.18 ± 0.29
	3.5-4.5 years	0.02 ± 0.01	0.01 ± 0.02	0.11 ± 0.14
	4.5-5.5 years	0.01 ± 0.02	0.01 ± 0.02	0.02 ± n.a.
	> 5.5 years	0.01 ± 0.01	0.01 ± 0.01	0.04 ± 0.03
	Total	0.02 ± 0.02	0.01 ± 0.02	0.08 ± 0.14
Proportion of Success	2.5-3.5 years	0.72 ± 0.14	0.73 ± 0.15	0.75 ± 0.10
	3.5-4.5 years	0.83 ± 0.02	0.84 ± 0.04	0.71 ± 0.15
	4.5-5.5 years	0.86 ± 0.02	0.88 ± 0.02	0.95 ± n.a.
	> 5.5 years	0.88 ± 0.01	0.88 ± 0.01	0.87 ± 0.04
	Total	0.84 ± 0.08	0.81 ± 0.05	0.81 ± 0.04

Table 2.13

*Results of either one-way between subject ANOVAs or Kruskal-Wallis H tests found significant differences between age groups in several tool-use characteristics (indicated by *)*

Food Type	Characteristic	<i>F</i> (2, 23)	<i>H</i> (3, <i>N</i> =27)	Sig.
All	Duration	1.53		0.23
	Strike Frequency	3.49		0.03*
	Strike Rate	0.63		0.60
	Accuracy Index		13.55	0.004*
	Tool Fidelity (Tool Changes/Bout)	4.86		0.01*
	Proportion of Success		7.99	0.05*
Sessile Oysters	Duration		1.97	0.58
	Strike Frequency	3.20		0.04*
	Strike Rate	0.90		0.46
	Accuracy Index		6.12	0.11
	Tool Fidelity (Tool Changes/Bout)		3.67	0.30
	Proportion of Success		6.14	0.11
Unattached Food	Duration		1.21	0.75
	Strike Frequency	0.52		0.61
	Strike Rate	3.24		0.07
	Accuracy Index	2.21		0.15
	Tool Fidelity (Tool Changes/Bout)		0.39	0.94
	Proportion of Success	1.37		0.29

Table 2.14

Tukey HSD (for ANOVAs) or Mann-Whitney U (for Kruskal Wallis) post-hoc tests indicated which age groups differed

Food Type	Characteristic	Age Group A	Age Group B	Tukey HSD	Mann-Whitney U
All	Strike Frequency	2.5 – 3.5 years	>5.5 years	$p = 0.047$	
	Tool Fidelity	2.5 – 3.5 years	4.5 – 5.5 years	$p = 0.01$	
			>5.5 years	$p = 0.02$	
	Accuracy Index	2.5 – 3.5 years	4.5 – 5.5 years		$U=0.00, z=-2.29, p=0.02$
			>5.5 years		$U=4.00, z=-2.09, p=0.04$
		3.5 – 4.5 years	4.5 – 5.5 years		$U=0.00, z=-2.76, p=0.01$
			>5.5 years		$U=1.00, z=-2.55, p=0.01$
	Proportion of Success	2.5 – 3.5 years	4.5 – 5.5 years		$U=0.00, z=2.34, p=0.03$
			>5.5 years		$U=4.00, z=-2.09, p=0.04$
		3.5-4.5 years	4.5-5.5 years		$U=4.00, z=-2.00, p=0.045$
Sessile	Strike Frequency	2.5 – 3.5 years	>5.5 years	$p = 0.04$

Figure 2.8 One-way between-subject ANOVAs or Kruskal-Wallis H tests found differences in the a i) strike frequencies, a ii) strike accuracies, a iii) rate of tool changes, and a iv) proportion of successful bouts of macaques in different age groups when analyzed across both food types, and in their b) strike frequencies when analyzed within tool-use on sessile oysters. Letters are used to denote statistical significance, and thus significantly different age groups do not share letters. Error bars represent one standard error of the mean.

Discussion

This is the first study on the ontogeny of stone-tool use skills in long-tailed macaques. I was able to examine manipulative behaviour, or lack thereof, in 69 individuals at different stages of development. I carried out longitudinal analyses of the object manipulation behaviour of five infants from birth, and one juvenile's tool-use behaviour from his first success, as well as cross-sectional comparisons between macaques divided into 1-year age groups. I combined the findings from these two lines of analyses to describe the developmental trajectory of macaque tool-use skills, from object manipulation, to competence, to changes in proficiency after skill acquisition.

Overall, results support predictions made from the perception-action perspective that tool use would develop over several years and that naïve macaques would first carry out simple manipulations, then a wide variety of non-functional combinatory manipulations, before manipulative behaviour is channeled towards the actions and object combinations necessary for tool use, that are then produced in various permutations until effective tool-use sequences are produced. The ontogeny of object manipulation and tool use in long-tailed macaques provides a new point of reference for comparison with the only two other nonhuman primate stone-tool users – chimpanzees (Biro et al., 2006; Inoue-Nakamura & Matsuzawa, 1997) and capuchins (Resende et al., 2014; Resende et al., 2008). Extending comparisons to patterns of development of stone-handling in closely related macaque species (Nahallage & Huffman, 2007; 2008; 2012), manipulative object play in other Old World monkeys (Fairbanks, 2000), and object percussion in human children (Kahrs, Jung, & Lockman, 2012; 2013; Frigaszy, Simpson, & Brakke, 2016), provides further insight into biological propensities and processes that underlie

developmental similarities in different organisms. Conversely, differences in the processes and outcomes of manipulative development between species, populations, and individuals, highlight areas where environmental and social influences interact with developmentally flexible behaviour. This augments our understanding of behavioral phenomenon viewed from the perception-action perspective of tool-use development.

Immature macaques carried out a wide variety of exploratory manipulations with the objects involved in tool use that changed in frequency and form, prior to achieving tool use competence. Macaque infants first began to manipulate stones and/or shell items between their first and third months of development. Interestingly, all but one infant first manipulated stones before shell items, and within shell items, infants first manipulated old and empty shells instead of those that still contained the living organism and potential food source. In older juveniles as well, single-item object manipulation more commonly involved only stones, rather than manipulation of shells and food items. Manipulating stones alone offers no possibilities for gaining food rewards, and suggests that manipulative activity on stones is intrinsically motivated in macaques, perhaps even biologically predisposed.

An underlying propensity for macaques to manipulate stones can be further evidenced by the resemblance between object manipulation preceding stone-tool use in these long-tailed macaques, and stone-handling in Japanese and rhesus macaques (Nahallage & Huffman, 2007a; 2007b; 2008). In all three species, infants begin manipulating stones with simple exploratory manipulations (e.g. picking up, biting) within their first to third months of age, and the variety and complexity of their manipulative actions increase to a peak between 2-4 years of age. Infant and juvenile stone handlers

carried out more frequent but shorter bouts than adults, while adults engaged in fewer but longer bouts of stone handling, predominantly consisting of sound-producing and other manually dexterous patterns. The close similarities between the ways that these two behaviours emerge, combined with current knowledge that stone handling has been documented in all macaque subspecies belonging to the *fascicularis* taxonomic subgroup of macaques (Nahallage & Huffman, 2008; 2016), suggests that stone-tool use in long-tailed macaques, first emerges out of biological predisposition towards object, and particularly stone manipulation. This accords with the perception-action perspective that tool use develops from perceptual learning that is first gained from performing predisposed action routines (Huffman & Quiatt, 1986; Lockman, 2000; Resende et al., 2008; Visalberghi & Frigaszy, 2006). Macaques could be discovering the properties and affordances of stones through their early manipulative behavior, for example, being hard and allowing one to strike other surfaces and objects. In coastal long-tailed macaques, these perceptual experiences take place in environments enriched with encased foods, facilitating the discovery of tool use as young incorporate their manipulative predispositions into foraging routines.

Infants begin to manipulate stones and shells within their first to third months, and rapidly develop a wide variety of manipulative actions on objects. As predicted, early manipulative actions were simple actions that did not involve combining objects, and were not directly instrumental to tool use sequences. Most commonly, infants will simply touch or pick up objects momentarily, manipulate them in the hands and mouth for short periods, or carry them over short distances. The earliest combinatorial manipulations in which infants brought objects in contact with each other, was observed in the second

month of manipulative development, and restricted to infants placing small stones onto larger stones or boulder surfaces. Rubbing stones and food items on surfaces were the next combinatorial manipulation to emerge. Percussive actions were the last to emerge, and were only observed in two infants under 6 months of age on single occasions. All combinatorial manipulations however, were rare for young macaques below 1.5 years of age, comprising an average of 4% of object manipulation bouts in infants under 6 months, increasing to 30% of bouts in juveniles aged 0.5-1.5 years (Age Group 2). Another notable change during the first 1.5 years of development is the relatively high frequency of object manipulation during the first six months, which then appears to decline after six months, until a re-emergent rise in activity beginning around 1.5 years.

The age of 1.5-2.5 years appears to represent a developmental time period of substantial changes in manipulative behavior. Individual differences become more apparent, with some juveniles maintaining only low rates of object manipulation, while others significantly increase in their frequency and complexity of manipulative behaviour. In this age group, combinatorial manipulations predominantly replaced simple manipulations, comprising an average of 80% of individual's manipulation bouts. In addition to the significant replacement of single item manipulations with combinatorial manipulations, widest variety of different manipulative actions are recorded in this age group. This variety in actions is contributed by the persistence of simple actions, and placing and rubbing stones and food items on anvils and substrates, and simultaneous increase in combinatorial manipulations involving percussion. These early percussive actions were mostly hitting stones onto anvil surfaces, again with no possibility of gaining food from this action, and sometimes directly percussing food items onto anvils, possibly

to crack and obtain the encased food source.

Qualitatively, percussive actions at this age often involved “swiping”, where objects were swung using haphazard lateral and roughly U-shaped sweeping motions, and would strike the substrate at the bottom of the U-shaped trajectory without particular precision. This resembled an action that looks intermediate between side-to-side rubbing actions used in rubbing objects on substrates, and the striking actions used in effective tool use, which utilized a more fixed up-down motion perpendicular to the plane on which the target object was oriented, and accurately hitting the same point (i.e. the sessile oyster) with reliability. This again accords with the perception-action perspective’s prediction that eventual tool use actions (proper striking), reflects earlier exploratory actions (rubbing items on surfaces). In addition, these early percussive actions in developing macaque tool users resemble the early inept and inconsistent strike trajectories of human infants’ object banging (Kahrs, Jung, & Lockman, 2012; 2013; 2014). In human infants, this developmental stage has been linked to a lack of control over postural stability and the distal arm joints (Fragaszy, Simpson, Cummins-Sebree, & Brakke, 2014; Kahrs, Jung, & Lockman, 2014). The common difficulties shared by the two species in developing percussion, suggests that similar limitations in physical maturation may also constrain macaque development.

Also between 1.5-2.5 years of age, manipulative behaviour begins to resemble tool use, although at this stage, sequences were often erroneous and all attempts were unsuccessful. Two individuals in this age group were observed to hit stones onto sessile oysters. This constitutes the correct tool-use sequence for cracking sessile oysters, but they were never successful. Their lack of success at this stage could be due to a lack of

physical strength, or poor mastery of proper striking actions and strike accuracy. At this age, one juvenile (Pld) also first began to manipulate all the objects involved in cracking unattached foods, and demonstrate all the actions necessary for cracking unattached foods but combined these actions in the wrong sequence. Two lines of evidence suggest that these erroneous tool-use sequences on motile food items likely persist for at least another year before the proper sequence is mastered. Firstly, these inept sequences were still part of the early tool-use bouts of the juvenile (Chk) who carried out his first successful tool use on motile items between 2.5-3.5 years of age. Also, when I subsequently returned to the study site in October 2016, Pld had not yet mastered the correct sequence of tool use on motile food items. These observations suggest that apart from developing and mastering effective striking actions, producing the appropriate action sequences and spatial relationships between the three objects involved in cracking unattached foods on anvils was a major challenge to macaque tool use competence.

At 2.5-3.5 years of age, some juvenile macaques achieve tool-use competence. Newly competent tool users still performed inept actions in their early tool use bouts, however, they no longer performed simple manipulations such as picking up, and manipulating stones and food items out of the contexts of tool use or trying to obtain food rewards from their actions. The effect of this is that the wide variety of manipulative actions observed in the preceding age group is sharply reduced and restricted to tool use behaviour. In the current study, I observed one juvenile male, Chk, in this age group use tools successfully for the first time. Two other individuals in that age group were already able to use tools when I began observations, and the remaining two individuals in that age group had not developed tool use abilities. Interestingly, exploratory object manipulations

were almost never carried out by the two individuals in Age Group 4 that had not started to use tools, and in macaques above Age Group 4 regardless of whether or not they were able to use tools, suggesting that the period of development up to around 3.5 years represents a critical period of learning for macaques, after which macaques do not develop tool use skills under natural conditions. A similar critical period for nut-cracking skill acquisition up to the age of 5 years has also been reported for chimpanzees, after which those who have not acquired the skill only scrounge from nut crackers (Biro et al., 2003).

Following initial competence, young tool users begin to improve in proficiency. The most significant rapid improvements appear to be in strike accuracy. For axe hammering of sessile oysters, Chk's strike accuracy improved significantly over the first three months of tool-use competence, and for pound hammering on motile organisms, strike accuracy improved more gradually, and significant improvements from initial levels of accuracy in the first month were only seen in the eighth month. These improvements in strike accuracy correlated with the significant improvements he made in his proportion of successful tool use bouts on both forms of tool use. There were no longer significant differences in strike accuracy between tool users in older age classes (3.5 years and above), suggesting that adult level accuracy is achieved by these early improvements. Some other aspects of tool-use proficiency appeared to improve more gradually as differences were not significant in the months following Chk's first competence, but were different between age groups. Tool users above 3.5 years of age (Age Group 5 and above), no longer incorporated irrelevant actions into their tool-use sequences, required fewer strikes on average to crack food items, particularly sessile oysters, and also showed greater tool fidelity, changing tools fewer times during bouts than tool users below 3.5

years of age. These patterns of improvement in proficiency, particularly the prominent improvements to strike accuracy that remains to be made after competence is achieved, again reflects the difficulty that macaques face in mastering effective striking.

There appears to be ontogenetic peaks and declines in the frequencies of manipulative behaviour, with associated differences in the types of manipulations that characterize these periods. The first peak in the frequency of object manipulation occurs soon after birth, with all infants beginning to manipulate stones and shells within the first 3 months of age. Overall object manipulation appears to decline after 6 months, with infants spending less time on and carrying out lower rates of manipulation. Overall manipulative activity rises sharply again at around 1.5 years of age. However, while the first peak in manipulative behavior is observed to be fairly uniform across individual infants, the increase in frequency and complexity of manipulative behaviour around 1.5 years is observed in only a proportion of individuals. These individual differences endure as individuals either achieve tool-use competence between 2.5-3.5 years, or remain non-tool users.

Comparisons with ontogenetic trajectories of object play of other Old World monkeys suggest that changes in maturing neural and motor systems underlie these observations of developmental peaks and critical periods for skill acquisition, and furthermore, that young individuals' experiences during earlier developmental stages affect developmental outcomes (Bourgeois & Rakic, 1993; 1996; Fairbanks, 2000; Jacobs, Chugani, Allada, Chen, & Phelps, et al., 1995; Rakic Bourgeois, Eckenhoff, Zecevic, & Goodman-Rakic., 1986; Zecevic, Bourgeois, & Rakic, 1989). In vervet monkeys and rhesus macaques, peaks in frequencies of object play occur when the formation of

synaptic connections between the cerebral cortices and motor neurons are increasing exponentially between 3 to 6 months of age, until rates of dendritic pruning overtakes growth at 6 months. Conversely, play declines with the myelination of neurons in the central nervous system (Gibson, 1991; Olivier, Edgley, Armand, & Lemon. 1997). This process is developmentally complete at 3.5 years, and renders neurons less plastic and responsive to behavioral experiences, and could therefore underlie the observation of the end of the critical learning period at 3.5 years, where some macaques no longer acquire tool use skills, and those who have restrict manipulative activities to the tool use patterns they have acquired.

Object manipulation in infancy therefore coincides with a period where the developing neural and motor systems are most amenable to experiential feedback (Fairbanks, 2000). The sensory input from the types of manipulations that infants practice at this stage, affect which motor-neural connections are strengthened or lost over development (e.g. Bourgeois & Rakic, 1996). Infants' behaviours are in turn influenced by the physical environments and social contexts surrounding their development. The effects of environmental factors on manipulative outcomes might be most apparent in species and population level differences. For example, although macaque species within the *fascicularis* taxonomic subgroup share a propensity for stone manipulation (Nahallage & Huffman, 2008; 2012), stone-handling emerges only in some populations where the macaques are provisioned. Infants in these groups can afford more time for stone play, reinforcing motor-neural connections and allowing the behaviour to be maintained into maturity. In long-tailed macaques, stone-tool use emerges only in some coastal populations. Coastal environments provide greater opportunities for infants to manipulate

stones in conjunction with hard-shelled food items, channeling manipulative experience towards those that prime motor-neural systems for the acquisition of tool use.

The influence of species-typical environments and natural histories on developmentally flexible behaviour, may also be seen in comparisons of the developmental challenges encountered by different species in mastering stone-tool use. Placing the challenges that macaques face in comparison with capuchins and chimpanzees reveals that the three species face different combinations of the same general challenges to varying extents. The three main difficulties that chimpanzees face when learning to crack nuts have been reported based on observations in both field and captive settings (Hiyashi, Mizuno, & Matsuzawa, 2005; Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa et al., 2001): 1) chimpanzees do not readily or regularly percuss objects on surfaces, 2) they do not extensively explore and manipulate stones, and 3) they face difficulty in mastering the correct sequence of producing two spatial relations between three objects out of several possible sequences. With macaques in the picture, the second challenge appears to be more chimpanzee specific. Capuchin development is not challenged by a lack of interest in stones (Resende et al., 2008), and as we have observed, several macaque species demonstrate a propensity for manipulating stones, and macaque infants on Koram Island readily explore and manipulate stones, even before manipulative interest in food items. On the other hand, the third challenge appears to be shared by all three species, with long periods of errors before juveniles are able to produce the proper sequences for nut-cracking, or pound hammering unattached foods in the case of macaques. Closer examinations however, have revealed that the source of difficulty in this aspect of tool use differs across species. In addition to managing multiple spatial relations, capuchins are

hindered from producing tool use sequences because of their apparent difficulty in performing the second action in the sequence, which is placing nuts on anvils (Resende et al., 2008). In contrast, placing actions are the first combinatory manipulations that infant chimpanzees develop (Inoue-Nakamura & Matsuzawa, 1997; Takeshita et al., 2005), and we have seen the same pattern in macaques. Therefore, it appears that macaques and chimpanzees both face the first challenge of producing percussive actions. This is not an issue for capuchins as percussion is a general feature of their foraging behaviour (Fragaszy et al., 2004), and emerges early in development (Fragaszy & Adams-Curtis, 1997; Resende et al., 2008).

The pattern of readiness to place objects but difficulty in percussion shared between macaques and chimpanzees support the ecological explanation proposed by Resende et al. (2008) to explain the reversed pattern of these differences between chimpanzees and capuchins. With the exception of these coastal populations that subsist on a high proportion of shelled marine organisms, long-tailed macaques are generally frugivorous, and their diets consist of food items that do not require percussive extraction (Gumert & Malaivijitnond, 2012). Therefore, the addition of macaques to the comparative picture previously consisting of capuchins and chimpanzees, strengthens support for the perception-action theory's prediction that there would be biases towards species-typical perception-action routines, and since tool-use develops from early exploratory routines, the developmental trajectory for each species will be influenced by its natural tendencies and ecologies.

While the ontogeny of stone-tool-use skills in macaques has been revealing, there is substantial individual variation that also calls for further investigation. Individuals vary

widely in the frequency at which they carry out manipulative and tool use behaviour, and in the developmental timing at which different manipulative actions and complexities emerge and change. For example, while many juveniles did not yet percuss items at 1.5-2.5 years, or carried out percussive actions with improper “swiping” actions, direct percussion of a food item onto a rock surface with the typical vertically oriented striking motions was recorded as early as the fifth month of manipulative development for infant Sai. Most illustrative of this variation in percussive behaviour is that only 76% of the macaques on Koram Island above 2.5 years old, developed tool use, and 88% of adults and adolescents at the other studied location, Piak Nam Yai Island. Amongst the non-tool users, some carried out direct percussion of food items on hard substrate, some rubbed food items on substrate but never percussed them, and yet others were never observed to process food items in combination with any other object or substrate. There are also indications that while cracking sessile oysters generally appear to emerge before cracking unattached food items, as would be expected because of the different levels of complexity in the required action sequences for the two tasks, even this is not true for all individuals. The first successful tool use of juvenile, Chk, was pound hammering of a *Planaxis sulcatus* snail. During this time, I observed him attempting to axe hammer sessile oysters unsuccessfully, striking all over the oyster-covered rock, appearing not to aim at any particular oyster target. His first successful axe hammering of oysters was observed later, and he began to target one oyster at a time. This raises the possibility that in addition to mastering accurate striking, another difficulty that some macaques face when learning how to crack sessile oysters could be in identifying individual oysters or focusing the attention on single oysters at a time, since oysters often grew in tight clusters or beds.

Also in relation to individual variation in mastering axing and pounding, one adult female, Nms, was never observed to carry out axe hammering on oysters. However, she did use tools on unattached foods and the way in which she cracked these foods appears to reflect incomplete development. Recall that juveniles attempt the sequence of pound hammering (take food and stone, place food on anvil, crack with stone) in several erroneous ways during development, one of which being taking a stone and food item, placing the food item in contact with the underside of the handheld stone, and attempting to bring both objects down onto the anvil simultaneously. While other individuals develop the typical sequence, Nms always cracks unattached foods using this action pattern, but appears to have refined it such that she is effective with this technique. These variations in individual macaques' ontogenetic trajectories highlight that tool-use learning is subject to other influences apart from species-typical perception-action routines and maturation of physical, neurological, and cognitive systems.

Investigations into the social influences on macaque tool-use development could be particularly illuminative to the aims of explaining inter-individual variation in developmental processes and outcomes. Studies conducted under natural settings have shown that both capuchin and chimpanzee young spend time in close proximity to tool users, attending both to tool users' behaviour and the products of their tool use (Biro et al., 2003; Biro et al., 2006; Coelho et al., 2015; Resende, Izar, & Ottoni, 2004; Matsuzawa et al., 2001; Ottoni, Resende, & Izar, 2005). These social interactions around tool use allow young individuals to gain more detailed information about the food types being processed, and the objects and action sequences involved in tool use. As such, each individual's pattern of social relationships and interactions with different tool users during the

formative stages of tool-use behaviour could influence its exposure to different food types, different tools, and different tool use actions, explaining the variation in developmental processes. In the chapters following, I investigate the influences of social interactions and relationships on developmental outcomes and the patterning of tool use behaviour in the Koram Island population.

CHAPTER 3:

PATTERNS OF SOCIAL-LEARNING INTERACTIONS WITH TOOL-USING GROUP MEMBERS OVER DEVELOPMENT

Introduction

In this chapter, I examine the social processes in the ontogeny of macaque tool-use skills starting with the ways in which naïve macaques may directly acquire tool-use-related information from skilled individuals through their interactions. Investigating how and which individuals interact allows examination of the likelihood and pathways of behavioral transmission, which can be more informative than using proxies of learning opportunities such as the size of foraging parties (Sanz & Morgan, 2013). Examining the types of interactions that animals engage in, can identify psychological mechanisms of social learning that may be involved in social information transmission in different species and contexts (Heyes, 1994; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004), or whether interactions would promote behavioral similarity or variation in a social group (Coussi-Korbel & Frigaszy, 1995). Documenting how these interactions change as individuals mature in age and competency can further contribute to understanding the skill-development processes, by informing explanations for ontogenetic phenomenon such as critical periods and the cessation of learning (Biro, Sousa, & Matsuzawa, 2006). Finally, examining how the characteristics of interaction partners such as dominance rank, sex, age, sociality, and expertise, influences and directs interactions unequally towards different individuals can reveal the likely pathways through which cultural information diffuses in different animal groups (Coussi-Korbel & Fragaszy, 1995; Huffman & Hirata,

2003), as well as strategies that individuals may use in their choice of social-learning interaction partners (Galef, 2009; Laland, 2004).

Young primates interact extensively with mature conspecifics in foraging contexts, especially before they learn species-typical diets and acquire the skills necessary for obtaining and processing foods (King, 1994; Rapaport & Brown, 2008). Young individuals maintain proximity with experienced individuals during foraging, and some may sync their feeding times and foraging locations, or “co-feed” on the same foods with older individuals (King, 1994; Schiel & Huber, 2006; Ueno & Matsuzawa, 2005; Whitehead, 1986). By staying close to foraging conspecifics, young individuals increase opportunities for obtaining food from mature conspecifics by scrounging discarded portions of food, taking food directly from foragers, or soliciting active food donations from adults by begging (Brown, Almond, & van Bergen, 2004; Rapaport & Brown, 2008). These associative interactions with knowledgeable group members during foraging therefore provide young primates with opportunities not only to gain nutritional benefits, but also acquire information about what foods to eat, and where and how to obtain them, with lesser need for lengthy and potentially dangerous exploration on their own (Galef & Giraldeau, 2001; Rapaport, 1999).

When obtaining food requires tool use, such interactions may be even more important, as foraging proficiency on tool-processed foods not only requires learning about the food items, but also about tools, object combinations, and action sequences, which requires a long period of learning and development. Scrounging or soliciting food from proficient tool users might be the only way that immature individuals can gain access to food that they are not yet able to extract or process. In addition to scrounging

and soliciting food, associating and interacting with tool users also exposes immature individuals to the tools and action sequences involved in the tasks. These exposures allow immatures to associate tools and actions with food rewards, which could encourage them to persist through multiple failures during the protracted tool-use learning process (Biro et al., 2006; Boesch, 2013; Sanz & Morgan, 2007). Studies of the interactions between naïve immatures and skilled tool users in tool-using chimpanzee and capuchin populations have documented that young individuals closely observed tool users, and obtained food predominantly via scrounging (Biro et al., 2003; Biro et al., 2006; Boesch & Boesch-Achermann, 2000; Coelho et al., 2015; Lonsdorf, 2005; Matsuzawa et al., 2001; Ottoni, Resende, & Izar, 2005), and more rarely by infants begging and adults actively or passively permitting food transfers (Boesch & Boesch-Achermann, 2000; Brown et al., 2004).

Immatures appear to interact with older individuals for more than just food rewards, as interactions that seem to focus on tools and tool-use actions have also been documented. At Bossou, where chimpanzees use stone tools for nut-cracking and leaf tools for drinking water from tree holes, infant chimpanzees touch anvils and tools while these are being used by their mothers for nut cracking and sometimes hold her arm as she hammers. Newly competent juveniles also scrounged adults' tools and tool sets, moving in to crack nuts with adults' hammers and anvils once the adult had walked away. Similar behaviours have been recorded in leaf-sponging interactions, where juveniles scrounge and use abandoned leaf sponges before they could make their own, and younger infants take leaf sponges from their mothers' hands for their own use during drinking bouts (Biro et al., 2006). The general pattern that emerges from these documented interactions, is thus

that primate infants actively and deliberately seek foraging information from experienced conspecifics, and are responsible for initiating the large majority of social interactions and information transfers (King, 1991, 1994; Rapaport & Brown, 2008).

Despite the consensus that young primates are agents of their own learning by initiating interactions with knowledgeable group members, there have been few direct investigations into whether young primates are strategic in terms of when, and from which group members they should preferentially seek information in order to optimize the nutritional and informational benefits of their interactions (Coelho et al., 2015; Laland, 2004). Several theoretical strategies have been proposed as to when, and from whom, individuals should socially learn (Galef, 2009; Laland, 2004). These are mostly based on theoretical economic payoffs associated with scrounging versus producing and copying versus self-exploration (Feldman, Aoki, & Kumm, 1996; Giraldeau & Beauchamp, 1999; Laland, 2004). A subset of these theories have been investigated using experiments and observations on animals such as flock-foraging birds (Giraldeau & Lefebvre, 1986; Lefebvre & Giraldeau, 1994; Templeton & Giraldeau, 1996) and schooling fish (Lachlan, Crooks, & Laland, 1998; Swaney, Kendal, Capon, Brown, & Laland, 2001), but empirical examinations in natural settings, and with a wider range of species is still lacking (Laland, 2004). The development of foraging interactions between naïve young primates and their experienced elders, offers several opportunities to further test the predictions of theoretical social learning strategies.

With regards to “when” individuals should learn from others, two related strategies proposed are that they should “copy when established behaviour is unproductive” (Laland, 2004) and “copy when asocial learning is costly” (Boyd &

Richerson, 1985; Feldman et al., 1996; Laland, 2004). Under these strategies, individuals would utilize socially-mediated ways of obtaining food or information when their own capabilities are inadequate, or when attempting to do so solely via individual learning and exploration is too time consuming or risky. These have been supported by observations of the extensive interactions that take place under tool-use contexts, since young individuals will be most incompetent when difficult tool-use tasks are involved. Further observations of the foraging interactions of several other primate species also show that interactions increased with foraging difficulty or risk. For example, infant howler monkeys co-fed more with adults when they were feeding on leaves as compared to fruits, purportedly because the former contains higher levels of toxins (Whitehead, 1986), and young baboons co-fed with mother more often when she was feeding on underground corms that young baboons could not yet dig up for themselves (King, 1994). Juvenile orangutans (Jaeggi, van Noordwijk, & van Schaik, 2008) and chimpanzees (Nishida & Turner, 1996; Silk, 1978), more often solicited foods that were difficult to acquire or process such as fruit that are defended by hard shells or thorns, while young white-faced capuchins observed more when conspecifics fed on foods requiring multi-step processing (Perry & Ordonez-Jimenez, 2006). Another prediction that can be drawn from these theoretical strategies, is that young primates' foraging interactions with experienced conspecifics should be more frequent or qualitatively different in early development when their own foraging behaviours are the least productive, and decrease as they become more capable foragers. In a tool-use context, this can happen when young individuals gain competence in tool use, allowing them to obtain whole foods, instead of scraps they obtain by scrounging from other tool users. Older individuals are also most tolerant of younger

infants and juveniles (Biro et al., 2003; Matsuzawa et al., 2001), and thus younger individuals have the most to gain from interacting, with the least risk of aggression.

In terms of “who” immature individuals direct learning interactions to, a robust finding across both primate and non-primate species is that individuals most often interacted with kin (Laland, 2004). This is explained most parsimoniously by the greater amounts of time that animals generally spend in close proximity to kin than non-kin. Most primate mothers are the primary caregivers to their infants and serve as the foremost model with which young individuals interact with during early experiences [e.g. chimpanzees (Biro et al., 2003; Biro et al., 2006; Boesch & Boesch-Achermann, 2000; Lonsdorf, 2006), orangutans (Jaeggi et al., 2008; van Noordwijk & van Schaik, 2005; van Schaik, Fox, & Fechtman, 2003), baboons (King, 1994), Japanese macaques (Nahallage & Huffman, 2007a)]. Patterns of dispersion and association during feeding, and ways in which certain food resources are distributed, may further limit the availability of interaction partners to mothers, kin, or close associates. For example, the sizes of orangutans’ foraging parties constrain the number of social partners that can provide opportunities for young orangutans to acquire tool skills (van Schaik et al., 2003). Also, amongst the chimpanzees of the Goualougo Triangle, termite nests are a clumped resource distributed through the home range, and the chimpanzees form smaller parties when feeding on termites than other food resources (Sanz & Morgan, 2007, 2013).

It has also been proposed that learners should “copy successful individuals” or those with “the most successful behaviour” (Laland, 2004). These strategies have rarely been directly tested as they imply the learner’s ability to evaluate the success of others, and the extent to which animals do so is unclear (Laland, 2004). Consequently, these have

mostly found indirect support, via evidence of related strategies such as “copy older individuals” (Kirkpatrick & Dugatkin, 1994; Laland, 2004). In the interactions surrounding tool use between young capuchins and chimpanzees and their group members, immature individuals showed strong biases towards observing tool users that were same aged or older, even though juvenile tool users may also be competent (Biro et al., 2003; Coelho et al., 2015). Presumably, older individuals are more proficient tool users given the lengthy amount of time it takes to refine tool-use skills (c.f. Chapter 2).

Tool-aided foraging provides a prime opportunity to directly evaluate the theoretical strategies that young individuals should preferentially interact with more successful or proficient tool users. Tool-use events are highly visible, and success and proficiency measures (e.g. whether or not a nut is cracked) can be more easily recorded than other foraging tasks (e.g. how much is ingested when feeding on leaves). However, only two studies on a single population of capuchin monkeys have directly investigated whether immature capuchins would more likely observe and scrounge from more proficient users. Both studies found that the more proficient and productive tool users were more often observed or scrounged from, and the authors attributed these findings to the possibility that scrounging from better tool users would lead to greater food payoffs (Coelho et al., 2015; Ottoni et al., 2005).

The tool-using long-tailed macaques on Koram Island are ideal for further examining the strategies that young primates may use in their foraging interactions, particularly in terms of “who” to interact with. The large group size means that young macaques have numerous tool-using models of different ages, sexes, and levels of proficiency, and with whom they have different levels of social association, facilitating

the testing of the different “who” strategies. Furthermore, the oysters and other shellfish that they process with tools are distributed fairly continuously along a relatively flat shore, so the group does not segregate into discrete foraging parties. This means that young macaques can potentially interact with most or all of the group’s tool users during foraging.

My objectives were therefore twofold. Firstly, to better understand a process by which tool-use learning could be socially transmitted in macaques, I characterized the interactions between non-tool users and skilled individuals, determining the types and relative prevalence of interactions macaques carry out, and how these differed between tool-use-naïve macaques at different ages. Secondly, to examine whether and how macaques strategically exploit social information, I tested for factors that influenced non-tool users’ choices of tool-user interaction partners. I made several predictions based on theoretical social learning strategies and findings regarding interactions around foraging and tool use in other primates. From the strategy “copy when established behaviour is unproductive”, I predicted that the youngest macaques would interact with skilled individuals most frequently, since they would be the least capable of obtaining food on their own, compared to older juveniles who had begun to develop tool-use skills or recently achieved competency. I also examined qualitative differences in the types of interactions that different aged macaques carried out. In terms of strategies regarding “who” macaques would preferentially direct interactions to, I examine whether tool users’, age, sex, dominance rank, and proficiency in tool use, and patterns of social affiliation and kinship influenced which tool users were more often interacted with by tool-naïve individuals. I predicted that like other primates, macaques would interact

preferentially with kin or closer social associates, and in particular with females, given the female philopatric social structure of long-tailed macaques. I also predicted that macaques would preferentially interact with older tool users and more proficient tool users, and examine what measures of tool-use proficiency influence macaques' choices of interaction partners. I discuss possible reasons for the observed relationships, and what these might imply about the learning strategies of macaques, and the social transmission of macaque tool-use behaviour.

Methods

Data Collection and Scoring

Data was collected within the same focal sampling protocol described in the preceding chapter. In addition to the general activity budget, object manipulation, and tool-use behaviours already explained in the preceding chapter, I also recorded all events in which the focal individual interacted with a tool-user in the midst of tool use, or the immediate products created during tool use, which are newly discarded food debris and tools. Henceforth, I refer to these interactions as tool-related interactions (TRI) to distinguish them from other social interactions (e.g. grooming). I recorded how individuals interacted with tool users or tool-use products, to create an ethogram of TRI behaviour (Table 3.1). For each TRI, I recorded the interaction type, the duration of each interaction, the identity of the tool user target, and the distance at which the focal individual was interacting with the tool-using target (within 1m, within 3m, or further than 3m). In some cases, focal individuals scrounged freshly cracked oysters from further than 3m to several tool users, making it difficult to determine the interaction partner, and I scored the tool user's identity as "unknown". If the focal individual entered within 1m to

the tool user, but supplanted the tool user from the tool site, these cases were scored as “supplant” instead of a distance measure.

Table 3.1

Descriptions of tool-related interaction behaviours

Interaction Type	Description
Observe closely	Gaze focused on tool user from within 3m
Scrounge Food	Retrieves and eats food abandoned or discarded by the tool user
Scrounge Tool	Retrieves and uses or manipulates a tool abandoned by the tool user
Reach	Stretch hand out towards a food item or tool being held by the user
Touch Food	Makes contact with a food item being processed, consumed, or held by the tool user.
Touch Tool	Makes contact with a tool being used or held by the tool user
Take Food	Takes over possession of a food item being processed or held by the tool user
Take Tool	Takes over possession of a tool being held by the tool user

In addition to recording and scoring TRIs, I also collected social data for determining patterns of social affiliation and the dominance hierarchy of the group. During focal samples, I recorded proximity and grooming associations, i.e. whenever the focal individual became and ceased to be within 1m of any other individuals, as well as the starts and ends of all grooming interactions involving the focal individual, also recording the identities of all proximity and grooming partners. I also made ad libitum observations of the subgroupings of individuals during times at which the group was predominantly engaged in rest or social affiliative (e.g. grooming, huddling) activities, particularly in the evening hours prior to roosting, as well as which individuals consistently affiliated with or around the same juveniles. I used this information to infer

kinship relations, as has previously been done with long-tailed macaques (Gumert, 2010). Lastly, I recorded ad libitum, all outcomes of agonistic and dominance related interactions (i.e. fights, supplants, submissions, and fear grins), in order to determine the dominance hierarchy of the group.

Analyses

Describing Tool-Related Interactions across Age Classes

To examine and describe age-related differences in tool-related interactions, I reclassified the macaques from the seven-group age classification used to examine the development of manipulative behaviour and tool use, into three groups. These were infants ($n = 19$; comprising individuals from Age Groups 1-2, below 1.5 years), juveniles ($n = 14$, Age Groups 3 and 4, 1.5 – 3.5 years), and adolescents and adults ($n = 35$; Age Groups 5 to 7, older than 3.5 years). I chose these age classifications based on the findings obtained in the preceding chapter, of how object-manipulation and tool-use behaviour changed over development, in order to test the hypothesis that naïve individuals' interactions with skilled group members change as their own tool skills develop.

I used Kruskal-Wallis H tests with Dunn's post-hoc tests to examine differences between the tool-related interactions in the three age classes in terms of a) the proportion of focal time spent on tool-related interactions, b) the rate of tool-related interactions carried out per minute, c) the average duration of tool-related interactions, d) the proportions of individuals' tool-related interactions that were observing, or e) scrounging, and f) the proportions of individuals' tool related interactions that were carried out from within 1m proximity to the tool user.

Identifying Factors that Influence Choice of Interaction Targets

Data Matrices

Tool-Related Interaction Matrices. I built directed interaction matrices based on the relative frequencies of non-tool users' choices of tool-user interaction partners (Appendix 2). In these matrices, cell values represent the frequency that individuals in the rows (non-tool users) interacted with individuals in the columns (tool users), as a percentage of the total frequency of tool-related interactions carried out by individuals in the row, obtained from focal samples. Separate rectangular matrices were built based on the ages of non-tool users (i.e. individuals in the rows). Since only tool users could be the targets of tool-related interactions, individuals in the columns of both matrices were all tool users ($n = 28$). In the first matrix, individuals in the rows were infants and juveniles below the tool-using age ($n = 27$). This matrix will be referred to as the "immature x user" matrix. In the second matrix, individuals in the rows were individuals that had reached tool-using age, i.e. above 2.5 years, but were not tool users ($n = 12$). This matrix will be referred to as the "mature non-user x user" matrix. In both matrices, individuals that did not carry out tool-related interactions were excluded from the rows of the matrices.

Matrices of Tool-Users' Attributes and Tool-Use Characteristics. I built corresponding "immature x user" and "mature non-user x user" matrices of tool-users' attributes, as well as of their tool-use characteristics (Appendix 2). In these matrices, cell values refer to the tool user (i.e. individuals in the columns) and not to dyads, therefore, the same values were assigned throughout each column.

Tool-users' demographic attributes examined were age, sex, and rank. In the age matrix, cells contained the tool user's age grouping, based on the seven-group classification. Since only individuals from age groups 4 to 7 used tools, cells contained either a 4, 5, 6, or 7, from youngest to oldest. In the sex matrix, males were assigned a value of 1, and females were assigned a value of 2. In the rank matrix, cells contained a 1 or 0 value, corresponding to whether the tool user (i.e. column individual), ranked higher or lower than the focal individual (i.e. row individual), or its mother, in the case of the immature x user matrix. I used mothers' ranks for immatures since on their own (i.e. without mothers' support during conflicts), they would be subordinate to the majority of older individuals. Relative ranks were based on the dominance hierarchy constructed using the outcomes of observed dyadic fights, supplants and submissions. Although I did not observe all dyads in dominance interactions, I could infer the ranks of all individuals because of the linear and transitive nature of the macaque hierarchical structure (i.e. if A is dominant to B, and B is dominant to C, then A is dominant to C), and the "youngest ascendency" pattern through which females acquire ranks just below their mothers but above older siblings (van Noordwijk & van Schaik, 1999).

Tool-use characteristics examined were measures of tool-users' productivity, i.e. measures of amounts of foods cracked, in terms of a) their proportion of foraging time spent using tools, and b) their rate of tool use in bouts per minute, as well as their tool-use proficiency in terms of c) strike efficiency, d) strike accuracy, e) tool fidelity, and f) their proportion of successful tool use bouts (explained in Chapter 2). These proficiency measures were chosen based on results of the preceding chapter, because these characteristics were found to improve over tool-use development.

I calculated proficiency measures c) to e) only separately for tool-related interactions and tool-use bouts carried out on sessile oysters and unattached foods, as these characteristics differed depending on whether tool use was being carried out on sessile oysters or unattached foods placed on anvils. Since tool use on unattached food was far less prevalent than tool use on sessile oysters, tool-related interactions carried out with tool users processing unattached foods were also less prevalent. Also, not all tool users processed unattached food. Amongst mature non-tool users, only 4 individuals interacted with users processing unattached foods, and only on single occasions. I therefore carried out matrix analyses involving unattached food interactions only between immature non-tool users who interacted with tool users processing unattached food ($n = 13$), and tool users with more than 10 bouts of tool use ($n = 18$).

Social Relationship Matrices. I built three different types of social relationship matrices, proximity-based association matrices, grooming-based association matrices, and inferred kinship matrices. In the proximity-based association matrices, cell values represent a proximity association index for each dyad, based on the amount of time that individuals spent within 1m to each other, and is equal to the total amount of time that individual A (in the row) and the individual B (in the column) spent in proximity, divided by the summed focal times of A and B. In the grooming-based association matrices, cell values represent a grooming association index for each dyad, and is equal to the total amount of time that individual A and individual B spent grooming each other, divided by the summed non-foraging focal time of A and B. Lastly, in the inferred kinship matrices, cell values of 1 are assigned to dyads that are inferred to be kin, based on observations of

how individuals consistently grouped during resting and pre-roosting arrangements and affiliation around juveniles, and cell values of 0 are assigned to non-kin dyads.

Testing Matrix Correlations. I first used Tau K_r tests for correlation between matrices (Hemelrijk, 1990a, 1990b), using the Matrix Tester add in for Microsoft Excel (Hemelrijk, 2015). I correlated the “immature x user” and “mature non-user x user” matrices of tool-related interactions with the corresponding matrices of social relationships, and tool users’ attributes and tool-use characteristics. Since I was interested in examining if macaques chose interaction partners based on more than social affiliations, I conducted partial Tau K_r tests to control for the effects of social relationships on partner choice when analyzing correlations between partner choice and tool-users’ attributes and tool-use characteristics. Probability for all tests was based on 10000 permutations. Sample size for tests involving immature individuals and tool users was 55, while sample size for tests involving mature non-users and tool users was 40 for analyses involving social relationships, tool user attributes, and tool-users’ proficiency measures on sessile oysters, and 31 for analyses involving tool-users’ proficiency measures on unattached food.

Results

Tool-Related Interactions across Age Classes

I recorded a total of 1280 tool-related interactions carried out by 51 individuals during their focal samples ($M = 19$, $SD = 22.51$, range = 0 – 81 interactions/individual). Tool-related interactions were most prevalent in the infant and juvenile age classes, with 100% of infants and juveniles, but only 48.6% of adolescents and adults, recorded to carry out tool-related interactions. Macaques in different age groups carried out tool-related interactions at different rates ($H = 32.65$, $p < 0.001$). Infants ($M = 4.28$, $SD = 2.46$ bouts/min; $t = 4.75$, $p < 0.001$) and juveniles ($M = 4.23$, $SD = 2.50$ bouts/min; $t = 4.53$, $p < 0.001$), carried out tool-related interactions at a higher rate than adults ($M = 1.48$, $SD = 1.21$ bouts/min) (Figure 3.1a). Macaques in different age groups also spent different proportions of their foraging time carrying out tool-related interactions ($H = 31.70$, $p < 0.001$), with infants ($M = 0.13$, $SD = 0.08$; $t = 5.06$, $p < 0.001$) and juveniles ($M = 0.10$, $SD = 0.06$; $t = 3.96$, $p < 0.01$) spending a larger proportion of foraging time carrying out tool-related interactions than adults ($M = 0.04$, $SD = 0.04$) (Figure 3.1b). Lastly, the duration of tool-related interaction bouts carried out by macaques in different age groups differed ($H = 13.81$, $p = 0.001$). Interaction bouts carried out by infants ($M = 72.62$ s, $SD = 62.79$ s; $t = 2.66$, $p = 0.02$) and juveniles ($M = 82.06$ s, $SD = 49.95$ s; $t = 3.31$, $p = 0.003$) lasted longer than those carried out by adults ($M = 72.48$ s, $SD = 50.50$ s) (Figure 3.1c).

Figure 3.1 Kruskal-Wallis H tests found differences between macaques of different age groups in the a) rates of initiating tool-related interactions, b) proportions of foraging time spent interacting with tool users, and c) the average durations of their interactions. Dunn's post-hoc tests showed which age groups significantly differed. Letters are used to denote statistical significance, such that significantly different age groups do not share letters. Error bars represent one standard error of the mean.

Scrounging from tool users was the predominant type of tool-related interaction, although the composition of tool-related interaction behaviours were different in different age groups (Figure 3.2). All individuals that carried out tool-related interactions scrounged food, and on average, scrounging occurred in 93% of individuals' tool-related interaction bouts. Infants scrounged food in a lower proportion of their tool-related interactions ($M = 0.83$, $SD = 0.20$) than juveniles ($M = 0.95$, $SD = 0.07$; $t = -2.42$, $p = 0.047$) and adults ($t = -4.98$, $p < 0.001$). The tool-related interactions of adults consisted only of scrounging. Juveniles and adults were not found to differ significantly.

Observing tool users was the next most common type of tool-related interaction, occurring in an average of 15% of infants' and juveniles' tool-related interaction bouts. In addition, infants and juveniles differed in the proportion of tool-related interactions in which they observed ($H = 28.10$, $p < 0.001$), and scrounged from ($H = 24.88$, $p < 0.001$) tool users. Infants observed tool users in a higher proportion of their tool-related interactions ($M = 0.21$, $SD = 0.18$) than both juveniles ($M = 0.06$, $SD = 0.09$; $t = 2.79$, $p = 0.02$) and adults ($t = 5.23$, $p < 0.001$) (Figure 3.2). Adults did not observe. Juveniles and adults were not found to differ significantly.

Other types of interactions were less prevalent. Infants and juveniles touched tools while tools were still being held by the users in an average of 3% of bouts. Sniffing tool user's mouths, reaching for tools and food items, taking food from users, touching food being held or consumed by tool users, and scrounging to manipulate tools just discarded by tool users all occurred in less than 1% of infants' and juveniles' interaction bouts. Infants ($M = 0.67$, $SD = 0.09$) carried out these types of interactions in a higher proportion of their bouts ($H = 18.07$, $p < 0.001$) than both juveniles ($M = 0.01$, $SD = 0.01$;

$t = 11.59, p = 0.02$) and adults who did not carry out these interactions ($t = 16.23, p < 0.001$). Juveniles and adults did not significantly differ.

Figure 3.2 Scrounging was the predominant type of tool-related interaction across all age classes, however, infants and juveniles also observed, and carried out other types of interactions with tool users (see Table 3.1), whereas adolescents and adults only scrounged. Kruskal-Wallis H tests found differences in the proportion of tool-related interactions in which infant and juvenile macaques scrounged, observed, and carried out other types of interactions. Dunn post-hoc tests were showed which age groups differed significantly, as denoted by letters, such as significantly different age groups do not share letters. Error bars represent one standard error of the mean.

There were differences between age groups in their proximity to the tool user while carrying out tool-related interactions (Figure 3.3). On average, 40% of individuals' tool-related interactions were carried out within 1m of the tool user, 9% from within 3m to the tool user, while 33% were carried out from more than 3m away from the tool user, and 19% of tool-related interactions were carried out by supplanting the tool user then

scrounging cracked food items. Macaques in different age groups differed in the proportion of their tool-related interactions that were carried out within 1m proximity to tool users ($H = 24.72, p < 0.001$), 3m proximity to tool users ($H = 8.04, p = 0.02$) and by supplanting the tool user ($H = 24.88, p < 0.001$). Infants carried out tool-related interactions in 1m proximity to tool users in a higher proportion of bouts ($M = 0.67, SD = 0.24$) than both juveniles ($M = 0.31, SD = 0.24; t = 3.22, p = 0.004$) and adults ($M = 0.17, SD = 0.17; t = 4.83, p < 0.001$), while juveniles ($M = 0.13, SD = 0.10$) carried out their interactions within 3m to the tool user in a higher proportion of bouts than infants ($M = 0.03, SD = 0.04; t = 14.08, p = 0.01$). Conversely, adults ($M = 0.43, SD = 0.33; t = 4.98, p < 0.001$) and juveniles ($0.13 \pm 0.15; t = 2.47, p = 0.04$) supplanted then scrounged from tool users in a higher proportion of tool-related interactions than infants ($M = 0.01, SD = 0.02$).

Figure 3.3 Tool-related interactions were carried out from within 1m proximity to the tool user particularly in infants, while adults' tool-related interactions were composed of a larger proportion of interactions in which the tool user was supplanted. Kruskal-Wallis H tests found differences in the proportions of tool-related interactions that were carried out within 1m and 3m to the tool user, and carried out by supplanting then scrounging from the tool users. Dunn post-hoc tests showed which age groups differed significantly, as denoted by letters, such as significantly different age groups do not share letters. Error bars represent one standard error of the mean.

Factors Influencing Choice of Interaction Targets

Social Relationships

Both immature and mature non-tool users more often interacted with tool users that were also closer social associates. Proximity-based matrices correlated with directed interaction matrices in both ages (immature x user: $\text{Tau } K_r = 0.37, p_r < 0.001$; mature non-user x user: $\text{Tau } K_r = 0.21, p_r < 0.001$) (Figure 3.4a), as did grooming-based association matrices (immature x user: $\text{Tau } K_r = 0.27, p_r < 0.001$; mature non-user x user: $\text{Tau } K_r =$

0.15, $p_r = 0.01$) (Figure 3.4b). In addition, the inferred kin matrix correlated with the tool-related interaction matrix in the immature x user analysis (Tau $K_r = 0.29$, $p_r < 0.001$), but not in the interactions of mature non-tool users (Figure 3.4c).

Demographic Attributes of Tool Users

Tool users' sex related to both age categories of non-tool users' TRI partners (Figure 3.5a). Females were more often interacted with by both immature and mature non-tool users (immature x user: Tau $K_r = 0.18$, $p_r = 0.02$; mature non-user x user: Tau $K_r = 0.17$, $p_r = 0.02$). To further examine whether females might be more often interacted with because they used tools more often, or because they had stronger social relationships with the non-tool users, I used partial Tau K_r tests to partial out the effects of tool users' proportions of foraging time spent on tool use, and social relationship matrices. The correlation between the tool-related interaction and sex matrices continued to be significant when the time-in-tool-use matrices were partialled out (immature x user: partial Tau $K_r = 0.20$, $p_r = 0.01$; non-user x user: partial Tau $K_r = 0.18$, $p_r = 0.01$). The effect of tool users' sex on the choice of interaction targets by mature non-tool users retained significance after grooming relationships were partialled out (partial Tau $K_r = 0.14$, $p_r = 0.04$), but not when other social relationships were partialled out. Tool user's sex had no relationship with the immature macaques' interaction targets after social relationships were partialled out. The bias towards female tool users therefore appears to be a product of social structure and relationships.

Tool user's age influenced immatures' interaction targets, but was not related to mature non-users' interactions. Older tool users were more often interacted with by immature non-users (Tau $K_r = 0.17$, $p_r = 0.02$) (Figure 3.5b), including when possible

differences in the time that younger and older tool users spent on tool use was partialled out (partial Tau $K_r = 0.13$, $p_r = 0.048$).

Tool user's rank saw the opposite effect, being significantly associated with mature non-users' interactions with tool users, but not with immatures'. Mature non-users more often scrounged from lower-ranked tool users (Tau $K_r = -0.23$, $p_l = 0.001$) (Figure 3.5c). These rank effects were not due to the findings that mature non-users scrounged more from females (partial Tau $K_r = -0.16$, $p_l = 0.01$), even though females generally ranked lower than mature males.

Tool Use Characteristics and Proficiency

More productive tool users, as measured by their proportions of foraging time spent using tools (Figure 3.6a) and rate of tool use (Figure 3.6b), were more often interacted with during tool-related interactions. Tool users that spent more time using tools were more often interacted with by both age groups of non-tool users. Tool-related interaction matrices correlated significantly with time-in-tool-use matrices (immature x users: Tau $K_r = 0.20$, $p_r = 0.002$; mature non-user x user: Tau $K_r = 0.14$, $p_r = 0.02$). Tool users that carried out tool use at a higher rate were also more often interacted with by both groups of non-users (immature x user: Tau $K_r = 0.16$, $p_r = 0.01$; mature non-user x user: Tau $K_r = 0.19$, $p_r = 0.001$).

I conducted further partial Tau K_r tests to rule out the possibility that these were spurious correlations with social relationships. These revealed that correlations between tool users' productivity measures and how often they were chosen as interaction targets were still significant for both measures of productivity and both age groups, when each

social relationship measure was partialled out; [time in tool use - proximity (immature x user: partial Tau $K_r = 0.16$, $p_r = 0.01$; mature non-user x user: partial Tau $K_r = 0.13$, $p_r = 0.03$), grooming, (immature x user: partial Tau $K_r = 0.21$, $p_r = 0.002$; mature non-user x user: partial Tau $K_r = 0.13$, $p_r = 0.02$), inferred kinship (immature vs user: partial Tau $K_r = 0.22$, $p_r = 0.001$; mature non-user vs user: partial Tau $K_r = 0.14$, $p_r = 0.02$)] and [rate of tool use - proximity (immature x user: partial Tau $K_r = 0.12$, $p_r = 0.003$; mature non-user x user: partial Tau $K_r = 0.17$, $p_r < 0.001$), grooming (immature x user: partial Tau $K_r = 0.17$, $p_r = 0.003$; mature non-user x user: partial Tau $K_r = 0.17$, $p_r < 0.001$), and inferred kinship matrices (immature x user: partial Tau $K_r = 0.17$, $p_r = 0.01$; mature non-user x user: partial Tau $K_r = 0.19$, $p_r = 0.001$)].

On sessile oysters, two measures of tool-use proficiency were also found to influence which tool users were more often interacted with. Tool users with higher strike efficiencies on oysters, i.e. requiring fewer strikes on average to crack open oysters, were more often interacted with during TRIs (immature vs user: Tau $K_r = -0.18$, $p_1 = 0.004$; mature non-user vs user: Tau $K_r = -0.20$, $p_1 < 0.001$) (Figure 3.7a). These significant correlations held when proximity (immature x user: partial Tau $K_r = -0.13$, $p_1 = 0.03$; mature non-user x user: partial Tau $K_r = -0.17$, $p_1 = 0.005$), grooming (immature x user: partial Tau $K_r = -0.15$, $p_1 = 0.01$; mature non-user x user: partial Tau $K_r = -0.19$, $p_1 < 0.001$), and inferred kinship (immature x user: partial Tau $K_r = -0.17$, $p_1 = 0.01$; mature non-user x user: partial Tau $K_r = -0.21$, $p_1 < 0.001$) matrices were partialled out. The preference for immature macaques to interact with tool users with higher strike efficiencies was also still significant after controlling for their preference for older tool users (partial Tau $K_r = -0.15$, $p_1 = 0.02$), even though older users may be more strike

efficient. Mature non-tool users also more often chose to scrounge from tool users with a higher proportion of successful tool-use bouts (Tau $K_r = 0.12$, $p_r = 0.03$) (Figure 3.7b), a correlation that was also significant when proximity (partial Tau $K_r = 0.12$, $p_r = 0.04$), grooming (partial Tau $K_r = 0.12$, $p_r = 0.04$), and inferred kinship (partial Tau $K_r = 0.13$, $p_r = 0.03$) matrices were partialled out.

On unattached foods, immatures interacted more often with tool users that had higher strike accuracies (Tau $K_r = 0.16$, $p_r = 0.01$), and higher proportions of successful tool-use bouts (Tau $K_r = 0.16$, $p_r = 0.02$). However, these correlations were no longer significant after social relationship matrices were partialled out.

Figure 3.4 Social relationships were associated with non-tool-using macaques' choices of tool users to interact with. a) Proximity-based and b) grooming-based association indices with tool users correlated positively with the proportions of bouts in which immature and mature non-tool-using macaques interacted with tool users. In addition c) immature, but not mature, macaques interacted with inferred kin tool users in a higher proportion of their TRI bouts.

Figure 3.5 Demographic attributes of tool users were associated with non-tool-users' choice of tool-users for TRI. a) Females were more often chosen as targets of interactions by both age classes although this was not significant for immatures after social relationships were partialled out in matrix analyses. b) Immature non-tool-using macaques more often interacted with older tool users, while c) mature more often interacted with lower-ranked tool users.

Figure 3.6 Tool users that were more productive in terms of the a) proportions of foraging time they spent using tools and b) rate of tool use, were more often interacted with by non-tool-using macaques.

Figure 3.7 Tool users that were more proficient in terms of a) strike efficiency, i.e. requiring fewer strikes to crack food items, were more often interacted with by both immature and mature non-tool users, while b) mature non-tool users also more often scrounged from tool users with a higher proportion of successful tool-use bouts.

Discussion

Age-related differences in tool-related interactions by the macaques of Koram Island support the predictions that younger and less competent individuals would interact with skilled group members more intensely, according with theoretical “copy when established behaviour is unproductive” strategies. Not only did infants and juveniles interact with tool users more frequently and more often within closer proximity, they also carried out a wider range of different types of interactions than did adolescent and adult individuals. The interactions of adolescent and adults were limited to scrounging, and therefore appear to solely focus on obtaining food payoffs from conspecifics’ tool use behaviours. On the other hand, infants and juveniles also observed tool users, touched tools that were being held or used by them, and occasionally engaged in exploratory object manipulation with tools had just been abandoned by tool users. These types of interactions involving close physical proximity and “co-action” (e.g. touching tools while in use), have been demonstrated to be important for the process of learning techniques in experiments on captive chimpanzees (Horner, 2010). Thus, these qualitative changes in the nature of interactions carried out by different-aged macaques, suggest that tool-related interactions by older macaques, particularly those who had already passed the critical period for acquiring tool-use skills, no longer function to promote further learning, whereas younger macaques who were still developing tool skills actively initiated interactions that facilitate obtaining information about foods, tools, and tool-use behaviours.

The most striking difference in the types of tool-related interactions carried out by different-aged macaques appears to be in the proportions of interactions in which the actor

observed the tool using partner. Not only did infants and juveniles observe tool users significantly more than adolescents and adults who did not observe, the difference in observation was further significantly higher in infants than older juveniles. That the youngest infants carried out the most observations, even more than juveniles, could be developmentally linked to weaning and changes in nutritional independence. Although macaque infants begin to forage and consume solid foods within the first month of development, they continue to suckle their mothers up till about one year of age before their nutritional needs must be fully met through their own foraging efforts (Karssemeijer, Vos, & van Hoof, 1990; van Noordwijk & van Schaik, 1999, 2005). This early supplementation of infants' nutrition with their mother's milk, a high-protein food source, could reduce their urgency to obtain tool-processed marine foods, and they can spend more time observing tool users rather than scrounging, facilitating the learning of foraging skills in early infancy. Similar links between the cessation of milk-provisioning with the scrounging and food-sharing of hard-to-process food has been suggested in chimpanzees (Corp & Byrne, 2002).

Cognitively, observation may play a heightened role in the learning of tool-use actions compared to other types of tool-related interactions. Neuroimaging studies have found that mirror neurons in macaque brains are activated both when performing an action or observing an action being performed (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996), and furthermore, there are "tool-responding mirror neurons" that respond even more strongly to actions with tools versus actions alone (Ferrari, Rossi, & Fogassi, 2005). These findings suggest a neural basis for observing tool use actions and later being able to produce them, implicating neural circuits in the observational learning and social

transmission of tool-use skills (Johnson-Frey, 2004). It would then be interesting to examine if differences in observation behaviour during infancy influences the acquisition of tool-use actions (next chapter).

In comparison to capuchins and chimpanzees, scrounging appears to compose a higher proportion of young individuals' interactions with tool users, relative to observation and other types of interactions. Between macaques and chimpanzees, observing tool users occupied approximately 2% of focal time in infant and juvenile macaques, and 1 – 3 % of observation time in chimpanzees between 0.5 – 3.5 years of age (Inoue-Nakamura & Matsuzawa, 2007). However, opposite to what is observed here in macaques, tool-related interactions are described as predominantly observation, with scrounging occurring in only a proportion of these interactions in both capuchins (Coelho et al., 2015; Ottoni et al., 2005) and chimpanzees (Biro et al., 2003; Biro et al., 2006; Boesch & Boesch-Achermann, 2000; Matsuzawa et al., 2001). Furthermore, capuchin infants scrounged nuts more than older juveniles (Coelho et al., 2015), contrary to what is observed here in macaques. This contrast may be explained by ecological differences in the way tool-processed foods and tool-use sites are distributed in the species' respective habitats. Nut-cracking in capuchins and chimpanzees center around anvils which would allow the tool user to easily control the possession of cracked nuts. Those interacting with the tool user may not always have the opportunity to scrounge, and therefore, observation would precede, and scrounging would follow. On the other hand, macaques predominantly crack sessile oysters that are distributed continuously along the shore. They move from one patch to another, making it easier for non-tool-using macaques to follow along and scrounge the remains of cracked oysters. These possibilities highlight an

avenue for further investigating the factors that influence the types of interactions that learners in different species initiate with skilled individuals. For example, field or laboratory experiments can investigate the tendency towards observing or scrounging if opportunities to do so were equal. Consequently, this would contribute towards testing how behavioral and habitat ecologies can shape the types of learning and cultural transmission that can occur in different species and contexts (e.g. Meulman, Sanz, Visalberghi, & van Schaik, 2010).

Compared to what has been reported for capuchins, macaques' preferential interactions with tool users appear to correlate more strongly with social relationships. In the present study, I found that both young and mature non-tool users more often scrounged and/or observed tool users with whom they also spent more time in proximity or grooming. The choices of young macaques in particular, also reflected inferred kin relationships. This contrasts with the model choices of capuchins, which were found to not (Ottoni et al., 2005), or only weakly relate to patterns of social affiliation (Coelho et al., 2015). This comparison may reflect differences in the levels of tolerance in capuchin and macaque social systems. Capuchin societies are characterized by a high degree of tolerance, with food sharing occurring outside of the parent-offspring context and between unrelated adults (Fragaszy, Visalberghi, & Fedigan, 2004). In contrast, long-tailed macaque societies are notoriously intolerant, with a high degree of nepotism (Aureli, Das, & Veenema, 1997; Matsumura, 1999; Thierry, 1985). Thus, it may more adaptive for macaques to behave in accordance with "copy kin" or "copy friends" strategies (Laland, 2004), since these individuals are less likely to react aggressively to them scrounging or observing in close quarters, and more likely to share information (or food) for reasons of

inclusive fitness (Hamilton, 1964). However, it is possible that populations with tool-use traditions may be more tolerant than what is typical for long-tailed macaque groups, which could have facilitated social transmission of the behavior in the first place, and so this hypothesis must be more rigorously tested. Scrounging and learning from kin is hypothesized to also better facilitate social learning because relatives more likely share genes, characteristics, and environments that increase the probability that they experience and react to information more similarly, and therefore, learning may be more likely to occur from watching kin than non-kin (Boyd & Richerson, 1985; Boyd & Richerson, 1988; Laland, 2004). It is also partly for this reason that kin or close affiliates are expected to more likely develop behavioral similarity through social learning, and I investigate this in Chapter 5.

In addition to scrounging and observing closer social affiliates or kin, macaques also appear to discriminate tool users based on their productivity and proficiency. Non-tool users preferentially interacted not only with tool users that carried out higher rates of tool use, which is likely linked to more productive scrounging, but also with tool users who required fewer strikes to crack food items. Recall from the preceding chapter that mastering effective striking was a major challenge to macaques when developing tool use skills; these results therefore suggest that macaques might be sensitive to these challenges, and interact with tool users to optimize not only scrounging, but learning payoffs.

It is unclear if and how macaques keep track of the relative proficiencies of conspecifics and payoffs obtained from interacting with unequally proficient tool users, but the results provide some evidence of these capabilities. Mature non-tool users appeared to be more sensitive to the relative proficiencies of tool users than young

macaques, since tool users' proportion of tool-use success influenced the partner choices of older but not younger macaques. This suggests a role for experience in accumulating knowledge about group members' tool use skills to further enhance scrounging payoffs. Furthermore, the macaques' preferential selection of more skilled tool users appeared to go beyond heuristic strategies such as "copy older individuals", since age did not influence mature individuals' partner choices, and the choices of immature individuals still related significantly to productivity and proficiency measures after tool users' age was statistically neutralized. It has also been suggested that animals may use a heuristic strategy of copying higher ranked individuals to identify the most successful individuals from whom to scrounge or learn from (Laland, 2004). However, contrary to this, lower-ranked macaque tool users were more often supplanted and scrounged from by mature non-tool users, while tool users' ranks did not appear to influence which tool users were more often observed or scrounged from by tool-use-naïve young. This age-related difference thus provides further evidence that macaques' actively select tool users to interact with, in order to maximize possible payoffs in accordance with their developmentally-linked scrounging or learning goals.

In summary, the macaques of Koram Island appear to actively initiate interactions with tool users in accordance with their age-related learning or scrounging motivations. This is evidenced by the greater emphasis on observation and wider variety of tool-related interactions focused on exploring tools carried out by immature macaques, in contrast with the sole focus on scrounging by mature macaques that did not develop tool-use skills. In addition, their choices of interaction partners not only reflected social affiliative and kin relationships within the group, which may in itself be strategic, they were also

biased towards more productive and proficient tool users. Theoretically, these strategies would optimize the food payoffs and learning opportunities that macaques can gain from their interaction with tool users, however, it remains to be tested if and how individual differences in tool-related interaction behaviours would influence the development of tool-use skills in young macaques. The findings also imply that the social transmission of tool-use behaviour in macaques should occur primary through kin and closer social affiliates, which could be investigated by examining if relatives or affiliates show greater similarity in tool use behaviour. These questions will be the focus of the next two chapters of this dissertation.

CHAPTER 4:

**THE EFFECTS OF SOCIAL LEARNING OPPORTUNITIES ON
DEVELOPMENT**

Introduction

The preceding two chapters have described the developmental trajectory of macaque tool-use competence and proficiency in the Koram Island population, and strongly implicate the involvement of social influences in the developmental process. The ontogeny of tool-use skills is governed to some extent by physical and cognitive maturation, but individual macaques vary widely in the extent of their exploratory manipulative behaviour and the emergence of developmental achievements, with some individuals never developing tool-use ability. During development, young macaques scrounge from and observe skilled tool users, occasionally touching tools while in use, and exploring abandoned tools. These interactions by immature macaques differ from the purely scrounging behaviour of older non-tool users, suggesting that these early interactions function to support tool use learning. Macaques preferentially interact with more productive and proficient tool users which would optimize scrounging and learning payoffs; however, their interactions are also closely linked to kin and social affiliative relationships. This suggests that social factors would influence the amount and quality of learning opportunities available to each individual, which could be related to the variation in individuals' tool-skill development.

Opportunity for social learning is crucial for the establishment and spread of behavioral traditions in animal communities (Fragaszy & Perry, 2003; van Schaik,

Deaner, & Merrill, 1999). This has been demonstrated by variation in the presence and extensiveness of tool-use traditions in different populations of the same species. In orangutans for example, only the more gregarious Sumatran populations in which individuals form larger foraging parties exhibit tool-aided foraging traditions, presumably because individuals have greater opportunity to observe the foraging behaviour of others (van Schaik et al., 1999). Similarly, chimpanzees exhibit a wide and complex tool repertoire in Goualougo, where population density is highest (Meulman, Seed, & Mann, 2013). These effects are not restricted to primates, as a comparative analysis involving birds and mammals has also highlighted gregariousness as a major life history variable influencing cross-species variation in the age at which individuals acquire skill competence (Schuppli, Isler, & van Schaik, 2012). On a more micro, inter-individual level, differences in learning opportunities from various sources during the formative stages of skill development, might be evident in individual variation in speeds of skill acquisition or eventual proficiency (van Schaik et al., 1999; van Schaik, Fox, & Fechtman, 2003).

Mothers are thought to be a crucial and primary source of opportunities for learning a behavior during early development, especially in primates where offspring dependence on and close association with mothers is relatively protracted (Humle, 2011; Lonsdorf, 2006; Nahallage & Huffman, 2007; van Schaik & Pradhan, 2003). Mothers differ in the frequency and proficiency at which they carry out a behaviour, directly affecting the quantity and quality of infants' first exposures to the behaviour. Amongst chimpanzees, offspring of mothers at Bossou who spent more time ant-dipping developed competence earlier, also spent more time ant-dipping, and were more proficient,

committing fewer dipping errors (Humble, Snowdon, & Matsuzawa, 2009). At Gombe, social correlates of the amounts of time mothers spent termite fishing related positively to the number of necessary actions for successful termite fishing achieved by their infants at 2.5 years of age, precisely when infants' skill differences become more apparent (Lonsdorf, 2006). The importance of a mother's behaviour on her offspring's behavioral development was also demonstrated in the non-functional stone-handling behaviour of Japanese macaques, with infants of a non-stone handler developing the behaviour later than peers whose mothers handled stones (Nahallage & Huffman, 2007a).

Despite the mother's central role in her offspring's early skill development, it is unlikely that she would be the exclusive source of learning opportunities for a young social primate. Firstly, social transmission solely from mothers to offspring would not have led to group-wide traditions since behaviours would have needed to spread between matrilineal lines (van Schaik et al., 2003; van Schaik & Pradhan, 2003). Secondly, mothers may fail to directly provide learning opportunities if she does not exhibit the behaviour, but offspring of non-performing mothers can acquire group traditions if the inability to learn from the mother is mitigated by opportunities to learn from other skilled models (van Schaik & Pradhan, 2003). For example, although Japanese macaques with non-stone-handling mothers were slower to develop the behaviour, they still did so after they began to associate more with stone-handling peers (Nahallage & Huffman, 2007a).

Mothers can influence their offspring's opportunities for learning from others through her associations with other group members. Mothers with more numerous or stronger affiliations with other conspecifics facilitate offspring's close exposure to other skilled models, increasing their learning opportunities (Lonsdorf, 2006; Meulman et al.,

2013; van Schaik et al., 2003). In orangutans, an individual's mean foraging party size which is stable over development and linked to its mothers' gregariousness, correlated with its specialization in tree-hole tool use (van Schaik et al., 2003). In chimpanzees however, mother's sociality during termite fishing did not correlate with offspring's skill acquisition and proficiency. This was attributed to termite fishing tending to be a solitary activity because of the clumped distribution of termite mounds (Lonsdorf, 2006). An individual's own sociality might therefore become important for seeking accessibility to learning opportunities especially as dependence on the mother reduces. For example, although these effects were not directly examined, it has been documented that after young chimpanzees are weaned at around 5 years of age, they increase their associations with other individuals during ant-dipping (Humle, 2011; Humle et al., 2009).

Apart from merely associating with others, young individuals can also augment their learning opportunities to the extent that they actively solicit interactions with skilled individuals during the behaviours of interest. As discussed in the preceding chapter, primate infants are responsible for the bulk of interactions with experienced individuals during skilled foraging behaviour since provisioning, food sharing, and active information transfer and teaching are rare (Galef, 2009; Jaeggi, van Noordwijk, & van Schaik, 2008; King, 1994; Rapaport & Brown, 2008). Furthermore, immature individuals can interact with skilled models in different ways, and some types of interactions such as observation or "co-action" (e.g. touching a model's arm during striking), in which learners directly participate in the model's behaviour are thought to be especially facilitative of learning, compared to less behaviorally-focused interactions such as scrounging (Humle, 2011). Therefore, it is plausible to expect that individual differences in learning outcomes might

also be linked to self-created learning opportunities via the interactions that immature individuals initiate with skilled group members.

Given the importance of learning opportunities on skill development, and the varied sources from which these opportunities could be contributed, I aimed to examine how differences in sociality-influenced, mother-related, and self-created opportunities for learning might explain the observed individual differences in the development and proficiency of tool use in young macaques. Young macaques potentially have the opportunity to learn from numerous tool-using models, because of the large group size and open distribution of tool-processed food resources in the habitat. Their opportunities for close-range learning are therefore restricted by their sociality and interactions with knowledgeable group members, rather than ecological constraints. I predicted that the amount and quality of opportunities for learning provided by their mother's rate and proficiency of tool use, and the number and strength of her associations with other group members, as well as their own sociality and rate of tool-related interactions, in particular how much they observed skilled group members, would correlate with the rate and complexity of object manipulation behaviours in younger infants and juveniles as measures of their speeds of development, and with measures of tool-use proficiency in newly competent older juveniles. I also examined if mature individuals' sociality related to their tool-use behaviour and proficiency, particularly in adult females, since current patterns of associations are more likely to reflect associations during development for the philopatric sex.

Methods

Measuring Speed of Development

I used data and results from the development of object manipulation and tool-use behaviour (Chapter 2), to select measures of speeds of development relevant to each age class (Table 4.1). Recall from the analyses on development that the macaques were divided into seven age groups: infants born during the study up to six months of age (with object manipulation behaviour analyzed in two time periods: 0-3 and 3-6 months), juveniles aged 0.5-1.5 years, 1.5-2.5 years, 2.5-3.5 years, adolescents and adults 3.5-4.5 years, 4.5-5.5 years, and >5.5 years. Since tool-use proficiency was found to improve rapidly after competence was achieved and relatively plateaued in adolescence and adulthood, I grouped adolescents and adults above 3.5 years into a single group for this analysis.

For age groups in which none of the juveniles had acquired tool-use competence (up to 2.5 years), measures of speed of development were based on their object-manipulation behaviour. Firstly, I measured how much individuals manipulated objects in terms of a) their proportion of focal time spent in object manipulation, and b) their rate of object manipulation bouts. Secondly, I measured how closely the objects manipulated matched the object combinations needed for tool use. From 0-3 months and 3-6 months, this was measured by the proportion of infants' bouts in which they manipulated both stones and shells, and for juveniles from 1.5-2.5 years, this was the proportion of bouts in which all items needed for a complete tool use sequence were involved. Thirdly, I measured the complexity of their object manipulation bouts in three ways, a) in terms of their proportions of manipulation bouts that fell into higher Hierarchical Classes, which

were class A-1-ii, A-2, and B-2 from 0-3 month and 3-6 months, and only class B-2 for 1.5-2.5 year olds, b) the average number of objects manipulated per bout, and c) the average number of actions carried out per bout. Lastly, I measured their action repertoire by a) the total number of different actions developed, b) the number of different Critical Actions they had developed, and additionally for those aged 1.5-2.5 years, c) the number of different percussive actions developed. For measures that were based on the proportion of bouts in which a characteristic was observed, and the average number of actions and objects per bout, I included only individuals with at least 10 bouts of manipulation. Only 2 juveniles aged 0.5-1.5 years met this criteria, and therefore, I could only examine their proportion of time and rate of object manipulation, and action repertoire, and not the other characteristics of their object manipulation bouts (recall from Chapter 2 that object-manipulation behaviour was generally low amongst juveniles aged 0.5-1.5 years).

For age groups in which at individuals had already attained tool-use competence (2.5 years and above), I examined how much each individual used tools in terms of their proportion of foraging time spent using tools and rate of tool-use bouts, and the proficiency measures of strike efficiency, strike accuracy, tool fidelity, and proportion of successful tool-use bouts. These measures were chosen since they were found to differ across age groups, and could therefore be useful for examining individual differences in proficiency. Similarly, I included only individuals with more than 10 bouts of tool use for measures of tool-use proficiency.

Measuring Opportunities for Learning

Sociality

I examined two measures of sociality that could relate to the number and quality of learning opportunities, 1) the number of social partners each individual has, and 2) strength of its associations, which is the sum of each individual's association indices with all other individuals. Therefore, strength increases if an individual interacts with more social partners, or if the individual interacts more often with its social partners (Whitehead, 2008). Association indices were calculated previously to build the proximity and grooming association matrices (Chapter 2). I examined each individual's measures of sociality separately for proximity-based and grooming-based associations, and with respect to all the individuals in the group, and when limited to other tool users in the group. Therefore, for each individual, I determined a) number of proximity partners, b) number of grooming partners, c) number of tool-user proximity partners, d) number of tool-user grooming partners, e) sum of proximity-based association indices, f) sum of grooming-based association indices, g) sum of proximity-based association indices with tool users, and h) sum of grooming-based association indices with tool users.

Mother-Related Opportunities for Learning

I measured opportunities for learning provided by mothers' tool-use behaviour and mother's sociality for young macaques below 3.5 years old, in which mother-offspring relationships were known or inferred. Measures of mothers' sociality is described in the preceding subsection above. Opportunities for learning provided by mothers' tool-use behaviour were her proportion of foraging time spent using tools, and rate of tool-use (bouts per minute). In addition to how often mothers used tools, I also examined the relationships between mother's tool-use proficiency measures and offspring speed of development or tool-use proficiency measures (Table 4.1).

Self-Created Opportunities for Learning via Tool-Related Interactions

In age classes where juveniles had not achieved tool-use competence (below 2.5 years), I measured self-created opportunities for learning by how much each individual carried out tool-related interactions (TRI) with tool users, and how much of these interactions involved observation. These were the proportion of focal time that each subject spent on TRI, and rate of TRI, and the proportion of individual's tool-related interactions in which they observed the tool user (only for individuals with more than 10 bouts of TRI).

Analyses

Tests of Predictions

I used a series of univariate analyses to identify significant relationships between each developmental or proficiency measure, with each measure of opportunities for learning. For analyses on the relationships between developmental and proficiency measures and mothers' tool-use characteristics and individuals' tool-related interaction behaviour, I ran separate univariate General Linear Models (GLM) in. In each model, a developmental or proficiency measure was entered as the dependent variable, and a maternal tool-use characteristic or tool-related interaction was entered as a covariate. The model included both the intercept, and the main effect of the covariate.

For analyses involving measures of sociality, GLMs could not be used as these were based on association indices that are not independent from each other, and randomization techniques must be used (Croft, James, & Krause, 2008). I used univariate permutation tests implemented with UCINET 6 (Borgatti, Everett, & Freeman, 2002), in

which each measure of sociality was regressed on each developmental or proficiency measure. For adolescent and adult individuals, I additionally examined the effects of sociality within only females, since in a female philopatric macaque society, their current sociality is likely to be a more representative indicator of their opportunities for learning during development, compared to immigrant males. Significant results were based on $p < 0.05$ and 10000 permutations.

Additional Analyses

The results obtained from the tests of predictions included some significant effects that were opposite to what was predicted. These are described in the Results section, but in particular, the proportions of foraging time spent using tools and the rates at which mothers carried out tool-use bouts, correlated negatively and significantly with measures of development in object manipulation of offspring above 1.5 years of age, and tool-use proficiency measures of offspring 2.5-3.5 years of age. A possible explanation for this unexpected effect is that more productive mothers provide greater opportunities for their offspring to obtain food via scrounging (also recall from Chapter 3 that immatures scrounged more often from more productive tool users). The increased opportunities for offspring of tool using mothers that used tools more prevalently to scrounge tool-processed food, could reduce their motivation to obtain food via their own tool-use efforts, and consequently their exploratory manipulations of stones and food items and proficiency in early tool use. To investigate if this was possible cause of the results obtained here, I ran additional univariate GLMs between offspring scrounging rates and their mother's proportion of time spent using tools and rate of tool use.

Results

Opportunities for learning measured from different possible sources i.e. an individual's own sociality, its mother's sociality and tool-use characteristics, and its own tool-related interaction behaviour, influenced the object-manipulation or tool-use behaviour of macaques in different age groups to different extents. Table 4.1 lists the means and standard deviations of measures of opportunities for learning, speeds of development, and tool-use proficiency for each age class.

0-3 months

Significant relationships between measures of opportunity for learning and development in object manipulation behaviour were most numerous in this age group. Various measures of opportunities for learning across all sources positively influenced how much infants carried out object manipulation, and several characteristics of their object manipulation behaviour (Table 4.2), suggesting a strong positive influence of learning opportunities on developmental progress at this age. Permutation tests found that infants with stronger proximity-based associations with tool users, spent more time on object manipulation, and carried out object manipulation bouts at higher rates, while the number of tool-user grooming associates that an infant had correlated with the number of different manipulative actions and Critical Actions that the infant had developed.

Mothers' sociality and tool-use characteristics also influenced their infants' object manipulation behaviour. Infants of mothers with a greater number of proximity associates, and more numerous and stronger grooming associations with both tool users and other group members in general spent more time on object manipulation. In addition, mothers'

numbers of proximity associates positively correlated with the number of different actions that infants had developed, and infants whose mothers had a greater number of tool-user proximity associates also manipulated more objects in each bout, and more often carried out multiple actions on a single object (i.e. bouts of Hierarchical Class A-1-ii complexity) versus single actions on single objects (Class A-1-i), which were common for this age. Infants whose mothers spent more time using tools, carried out tool use at faster rates, and were more proficient in terms of strike efficiency, spent more time on object manipulation. Mother's strike efficiency also correlated with the number of Critical Actions that infants had developed, and her proficiency in terms of tool-selection efficiency correlated with the proportion of infants' object manipulation bouts in which they carried out multiple actions on multiple objects (i.e. HC A-2 complexity, the highest level of complexity observed at this age).

Lastly, infants self-created opportunities for learning via their interactions with skilled models during tool use also influenced their level of development in object manipulation behaviour. Infants that carried out higher rates of tool-related interactions spent more time engaged in object manipulation, and the time they spent on tool-related interactions correlated with the number of actions they had developed. In addition, infants who observed tool users in a higher proportion of their tool-related interactions, more often carried out the most complex type of object manipulation bouts observed by this age (HC A-2).

Table 4.1

Means and standard deviations of predictor variables (measures of learning opportunities) and dependent variables (measures of development in object manipulation or tool-use proficiency) examined in each age group.

Variable	0 -3mth ²	3-6mth ²	0.5-1.5yr	1.5-2.5yr	2.5-3.5yr	>3.5yr	>3.5yr [F]
Predictors (Learning Opportunities)							
<u>Sociality¹</u>							
Proximity count	56 ± 3		54 ± 4	50 ± 4	42 ± 8	43 ± 16	55 ± 5
Proximity count (tool users)	21 ± 1		21 ± 3	19 ± 3	17 ± 1	16 ± 5	19 ± 3
Proximity strength	1.71 ± 0.40		1 ± 0.24	0.76 ± 0.43	0.39±0.09	0.86 ± 0.69	1.29 ± 0.61
Proximity strength (tool users)	0.55 ± 0.18		0.38 ± 0.16	0.29 ± 0.16	0.21±0.06	0.25 ± 0.17	0.36 ± 0.14
Grooming count	3 ± 2		5 ± 3	8 ± 3	7 ± 3	11 ± 7	14 ± 6
Grooming count (tool users)	2 ± 2		3 ± 2	5 ± 2	5 ± 2	5 ± 3	7 ± 3
Grooming strength	0.01 ± 0.01		0.08 ± 0.04	0.15 ± 0.10	0.09±0.06	0.15 ± 0.10	0.20 ± 0.09
Grooming strength (tool users)	0.01 ± 0.01		0.05 ± 0.04	0.10 ± 0.05	0.06±0.05	0.07 ± 0.05	0.09 ± 0.05
<u>Mother's Tool-Use</u>							
Prop. time in TU	0.38 ± 0.32		0.35 ± 0.34	0.37 ± 0.34	0.38 ± 0.30	Not analyzed for this age group.	
Rate of tool use (bouts/min)	0.88 ± 0.73		0.86 ± 0.91	0.82 ± 0.76	0.77 ± 0.63		
Strike efficiency (strikes/bout)	8.67 ± 1.32		8.53 ± 1.48	8.19 ± 1.97	8.58 ± 0.75		
Strike accuracy (prop. of accurate strikes)	0.99 ± 0.22		0.99 ± 0.02	0.96 ± 0.06	0.99 ± 0.01		
Tool-selection efficiency (tool changes/bout)	0.02 ± 0.02		0 ± 0.01	0.02 ± 0.02	0.02 ± 0.02		
Prop. of successful bouts	0.86 ± 0.06		0.89 ± 0.03	0.87 ± 0.05	0.90 ± 0.02		
<u>Mother's Sociality¹</u>							
Proximity count	56 ± 4		56 ± 3	57 ± 3	55 ± 3		
Proximity count (tool users)	19 ± 2		20 ± 2	21 ± 3	20 ± 2		
Proximity strength	1.85 ± 0.30		1.36 ± 0.56	1.69 ± 0.63	1.56 ± 0.72		
Proximity strength (tool users)	0.48 ± 0.09		0.38 ± 0.15	0.42 ± 0.15	0.39 ± 0.17		
Grooming count	19 ± 7		14 ± 4	17 ± 6	17 ± 4		
Grooming count (tool users)	8 ± 3		7 ± 2	7 ± 3	6 ± 3		
Grooming strength	0.20 ± 0.09		0.22 ± 0.08	0.26 ± 0.09	0.26 ± 0.06		
Grooming strength (tool users)	0.09 ± 0.04		0.09 ± 0.04	0.09 ± 0.05	0.09 ± 0.06		
<u>Tool-Related Interactions</u>							
Prop. time in TRI	0.12 ± 0.09		0.13 ± 0.07	0.12 ± 0.04			
Rate of TRI (bouts/hr)	2.93 ± 1.81		5.47 ± 2.78	5.10 ± 2.31			
Prop. bouts of observation	0.24 ± 0.22		0.18 ± 0.14	0.08 ± 0.10			

Variable	0 -3mth ²	3-6mth ²	0.5-1.5yr	1.5-2.5yr	2.5-3.5yr	>3.5yr	>3.5yr [F]
Dependent Variables (Developmental/Proficiency Measures)							
<u>Characteristics of Object Manipulation</u>							
Prop. time in object manipulation	0.02 ± 0.01	0.03 ± 0.02	0.01 ± 0.01	0.04 ± 0.05			
Rate of object manipulation (bouts/min)	0.04 ± 0.02	0.05 ± 0.03	0.09 ± 0.06	0.28 ± 0.27			
Duration of bouts (s)	15.92 ± 6.15	25.59 ± 4.98		46.18 ± 30.97			
Prop. involving stones and shells	0.05 ± 0.06	0.10 ± 0.11					
Prop. involving complete objects				0.15 ± 0.08			
Average objects per bout	1 ± 2	1 ± 1		2 ± 3			
Prop. of Hierarchical Class (HC) A-1-ii	0.44 ± 0.09	0.52 ± 0.20					
Prop. of HC A-2	0.07 ± 0.07	0.06 ± 0.08		0.82 ± 0.09			
Prop. of HC B-2	0.04 ± 0.06	0.09 ± 0.09		0.97 ± 0.03			
Prop. with Critical Actions	0.38 ± 0.14	0.61 ± 0.16		0.59 ± 0.33			
Number of different actions developed	12 ± 4	14 ± 3	7 ± 4	12 ± 11			
Number of Critical Actions developed	3 ± 1	4 ± 2	2 ± 1	6 ± 5			
Number of percussive actions developed				2 ± 3			
Average actions per bout				3 ± 1			
<u>Tool-Use Characteristics</u>							
Prop. time in TU					0.29 ± 0.27	0.40 ± 0.29	0.36 ± 0.31
Rate of tool use (bouts/min)					0.68 ± 0.65	0.90 ± 0.72	0.85 ± 0.75
Strike efficiency (strikes/bout)					12.95 ± 3.50	9.94 ± 3.23	8.38 ± 1.63
Strike accuracy (prop. of accurate strikes)					0.92 ± 0.06	0.98 ± 0.04	0.98 ± 0.04
Tool-selection efficiency (tool changes/bout)					0.05 ± 0.04	0.02 ± 0.06	0.02 ± 0.02
Prop. of successful bouts					0.73 ± 0.14	0.80 ± 0.08	0.86 ± 0.54

¹ “Count” variables refer to the total number other individuals with which the subject shared either proximity or grooming associations. “Strength” variables refer to the overall strength a subject’s associations within the group, calculated by summing all proximity or grooming-based association indices.

² Infants in the 0-3 month and 3-6 month analyses were the same subjects, therefore, a single measure of their sociality averaged across all months and mother’s characteristics were used as predictor variables for analyses.

Table 4.2

Significant relationships between measures of learning opportunities and development in object manipulation at 0-3 months.

Predictor	Dependent Variable	Test Statistics ¹
<u>Sociality</u>		
Proximity strength (tool users)	Prop. time in OM	$F_{(n=8)}=38.22, p=0.001, R^2=0.86$
	Rate of OM	$F_{(n=8)}=19.33, p=0.01, R^2=0.76$
Grooming count (tool users)	Number of different actions	$F_{(n=8)}=8.85, p=0.02, R^2=0.57$
	Number of Critical Actions	$F_{(n=8)}=5.50, p=0.04, R^2=0.48$
<u>Mother's Tool-Use</u>		
Prop. time in TU	Prop. time in OM	$F_{(n=8)}=7.10, p=0.04, R^2=0.54$
Rate of TU	Prop. time in OM	$F_{(n=8)}=7.72, p=0.03, R^2=0.56$
Strike efficiency	Prop. time in OM	$F_{(n=5)}=12.23, p=0.04, R^2=0.80$
	Number of Critical Actions	$F_{(n=5)}=15.24, p=0.03, R^2=0.84$
Tool Fidelity	Prop. bouts of HC A-2	$F_{(n=5)}=2101.74, p=0.01, R^2=0.99$
<u>Mother's Sociality</u>		
Proximity count (all group)	Prop. time in OM	$F_{(n=5)}=9.06, p=0.03, R^2=0.60$
	Rate of OM	$F_{(n=5)}=7.18, p=0.03, R^2=0.54$
	Number of different actions	$F_{(n=5)}=7.41, p=0.04, R^2=0.55$
Proximity strength (tool users)	Duration of OM bouts	$F_{(n=4)}=10.60, p<0.001, R^2=0.98$
	Prop. bouts HC A-1-ii	$F_{(n=4)}=11.24, p<0.001, R^2=0.85$
	Ave. objects per bout	$F_{(n=4)}=11.73, p<0.001, R^2=0.98$
Grooming count (all group)	Prop. time in OM	$F_{(n=8)}=7.48, p=0.03, R^2=0.55$
Grooming strength (all group)	Prop. time in OM	$F_{(n=8)}=9.52, p=0.02, R^2=0.61$
Grooming count (tool users)	Prop. time in OM	$F_{(n=8)}=5.14, p=0.04, R^2=0.51$
Grooming strength (tool users)	Prop. time in OM	$F_{(n=8)}=43.38, p=0.002, R^2=0.88$
	Rate of OM	$F_{(n=8)}=8.99, p=0.02, R^2=0.60$
<u>Tool-Related Interactions</u>		
Prop. time in TRI	Number of different actions	$F_{(n=8)}=13.84, p=0.01, R^2=0.65$
Rate of TRI	Prop. time in OM	$F_{(n=8)}=15.40, p=0.01, R^2=0.72$
Prop. observation	Prop. bouts of HC A-2	$F_{(n=4)}=28.02, p=0.03, R^2=0.93$

¹ analyses involving sociality measures as predictors were carried out using univariate permutation tests, while the effects of mother's tool-use characteristics and TRI behavior were analyzed with univariate General Linear Models.

3 – 6 months

There were fewer significant and positive effects of opportunities for learning on infants' speeds of development measured between 3-6 months (Table 4.3). The number of tool-user grooming associates that infants had, number of proximity-based associates their mothers had, and the amount of time they spent on tool-related interactions continued to correlate with the number of different manipulative actions they had developed, and

infants who observed tool users in a higher proportion of their tool-related interactions had developed more Critical Actions. Contrary to expectations, mother's tool-use proficiency in terms of her strike efficiency and tool-selection efficiency now had negative effects on how often infants carried out more complex object manipulation bouts (HC A-1-ii and B-2), and involved Critical Actions in their manipulations.

Table 4.3

Significant relationships between measures of learning opportunities and development in object manipulation at 3-6 months. # indicates significance opposite to predictions.

Predictor	Dependent Variable	Test Statistics
<u>Sociality</u>		
Grooming count (tool users)	Number of different actions	$F_{(n=8)}=8.91, p=0.03, R^2=0.60$
<u>Mother's Tool-Use</u>		
Strike efficiency [#]	Prop. bouts of HC B-2	$F_{(n=4)}=37.36, p=0.03, R^2=0.95$
	Prop. bouts with Critical Actions	$F_{(n=4)}=108.62, p=0.01, R^2=0.98$
Tool Fidelity [#]	Prop. bouts of HC A-1-ii	$F_{(n=4)}=21.98, p=0.04, R^2=0.91$
<u>Mother's Sociality</u>		
Proximity count (all group)	Number of different actions	$F_{(n=8)}=6.69, p=0.047, R^2=0.53$
<u>Tool-Related Interactions</u>		
Prop. time in TRI	Number of different actions	$F_{(n=8)}=7.37, p=0.04, R^2=0.55$
Prop. observation	Number of Critical Actions	$F_{(n=8)}=6.41, p=0.045, R^2=0.52$

0.5 – 1.5 years

Juveniles between 0.5 to 1.5 years of age carried out very little object manipulation overall (Table 4.1, and also see Chapter 2); however, those with stronger proximity-based associations both across all group members and with tool users carried out higher rates of object manipulation, and those whose mothers spent more time using tools, also spent more time on object manipulation (Table 4.4). The strength of juveniles' general proximity based associations also correlated with the number of different actions they had developed.

Table 4.4

Significant relationships between learning opportunities and development in object manipulation at 0.5-1.5 years. Characteristics of object manipulation were not examined for this age group because only two subjects provided more than 10 bouts for analyses.

Predictor	Dependent Variable	Test Statistics
<u>Sociality</u>		
Proximity strength (all group)	Rate of OM	$F_{(n=9)}=14.76, p=0.01, R^2=0.68$
	Number of different actions	$F_{(n=9)}=6.49, p=0.04, R^2=0.48$
Proximity strength (tool users)	Rate of OM	$F_{(n=9)}=15.36, p=0.001, R^2=0.69$
<u>Mother's Tool-Use</u>		
Prop. time in TU	Prop. time in OM	$F_{(n=9)}=7.75, p=0.03, R^2=0.53$
Rate of TU	Prop. time in OM	$F_{(n=9)}=14.22, p=0.01, R^2=0.67$

1.5-2.5 years

At age 1.5 to 2.5 years, juveniles' own sociality, in the strength of its grooming-based associations, correlated positively with their rates of object manipulations, and rates of engaging in tool-related interactions correlated with how often their object-manipulation behaviour involved all the necessary items for tool use (Table 4.5). Contrary to expectations, there were significant negative relationships between mothers' tool-use characteristics and juveniles' object manipulation behaviour.

Table 4.5

Significant relationships between learning opportunities and development in object manipulation at 1.5-2.5 years. # indicates significance opposite to prediction.

Predictor	Dependent Variable	Test Statistics
<u>Sociality</u>		
Grooming strength (all group)	Rate of OM	$F_{(n=9)}=3.69, p=0.048, R^2=0.35$
<u>Mother's Tool-Use</u>		
Prop. time TU [#]	Prop. bouts of HC B-2	$F_{(n=5)}=11.31, p=0.04, R^2=0.79$
Rate TU [#]	Prop. bouts of HC B-2	$F_{(n=5)}=10.36, p=0.049, R^2=0.78$
Prop. Success	Prop. bouts with complete items	$F_{(n=4)}=23.45, p=0.04, R^2=0.92$
<u>Mother's Sociality</u>		
Grooming count (all group) [#]	Rate of OM	$F_{(n=9)}=9.49, p=0.01, R^2=0.58$
<u>Tool-Related Interactions</u>		
Rate of TRI	Prop. bouts with complete items	$F_{(n=5)}=21.64, p=0.02, R^2=0.88$

2.5-3.5 years

Three out of the five juveniles in the 2.5-3.5-year age group had already achieved tool use competence. Supporting the importance of a mother's skill on their offspring's tool-use development, the two juveniles who did not develop tool use had a mother that was a non-tool-user, and a mother who used tools infrequently and in an idiosyncratic way (see discussion on individual Nms in Chapter 1). The three tool-using juveniles all had mothers who were frequent tool users. Apart from these observations, juvenile's rates of tool use correlated with their number of grooming associates, and the proportions of time they spent using tools correlated with their mother's time and rate of tool use, and her proficiency in terms of strike efficiency (Table 4.6). Again, contrary to prediction, some of mother's tool-use characteristics appeared to have negative effects on juvenile's proficiency. In particular, young tool users whose mother's spent more time using tools and carried out higher rates of tool use, had lower tool fidelity and were less efficient in striking.

Table 4.6

Significant relationships between measures of learning opportunities and tool-use behaviour at 2.5-3.5 years. # indicates significance opposite to predictions.

Predictor	Dependent Variable	Test Statistics
<u>Sociality</u>		
Grooming count (all group)	Rate of tool use	$F_{(n=5)}=4.85, p<0.001, R^2=0.62$
<u>Mother's Tool-Use</u>		
Prop. time in TU	Prop. time in TU	$F_{(n=5)}=14.62, p=0.03, R^2=0.83$
	Tool Fidelity [#]	$F_{(n=3)}=213.73, p=0.04, R^2=0.99$
Rate of TU	Prop. time in TU	$F_{(n=5)}=11.17, p=0.04, R^2=0.79$
	Strike efficiency [#]	$F_{(n=3)}=870.40, p=0.02, R^2=0.99$
Strike accuracy	Prop. time in TU	$F_{(n=4)}=20.71, p=0.045, R^2=0.91$
Tool-selection efficiency	Prop. success	$F_{(n=3)}=440.49, p=0.03, R^2=0.99$

>3.5 years

In adolescent and adult tool users above 3.5 years old, sociality did not affect how much individuals used tools when analyzed across males and females. However, when analysis was restricted to only females, the philopatric sex for which current sociality should be a better proxy for learning opportunities during development, females with more numerous and stronger grooming associations with other tool users, spent a greater proportion of their foraging time in tool use (Table 4.7). Across all adolescents and adults, those with more numerous proximity-based associations generally and with tool users, as well as the stronger grooming-based associations, were found to have better strike efficiencies.

Table 4.7

Significant relationships between measures of sociality, as proxy measures for learning opportunities during development, with mature individuals' tool-use behaviour and proximity. [F] indicates results of analyses when restricted to females only.

Predictor	Dependent Variable	Test Statistics
<u>Sociality</u>		
[F] Grooming count (tool users)	Prop. time in TU	$F_{(n=20)}=6.41, p=0.02, R^2=0.26$
[F] Grooming strength (tool users)	Prop. time in TU	$F_{(n=20)}=6.41, p=0.02, R^2=0.26$
Proximity count (all group)	Strike efficiency	$F_{(n=25)}=6.73, p=0.03, R^2=0.23$
Proximity count (tool users)	Strike efficiency	$F_{(n=25)}=6.81, p=0.03, R^2=0.23$
Grooming strength (tool users)	Strike efficiency	$F_{(n=25)}=6.55, p=0.03, R^2=0.22$

Associations between maternal tool use and offspring scrounging

Univariate GLMs revealed significant positive correlations between the prevalence of maternal tool-use behavior and offspring scrounging behavior in offspring aged up to 1.5 years. In the 0 - 0.5 year age group, offspring rates of scrounging correlated with the proportion of foraging time that mothers spent using tools ($F = 7.84, p = 0.03, R^2 = 0.41$)

and mothers' rates of tool use ($F = 6.99, p = 0.03, R^2 = 0.37$). In this age group, the proportion of foraging time that offspring spent scrounging also correlated positively with maternal rates of tool use ($F = 6.55, p = 0.04, R^2 = 0.36$). In the 0.5 – 1.5 year age group, the proportion of foraging time that mothers spent using tools correlated positively with both the proportion of foraging time that offspring spent scrounging ($F = 11.81, p = 0.02, R^2 = 0.56$) and their rates of scrounging ($F = 6.17, p = 0.046, R^2 = 0.39$).

Discussion

The results are largely consistent with the hypothesis that individuals differ in the speeds at which they develop tool-use skills and their eventual tool-use abilities at least in part because of differences in their opportunities for social learning. Since learning opportunities could stem from multiple sources I examined several of these, namely opportunities for learning from maternal tool-use behaviour and opportunities to learn from non-maternal models afforded by both maternal and individual patterns of association with others, and individuals' active interactions with skilled conspecifics. I found that all these factors to some extent influenced learning outcomes. The main difference between age groups was that the most numerous and positive influences of learning opportunities on development were observed in the youngest macaques. This could relate to the closeness between infants, their mothers, and other close associates at this age, and highlights a developmental period in which social influence might be most critical. Closer examination of the observed effects at different ages further suggest that influences are developmentally linked, and highlight the importance of different influences during different developmental time periods.

Based on commonalities in the observed results across different age groups, macaques' own patterns of association appear to exert the most consistent influence on their opportunities for learning. Differences in sociality appear to primarily influence how much young macaques carry out exploratory object manipulation, which could then translate to individual differences in tool-use behaviour in maturity. An individual's own sociality, measured either by the number or strength of its proximity or grooming relationships, positively correlated with the times that individuals spent on, or the rate at which they carried out object manipulation or tool-use behaviour, an effect that was ubiquitous across all age groups. One difference between age groups is that in younger macaques up to 1.5 years, associations with tool users in particular accounted for these correlations, while general affiliation with both tool-using and non-tool-using group members explained the correlations observed in older macaques. Recall from chapter 2 that juveniles below 1.5 years of age often carried out tool-related interactions from within 1m proximity to tool users than older macaques. Taken together, these results suggest that exposure to tool-use behaviours in other group members could support learning because of the facilitative effect that exposure to the behaviour of others has on an individual's own behaviour, in accordance with social facilitation, and local and stimulus enhancement mechanisms of social learning (Heyes, 1994; Laland & Hoppitt, 2013). Macaques, especially the young, that have close relationships with tool users, are likely to more often be in close proximity to their behaviour, and be motivated to engage in their own exploratory behaviours which then support their development of tool-use skills. When juveniles are older and spend less time in proximate interactions with tool users (Chapter 2), individuals that are more strongly affiliated within the group are still

more likely to be in the midst of the group's tool-use behaviour, and encouraged to manipulate objects, than peripheral individuals. This effect might be more conclusively explored by examining sequential relationships between carrying out tool-related interaction with tool users, or the group's tool-use activity, on young individuals' own object manipulation as has recently been done with capuchins (Eshchar et al., 2016). A further difference between age groups is that the influence of sociality is much weaker on adult macaques' tool-use behaviour than on measures of rates of development in juveniles, as seen in the smaller effect sizes (R^2 values) of results (Table 4.7 vs. Tables 4.2 – 4.6). This could relate to the likelihood of a critical period for learning as described in Chapter 2, and reinforces the importance of opportunities for learning, particularly during the formative stages of development, on behavioral outcomes in maturity.

While sociality had pervasive influences on how much young macaques of all ages manipulated objects, measures of developmental speed in terms of the complexity of their manipulative behaviour appeared to be better predicted by the opportunities for learning that young macaques create via their interactions with tool-using skilled models. Sociality was positively correlated to the number of different actions that infants and juveniles had developed at 3 months, 6 months, and between 0.5-1.5 years, but more numerous relationships were found between tool-related interaction behaviour and object-manipulation complexity. The rate at which infants carried out tool-related interactions correlated not only with the proportions of time they spent on object manipulation, but also with the number of different manipulative actions in their repertoire at 6 months of age. The positive effects of juvenile's rates of tool-related interactions on developmental progress were still observed in those aged between 1.5 to 2.5 years, when sociality no

longer produced significant relationships, correlating positively with how much these juveniles carried out object manipulation bouts with all the items involved in complete tool-use sequences. Additionally, the proportion of tool-related interactions in which infants observed tool users correlated with the proportions of manipulation bouts in which they performed multiple actions on multiple objects (as opposed to single actions or objects) at 3 months of age, and the number of Critical Actions they had developed at 6 months of age. These results thus provide another line of support for the importance of interaction with tool users, especially more active and involved forms of interaction, to the learning of tool-use skills.

Maternal effects on macaques' speeds of development or tool-use proficiency were not as consistent across different age groups, which is to be expected with the processes of weaning and young individuals gaining independence as they mature. Mothers' sociality only had positive correlations with the amount of time that their infants spent on object manipulation up to 3 months of age. This accords with observed changes in mother-infant contact time over the first few months of life, with long-tailed macaque infants spending the majority of their first month in contact with their mothers but decreasing contact drastically by the second to third month (Karssemeijer, Vos, & van Hoof, 1990). As discussed above, young individuals' own sociality and active interactions with tool users then become important for their continued exposure to learning opportunities.

The characteristics of mothers' tool-use behaviour had mixed effects on their offspring's speeds of development and tool-use proficiency. As predicted, the amounts of time and rates at which mothers carried out tool use correlated positively with how much

and how frequently younger offspring carried out object manipulation and older offspring used tools. However, mothers' tool-use proficiency largely had negative influences on older offspring's complexity in object manipulation at 1.5-2.5 years, and on the tool-use proficiency of offspring aged between 2.5-3.5 years. These findings are contrary to the prediction that more proficient mothers would provide better quality learning opportunities, and enhance the skill development of her offspring. I found support for the possibility that this unpredicted pattern is due to more productive maternal tool-use behaviour resulting in an increase in offspring scrounging behaviour, which could negatively affect offspring tool-skill development. The inhibitory effects of scrounging on an individual's motivation or ability to learn the producing behaviour (Laland, 2004) has also been demonstrated by experimental findings that obtaining food payoffs via scrounging negatively affected the learning of food cues and techniques for obtaining food in birds (Beauchamp & Kacelnik, 1991; Giraldeau & Lefebvre, 1987) and capuchin monkeys (Fragaszy & Visalberghi, 1990). However, the opposite effect, that scrounging facilitates learning however, has also been demonstrated in other species (Caldwell & Whiten, 2003; Fritz & Kotrschal, 1999). In this study in particular, I found that more productive maternal tool use was related to higher levels of scrounging behaviour in offspring in the 0 – 0.5 year and 0.5 - 1.5-year age groups. Whether and how these behavioral patterns during early development would relate to the development and proficiency of tool-use skills in later juvenility will have to be further explored with longitudinal study before more conclusive explanations can be made.

In summary, the results of the current analyses support hypotheses that opportunities for learning from skilled individuals influences the developmental process

and outcomes of learning stone-tool use in macaques. The most likely pathway through which these influences occur is via associations with skilled individuals, which appears to primarily influence how much young individuals carried out object manipulation, a necessary process in the development of tool-use skills. Results also suggest that opportunities for learning about tool use, created via the extent and type of interactions that young individuals carry out with tool users also influences their skill development, relating to the complexity of their manipulative repertoire relative to their peers. Maternal influences on learning opportunities appears limited in macaques, positively influencing developmental progress particularly in the first three months of life when infants' relationships with their mothers is closest, and following which, mother's productivity and proficiency in tool use might even inhibit the behavioral development of older offspring. The current analyses face several limitations. Learning outcomes and speeds of development had to be measured in several ways that further varied for different-aged macaques at different stages of development. This generated a large number of test variables, within a small sample size, restricting statistical analyses to univariate tests, that make it difficult to conclude on relative influences of different factors, and possible interactions between factors. Accumulating a larger dataset over time will enable more rigorous testing of the factors that likely affect development as revealed in this first exploration. Longitudinal examinations into how the relationships between learning opportunities and developmental progress observed at different stages of maturity eventually develop into an individual's tool-use behaviour, will also allow us to more thoroughly decipher the interactions between various learning opportunities, and more specific mechanisms through which different learning opportunities affect behaviour.

CHAPTER 5

THE EFFECTS OF SOCIAL RELATIONSHIPS ON CONFORMITY IN TOOL- USE BEHAVIORAL PATTERNS

Introduction

Processes of conformity, defined as “the tendency for individuals to preferentially exhibit behavioral alternatives that they witness most frequently in their peers who are considered most prestigious or successful, or those peers with whom they have the highest quality social relationships” (Perry, 2009), have become prominent in recent attempts to further identify the influences underlying the complex patterning of animal traditions (Whiten & Claidière, 2012). Behavioral variation both between and within geographic populations has been comprehensively documented for a wide array of species and behaviours (Leca, Gunst, & Huffman, 2007; Luncz, Mundry, & Boesch, 2012; Panger et al., 2002; Perry, 2011; Whiten et al., 1999). Studies of the developmental process of many of these behaviours have followed, and have implicated social learning as an important factor in the continued acquisition of the behaviours by new individuals (Biro, Sousa, & Matsuzawa, 2006; Humle, Snowden, & Matsuzawa, 2009; Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2005; 2006). These lines of inquiry have established the capacity for social learning and presence of traditions and cultures in primate societies. However, deeper investigations are now needed for identifying and understanding additional environmental, psychological, and social processes that can contribute to the detailed and diverse behavioral patterns across species and within behavioral traditions

(Claidière & Sperber, 2010; Whiten & Claidière, 2012; Whiten & van Schaik, 2007).

Originating from research in human social psychology, interest in conformity in primate societies is boosted by its potential for understanding how cultural behavioral variants arise (Huffman, Spiezio, Sgaravatti, & Leca, 2010). Consequently, this increases scientific understanding of evolutionary origins and analogous processes that might have shaped human cultural uniqueness (Whiten, Hinde, Laland, & Stringer, 2011).

Studies employing two-action paradigms and diffusion chain experiments with captive primates have found that individuals often adopt the technique of the model that they had the most opportunity to observe, and that new practitioners maintain fidelity to the seeded behavioral variant (Dindo, Stoinski, & Whiten, 2010; Dindo, Thierry, & Whiten, 2008; Horner, Whiten, Flynn, & de Waal, 2006; Huffman, Spiezio, Sgaravatti, & Leca, 2010; Whiten, Horner, & de Waal, 2005). In one study (Dindo et al. 2008), capuchins were allowed to observe a model using either of two techniques (lift or slide) to open the door of a foraging apparatus. Initial observers developed the techniques used by their models, and the technique was transmitted with fidelity along two diffusion chains of 4 and 5 individuals. Similar results have been obtained with other species, including orangutans (Dindo et al. 2010), chimpanzees (Huffman, Spiezio, Sgaravatti, & Leca, 2010), and human children (Horner et al. 2006). These studies thus demonstrate the potential for the emergence and maintenance of conformity biases in primate groups, and suggest that these biases might be a mechanism via which variants within behavioral traditions could be established and maintained.

Despite its potential, opportunities for studying processes of conformity within wild populations are rare. The behaviours in which social processes of conformity are

most likely to operate and produce similarities between close individuals are those that are too complex for individuals to acquire without social learning, commonly skilled foraging tasks (Byrne, 2007). Yet, because of the adaptive values of these skills or specific processing requirements imposed by the food items, many of these behaviours are fairly homogenous within populations, with individuals developing the most efficient and typically the same techniques, making it impossible to separate these ecological constraints from social influences in producing behavioral similarity (Perry, 2009).

Opportune cases in which several variants of behaviors or alternative processing techniques for single food types were present within populations have enabled researchers to identify conformity biases by examining relationships between inter-individual behavioral similarity and patterns of association. Several studies on populations of white-faced capuchins at different field sites, have revealed that for certain types of food with rare or multiple processing techniques (although not involving tool use), dyad partners that shared techniques were also those that spent more time in close proximity [Palo Verde National Park: mango rubbing, and *Annoma* and *Randia* fruit pounding (Panger et al., 2002); Santa Rosa NP: *Luehia candida* fruit pounding (O'Malley & Fedigan, 2005); Lomas Barbudal: rubbing vs. pounding *Sloanea terniflora* (Perry & Ordonez Jimenez, 2006); Tiputini Biodiversity Station: palm-tree breaking and unimanual vs. bimanual *Sloanea terniflora* pounding: (Matthews, 2009)]. A longitudinal assessment of the development of *Luehea* processing at Lomas Barbudal further identified that while young unskilled capuchins practiced both technique variants present in the group (scrubbing/pounding), they eventually conformed to the technique which they had observed most during early development, with females in particular adopting their

mother's technique (Perry, 2009). Similarly, female chimpanzees who spent more time observing their mothers' termite fishing behaviour were found to conform to her technique, while less closely-observant male offspring did not (Lonsdorf, 2005). These studies demonstrate conformity biases in wild populations, akin to those generated in captive two-action experiments described earlier, where individuals tended towards behavioral similarity with the group members whose behaviours they had the most exposure to as a result of social relationships.

The macaques on Koram Island provide another rare opportunity to examine within-population conformity biases in natural settings. So far, the current analyses have detailed the typical ontogenetic pattern of stone-tool use amongst the macaques on Koram Island, revealed how young macaques strategically direct learning interactions to more closely affiliated and proficient tool users, and identified factors that influence opportunities for learning and consequent developmental progress. However, several patterns of macaque tool-use behaviour both on Koram Island, and across other tool-using macaque populations are not well explained by these findings. For example, opportunities for learning may explain the observations that individuals differ in whether, and how much or well they use tools, but tool users also vary in more qualitative ways. Macaques may use either the face, edge, or point of stone tools to strike foods, and on Koram Island, there are 13 action patterns (action variations in the way tools are handled) within these hammering classes (Table A1.2 in Appendix 1). Individuals also differ in the proportions of food types that make up their tool-processed diets, with some individuals processing more oysters or motile shellfish relative to others. Based on observations, individual macaques may also have preferences for certain tool materials, shapes, and sizes.

These differences are further highlighted when we compare the behavioral patterns of the Koram Island macaques with another tool-using population that we have previously studied on Piak Nam Yai Island (Gumert, Kluck, & Malaivijitnond, 2009; Gumert & Malaivijitnond, 2012; Tan, Tan, Vyas, Malaivijitnond, & Gumert, 2015). With regards to hammering classes, the macaques on Koram more predominantly used point hammering (76% of tool-use bouts versus 10% being face hammering and 4% being edge hammering, while the distribution of point and face hammering usage appears to be more equal at Piak Nam Yai (50% point hammering and 42% face hammering). This appears to be due at least in part to the less strict association between point hammering and sessile food items on KR, with 18% of tool users also using point hammering when processing unattached food items, and 10% using point hammering regardless of whether they were processing sessile oysters or unattached food items. Also, although edge hammering was less frequently used than point and face hammering at both sites, a larger percentage of the tool-using population on Koram (50%) used edge hammering than at Piak Nam Yai (13%). Furthermore, there is a wider variety of action patterns on Piak Nam Yai, and macaques there also more commonly use both hands and larger stones, whereas bimanual action patterns are a behavioural idiosyncrasy of only two individuals on Koram Island. These comparisons between populations suggest that inter-individual are not merely the consequences of individual trial-and-error learning, but could also be influenced by social processes that promote inter-individual similarity, and that can be seen in overall different behavioral trends at the inter-population level.

In this chapter, I therefore aimed to test the hypothesis that behavioral variation within the Koram Island macaque population is influenced by conformity biases between

closely associated individuals, by investigating if patterns of proximity, grooming, and inferred kinship associations related to inter-individual similarities in tool-use behaviour. The importance of social relationships has been a prevalent finding across the current investigations into the social aspects of macaque tool-use development. Patterns of close proximity and grooming associations, as well as inferred kinships closely related to young macaques' choices of tool users they preferentially observed and scrounged from (Chapter 3). The number and strength of individuals' associations with other group members exerted the predominant and most consistent influence on individuals' learning opportunities, consequently relating to their manipulative progress and tool-use behaviour over development (Chapter 4). Coupled, these findings suggest that during development, macaques have different levels of exposure to different group members' tool-use behaviour that is related to their patterns of proximity, grooming, and kinship associations. Specifically, I predicted that dyadic association indices will correlate with dyadic behavioral similarity in terms of partners being either both tool users or non-tool users, and tool-using dyads being similar in the amounts of tool use they carry out, the ways in which they handled and used tools, the proportions of different foods in their tool-processed diets, and their preference for similar sized tools.

Methods

Data Collection

Data used to examine individuals' tool-use behaviour, proximity and grooming associations, and inferred kinship, were collected via focal and ad libitum sampling already explained in prior chapters. In addition to these behavioral data, I also collected used tools from known individuals, for the current analysis on inter-individual similarity

in tool preferences. Tools were collected ad libitum over two time periods, with the considerations of minimizing possible impact on immature macaques' learning behaviour (e.g. their exploration of discarded tools). As such, tools were only collected if they were discarded in inconspicuous locations, i.e. they were not left on anvils or oyster beds, but dropped amongst other stones as the user walked along the shore, and not in the presence or view of other individuals, particularly immatures. For each tool collected, the identity of the user, how the tool was used, i.e. in face, edge, or point hammering, and the food type it was used to process was recorded. Tools were weighed to obtain a measure of tool size to examine tool-choice similarity. A total of 582 tools from 20 users were analyzed (range = 11 – 44 tools/user; $M = 29$ tools/user), after including only users with more than 10 collected tools for analysis.

Identifying Similarities in Tool-Use Behaviour

I investigated similarity in tool-use behaviour in terms of whether or not individuals were tool users, how often individuals used tools, their use of different hammering classes (i.e. which tool surface they struck foods with, refer to Tan et al. 2015 for detailed description), the food types they processed with tools, and their choice of tools. I identified similar and dissimilar dyads in each measure of tool-use similarity, and represent these dyads in similarity matrices for statistical analyses. The following data matrices were built (Appendix 3):

- a) “user similarity” matrices, based on whether or not individuals were tool users
- b) “time similarity” matrices based on the proportion of foraging time that individuals spent on tool use
- c) “rate similarity” matrices based on individuals' rates of tool use

- d) “hammering similarity” matrices based on the proportion of tool-use bouts in which individuals used i) edge, and ii) face hammering
- e) “food similarity” matrices based on the proportion of tool-use bouts in which individuals processed unattached foods
- f) “tool similarity” matrices based on the average weights of tools collected from each individual.

In investigating similarities in hammering and foods processed, the proportions of tool use in which point hammering was used, and oysters were processed respectively, were not investigated. These characteristics were more homogenous in the population, and predominant for all individuals except one adult female, Nms (see discussion in Chapter 2), making it less productive to identify inter-individual similarity. Also, since the data were based on the proportions of each individual’s tool-use bouts in which a characteristic was observed, it would be redundant to examine all characteristics in each category.

In the similarity matrices, cell values of 1 were assigned if the individuals in the row and column formed a similar dyad, and cell values of 0 were assigned if the individuals in the row and column formed dissimilar dyad. For a) “user similarity”, similar dyads were those in which members were either both tool users or both non-tool users. For b) to f), similar dyads were those in which members were either above or below the group median for the respective characteristics. For example, in b) “time similarity” matrix, similar dyads would be dyads in which both members carried out tool use in a proportion of their foraging time that was either above or below the group median, and were therefore either both individuals that used tools often or not, relative to the group.

Association Matrices and Matrix Correlations

The association matrices used in the current analyses were reduced from the previously constructed proximity based, grooming based, and inferred kinship matrices, to include the relevant individuals in each analyses (Appendix 3). I used Tau K_r tests (Hemelrijk, 1990a, 1990b) to examine correlations between similarity matrices and three corresponding social relationship matrices. The “user similarity” and corresponding proximity, grooming, and inferred kinship matrices included only macaques in tool-using age classes (2.5 years and above). For analyses involving tool-use characteristics, the similarity matrices b) to e) described above, and corresponding association matrices contained tool users with more than 10 bouts of tool use. For the analysis on tool similarity, the “tool similarity” and association matrices contained tool users for whom I managed to collect at least 10 tools. An additional consideration is that these analyses are based on the current association patterns of macaques that had already acquired tool use, and therefore may not accurately reflect patterns of association during the time when they were developing tool use, precisely when patterns of association would have the strongest influence on potential behavioral conformity (Perry, 2009). Therefore, I repeated all the analyses with matrices containing only females. Since females are the philopatric sex in macaques, females’ current associations are more likely than males’ to reflect their associations during development. Significance at $p < 0.05$ were based on 10000 permutations for all tests.

Results

When analyzed across all individuals, there were significant correlations between dyadic association indices and similarity in tool-use behaviour in terms of dyad partners’

use of edge hammering action patterns, and their tool-processed diets. Mean proximity-based association indices (Table 5.1) were higher amongst similar than dissimilar dyads in terms of all similarity characteristics except the likelihood of both being tool users (Figure 5.1a), and grooming-based association indices were higher for similar than dissimilar dyads in all characteristics (Figure 5.1b). Matrix analysis found significant correlations between the proximity-based association matrix containing all tool users (Appendix 3, matrix Prox 2), and the food similarity matrix (Appendix 3, matrix Unattached) in terms of the proportion of tool-use bouts in which all unattached foods were processed (Tau K_r = 0.13, p_r = 0.01), as well as the grooming-based association matrix containing all users (Appendix 3, matrix Groom 2) with the hammering similarity matrix in terms of the proportion of tool-use bouts in which edge hammering was used (Appendix 3, matrix Edge) (Tau K_r = 0.11, p_r = 0.01) (Table 5.2). Near significant correlations were obtained between the all-user grooming-based association matrix and the food similarity matrices in terms of the proportion of tool-use bouts in which all unattached food were processed (Tau K_r = 0.09, p_r = 0.051). A higher proportion of kin dyads were found to be similar dyads than non-kin dyads in all characteristics except the proportion of time spent using tools and rate of tool use (Figure 5.1c). Matrix correlations found a significant correlation between the all-user inferred kinship matrix (Appendix 3, matrix Kin 2), and edge hammering similarity matrix (Appendix 3, matrix Edge) (Tau K_r = 0.20, p_r = 0.02). A near significant correlation (Tau K_r = 0.09, p_r = 0.052) was found between the all-user inferred kinship matrix and the user similarity matrix (Table 5.2).

Fewer significant correlations were obtained when the analysis was restricted to females. Mean proximity based association indices were higher amongst similar than

dissimilar dyads in the proportion of time spent using tools, rate of tool use, proportion of bouts in which edge hammering was used, and proportion of bouts in which all unattached food were processed (Figure 5.2a). Mean grooming based association indices were higher amongst similar than dissimilar dyads in all characteristics except the proportion of bouts in which face hammering was used, unattached food were processed, and tool size (Figure 5.2b). Matrix analyses found significant correlations between the female-only proximity-based association matrix (Appendix 3, matrix Prox 2F) and the rate of tool-use similarity (Appendix 3, matrix Rate F) (Tau $K_r = 0.16$, $p_r = 0.03$), as well as the edge hammering similarity matrix (Appendix 3, matrix Edge F) (Tau $K_r = 0.15$, $p_r = 0.03$). A significant correlation was also found between the female-only grooming-based association matrix (Appendix 3, matrix Groom 2F) and the edge hammering similarity matrix (Tau $K_r = 0.26$, $p_r = 0.01$) (Table 5.2). Unlike when analyzed across all individuals, there were no significant relationships between inferred kinship and similarity matrices.

Dyadic similarity in average tool weight used did not correlate significantly with any dyadic association or relationship measure.

Table 5.1

Means $\pm$ standard deviations of proximity and grooming based association indices of similar versus dissimilar dyads for each similarity characteristics, analyzed across all individuals and amongst female-female dyads only.

Similarity Characteristic	All				Females			
	Proximity		Grooming		Proximity		Grooming	
	Similar	Dissimilar	Similar	Dissimilar	Similar	Dissimilar	Similar	Dissimilar
User	0.01 $\pm$ 0.02	0.01 $\pm$ 0.02	0.002 $\pm$ 0.01	0.002 $\pm$ 0.01	0.02 $\pm$ 0.02	0.03 $\pm$ 0.02	0.004 $\pm$ 0.01	0.003 $\pm$ 0.01
Time	0.01 $\pm$ 0.02	0.01 $\pm$ 0.01	0.003 $\pm$ 0.01	0.003 $\pm$ 0.01	0.03 $\pm$ 0.02	0.02 $\pm$ 0.02	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01
Rate	0.01 $\pm$ 0.02	0.01 $\pm$ 0.01	0.003 $\pm$ 0.01	0.002 $\pm$ 0.01	0.03 $\pm$ 0.03	0.02 $\pm$ 0.01	0.01 $\pm$ 0.01	0.004 $\pm$ 0.01
Face Hammering	0.01 $\pm$ 0.01	0.01 $\pm$ 0.02	0.003 $\pm$ 0.01	0.002 $\pm$ 0.01	0.02 $\pm$ 0.02	0.03 $\pm$ 0.02	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01
Edge Hammering	0.01 $\pm$ 0.02	0.01 $\pm$ 0.01	0.004 $\pm$ 0.01	0.001 $\pm$ 0.01	0.03 $\pm$ 0.03	0.02 $\pm$ 0.02	0.01 $\pm$ 0.01	0.003 $\pm$ 0.01
Unattached Food	0.01 $\pm$ 0.02	0.01 $\pm$ 0.01	0.003 $\pm$ 0.01	0.002 $\pm$ 0.01	0.02 $\pm$ 0.02	0.02 $\pm$ 0.02	0.003 $\pm$ 0.01	0.01 $\pm$ 0.01
Snails	0.01 $\pm$ 0.02	0.01 $\pm$ 0.1	0.003 $\pm$ 0.01	0.002 $\pm$ 0.01	0.03 $\pm$ 0.02	0.02 $\pm$ 0.02	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01
Clams	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.003 $\pm$ 0.01	0.003 $\pm$ 0.01	0.02 $\pm$ 0.02	0.02 $\pm$ 0.02	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01
Tool	0.01 $\pm$ 0.02	0.01 $\pm$ 0.02	0.004 $\pm$ 0.01	0.004 $\pm$ 0.01	0.02 $\pm$ 0.02	0.03 $\pm$ 0.02	0.003 $\pm$ 0.01	0.01 $\pm$ 0.01

Table 5.2

*Data showed significant correlations between dyadic association indices and similarity in tool-use behavior in terms of dyad partners' likelihood of being tool users, rates of tool use, use of face and edge hammering, and tool-processed diets., as indicated by bold typeface with **. Near significant results are indicated by bold typeface and *.*

Similarity Characteristic	All Individuals				Females			
	N	Proximity	Grooming	Kinship	N	Proximity	Grooming	Kinship
User	40	Tau K_r = -0.01 p_l = 0.48	Tau K_r = 0.03 p_r = 0.21	Tau K_r = 0.09 p_r = 0.052*	21	Tau K_r = -0.08 p_l = 0.06	Tau K_r = 0.05 P_r = 0.21	Tau K_r = 0.03 P_r = 0.32
Time	28	Tau K_r = 0.05 p_r = 0.12	Tau K_r = 0.03 p_r = 0.24	Tau K_r = -0.02 p_l = 0.49	13	Tau K_r = 0.03 p_r = 0.39	Tau K_r = 0.11 P_r = 0.15	Tau K_r = -0.12 P_r = 0.44
Rate	28	Tau K_r = 0.03 p_r = 0.22	Tau K_r = 0.04 p_r = 0.23	Tau K_r = -0.07 p_l = 0.24	13	Tau K_r = 0.16, p_r = 0.03**	Tau K_r = 0.09 P_r = 0.21	Tau K_r = -0.08 P_r = 0.51
Face Hammering	28	Tau K_r = -0.01 p_l = 0.44	Tau K_r = -0.01 p_l = 0.43	Tau K_r = 0.15, p_r = 0.08	13	Tau K_r = -0.10 p_l = 0.10	Tau K_r = -0.15 P_r = 0.06	Tau K_r = -0.15 P_r = 0.49
Edge Hammering	28	Tau K_r = 0.03 p_r = 0.21	Tau K_r = 0.13 p_r = 0.01**	Tau K_r = 0.20, p_r = 0.02**	13	Tau K_r = 0.15, p_r = 0.03**	Tau K_r = 0.26, P_r = 0.01**	Tau K_r = 0.44 P_r = 0.19
Unattached Food	28	Tau K_r = 0.11 p_r = 0.01**	Tau K_r = 0.09 p_r = 0.051*	Tau K_r = 0.13 p_r = 0.08	13	Tau K_r = -0.09 p_l = 0.22	Tau K_r = -0.04 P_r = 0.39	Tau K_r = -0.19 P_r = 0.50
Tool	20	Tau K_r = 0.07 p_r = 0.10	Tau K_r = -0.15 p_l = 0.06	Tau K_r = 0.12 p_r = 0.21	13	Tau K_r = -0.10 p_l = 0.16	Tau K_r = -0.06 P_r = 0.33	Tau K_r = -0.15 P_r = 0.49

Figure 5.1 When analyzed across all dyads, a) the average proximity-based association indices of similar dyads were higher than those of dissimilar dyads in all characteristics except the likelihood of both being tool users, while b) the average grooming-based association indices of similar dyads were higher than those of dissimilar dyads in all characteristics. c) A higher proportion of kin dyads were found to be similar dyads than non-kin dyads in all characteristics except the proportion of time spent using tools and rate of tool use. * indicates characteristics for which Tau Kr matrix analyses found significant correlations between the association and similarity matrices (Table 5.2). Error bars represent one standard error of the mean.

Figure 5.2 When analyzed across female-female dyads only, a) average proximity based association indices were higher amongst similar than dissimilar dyads in the proportion of time spent using tools, rate of tool use, proportion of bouts in which edge hammering was used, and proportion of bouts in which unattached food were processed, while b) average grooming based association indices were higher amongst similar than dissimilar dyads in all characteristics except the proportion of bouts in which face hammering was used, unattached food were processed, and tool weight. * indicates characteristics for which Tau Kr matrix analyses found significant correlations between the association and similarity matrices (Table 5.2). Error bars represent one standard error of the mean.

Discussion

The results of the current analyses provide support for the hypothesis that processes of conformism amongst more closely associated group members contribute to the patterning of behavioral variation within, and consequently, between stone-tool-using macaque populations. Within the population on Koram Island, we found relationships between patterns of social association and inter-individual similarity in tool-use behaviour in terms of the rates of tool use by female tool users, and in terms of tool users' hammering patterns and tool-processed diets. Several patterns in the results obtained highlight areas for further discussion and consideration of alternative explanations accounting for the observed behavioral similarity between some groups of closer associates. In particular, there were more correlations between association patterns and behavioral similarity across all individuals rather than amongst females contrary to predictions, and the use of edge hammering action patterns and composition of the tool-processed diets appeared to be the behavioural characteristics of tool use that were most strongly influenced by association patterns.

The fewer significant correlations between social relationships and behavioural similarity when examined amongst only the females in the group appears to contradict what might be expected. As discussed, patterns of association amongst mature macaques should more closely reflect social influences during development for the philopatric sex, and so, correlations should be more pronounced when examined amongst female group members. It is possible that the contradiction might have a methodological explanation. When analyzed across all individuals in the group, inferred kin dyads included 5 pairs of adult females with their juvenile or adolescent male offspring that had not yet emigrated

from the group (Kmk-Chk, Pet-Hee, Kwg-Moo, Lhm-Nak, Lhm-Dto). In analyses involving only females, these female and male offspring dyads were excluded, thus removing behaviorally similar dyads. Inferred kinship was nearly significantly related to dyadic similarity in the likelihood that partners were tool users, and significantly in tool using dyads' similarity in their proportions of edge hammering used when examined across all individuals, but inferred kinship amongst only females did not relate significantly to behavioral similarity for any characteristic. This further suggests that within kin relationships, the potential for conformity may be strongest between offspring and their mothers.

The effect of inferred kinship on behavioral similarity both supports hypothesis that social conformity processes underlie behavioral patterning, but does not rule out possible biological explanations. Of the three types of associations examined, proximity, grooming, and inferred kinship, inferred kinship would most accurately reflect patterns of association during development, particularly between mothers and offspring. Recall from Chapter 3 that young macaques preferentially observed and scrounged from inferred kin. The finding that inferred kinship related to some measures of dyadic behavioral similarity, thus provides additional evidence that individuals tend to develop similar behavioral patterns to conspecifics with whom they had the most opportunity to observe or shared the closest relationship with during behavioral development, in line with conformism (Perry, 2009). On the other hand, associations between kinship and behavioral similarity, particularly if similarities are greatest between mothers and offspring, raises the possibility that genetic similarities predispose individuals to adopt similar behavioral patterns. This would plausibly occur if biological similarities lead kin to experience more

similar sensations of reinforcement from their behaviours (Laland, 2004). In this case, related individuals could experience the same affective feedback from handling stones in certain ways, or from consuming certain foods, resulting in their shared tendency towards those behavioral patterns.

There were also significant relationships between proximity and grooming associations in terms of dyadic similarity in how much partners consumed unattached foods, and in their use of edge hammering action patterns. Dyadic similarity in the proportion of individuals' tool use in which they used edge hammering action patterns was significantly related to grooming associations in both analyses across the group and amongst females. These findings highlight three further areas for discussion. Firstly, the particular significance of behavioral similarity in the use of edge hammering within the Koram Island population is potentially revealing, especially when compared with the behavioral patterns of the Piak Nam Yai population. Secondly, what possible mechanisms could lead to conformism in diet composition, and such a specific and material-associated characteristic of tool-use behaviour as the use of tool edges (vs. faces or points) for hammering? And thirdly, how might processes of conformity explain relationships between mature macaques' current proximity and grooming associations with similarities in their tool use behaviour, given the possibility that these associations were developed after the macaques had already formed adult behavioral patterns, and, what alternative explanations might account for the observed results?

Behavioral similarity in the use of edge hammering amongst more closely associated individuals in the Koram Island population is interesting for two reasons. Firstly, it suggests that processes of conformism can facilitate the spread of behavioral

patterns in one population that is rare in another. Compared with a previously studied population on Piak Nam Yai Island, edge hammering is used more often on Koram Island, and by a larger proportion of the population. On Piak Nam Yai Island, the macaques predominantly used the points of tools to crack sessile oysters, and the broader faces of tools on unattached foods, with edge hammering being rarely used for either food type (Tan et al., 2015). Based on logical deductions from our observations, the association between striking surfaces and food types may be due to the effectiveness of using different tool surfaces on different types of food. Using tool points provided a sharper and more precise surface for chipping open oysters, while the larger striking surface afforded by tool faces to crack open unattached food items placed on anvils would reduce the likelihood that food items ricochet off the anvils when struck. Edge hammering then, might not be optimally effective for either food type, providing neither the most precise surface for chipping open oysters, or the widest surface for pounding open unattached foods. This makes the prevalence of edge hammering on Koram Island even more interesting as it suggests that processes of conformism might be able to outweigh the adaptive values of behavioral variants.

What mechanisms might lead to individuals developing conformity in such a specific and material-associated characteristic of tool use? Macaques do not simply imitate the tool choice or tool-use actions of their associates, as young macaques proceed through developmental stages of high variability in sizes of stones and striking actions, and extensive trial and error before developing competency and mature behavioral patterns. Material conformity has also been found in the tool manufacture of New Caledonian crows, and researchers have suggested a mechanism of “external memory” for

the materials experienced during developmental explorations as a possible explanation (Holzhaider, Hunt, & Gray, 2010). Under this hypothesis, social associations during development would bias young macaques' explorations of tools to those used and abandoned by group members with whom they spent more time in closer contact. This would then influence young macaques' memories for certain properties of the tools they had explored, for example, experiences that food debris was more often found on the edges of tools, which then biases the outcomes of individuals' own explorations towards similarity to these experiences. This might possibly explain the relationships between associations during development and learning, and eventual behavioral similarities. However, what reasons might better explain the findings that current association patterns also correlated with shared tendencies to consume unattached foods and use tool edges for hammering?

One study provides limited evidence that processes of conformism can operate to produce behavioral similarity amongst wild primates, even after adult behavioral patterns have already been formed (Luncz & Boesch, 2014). Amongst neighbouring chimpanzee communities in the Taï National Park, chimpanzee groups have maintained group-specific patterns in terms of their usage of different sized stone or wooden nut-cracking tools over at least 25 years. This is despite the immigration of adult females that had already formed mature tool-use repertoires, and thus potentially introduce the behavioral patterns of their natal groups into their new communities. In addition, when researchers tracked the tool-use behaviour of an immigrant female, they found that her behaviour became increasingly similar to the existing patterns of her new group over the course of two years, even though there were no ecological constraints preventing her from persisting in her original

behaviour. The authors propose that immigrant females alter their original behaviours to conform to their new group's for reasons of "informational conformity" or "normative conformity" (Whiten & Claidière, 2012). In informational conformity, females adapt to their new group's behaviour in order to rapidly gain information about locating and exploiting resources in their new territories. In normative conformity on the other hand, immigrant females conform to the behavioral patterns of their new groups in order to reduce xenophobic aggression and integrate socially into their new community (Luncz & Boesch, 2014). These hypotheses however, were not directly tested in the study.

In the Koram Island macaque population, it might be difficult to ascribe processes of informational and normative conformity to the finding that current social association patterns correlate with similarity in food choice and the use of tool edges for hammering. Informational conformity by immigrant macaque males is unlikely, since new males on Koram Island can only originate from the one other small group that inhabit the island. This smaller group also carries out tool use on the same shores as the study group albeit much less frequently, and therefore, immigrant males would already have knowledge of available food and tool resources. Explanations invoking normative conformity are more useful for explaining conformity to social behavioral customs (Whiten & Claidière, 2012), perhaps for example, forms of grooming like hand-clasp grooming observed in chimpanzees (Whiten et al., 1999) or social play like various play and affiliative behaviors observed in white-faced capuchins (Perry, 2011). It is highly unlikely that macaques would reduce aggression towards immigrants simply because they ate more similar foods or used the same tool surfaces to crack those foods. In fact, foraging on the same foods is

more likely to increase rather than decrease xenophobic aggression because of food competition.

It is therefore prudent to consider explanations other than processes of social conformity, which could explain the observed behavioral similarity between closely associated individuals. The most obvious explanation might be that individuals who spend more time in close proximity are more likely to forage in the same areas. This explanation might be particularly accountable for inter-individual similarity in food choices, since different foods are found in different concentrations in different parts of Koram Island's shore. For example, oysters are located further down in the littoral zone than are the commonly processed gastropods such as periwinkles (*Planaxis sulcatus*) and tooth-lipped snails (*Monodonta labio*), and the smooth-beach clam (*Atactodea glabrata*) is predominantly harvested along one section of sandy beach and only at an appropriate tidal level. Individuals who forage together, are thus more likely to consume more of the same foods. Since food types are linked to the use of different tool surfaces for hammering (Tan et al., 2015), this explanation might partially account for dyadic similarity in the use of edge hammering. However, this still does not account for the higher group level prevalence of point and edge hammering on Koram Island regardless of food type, when face hammering is likely more effective on unattached foods, and more common in the Piak Nam Yai population.

An addition caveat is that ecological differences between the Koram Island and Piak Nam Yai Island study sites have not been systematically examined. One factor in particular, which may contribute to the differences in stone usage and hammering patterns of the two populations, is differences in the material properties of the stones available on

the two islands. The rocky shores of Koram Island are composed of primarily limestone boulders that are small and craggy in appearance, while the rocky shores of Piak Nam Yai Island consist of primarily basalt boulders that are larger and smoother, and form large, smooth, stacked rock structures. Consequently, there could be differences in the stones available for use as tools on each island, that influence the ways in which the macaques can most effectively handle and utilize them. For example, it is possible that the limestone tools that the macaques on Koram Island primarily utilize are more prone to fracturing if the faces of stones are used to strike food items, as compared to the harder basalt tools on Piak Nam Yai Island, resulting in the development of more frequent tool point or edge usage for striking in the Koram population. These possibilities must be explored with more detailed analyses of the properties of tool stones used in each population. Further examining tool properties would also be useful for examining the tool preferences of individual macaques. In the current study, I used only the coarse measure of tool weight, but it is possible that macaques also base their tool choices on other lithic properties such as material and various shape and textural features, and these preferences could be socially influenced.

In summary, support for conformity in the tool-use behavioral patterns of macaques based on the findings of the current analyses is promising but not yet conclusive. Conformity appears to be especially evident in the ways in which macaques use different tool surfaces to strike foods, and in their food preferences. The possibility of genetic influences on behaviour, simpler explanations such as more closely affiliated individuals more often foraging in the same areas and thus converging on the same foods, and ecological differences influencing behavioural differences between study sites

however, have not been ruled out. The results here have therefore highlighted areas in which further research would be most productive. The large population on Koram Island, and other yet unstudied populations, could provide a good sample size for various longitudinal studies. For example, the changes in the social associations of a large number of developing individuals could be documented and correlated with behavioral outcomes (e.g. Perry, 2009). This would enable stronger inferences regarding which individuals most strongly influenced eventual behavioral conformity, and time points during young macaques' development at which their behavior is most susceptible to conformity biases. Study could extend into macaques' maturity, to examine the extent to which changes in patterns of social association could effect changes in the tool-use behaviour of mature macaques. Further research could also go beyond examining similarity between dyads, to identifying conformity biases amongst clusters within groups (e.g. Matthews, 2009). This would provide greater clarity into the extent to which more detailed inter-individual relationships and behavioral similarities produce larger scale group-level behavioral variation. Ultimately, these continued examinations into the detailed influences on both inter-individual and population-level behavioral patterning will advance scientific understanding of cultural processes in animals.

CHAPTER 6

GENERAL DISCUSSION AND FUTURE DIRECTIONS

The findings of this dissertation have provided the first description of the behavioral processes involved in the ontogeny of stone-tool use by long-tailed macaques. I found that the development of stone-tool use by the macaques on Koram Island is a 2 to 3-year process in which infants and juveniles extensively manipulate relevant materials, and engage in persistent trial-and-error before achieving tool use. It begins with all infants carrying out simple, mostly non-combinatorial manipulations, particularly on stones separately from food items. These simple manipulations are gradually replaced by combinatorial and percussive activity that peak in diversity at around 1.5 years of age, then begin to canalize towards manipulative activity that closely resembles those involved in tool use, with the object and action sequences for axe hammering generally preceding pound hammering. Inept percussive actions and erroneous object and action combinations and sequences persist for approximately another year before juveniles achieve their first successful tool use, suggesting that these aspects of tool use were the greatest challenges for young macaques. New tool users continue to refine their skills most drastically in the months following competence, and particularly in terms of strike accuracy and efficiency. Within this general pattern is considerable individual variation in terms of individuals' overall prevalence of manipulative and tool use activity, the emergence of different developmental mile stones, and for individuals that do achieve tool use, in their proficiency, the action patterns they use, and the food and tool choices they prefer.

Results suggest that variation in developmental outcomes are influenced both by developing individuals' active interaction with their environments and social partners, and

opportunities for social learning are further influenced by maternal behaviour and social relationships. I found that infant and juvenile macaques interacted extensively with tool-using group members, observing their tool use, and exploring their tools, including touching the tools while in use. These interactions contrast with the purely scrounging interactions of older macaques that did not develop tool use, therefore suggesting that young macaques carry out these interactions to obtain both food payoffs and information about tool use actions and materials. There was evidence for strategic interactions with tool users that were more productive and proficient, as these individuals were more often the targets of scrounging and observation. Further evidence for the importance of active interactions with tool users to tool-use development was provided by the finding that the rates of young macaques' interactions with tool users correlated with the frequency and complexity of their object manipulation behaviour. I also found that patterns of social relationships were a pervasive social influence on the development of tool skills in macaques. Patterns of social affiliation and inferred kinship not only strongly guided naïve macaques' interactions with tool users, but an individual's sociality was also the most significant source of social learning opportunities that influenced developmental speeds and outcomes, particularly after the early influences of mother's tool-use behaviour and sociality waned. Patterns of social affiliation and kinship also related to inter-individual behavioral similarity, with the tool use behaviour of more closely affiliated dyads evidencing conformity in terms of whether or not the pairs were tool users, and if so, in their hammering patterns and food choices.

This overview of how macaques are learning and developing tool-use skills through their active interactions with their physical and social environments, and how

these behavioral processes might be shaping their lithic traditions can contribute to ongoing discussion in the wider field of evolutionary biology. Some evolutionary biologists propose that conceptions of evolution should shift from viewing organisms and their behaviour as products of natural selection in response to environmental pressures, toward a “niche-construction perspective”, that perceives organisms simultaneously as agents in influencing how they evolve because they continuously modify their environments through their activities, and therefore co-engineer the selective pressures acting back on them and those that share their environments (Laland, Odling-Smee, & Feldman, 1996; 1999; 2001; Laland, Odling-Smee, & Gilbert, 2008; Laland & Sterelny, 2006; Odling-Smee, Laland, & Feldman, 1996; 2003; Sterelny, 2001). For cultural evolution, the implications are that behavioral traditions develop from complex, bidirectional interactions between genes, behaviours, and environments over extended time scales. Animals’ activities feed back into environmental and biological evolutionary processes in ways that augment the emergence and transmission of behaviour to conspecifics that share and inherit these niche constructed biological predispositions and environments. From this perspective, stone-tool use would have developed from a history of interactions between macaques that began to occupy coastal or island habitats and the conditions of their new environments, with the ways in which they adapted to and behaved in these environments influenced partially by existing biological predispositions. For example, macaques on islands could have begun foraging along the coasts in response to a limited availability of plant foods, a behavior facilitated by their generalist diets. They would have encountered and began exploring hard-shelled marine invertebrates, perhaps using predisposed action routines such as manipulating foods in combination with

surrounding rocky substrate. This may have led to the innovation of stone-tool use by one or several individuals, and later spread horizontally and vertically through the group via direct and indirect social learning processes. At any time during the history of these interactions, the ways in which macaques behaved would have altered the environment, or led to biological changes, which then influenced subsequent behaviour. Early stone and food manipulation or tool use by some individuals in the population may have created accumulation of stones in conjunction with food debris that were salient in the landscape. This altered environment could have fostered greater exploration by conspecifics and new macaques born into the population. Increased consumption of seafood may over time lead to biological changes in food preferences, and an increase in manipulative behaviour could need to changes in motor-neural connections and the manipulative capabilities of macaques (c.f. Chapter 2). These are just some examples of how an ongoing cycle of interactions, feedback, and changes could occur in ways that facilitate and reinforce the development of stone-tool use in new practitioners and its maintenance in the population.

The behavioral and social processes in the ontogeny of tool-use behaviour described in this dissertation, can be placed into a niche construction model of cultural evolution (Figure 6.1), as developing individuals not only inherit environments, but actively direct their learning behaviour and therefore participate in niche construction by influencing their own learning outcomes (Flynn, Laland, Kendal, & Kendal, 2013). The results of the current research show that young macaques are actively exploring stones and food items in their environments, persistently practicing tool-use skills, and preferentially seeking tool-use related information from group members. Findings also show that individuals' active learning behaviours interact with their physical and social

environments to result in different learning outcomes. Ontogenetic processes thus introduce behavioral variation into population and affect the ways in which the environment is modified by each generation. These processes would be occurring in different populations of macaques, with environmental, biological, and behavioral differences all contributing to variation in the stone-tool use traditions of different macaque populations.

Figure 6.1 A niche-construction model for the emergence, maintenance, and evolution of lithic traditions a coastal-living long-tailed macaque population. The ways in which macaques behave, that facilitate the emergence and maintenance of tool use, are not only products of existing biological and environmental conditions (inner circles), but create feedback (bidirectional arrows) that alter their environments and biology over evolutionary time (expanding circles). As found in the current research, young macaques actively interact with stones, shells, and food items in their environments, and their social partners, with effects on their development of tool use and patterns of behavioral variation. Through their learning processes, young macaques are therefore co-directors of the continued evolution of their stone-tool-use traditions.

Research into the lithic traditions of long-tailed macaques is still in its infancy, and many details regarding biological, environmental, and behavioural processes influencing stone-tool traditions remain to be understood. Continuing research can accumulate longitudinal data on individuals' behavioral patterns and social relationships over their lifespans. This will enable more direct examinations of how and when social and environmental influences present during formative periods affect developmental outcomes, and the extent to which these influences persist in behavioral patterns during maturity. The ongoing discovery of other populations of stone-tool-using long-tailed macaques will enable comparisons of the diversity of macaque stone-tool use across a greater number of individuals and groups living under different environmental conditions. Examinations of the relationships between individual, social, and ecological variables, with the patterning of behaviour across this larger sample will enable a better understanding of the relative effects of these factors underlying the macaque account of a rare lithic tradition. Over time, comparing how the different behavioral patterns of different populations of macaques affect their environments, and tracking the effects of these changes on the ontogeny and behaviour of subsequent generations would facilitate tests of the predictions of niche constructivist theories of cultural evolution, contributing to conceptual advances in the wider field of evolutionary biology.

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Appendix 1.

Current knowledge of long-tailed macaque stone-tool use

Populations exhibiting stone-tool use

Piak Nam Yai and Thao Islands

Piak Nam Yai (PNY) and Thao (TH) Islands are two adjacent islands located in Laem Son National Park (LSNP), Ranong province, Thailand. LSNP is located on the western seaboard of Thailand, and encompasses part of the coastal mainland, the Andaman Sea, and 15 islands within. Of these 15 islands, long-tailed macaques inhabit only PNY and TH. The islands are situated approximately 750m from the mainland. PNY is larger, with an area of 1.7km² and 5.4km of coastline, while TH is approximately 1.3km², with 5.3km of coastline. The islands' coasts are comprised of rocky shores, mangroves, and some sandy beaches.

The macaques on PNY and TH are unhabituated and will flee from human approach. They forage daily along the coast, which contain a wide variety of marine invertebrates and shore plants, and carry out tool use mainly on the rocky shores and in the mangroves. The population on PNY has been studied since 2005, and is the population on which all published work has been based thus far. The majority of macaques on PNY were individually identified during a population census in 2011, and the census estimated the population to consist of 192 individuals distributed across nine groups with overlapping home ranges. At least 88% of adults and adolescents, and 58% of the population were tool users (Gumert, Hamada, & Malaivijitnond, 2013). The population on TH is estimated at 60-100 individuals, but has not been formally surveyed.

Koram and Nom Sao Islands

Koram (KR) (N12°14'32", E100°0'34") and Nom Sao (NS) (N12°13'51", E100°0'17") Islands are two adjacent islands in Khao Sam Roi Yot National Park (KSRY), Prachuap Khiri Khan province, Thailand. KSRY is Thailand's first marine national park, and protects a coastal region on the eastern coast of Thailand, comprising areas of the mainland, islands, and waters of the Gulf of Thailand. KR is located in the Thai Gulf, about 1km offshore from the mainland. It is approximately 0.45km² in area, with 3.5km of coastline comprising of limestone cliff shore where it faces the open gulf, and rocky shores and sandy beaches on the side of the coast facing the mainland. NS is 0.37km southwest of KR, with a smaller area of 0.10km², with 1.32km of coastline. Both islands are arid and contain no freshwater bodies, with limestone karst interiors that are covered with dwarf evergreens and deciduous scrub flora.

The macaques on KR and NS are habituated as a result of regular provisioning by locals and tourists, but still forage naturally and carry out tool use. On KR, there are two groups of macaques, the larger of which was the group studied for this dissertational research. As of December 2014, the larger group contained 64 individuals, however, a total of 69 individuals contributed data to the current research (Table 2.1). 28 out of 39, or 76.3% of macaques in age classes in which tool use was observed (i.e. > 2.5 years) were tool users. The smaller group is not easily observed as they do not frequent the island's shore, but so far, six adults (♂ = 4 ♀ = 2), three adolescent males, and one juvenile male have been observed, with at least 1 adult male, 1 adult female, and 1 adolescent male using tools. On NS, there are at least nine adult males that have been individually identified, with at least 4 being tool users. There are no females or juveniles

on NS, and it is likely that the males were displaced from KR. Study of the KR population began in 2012, and is the population on which the current work is based.

Other reported but unstudied locations

Stone-tool-using long-tailed macaques have also been identified at several other locations in Thailand and Myanmar. Nearby to Piak Nam Yai Island, near Ranong City long-tailed macaques crack oysters around mangrove forest areas near the Pracharatrangsarith Temple, and possibly on Baan Koh Lao Island. These reports however, were based on information provided by locals of the area, and have not been witnessed firsthand by the researchers (Malaivijitnond et al., 2007). Ongoing explorations are discovering stone-tool using macaques at several other locations in Thailand and on islands of southern Myanmar (Gumert, unpublished data). The earliest report of long-tailed macaques using stone tools to crack oysters was actually based on serendipitous observations of islands in the Mergui Archipelago, off the coast of Myanmar (Carpenter, 1887). The current findings are suggesting that stone-tool use originated in long-tailed macaque populations in the Mergui Archipelago region, and that the Thai populations represent the tail-end of this rare behaviour's limited distribution.

Foods processed with stone tools

On PNY, the tool-processed diets of macaques consist of a wide variety of naturally occurring marine animal and plant species (Gumert & Malaivijitnond, 2012). In total, 47 species of foods processed with tools were identified, but the macaques concentrated on a small subset of the more abundant, accessible, and adequately sized prey. Four species of marine bivalves and gastropods made up 83% of the total sample food items surveyed, and these were predominantly rock oysters (*Saccostrea cucullata*),

nerite snails (*Nerita chamaeleon*), drills (*Thais bitubercularis*), and tooth-lipped snails (*Monodonta labio*). The rest of the food species comprised of various species of bivalves (clams, mussels, and cockles), gastropods (marine snails, conches, and limpets), crustaceans, and parts of several species of coastal plants: sea almonds (*Terminalia catappa*), coconut (*Cocos nicifera*), and pandan fruits (*Pandanus tectorius*).

Techniques and tool selection in relation to food characteristics

The food species described above can be most broadly categorized into two types: 1) sessile rock oysters, i.e. cemented onto its growth substrate, and 2) unattached or motile, i.e. capable of movement or being transportable (in the case of nuts and fruits), and are processed different by the macaques (Gumert, Kluck, & Malaivijitnond, 2009; Tan, Tan, Vyas, Malaivijitnond, & Gumert, 2015). Macaques process sessile rock oysters by striking at and cracking the outward facing valve of the oysters to obtain the flesh, typically using the precise points of smaller handheld stones, in a technique termed “axe hammering”. When processing unattached foods, they place the food item on an anvil surface before cracking it open, typically with the broader surfaces of larger tools, termed “pound hammering”. These behavioral observations of associations between techniques and food types have been corroborated by examinations of use-wear on stones used to process each food type (Gumert et al., 2009; Haslam, Gumert, Biro, Carvalho, & Malaivijitnond, 2013), however, there are variations within these two main techniques that will be described in the next section.

Apart from being sessile or unattached, food species also differ on other characteristics such as size and toughness, the macaques have been found to select stones of different mass accordingly (Gumert & Malaivijitnond, 2013). Field quasi experiments

were conducted in the form of “tool tests”, whereby four stones in different mass categories (X: 40-60g, S: 90-100g, M: 150-200g, L: 400-100g) were laid out at various locations along the shores of PNY, then monitored for use by macaques, to record the food types that chosen stones were used to process based on analyses of associated food debris. These tests revealed that macaques selected smaller to larger stones for processing sessile oysters, small gastropods, and large gastropods. Examinations of tool masses and associated food debris at natural tool sites further revealed that the macaques used tools of significantly different and increasing weight, when processing sessile oysters, nerite and snails, bivalves, drills and conches, with the largest stones being used to process nuts.

Variation in hammering and action patterns

Within the broad categorization of axe and pound hammering, there is considerable variation in the ways in which macaques handle tools, including idiosyncratic actions patterns used by a few or single individuals in the population (Tan et al., 2015). We found that macaques used either tool points, faces, or edges to strike food items, and defined three hammering classes as point hammering, face hammering, and edge hammering. The macaques on PNY commonly used point (42% of scan sampled tool-use instances) and face hammering (50%), but rarely used edge hammering (2%). Point and face hammering corresponded to the earlier descriptions of axe and pound hammering in terms of the food types and tool sizes they were associated with. Edge hammering was not particularly associated with either sessile or unattached food, this non-specificity and its rarity in the population could suggest it is a less effective or preferred technique for processing either food type at PNY.

We also identified 17 different actions patterns within point, face, and edge hammering, which are distinguished based on their combinations of tool material (stone or shell), hand use (unimanual or bimanual), posture (either seated or standing statically, or dynamically rising from seated to standing before striking), and striking motion (overhand, underhand, clapping, flipping, fulcrum) (descriptions and video of actions patterns in Tan et al. 2015). Individual macaques used between 1 – 4 action patterns. Both unimanual and bimanual actions patterns were common on PNY, with the most common action patterns being unimanual point hammering (58% of individuals sampled), symmetrical-bimanual face hammering (47%), and unimanual face hammering (37%). Unimanual edge hammering was relatively common (13%) compared to all other action patterns, which were recorded in less than 5% of the sampled population, thus reflecting more idiosyncratic behaviour.

Sex and age differences

Female and male macaques differed slightly in their tool-use behavioral patterns (Gumert, Low, & Malaivijitnond, 2011). Overall, females foraged with tools more often than males, and they more often processed sessile oysters with axe hammering than did males. Males processed unattached foods with pound hammering more often than females, although they also regularly axe hammered and consumed sessile oysters. Associated with these differences, are that females utilized smaller tools, and struck more frequently and at faster rates with tools than males did.

The same study also found several age-related differences in tool use behaviour. Immature tool users were found to use tools less than adults, used smaller tools, and struck sessile oysters faster but unattached foods slower than adult users. Tool use was

reportedly observed in macaques as young as one-year old, and stone-handling behaviours were seen in infant macaques that could not yet use tools.

Effects of human activity

Although PNY is protected and relatively pristine, there is increasing anthropogenic activity on the island, to the possible detriment of the macaques' stone-tool use behaviour (Gumert et al., 2013). The most significant form of human disturbance on PNY occurs appears to be the clearing of land to make way for oil palm, rubber, bitter bean, and coconut plantations, and the accompanying workers' settlements. Perhaps as a by-product of these establishments, domestic dogs have been introduced onto the island. Macaque groups that overlapped more greatly with plantations were found to have fewer juveniles, and frequented the island's shores less than groups that were more removed from human activity. Domestic dogs also often displaced the macaques from shores, and more intense dog activity was related to higher infant mortality in macaque groups. Over time, it is possible that the reduction of macaques' foraging opportunities on the island's shores, and the increased mortality rate of new individuals to the population will interfere with the continued transmission of stone-tool use behaviour to new practitioners, and diminish this rare behavioral tradition.

Preliminary comparisons between Piak Nam Yai and Koram Islands

A systematic comparison of the environments and tool-use behaviour on PNY and KR has not been carried out, but several differences are apparent. Some have been described above, i.e. the differences in levels of habituation and anthropogenic influences, and the lower overall prevalence of tool use in the KR versus the PNY population. In

addition to these, there are clear differences in the food types processed, and usage of different hammering classes and action patterns at KR.

The macaques on KR process a smaller variety of food species, and we have identified at least 24 species including both naturally occurring and provisioned foods (Table A1.1). Similar to PNY, the macaques on KR processed mainly sessile oysters, however, snails on KR are smaller, and the main snail species processed on KR are the tropical periwinkle, bifasciated ceriths, and tooth-lipped snails. Tropical periwinkles and bifasciated ceriths are also present but not preferred on PNY where the larger nerites, drills, and tooth-lipped snails are favoured. The macaques on KR also process a small proportion of bivalves and crabs, like on PNY. The plant seeds and nuts processed on PNY do not grow on KR, but the macaques on KR also process plant matter in the form of coconuts that occasionally wash ashore, and the dried seeds of mangoes that are seasonally provisioned to them. Other non-naturally occurring items that macaque crack with stones are glass drink bottles that occasionally wash onto shore.

There are several notable differences with regards to the types of hammering and diversity of action patterns used at KR versus PNY. As described in Chapter 5 of this dissertation, the macaques on KR more predominantly used point hammering, while the distribution of point and face hammering usage appears to be more equal at PNY. This appears to be due at least in part to the less strict association between point hammering and sessile food items on KR, with 18% of tool users also using point hammering when processing unattached food items, and 10% using point hammering regardless of whether they were processing sessile oysters or unattached food items. Also, although edge hammering was less frequently used than point and face hammering at both sites, a larger

percentage of the tool-using population on KR (50%) used edge hammering than at PNY (13%).

With regards to action patterns, there is a lower diversity of variation in the KR population than at PNY, with only 13 action patterns recorded (Table A1.2). Of these however, three of the action patterns observed on KR were not recorded at PNY, and these were bimanual asymmetrical point hammering, and bimanual asymmetrical food-to-stone face and edge hammering. Food-to-stone hammering action patterns are the idiosyncratic action patterns of one adult female in the group (Nms). Another distinct observation, is that the macaques on KR do not carry out bimanual action patterns, except for two individuals (Nms and Nhk) that exclusively do so and never use unimanual action patterns.

Table A1.1

Tool-processed foods by macaques on Koram Island, Khao Sam Roi Yot National Park. (#) indicate foods that were provisioned. Asterisks () indicate foods that have not been recorded in the tool-processed diets of macaques at the previously studied site, Piak Nam Yai Island, Laem Son National Park.*

Group	Genera	Species	Vernacular Names
Bivalve	<i>Saccostrea</i>	<i>cucullata</i>	Rock oyster
Bivalve	<i>Isognomon</i>	<i>isognomum</i>	Wader Tree Oyster*
Bivalve	<i>Gafrarium</i>	<i>divaricatum</i>	Forked venus clam
Bivalve	<i>Asaphis</i>	<i>violascens</i>	Pacific asaphis
Bivalve	<i>Atactodea</i>	<i>glabrata</i>	Smooth beach clam*
Bivalve	<i>Perna</i>	<i>viridis</i>	Asian green mussel [#]
Bivalve	<i>Anadara</i>	<i>granosa</i>	Blood cockle* [#]
Bivalve	<i>Paphia</i>	<i>undulata</i>	Short-necked clam* [#]
Gastropod	<i>Planaxis</i>	<i>sulcatus</i>	Tropical periwinkle
Gastropod	<i>Clypeomorus</i>	<i>bifasciatus</i>	Bifasciated cerith
Gastropod	<i>Pugilina</i>	<i>cochlidium</i>	Crown conch
Gastropod	<i>Monodonta</i>	<i>labio</i>	Tooth-lipped snail
Gastropod	<i>Tenguella</i>	<i>musiva</i>	Drupe or Rock Snail
Gastropod	<i>Echinolittorina</i>	<i>malaccana</i>	Knobbly Periwinkle*
Crab	<i>Grapsus</i>	<i>albolineatus</i>	Mottled Sally light-foot
Crab	<i>Thalamita</i>		Swimming crab
Crab	<i>Myomenippe</i>	<i>hardwickii</i>	Stone or Thunder crab
Crab	<i>Eriphia</i>	<i>ferox</i>	Ferocious reef crab*
Crab	<i>Atergatis</i>	<i>integerrimus</i>	Red egg crab*
Crab	<i>Clibanarius</i>	<i>vittatus</i>	Hermit crab*
Crab	<i>Leptodius</i>	<i>affinis</i>	Brachyuran crab
Crab	<i>Petrolisthes</i>	<i>aff hastatus</i>	Porcelain crab
Plant	<i>Cocos</i>	<i>nicifera</i>	Coconut
Plant	<i>Mangifera</i>	<i>indica</i>	Mango* [#]

Table A1.2

Hammering classes and action patterns observed in the stone-tool use of macaques on Koram Island. Asterisks () indicate action patterns that have not been observed at Piak Nam Yai and Thao Islands.*

Hammering Class / Action Pattern	Description
<i>Point Hammering</i>	<i>Hammering in which corners and pointed protuberances of a tool are used to strike food items.</i>
Unimanual	Point hammering where the tool is held in either the left or right hand.
Bimanual Point	Point hammering using two hands, where both hands handle the tool with the same grip and exert similar force in striking the food item.
Asymmetrical Bimanual Point	Point hammering using two hands, where one hand grips the stone and provides downward force during striking, while the other hand supports the stone and assists in lifting the tool.
Unimanual Supported	Unimanual point hammering where the food item is attached to a mobile rock that is supported by the non -striking hand.
<i>Face Hammering</i>	<i>Hammering in which the faces of a tool, i.e. the flat open surfaces of the stone that spanned the full length and width of stones were used to strike food items.</i>
Unimanual	Face hammering where the tool is held in either the left or right hand.
Bimanual Symmetrical	Face hammering using two hands, where both hands handle the tool with the same grip and exert similar force in striking the food item.
Bimanual Asymmetrical	Face hammering using two hands, where one hand grips the stone and provides downward force during striking, while the other supports the stone and assists in lifting the tool.
Bimanual Asymmetrical	Face hammering using two hands, where one hand grips the stone and provides downward force during striking, while the other hand brings the food into contact with the bottom face of the stone and holds it in place before both the stone and food item are struck down onto the anvil together. The hand holding the food item is quickly withdrawn before contact with the anvil is made.
Food-to-Stone *	
Flip	Bimanual asymmetrical face hammering where the stone is raised and flipped before it is brought down onto the food item.
<i>Edge Hammering</i>	<i>Hammering in which the edges of a tool, i.e. the sides along the lengths and widths of the tools were used to strike food items.</i>
Unimanual	Edge hammering where the tool is held in either the left or right hand.
Bimanual Symmetrical	Edge hammering using two hands, where both hands handle the tool with the same grip and exert similar force in striking the food item.
Bimanual Asymmetrical	Edge hammering using two hands, where one hand grips the stone and provides downward force during striking, while the other supports the stone and assists in lifting the tool.

<i>Hammering Class / Action Pattern</i>	Description
Bimanual Asymmetrical Food-to-Stone *	Edge hammering using two hands, where one hand grips the stone and provides downward force during striking, while the other hand brings the food into contact with the bottom face of the stone and holds it in place before both the stone and food item are struck down onto the anvil together. The hand holding the food item is quickly withdrawn before contact with the anvil is made.

APPENDIX 2

List of Matrices (Chapter 3)

Tool-Related Interaction Matrices

TRI I. Directed interaction matrix between immatures and tool users (Immature x User), where cell values represent the % of each immature's (rows) interactions that each tool user (column) was the target.

TRI I(S). Directed interaction matrix between immatures and tool users (Immature x User) processing sessile oysters, where cell values represent the % of each immature's (rows) interactions that each tool user (column) was the target.

TRI I(U). Directed interaction matrix between immatures and tool users (Immature x User) processing unattached food, where cell values represent the % of each immature's (rows) interactions that each tool user (column) was the target.

TRI M. Directed interaction matrix between mature non-users and tool users (Mature Non-User x User), where cell values represent the % of each non-user's (rows) interactions that each tool user (column) was the target.

TRI M(S). Directed interaction matrix between mature non-users and tool users (Mature Non-User x User) processing sessile oysters, where cell values represent the % of each non-user's (rows) interactions that each tool user (column) was the target.

Social Relationship Matrices (Used in Tau *Kr* tests with corresponding TRI matrices, and partialled out in partial Tau *Kr* tests between TRI matrices and tool-users' demographic attributes and tool-use characteristics matrices).

Prox I(S). Proximity-based association matrix corresponding to TRI I and TRI I(S)

Prox I(U). Proximity-based association matrix corresponding to TRI I(U)

Prox M(S). Proximity-based association matrix corresponding to TRI M and TRI M(S)

Groom I(S). Grooming-based association matrix corresponding to TRI I and TRI I(S)

Groom I(U). Grooming-based association matrix corresponding to TRI I(U)

Groom M(S). Grooming-based association matrix corresponding to TRI M and TRI M(S)

Kin I(S). Inferred kinship matrix corresponding to TRI I and TRI I(S)

Kin I(U). Inferred kinship matrix corresponding to TRI I(U)

Kin M(S). Inferred kinship matrix corresponding to TRI M and TRI M(S)

Tool-Users' Demographic Attributes

Age I. Tool user's age corresponding to TRI I

Age M. Tool users' sex corresponding to TRI M

Sex I. Tool user's age corresponding to TRI I

Sex M. Tool users' sex corresponding to TRI M

Rank I. Tool user's rank relative to partner corresponding to TRI I

Rank M. Tool users' rank relative to partner corresponding to TRI M

Tool-Users' Tool-Use Characteristics

Prop I. Proportion of foraging time spent using tools corresponding to TRI I

Prop M. Proportion of foraging time spent using tools corresponding to TRI M

Rate I. Rate of tool use corresponding to TRI I

Rate M. Rate of tool use corresponding to TRI M

Strike I(S). Average strike frequency on sessile oysters, corresponding to TRI I(S)

Strike I(U). Average strike frequency on unattached foods, corresponding to TRI I(U)

Strike M(S). Average strike frequency on sessile oysters, corresponding to TRI M(S)

Accuracy I(S). Average proportion of accurate strikes on sessile oysters, corresponding to TRI I(S)

Accuracy I(U). Average proportion of accurate strikes on unattached food, corresponding to TRI I(U)

Accuracy M(S). Average proportion of accurate strikes on sessile oysters, corresponding to TRI M(S)

Fidelity I(S). Average frequency of tool changes per bout of cracking sessile oysters, corresponding to TRI I(S)

Fidelity I(U). Average frequency of tool changes per bout of cracking unattached food, corresponding to TRI I(U)

Fidelity M(S). Average frequency of tool changes per bout of cracking sessile oysters, corresponding to TRI M(S)

Success I(S). Proportion of successful bouts on sessile oysters, corresponding to TRI I(S)

Success I(U). Proportion of successful bouts on unattached food, corresponding to TRI I(U)

Success M(S). Proportion of successful bouts on sessile oysters, corresponding to TRI M(S)

Tool-Related Interaction Matrices

TRI I

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	6	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	2	0	0	67	0	8	0	0	3	6	2
Dam	52	0	0	9	4	0	0	0	4	0	0	0	9	0	0	0	0	0	0	0	17	0	0	4	0	0	4	0
Dat	8	0	0	2	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	2	0	4	10	10
Dwg	0	0	0	0	0	0	0	0	93	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Fgn	3	13	0	0	3	6	0	3	3	6	16	3	3	0	0	0	3	3	0	9	0	0	16	0	0	9	0	0
Gbi	0	4	0	4	0	0	0	0	0	0	0	4	18	7	0	0	0	0	0	0	11	0	0	11	0	0	18	14
Hmp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	50	0	0
Jgr	0	0	5	0	0	5	0	0	5	5	5	0	0	10	0	0	0	0	24	10	0	5	0	0	0	24	0	10
Jrk	41	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	6	0	0	0	6	0	0	6	0	18	6	6
Kgk	4	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	13	0	4	61	0	9	4	0
Kng	5	5	5	5	5	5	0	5	0	0	0	5	0	0	0	0	0	0	10	0	5	5	10	0	0	24	0	0
Mek	33	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	33	0	11	0	33
Mnm	3	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	6	0	69	3	3	0	0	3	0	0	0	3
Mpr	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	33	33	33	33	33	33	67	33
Mty	15	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	4	0	0	0	19	0	4	0	0	12	8	0
Nmk	11	0	5	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	3	0	0	3	0	0	66	0
Nmt	30	10	0	0	10	0	0	0	20	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10	0
Nrk	67	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	8	8	0	0	0	0
Otn	0	0	0	3	0	12	0	0	0	0	0	44	0	3	0	0	0	3	3	0	0	0	6	6	0	6	0	3
Pld	14	0	0	2	2	0	0	4	0	0	2	0	2	0	0	0	0	0	0	0	0	0	2	0	0	4	62	0
Pri	9	3	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	3	0	0	0	0
Pyn	9	2	0	18	0	0	0	7	0	0	0	2	0	4	0	0	2	0	4	0	4	0	0	2	0	42	2	0
Sai	12	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	65	4	0	0	0	4
Tng	15	0	0	0	4	0	0	0	0	0	0	0	4	0	0	0	46	0	12	0	8	0	0	8	0	4	0	0
Tpt	2	0	0	0	0	0	0	0	0	0	2	0	65	0	0	0	2	7	2	0	0	0	0	0	0	0	7	13
Tuk	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0
Waw	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	2	87	0	1	3	1

TRI I(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	6	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	2	0	0	67	0	8	0	0	3	6	2
Dam	52	0	0	9	4	0	0	0	4	0	0	0	9	0	0	0	0	0	0	0	17	0	0	4	0	0	4	0
Dat	8	0	0	2	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	2	0	4	10	10
Dwg	0	0	0	0	0	0	0	0	93	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Fgn	3	13	0	0	3	6	0	3	3	6	16	3	3	0	0	0	3	3	0	9	0	0	16	0	0	9	0	0
Gbi	0	4	0	4	0	0	0	0	0	0	0	4	18	7	0	0	0	0	0	0	11	0	0	11	0	0	18	14
Hmp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	50	0	0
Jgr	0	0	5	0	0	5	0	0	5	5	5	0	0	10	0	0	0	0	24	10	0	5	0	0	0	24	0	10
Jrk	41	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	6	0	0	0	6	0	0	6	0	18	6	6
Kgk	4	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	13	0	4	61	0	9	4	0
Kng	5	5	5	5	5	5	0	5	0	0	0	5	0	0	0	0	0	0	10	0	5	5	10	0	0	24	0	0
Mek	33	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	33	0	11	0	33
Mnm	3	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	6	0	69	3	3	0	0	3	0	0	0	3
Mpr	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	33	33	33	33	33	33	67	33
Mty	15	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	4	0	0	0	19	0	4	0	0	12	8	0
Nmk	11	0	5	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	3	0	0	3	0	0	66	0
Nmt	30	10	0	0	10	0	0	0	20	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10	0
Nrk	67	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	8	8	0	0	0	0
Otn	0	0	0	3	0	12	0	0	0	0	0	44	0	3	0	0	0	3	3	0	0	0	6	6	0	6	0	3
Pld	14	0	0	2	2	0	0	4	0	0	2	0	2	0	0	0	0	0	0	0	0	0	2	0	0	4	62	0
Pri	9	3	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	3	0	0	0	0
Pyn	9	2	0	18	0	0	0	7	0	0	0	2	0	4	0	0	2	0	4	0	4	0	0	2	0	42	2	0
Sai	12	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	65	4	0	0	0	4
Tng	15	0	0	0	4	0	0	0	0	0	0	0	4	0	0	0	46	0	12	0	8	0	0	8	0	4	0	0
Tpt	2	0	0	0	0	0	0	0	0	0	2	0	65	0	0	0	2	7	2	0	0	0	0	0	0	0	7	13
Tuk	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0
Waw	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	2	87	0	1	3	1

TRI I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	0	0	0	0	0	0	0	40	0	0	0	0	60	0	0	0	0	0
Dat	0	0	0	0	0	0	0	0	0	67	0	0	0	0	0	0	0	0
Dwg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0
Gbi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0
Jrk	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0
Mek	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0
Mnm	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0
Mpr	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0
Nmk	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0
Tpt	0	0	0	0	0	0	25	0	75	0	0	0	0	0	0	0	0	0
Waw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0

TRI M

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	43	0	0	36	0	0
Hkr	6	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	44	0	0	19	0	6
Jsl	0	10	0	0	20	0	0	10	0	10	0	10	0	0	0	10	0	0	0	20	0	0	0	0	0	10	0	0
Mgp	0	0	0	0	0	0	0	13	0	19	6	6	6	0	0	0	6	0	0	0	6	6	19	13	0	0	6	6
Nee	0	0	0	0	0	0	7	0	0	7	7	7	0	13	0	0	13	7	0	0	0	0	0	0	0	27	13	0
Ngk	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	11	0	0	0	0	0	0	0	0	0	56
Pla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	0	33	0	33	0	0
Poo	5	0	0	0	0	0	0	0	0	0	5	18	0	0	0	0	9	0	23	5	14	0	5	5	0	5	0	0
Som	5	0	0	0	0	19	0	5	5	5	0	0	5	0	0	0	0	0	10	0	0	38	0	0	0	5	5	0
Suy	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	33
Yak	0	0	0	0	0	33	0	22	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	33	0	0
Yng	0	0	0	0	0	0	0	7	7	0	0	7	0	0	0	0	7	0	0	7	0	0	0	43	0	7	7	0

TRI M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	43	0	0	36	0	0
Hkr	6	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	44	0	0	19	0	6
Jsl	0	10	0	0	20	0	0	10	0	10	0	10	0	0	0	10	0	0	0	20	0	0	0	0	0	10	0	0
Mgp	0	0	0	0	0	0	0	13	0	19	6	6	6	0	0	0	6	0	0	0	6	6	19	13	0	0	6	6
Nee	0	0	0	0	0	0	7	0	0	7	7	7	0	13	0	0	13	7	0	0	0	0	0	0	0	27	13	0
Ngk	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	11	0	0	0	0	0	0	0	0	0	56
Pla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	0	33	0	33	0	0
Poo	5	0	0	0	0	0	0	0	0	0	5	18	0	0	0	0	9	0	23	5	14	0	5	5	0	5	0	0
Som	5	0	0	0	0	19	0	5	5	5	0	0	5	0	0	0	0	0	10	0	0	38	0	0	0	5	5	0
Suy	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	33
Yak	0	0	0	0	0	33	0	22	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	33	0	0
Yng	0	0	0	0	0	0	0	7	7	0	0	7	0	0	0	0	7	0	0	7	0	0	0	43	0	7	7	0

Social Relationship Matrices – Proximity-Based Association Matrices

Prox I(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.03	0.08	0.00	0.00	0.00	0.04	0.01	0.01	0.00	0.41	0.00	0.05	0.04	0.01	0.00	0.03	0.02
Dam	0.13	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.05	0.01	0.01	0.03	0.01	0.00	0.05	0.00
Dat	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.04	0.00	0.00	0.00	0.34	0.00	0.01	0.00	0.04	0.01	0.03	0.02	0.01	0.00	0.01	0.01
Dwg	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Fgn	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.07	0.02	0.00	0.01
Gbi	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.07	0.01	0.00	0.00	0.02	0.01	0.01	0.00	0.05	0.00	0.05	0.05	0.01	0.00	0.04	0.01
Hmp	0.03	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.02	0.00	0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.01	0.01	0.00
Jgr	0.01	0.01	0.01	0.00	0.00	0.02	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.02	0.00	0.05	0.00	0.00	0.00	0.00	0.01	0.01
Jrk	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.03	0.03	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.02	0.01	0.01	0.02	0.02	0.02	0.03	0.01
Kgk	0.03	0.00	0.01	0.01	0.00	0.00	0.00	0.02	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.03	0.00	0.01	0.05	0.01	0.01	0.03	0.00
Kng	0.02	0.01	0.01	0.00	0.00	0.01	0.00	0.03	0.00	0.02	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.05	0.01	0.01	0.01	0.00	0.00	0.02	0.00
Mek	0.02	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.03	0.07	0.01	0.00	0.00	0.03	0.01	0.02	0.00	0.03	0.00	0.02	0.03	0.01	0.00	0.05	0.06
Mnm	0.02	0.00	0.00	0.01	0.00	0.02	0.00	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02	0.00	0.25	0.01	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.00
Mpr	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.07	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.02	0.00	0.03	0.02	0.01	0.01	0.02	0.01
Mty	0.06	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.02	0.21	0.00	0.00	0.00	0.02	0.00	0.01	0.00	0.04	0.00	0.02	0.02	0.02	0.01	0.03	0.00
Nmk	0.02	0.00	0.01	0.03	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.04	0.01	0.00	0.00	0.00	0.01	0.02	0.00	0.03	0.03	0.01	0.01	0.01	0.01	0.27	0.02
Nmt	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.01	0.01	0.00	0.01	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.02	0.02	0.01	0.01	0.01	0.00
Nrk	0.06	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.04	0.00	0.04	0.02	0.00	0.01	0.00	0.00
Otn	0.02	0.00	0.01	0.03	0.00	0.01	0.00	0.01	0.01	0.00	0.06	0.26	0.02	0.02	0.00	0.00	0.02	0.00	0.01	0.00	0.03	0.02	0.03	0.04	0.02	0.01	0.01	0.01
Pld	0.02	0.00	0.00	0.00	0.01	0.01	0.00	0.03	0.02	0.00	0.02	0.01	0.02	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.02	0.00	0.02	0.04	0.01	0.02	0.30	0.01
Pri	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.02	0.02	0.00	0.00	0.00	0.00
Pyn	0.01	0.00	0.00	0.03	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.03	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.00	0.03	0.03	0.00	0.15	0.02	0.00
Sai	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.04	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.03	0.00	0.39	0.02	0.02	0.01	0.02	0.02
Tng	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.02	0.00	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.16	0.01	0.01	0.02	0.00	0.00	0.00	0.01	0.02	0.02	0.01	0.01
Tpt	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.50	0.01	0.00	0.00	0.02	0.02	0.01	0.00	0.02	0.00	0.03	0.01	0.02	0.00	0.07	0.04
Tuk	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.01	0.07	0.01	0.00	0.00	0.01	0.01	0.02	0.00	0.01	0.00	0.00	0.02	0.01	0.00	0.47	0.03
Waw	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.03	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.03	0.00	0.03	0.31	0.01	0.00	0.02	0.02

Prox I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.08	0.04	0.01	0.00	0.41	0.00	0.05	0.04	0.01	0.03
Dat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.04	0.34	0.01	0.00	0.04	0.01	0.03	0.02	0.01	0.01
Dwg	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Gbi	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.07	0.02	0.01	0.00	0.05	0.00	0.05	0.05	0.01	0.04
Jrk	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.03	0.03	0.02	0.00	0.00	0.02	0.01	0.01	0.02	0.02	0.03
Mek	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.03	0.07	0.03	0.02	0.00	0.03	0.00	0.02	0.03	0.01	0.05
Mnm	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.01	0.02	0.25	0.01	0.00	0.00	0.01	0.00	0.01	0.01
Mpr	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.07	0.03	0.01	0.00	0.02	0.00	0.03	0.02	0.01	0.02
Nmk	0.00	0.01	0.00	0.00	0.04	0.00	0.00	0.00	0.04	0.00	0.02	0.00	0.03	0.03	0.01	0.01	0.01	0.27
Pyn	0.00	0.00	0.01	0.00	0.01	0.00	0.01	0.00	0.03	0.02	0.00	0.00	0.03	0.00	0.03	0.03	0.00	0.02
Tng	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.01	0.00	0.16	0.01	0.02	0.00	0.00	0.00	0.01	0.02	0.01
Tpt	0.00	0.02	0.00	0.00	0.01	0.00	0.00	0.01	0.50	0.02	0.01	0.00	0.02	0.00	0.03	0.01	0.02	0.07
Waw	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.03	0.03	0.01	0.00	0.03	0.00	0.03	0.31	0.01	0.02

Prox M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.03	0.00	0.03	0.02	0.01	0.00	0.00	0.00	0.05	0.00	0.01	0.00	0.03	0.00	0.02	0.05	0.00	0.01	0.01	0.01
Hkr	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.02	0.00	0.02	0.01	0.02	0.01	0.01	0.03
Jsl	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Mgp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00
Nee	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.03	0.02	0.04	0.01	0.00	0.00	0.03	0.01	0.01	0.00	0.06	0.00	0.03	0.05	0.02	0.04	0.01	0.02
Ngk	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.02	0.00	0.00	0.01	0.01	0.00	0.00	0.03	0.00	0.03	0.01	0.02	0.02	0.01	0.04
Pla	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.02	0.02	0.05	0.00	0.00	0.00	0.04	0.00	0.04	0.00	0.04	0.00	0.08	0.03	0.03	0.01	0.00	0.00
Poo	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.03	0.03	0.06	0.00	0.00	0.00	0.04	0.00	0.04	0.00	0.09	0.00	0.07	0.10	0.07	0.01	0.04	0.01
Som	0.01	0.02	0.01	0.01	0.00	0.04	0.01	0.07	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.09	0.00	0.01	0.01	0.00	0.00	0.00
Suy	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.04	0.04	0.01	0.01	0.00	0.01	0.00	0.01	0.00	0.02	0.00	0.01	0.03	0.02	0.00	0.01	0.03
Yak	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Yng	0.00	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.02	0.01	0.06	0.03	0.07	0.01	0.00	0.00	0.05	0.00	0.03	0.00	0.11	0.00	0.05	0.04	0.03	0.02	0.04	0.01

Social Relationship Matrices – Grooming-Based Association Matrices

Groom I(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dam	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dwg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fgn	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00
Gbi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hmp	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.02	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Jgr	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
Jrk	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Kgk	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Kng	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.01	0.00	0.00	0.01	0.00
Mek	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mnm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mpr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mty	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Nmk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00
Nmt	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nrk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Otn	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pld	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00
Pri	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Pyn	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00
Sai	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tng	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Tpt	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tuk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Waw	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00

Groom I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Dat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dwg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gbi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jrk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Mek	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mnm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mpr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nmk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06
Pyn	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tng	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
Tpt	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Waw	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00

Groom M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Hkr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.04
Jsl	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Mgp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nee	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.04	0.00	0.03
Ngk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Pla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Poo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Som	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Suy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.04
Yak	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Yng	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.02	0.00	0.00	0.00	0.00	0.02	0.00	0.00

Social Relationship Matrices – Inferred Kinship Matrices

Kin I(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dam	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Dat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Dwg	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fgn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gbi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hmp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jgr	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Jrk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kgk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Kng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mek	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mnm	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Mpr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mty	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nmk	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nmt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nrk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Otn	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pld	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pyn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Sai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Tpt	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tuk	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Waw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Kin I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Dat	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Dwg	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Gbi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Jrk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mek	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mnm	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Mpr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nmk	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Pyn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tng	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Tpt	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Waw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Kin M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hkr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Jsl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mgp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ngk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Som	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Suy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yak	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Tool-Users' Demographic Attributes Matrices

Age I

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Dam	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Dat	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Dwg	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Fgn	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Gbi	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Hmp	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Jgr	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Jrk	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Kgk	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Kng	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Mek	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Mnm	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Mpr	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Mty	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Nmk	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Nmt	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Nrk	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Otn	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Pld	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Pri	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Pyn	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Sai	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Tng	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Tpt	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Tuk	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Waw	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7

Age M

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Hkr	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Jsl	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Mgp	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Nee	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Ngk	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Pla	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Poo	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Som	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Suy	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Yak	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7
Yng	7	5	4	7	5	5	6	5	7	5	5	7	7	6	7	7	7	6	7	4	7	4	7	6	7	7	7	7

Sex I

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Dam	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Dat	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Dwg	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Fgn	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Gbi	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Hmp	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Jgr	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Jrk	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Kgk	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Kng	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Mek	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Mnm	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Mpr	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Mty	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Nmk	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Nmt	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Nrk	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Otn	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
PI d	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Pri	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Pyn	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Sai	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Tng	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Tpt	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Tuk	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Waw	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1

Sex M

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Hkr	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Jsl	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Mgp	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Nee	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Ngk	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Pla	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Poo	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Som	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Suy	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Yak	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1
Yng	1	1	1	1	2	1	1	1	2	1	2	2	2	1	1	1	2	1	2	1	2	1	2	2	2	2	2	1

Rank I

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Dam	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Dat	1	1	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	1
Dwg	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	1
Fgn	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1
Gbi	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Hmp	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1
Jgr	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	1	1	0	1	0	0	1	0	0	1	1
Jrk	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Kgk	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Kng	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Mek	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Mnm	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	0	1	1	0	1	0	0	1	0	0	1	1
Mpr	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Mty	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1
Nmk	1	1	0	1	0	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1
Nmt	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Nrk	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Otn	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	1	1
Pld	1	1	0	1	0	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1
Pri	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1
Pyn	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
Sai	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tng	1	1	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	1
Tpt	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1
Tuk	1	1	0	1	0	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1
Waw	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	1	0	1	1

Rank M

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Hkr	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Jsl	1	0	1	1	0	1	1	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1
Mgp	1	0	1	1	0	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Nee	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	1	1
Ngk	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Pla	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Poo	1	1	1	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1
Som	1	1	0	1	0	1	1	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Suy	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Yak	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Yng	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1

User's Tool-Use Characteristics – Productivity Matrices

Prop I

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Dam	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Dat	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Dwg	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Fgn	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Gbi	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Hmp	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Jgr	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Jrk	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Kgk	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Kng	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Mek	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Mnm	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Mpr	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Mty	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Nmk	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Nmt	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Nrk	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Otn	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Pld	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Pri	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Pyn	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Sai	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Tng	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Tpt	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Tuk	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Waw	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82

Prop M

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Hkr	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Jsl	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Mgp	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Nee	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Ngk	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Pla	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Poo	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Som	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Suy	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Yak	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82
Yng	0.64	0.49	0.42	0.69	0.48	0.63	0.63	0.65	0.46	0.56	0.50	0.57	0.70	0.57	0.15	0.55	0.55	0.57	0.50	0.48	0.62	0.57	0.74	0.46	0.09	0.79	0.71	0.82

Rate I

	Asg	Chg	Chk	ChI	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Dam	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Dat	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Dwg	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Fgn	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Gbi	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Hmp	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Jgr	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Jrk	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Kgk	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Kng	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Mek	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Mnm	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Mpr	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Mty	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Nmk	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Nmt	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Nrk	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Otn	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Pld	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Pri	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Pyn	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Sai	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Tng	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Tpt	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Tuk	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Waw	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08

Rate M

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Hkr	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Jsl	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Mgp	0.97	1.32	0.93	0.93	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Nee	0.97	1.32	0.93	0.93	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Ngk	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Pla	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Poo	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Som	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Suy	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Yak	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08
Yng	0.97	1.32	0.93	1.34	1.19	1.18	1.97	1.61	0.79	1.19	1.06	1.47	1.43	0.99	0.17	0.98	1.27	0.85	0.95	1.00	1.62	1.47	1.50	1.38	0.22	2.41	1.68	2.08

User's Tool-Use Characteristics – Proficiency Matrices

Strike I(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Dam	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Dat	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Dwg	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Fgn	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Gbi	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Hmp	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Jgr	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Jrk	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Kgk	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Kng	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Mek	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Mnm	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Mpr	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Mty	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Nmk	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Nmt	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Nrk	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Otn	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Pld	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Pri	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Pyn	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Sai	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Tng	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Tpt	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Tuk	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Waw	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11

Strike I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Dat	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Dwg	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Gbi	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Jrk	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Mek	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Mnm	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Mpr	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Nmk	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Pyn	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Tng	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Tpt	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92
Waw	3.95	11.51	13.93	2.76	9.40	5.04	6.45	7.89	8.83	6.86	3.41	9.36	4.93	5.31	5.70	4.27	2.80	10.92

Strike M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Hkr	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Jsl	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Mgp	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Nee	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Ngk	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Pla	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Poo	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Som	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Suy	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Yak	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11
Yng	10	9.5	16	12	10	6.1	11	13	10	8.8	9	9.1	9.3	14	21	9.2	7.8	14	8.6	14	8.5	9.1	7.5	7	4.7	6.6	11	11

Accuracy I(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Dam	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Dat	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Dwg	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Fgn	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Gbl	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Hmp	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Jgr	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Jrk	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Kgk	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Kng	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Mek	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Mnm	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Mpr	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Mty	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Nmk	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Nmt	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Nrk	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Otn	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Pld	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Pri	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Pyn	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Sai	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Tng	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Tpt	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Tuk	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Waw	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00

Accuracy I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Dat	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Dwg	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Gbi	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Jrk	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Mek	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Mnm	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Mpr	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Nmk	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Pyn	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Tng	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Tpt	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77
Waw	0.63	0.59	0.37	0.95	0.56	0.76	0.98	0.85	0.97	1.00	1.00	0.87	0.92	0.77	0.91	0.91	0.70	0.77

Accuracy M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Hkr	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Jsl	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Mgp	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Nee	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Ngk	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Pla	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Poo	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Som	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Suy	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Yak	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00
Yng	0.99	0.94	0.86	1.00	0.95	0.99	0.99	0.99	1.00	0.91	0.99	1.00	1.00	1.00	0.95	1.00	1.00	1.00	0.99	0.97	0.99	0.95	0.99	0.99	0.85	1.00	0.96	1.00

Fidelity I(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Dam	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Dat	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Dwg	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Fgn	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Gbl	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Hmp	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Jgr	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Jrk	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Kgk	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Kng	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Mek	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Mnm	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Mpr	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Mty	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Nmk	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Nmt	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Nrk	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Otn	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Pld	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Pri	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Pyn	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Sai	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Tng	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Tpt	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Tuk	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Waw	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00

Fidelity I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Dat	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Dwg	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Gbi	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Jrk	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Mek	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Mnm	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Mpr	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Nmk	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Pyn	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Tng	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Tpt	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08
Waw	0.03	0.51	0.27	0.02	0.30	0.02	0.01	0.02	0.06	0.04	0.00	0.00	0.00	0.02	0.07	0.02	0.03	0.08

Fidelity M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Hkr	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Jsl	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Mgp	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Nee	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Ngk	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Pla	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Poo	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Som	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Suy	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Yak	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Yng	0.00	0.00	0.09	0.01	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.01	0.04	0.00	0.29	0.00	0.01	0.00	0.00	0.04	0.00	0.02	0.01	0.04	0.03	0.00	0.00	0.00

Success I(S)

	Asg	Chg	Chk	ChI	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Cha	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Dam	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Dat	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Dwg	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Fgn	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Gbl	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Hmp	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Jgr	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Jrk	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Kgk	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Kng	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Mek	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Mnm	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Mpr	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Mty	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Nmk	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Nmt	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Nrk	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Otn	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Pld	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Pri	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Pyn	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Sai	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Tng	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Tpt	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Tuk	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Waw	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88

Success I(U)

	Chg	Chk	Cht	Dto	Hee	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Pet
Cha	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Dat	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Dwg	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Gbi	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Jrk	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Mek	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Mnm	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Mpr	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Nmk	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Pyn	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Tng	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Tpt	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00
Waw	0.67	0.65	0.53	0.93	0.80	0.64	0.85	0.88	0.97	1.00	0.88	0.84	0.80	0.77	0.70	0.95	0.74	1.00

Success M(S)

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Fhn	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Hkr	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Jsl	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Mgp	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Nee	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Ngk	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Pla	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Poo	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Som	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Suy	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Yak	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88
Yng	0.87	0.79	0.57	0.90	0.82	0.92	0.95	0.83	0.76	0.82	0.81	0.89	0.88	0.88	0.57	0.90	0.90	0.86	0.92	0.80	0.87	0.83	0.93	0.83	0.79	0.91	0.84	0.88

APPENDIX 3

List of Matrices (Chapter 5)

Social Relationship Matrices

Proximity Based Association Matrices

- Prox 1. Proximity-based association matrix containing all individuals of tool-using age
- Prox 1F. Proximity-based association matrix containing all females of tool-using age
- Prox 2. Proximity-based association matrix containing tool users
- Prox 2F. Proximity-based association matrix containing female tool users
- Prox 3. Proximity-based association matrix containing tool users with > 10 collected tools
- Prox 3F. Proximity based association matrix containing female tool users with > 10 collected tools

Grooming Based Association Matrices

- Groom 1. Grooming-based association matrix containing all individuals of tool-using age
- Groom 1F. Grooming-based association matrix containing all females of tool-using age
- Groom 2. Grooming-based association matrix containing tool users
- Groom 2F. Grooming-based association matrix containing female tool users
- Groom 3. Grooming-based association matrix containing tool users with > 10 collected tools
- Groom 3F. Grooming-based association matrix containing female tool users with > 10 collected tools

Inferred Kinship Matrices

- Kin 1. Inferred kinship matrix containing all individuals of tool-using age
- Kin 1F. Inferred kinship matrix containing all females of tool-using age
- Kin 2. Inferred kinship matrix containing tool users
- Kin 2F. Inferred kinship matrix containing tool users
- Kin 3. Inferred kinship matrix containing tool users with > 10 collected tools
- Kin 3F. Inferred kinship matrix containing female tool users with > 10 collected tools

Similarity Matrices

- User. User similarity matrix corresponding to Prox 1, Groom 1, and Kin 1
- User F. User similarity matrix of females, corresponding to Prox 1F, Groom 1F, and Kin 1F

Time. Time similarity matrix corresponding to Prox 2, Groom 2, and Kin 2

Time F. Time similarity matrix of female tool users, corresponding to Prox 2F, Groom 2F, and Kin 2F

Rate. Rate similarity matrix corresponding to Prox 2, Groom 2, and Kin 2

Rate F. Rate similarity matrix of female tool users, corresponding to Prox 2F, Groom 2F, and Kin 2F

Edge. Edge hammering similarity matrix corresponding to Prox 2, Groom 2, and Kin 2

Edge F. Edge hammering similarity matrix of female tool users, corresponding to Prox 2F, Groom 2F, and Kin 2

Face. Face hammering similarity matrix corresponding to Prox 2, Groom 2, and Kin 2

Face F. Face hammering similarity matrix of female tool users, corresponding to Prox 2F, Groom 2F, and Kin 2

Unattached. Unattached food similarity matrix corresponding to Prox 2, Groom 2, and Kin 2

Unattached F. Unattached food similarity matrix of female tool users, corresponding to Prox 2F, Groom 2F, and Kin 2F

Tool. Tool weight similarity matrix corresponding to Prox 3, Groom 3, and Kin 3

Tool F. Tool weight similarity matrix of female tool users, corresponding to Prox 3F, Groom 3F, and Kin 3F

Prox 1

258

Prox 1F

	Cht	Fhn	Hep	Hkr	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Nee	Ngk	Ngr	Nhk	Nms	Noi	Pet	Pla	Poo	Suy	Yng
Cht		0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.00	0.00
Fhn	0.01		0.03	0.00	0.03	0.02	0.01	0.05	0.01	0.03	0.02	0.03	0.02	0.05	0.00	0.01	0.01	0.02	0.03	0.01	0.01
Hep	0.00	0.03		0.01	0.10	0.01	0.01	0.02	0.01	0.03	0.04	0.00	0.01	0.02	0.01	0.00	0.01	0.01	0.01	0.01	0.02
Hkr	0.01	0.00	0.01		0.00	0.01	0.01	0.01	0.00	0.02	0.00	0.00	0.02	0.01	0.02	0.01	0.01	0.02	0.00	0.01	0.00
Htk	0.01	0.03	0.10	0.00		0.07	0.04	0.02	0.01	0.04	0.03	0.00	0.01	0.03	0.02	0.01	0.01	0.02	0.03	0.01	0.06
Jan	0.01	0.02	0.01	0.01	0.07		0.02	0.02	0.01	0.03	0.02	0.02	0.04	0.04	0.01	0.00	0.02	0.02	0.03	0.04	0.03
Kmk	0.01	0.01	0.01	0.01	0.04	0.02		0.04	0.01	0.06	0.04	0.04	0.03	0.03	0.02	0.03	0.07	0.05	0.06	0.04	0.07
Kwg	0.01	0.05	0.02	0.01	0.02	0.02	0.04		0.03	0.06	0.03	0.01	0.05	0.05	0.02	0.01	0.02	0.04	0.04	0.01	0.05
Lhm	0.00	0.01	0.01	0.00	0.01	0.01	0.01	0.03		0.01	0.01	0.00	0.02	0.03	0.01	0.00	0.02	0.04	0.04	0.01	0.03
Mrk	0.00	0.03	0.03	0.02	0.04	0.03	0.06	0.06	0.01		0.06	0.03	0.06	0.09	0.01	0.02	0.03	0.04	0.09	0.02	0.11
Nee	0.00	0.02	0.04	0.00	0.03	0.02	0.04	0.03	0.01	0.06		0.01	0.03	0.05	0.02	0.04	0.01	0.03	0.06	0.01	0.03
Ngk	0.01	0.03	0.00	0.00	0.00	0.02	0.04	0.01	0.00	0.03	0.01		0.03	0.01	0.02	0.02	0.01	0.03	0.01	0.01	0.01
Ngr	0.01	0.02	0.01	0.02	0.01	0.04	0.03	0.05	0.02	0.06	0.03	0.03		0.05	0.04	0.03	0.01	0.08	0.07	0.01	0.05
Nhk	0.01	0.05	0.02	0.01	0.03	0.04	0.03	0.05	0.03	0.09	0.05	0.01	0.05		0.01	0.00	0.03	0.03	0.10	0.03	0.04
Nms	0.00	0.00	0.01	0.02	0.02	0.01	0.02	0.02	0.01	0.01	0.02	0.02	0.04	0.01		0.00	0.01	0.03	0.07	0.02	0.03
Noi	0.01	0.01	0.00	0.01	0.01	0.00	0.03	0.01	0.00	0.02	0.04	0.02	0.03	0.00	0.00		0.03	0.01	0.01	0.00	0.02
Pet	0.01	0.01	0.01	0.01	0.01	0.02	0.07	0.02	0.02	0.03	0.01	0.01	0.01	0.03	0.01	0.03		0.00	0.04	0.01	0.04
Pla	0.01	0.02	0.01	0.02	0.02	0.02	0.05	0.04	0.04	0.04	0.03	0.03	0.08	0.03	0.03	0.01	0.00		0.06	0.01	0.04
Poo	0.01	0.03	0.01	0.00	0.03	0.03	0.06	0.04	0.04	0.09	0.06	0.01	0.07	0.10	0.07	0.01	0.04	0.06		0.05	0.07
Suy	0.00	0.01	0.01	0.01	0.01	0.04	0.04	0.01	0.01	0.02	0.01	0.01	0.01	0.03	0.02	0.00	0.01	0.01	0.05		0.03
Yng	0.00	0.01	0.02	0.00	0.06	0.03	0.07	0.05	0.03	0.11	0.03	0.01	0.05	0.04	0.03	0.02	0.04	0.04	0.07	0.03	

Prox 2

	ASG	CHG	CHK	CHL	CHT	DTO	GRB	HEE	HEP	HGP	HTK	JAN	KMK	KMY	KRB	KRG	KWG	KWN	LHM	MOC	MRK	NAK	NGR	NHK	NMS	NOI	PET	PLW
ASG		0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0.01	0.00
CHG	0.00		0.00	0.02	0.00	0.02	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
CHK	0.00	0.00		0.00	0.00	0.01	0.00	0.05	0.00	0.01	0.00	0.01	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.00
CHL	0.00	0.02	0.00		0.01	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0.03	0.00
CHT	0.01	0.00	0.00	0.01		0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.01	0.00
DTO	0.01	0.02	0.01	0.00	0.00		0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.01	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
GRB	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
HEE	0.01	0.01	0.05	0.02	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.00	0.01	0.07
HEP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.10	0.01	0.01	0.00	0.00	0.00	0.02	0.00	0.01	0.00	0.03	0.00	0.01	0.02	0.01	0.00	0.01	0.00
HGP	0.00	0.02	0.01	0.00	0.00	0.01	0.00	0.00	0.00		0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
HTK	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.10	0.01		0.07	0.04	0.00	0.00	0.00	0.02	0.00	0.01	0.00	0.04	0.00	0.01	0.03	0.02	0.01	0.01	0.01
JAN	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.07		0.02	0.01	0.00	0.00	0.02	0.02	0.01	0.00	0.03	0.00	0.04	0.04	0.01	0.00	0.02	0.01
KMK	0.01	0.00	0.03	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.04	0.02		0.00	0.01	0.00	0.04	0.01	0.01	0.00	0.06	0.00	0.03	0.03	0.02	0.03	0.07	0.01
KMY	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.00		0.00	0.00	0.00	0.04	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.05
KRB	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KRG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
KWG	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02	0.00	0.02	0.02	0.04	0.00	0.00	0.00		0.00	0.03	0.05	0.06	0.00	0.05	0.05	0.02	0.01	0.02	0.01
KWN	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.04	0.00	0.00	0.00		0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.03	0.01
LHM	0.00	0.01	0.00	0.00	0.00	0.04	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.03	0.01		0.00	0.01	0.02	0.02	0.03	0.01	0.00	0.02	0.02
MOO	0.01	0.00	0.01	0.01	0.00	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00		0.01	0.04	0.00	0.00	0.00	0.00	0.00	0.00
MRK	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.03	0.00	0.04	0.03	0.06	0.01	0.00	0.00	0.06	0.00	0.01	0.01		0.01	0.06	0.09	0.01	0.02	0.03	0.00
NAK	0.01	0.01	0.00	0.01	0.00	0.06	0.01	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.01		0.00	0.00	0.00	0.00	0.00	0.00
NGR	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.01	0.04	0.03	0.00	0.00	0.00	0.05	0.00	0.02	0.00	0.06	0.00		0.05	0.04	0.03	0.01	0.00
NHK	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.02	0.00	0.03	0.04	0.03	0.00	0.00	0.00	0.05	0.01	0.03	0.00	0.09	0.00	0.05		0.01	0.00	0.03	0.00
NMS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.01	0.02	0.00	0.00	0.01	0.02	0.01	0.01	0.00	0.01	0.00	0.04	0.01		0.00	0.01	0.01
NOI	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.03	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.02	0.00	0.03	0.00	0.00		0.03	0.01
PET	0.01	0.00	0.01	0.03	0.01	0.00	0.00	0.07	0.01	0.00	0.01	0.02	0.07	0.02	0.00	0.00	0.02	0.03	0.02	0.00	0.03	0.00	0.01	0.03	0.01	0.03		0.01
PLW	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.05	0.00	0.00	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	

Prox 2F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.01	0.01
Hep	0.00		0.10	0.01	0.01	0.02	0.01	0.03	0.01	0.02	0.01	0.00	0.01
Htk	0.01	0.10		0.07	0.04	0.02	0.01	0.04	0.01	0.03	0.02	0.01	0.01
Jan	0.01	0.01	0.07		0.02	0.02	0.01	0.03	0.04	0.04	0.01	0.00	0.02
Kmk	0.01	0.01	0.04	0.02		0.04	0.01	0.06	0.03	0.03	0.02	0.03	0.07
Kwg	0.01	0.02	0.02	0.02	0.04		0.03	0.06	0.05	0.05	0.02	0.01	0.02
Lhm	0.00	0.01	0.01	0.01	0.01	0.03		0.01	0.02	0.03	0.01	0.00	0.02
Mrk	0.00	0.03	0.04	0.03	0.06	0.06	0.01		0.06	0.09	0.01	0.02	0.03
Ngr	0.01	0.01	0.01	0.04	0.03	0.05	0.02	0.06		0.05	0.04	0.03	0.01
Nhk	0.01	0.02	0.03	0.04	0.03	0.05	0.03	0.09	0.05		0.01	0.00	0.03
Nms	0.00	0.01	0.02	0.01	0.02	0.02	0.01	0.01	0.04	0.01		0.00	0.01
Noi	0.01	0.00	0.01	0.00	0.03	0.01	0.00	0.02	0.03	0.00	0.00		0.03
Pet	0.01	0.01	0.01	0.02	0.07	0.02	0.02	0.03	0.01	0.03	0.01	0.03	

Prox 3

	Chg	Chk	Cht	Dto	Hee	Hep	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet
Chg		0.00	0.00	0.02	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Chk	0.00		0.00	0.01	0.05	0.00	0.01	0.00	0.01	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.01	0.01
Cht	0.00	0.00		0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.01
Dto	0.02	0.01	0.00		0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.04	0.01	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Hee	0.01	0.05	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.01	0.07
Hep	0.00	0.00	0.00	0.00	0.00		0.00	0.10	0.01	0.01	0.02	0.01	0.00	0.03	0.00	0.01	0.02	0.01	0.00	0.01
Hgp	0.02	0.01	0.00	0.01	0.00	0.00		0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Htk	0.00	0.00	0.01	0.00	0.00	0.10	0.01		0.07	0.04	0.02	0.01	0.00	0.04	0.00	0.01	0.03	0.02	0.01	0.01
Jan	0.00	0.01	0.01	0.00	0.00	0.01	0.00	0.07		0.02	0.02	0.01	0.00	0.03	0.00	0.04	0.04	0.01	0.00	0.02
Kmk	0.00	0.03	0.01	0.00	0.00	0.01	0.00	0.04	0.02		0.04	0.01	0.00	0.06	0.00	0.03	0.03	0.02	0.03	0.07
Kwg	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.02	0.02	0.04		0.03	0.05	0.06	0.00	0.05	0.05	0.02	0.01	0.02
Lhm	0.01	0.00	0.00	0.04	0.00	0.01	0.00	0.01	0.01	0.01	0.03		0.00	0.01	0.02	0.02	0.03	0.01	0.00	0.02
Moo	0.00	0.01	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.00	0.05	0.00		0.01	0.04	0.00	0.00	0.00	0.00	0.00
Mrk	0.00	0.00	0.00	0.00	0.01	0.03	0.00	0.04	0.03	0.06	0.06	0.01	0.01		0.01	0.06	0.09	0.01	0.02	0.03
Nak	0.01	0.00	0.00	0.06	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.04	0.01		0.00	0.00	0.00	0.00	0.00
Ngr	0.00	0.00	0.01	0.00	0.01	0.01	0.00	0.01	0.04	0.03	0.05	0.02	0.00	0.06	0.00		0.05	0.04	0.03	0.01
Nhk	0.00	0.01	0.01	0.00	0.01	0.02	0.00	0.03	0.04	0.03	0.05	0.03	0.00	0.09	0.00	0.05		0.01	0.00	0.03
Nms	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.01	0.02	0.02	0.01	0.00	0.01	0.00	0.04	0.01		0.00	0.01
Noi	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.03	0.01	0.00	0.00	0.02	0.00	0.03	0.00	0.00		0.03
Pet	0.00	0.01	0.01	0.00	0.07	0.01	0.00	0.01	0.02	0.07	0.02	0.02	0.00	0.03	0.00	0.01	0.03	0.01	0.03	

Prox 3F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.01	0.01
Hep	0.00		0.10	0.01	0.01	0.02	0.01	0.03	0.01	0.02	0.01	0.00	0.01
Htk	0.01	0.10		0.07	0.04	0.02	0.01	0.04	0.01	0.03	0.02	0.01	0.01
Jan	0.01	0.01	0.07		0.02	0.02	0.01	0.03	0.04	0.04	0.01	0.00	0.02
Kmk	0.01	0.01	0.04	0.02		0.04	0.01	0.06	0.03	0.03	0.02	0.03	0.07
Kwg	0.01	0.02	0.02	0.02	0.04		0.03	0.06	0.05	0.05	0.02	0.01	0.02
Lhm	0.00	0.01	0.01	0.01	0.01	0.03		0.01	0.02	0.03	0.01	0.00	0.02
Mrk	0.00	0.03	0.04	0.03	0.06	0.06	0.01		0.06	0.09	0.01	0.02	0.03
Ngr	0.01	0.01	0.01	0.04	0.03	0.05	0.02	0.06		0.05	0.04	0.03	0.01
Nhk	0.01	0.02	0.03	0.04	0.03	0.05	0.03	0.09	0.05		0.01	0.00	0.03
Nms	0.00	0.01	0.02	0.01	0.02	0.02	0.01	0.01	0.04	0.01		0.00	0.01
Noi	0.01	0.00	0.01	0.00	0.03	0.01	0.00	0.02	0.03	0.00	0.00		0.03
Pet	0.01	0.01	0.01	0.02	0.07	0.02	0.02	0.03	0.01	0.03	0.01	0.03	

Groom 1

264

Groom 1F

	Cht	Fhn	Hep	Hkr	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Nee	Ngk	Ngr	Nhk	Nms	Noi	Pet	Pla	Poo	Suy	Yng
Cht		0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fhn	0.00		0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hep	0.00	0.00		0.00	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hkr	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.02	0.00
Htk	0.00	0.00	0.02	0.00		0.04	0.00	0.00	0.00	0.03	0.04	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Jan	0.00	0.00	0.00	0.00	0.04		0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kmk	0.02	0.00	0.00	0.00	0.00	0.00		0.00	0.01	0.02	0.00	0.00	0.00	0.01	0.00	0.06	0.01	0.00	0.00	0.01	0.02
Kwg	0.00	0.01	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lhm	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.02
Mrk	0.00	0.00	0.01	0.00	0.03	0.01	0.02	0.00	0.00		0.01	0.00	0.03	0.03	0.00	0.01	0.01	0.00	0.03	0.00	0.02
Nee	0.00	0.01	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.01		0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.01	0.00
Ngk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00		0.01	0.01	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Ngr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.03	0.00	0.01		0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.00
Nhk	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.03	0.00	0.01	0.00		0.00	0.00	0.00	0.00	0.01	0.00	0.00
Nms	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.01	0.00	0.01	0.00
Noi	0.00	0.00	0.00	0.00	0.01	0.00	0.06	0.00	0.00	0.01	0.04	0.00	0.02	0.00	0.00		0.03	0.00	0.00	0.00	0.02
Pet	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.03		0.00	0.00	0.00	0.00
Pla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.00		0.02	0.00	0.00
Poo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.02		0.01	0.00
Suy	0.00	0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01		0.00
Yng	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	

Groom 2

	ASG	CHG	CHK	CHL	CHT	DTO	GRB	HEE	HEP	HGP	HTK	JAN	KMK	KMY	KRB	KRG	KWG	KWN	LHM	MOC	MRK	NAK	NGR	NHK	NMS	NOI	PET	PLW
ASG		0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHG	0.00		0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHK	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHL	0.00	0.03	0.00		0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.01	0.00
CHT	0.01	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
DTO	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GRB	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
HEE	0.01	0.00	0.00	0.02	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
HEP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HGP	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HTK	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00		0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.01	0.00	0.00
JAN	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00
KMK	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.01	0.00	0.06	0.01	0.00	0.00
KMY	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
KRB	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KRG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
KWG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.05	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00
KWN	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
LHM	0.02	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.03	0.00	0.00	0.00	0.00	0.02	0.00	0.00
MOO	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00		0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00
MRK	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.01		0.00	0.03	0.03	0.00	0.01	0.01	0.00	0.00
NAK	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
NGR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.00		0.00	0.00	0.02	0.00	0.00	0.00
NHK	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.03	0.00	0.00		0.00	0.00	0.00	0.00
NMS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
NOI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.00		0.03	0.00	0.00
PET	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.02	0.00	0.01	0.00	0.00	0.00	0.00	0.03		0.00	0.00
PLW	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00

Groom 2F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Hep	0.00		0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Htk	0.00	0.02		0.04	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.01	0.00
Jan	0.00	0.00	0.04		0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00
Kmk	0.02	0.00	0.00	0.00		0.00	0.01	0.02	0.00	0.01	0.00	0.06	0.01
Kwg	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.02	0.01	0.00	0.00	0.00
Lhm	0.00	0.00	0.00	0.00	0.01	0.00		0.00	0.00	0.00	0.00	0.00	0.02
Mrk	0.00	0.01	0.03	0.01	0.02	0.00	0.00		0.03	0.03	0.00	0.01	0.01
Ngr	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.03		0.00	0.00	0.02	0.00
Nhk	0.01	0.00	0.01	0.01	0.01	0.01	0.00	0.03	0.00		0.00	0.00	0.00
Nms	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00
Noi	0.00	0.00	0.01	0.00	0.06	0.00	0.00	0.01	0.02	0.00	0.00		0.03
Pet	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.01	0.00	0.00	0.00	0.03	

Groom 3

	Chg	Chk	Cht	Dto	Hee	Hep	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet
Chg		0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chk	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cht	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Dto	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hee	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.04
Hep	0.00	0.00	0.00	0.00	0.00		0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Hgp	0.01	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Htk	0.00	0.00	0.00	0.00	0.00	0.02	0.00		0.04	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.01	0.00
Jan	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.04		0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00
Kmk	0.00	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.01	0.00	0.02	0.00	0.00	0.01	0.00	0.06	0.01
Kwg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.05	0.00	0.00	0.02	0.01	0.00	0.00	0.00
Lhm	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.01	0.00		0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.02
Moo	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.05	0.00		0.01	0.02	0.00	0.00	0.00	0.00	0.00
Mrk	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03	0.01	0.02	0.00	0.00	0.01		0.00	0.03	0.03	0.00	0.01	0.01
Nak	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.00		0.00	0.00	0.00	0.00	0.00
Ngr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.03	0.00		0.00	0.00	0.02	0.00
Nhk	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.03	0.00	0.00		0.00	0.00	0.00
Nms	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00
Noi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.06	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.00		0.03
Pet	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.01	0.00	0.00	0.00	0.00	0.03	

Groom 3F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Hep	0.00		0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Htk	0.00	0.02		0.04	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.01	0.00
Jan	0.00	0.00	0.04		0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00
Kmk	0.02	0.00	0.00	0.00		0.00	0.01	0.02	0.00	0.01	0.00	0.06	0.01
Kwg	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.02	0.01	0.00	0.00	0.00
Lhm	0.00	0.00	0.00	0.00	0.01	0.00		0.00	0.00	0.00	0.00	0.00	0.02
Mrk	0.00	0.01	0.03	0.01	0.02	0.00	0.00		0.03	0.03	0.00	0.01	0.01
Ngr	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.03		0.00	0.00	0.02	0.00
Nhk	0.01	0.00	0.01	0.01	0.01	0.01	0.00	0.03	0.00		0.00	0.00	0.00
Nms	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00
Noi	0.00	0.00	0.01	0.00	0.06	0.00	0.00	0.01	0.02	0.00	0.00		0.03
Pet	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.01	0.00	0.00	0.00	0.03	

Social Relationship Matrices – Inferred Kinship Matrices

Kin 1

	Asg	Chg	Chk	Chl	Cht	Dto	Fhn	Grb	Hee	Hep	Hgp	Hkr	Htk	Jan	Jsl	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Mgp	Moo	Mrk	Nak	Nee	Ngk	Ngr	Nhk	Nms	Noi	Pet	Pla	Plw	Poo	Som	Suy	Yak	Yng				
Asg			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Chg	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Chk	0	0			0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Chl	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cht	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dto	0	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fhn	0	0	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grb	0	0	0	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hee	0	0	0	0	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hep	0	0	0	0	0	0	0	0	0			0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hgp	0	0	0	0	0	0	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hkr	0	0	0	0	0	0	0	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Htk	0	0	0	0	0	0	0	0	0	1	0	0		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan	0	0	0	0	0	0	0	0	0	0	1	0	0	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jsl	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kmk	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kmy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Krb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Krg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kwg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kwn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lhm	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mgp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Moo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mrk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nak	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0						

Kin 1F

	Cht	Fhn	Hep	Hkr	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Nee	Ngk	Ngr	Nhk	Nms	Noi	Pet	Pla	Poo	Suy	Yng
Cht		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fhn	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hep	0	0		0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hkr	0	0	0		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Htk	0	0	1	0		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan	0	0	1	0	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kmk	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kwg	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0
Lhm	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0
Mrk	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0
Nee	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Ngk	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Ngr	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0
Nhk	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	1	1	0
Nms	0	0	0	1	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
Noi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0
Pet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0
Pla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0
Poo	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		1	0
Suy	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1		0
Yng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Kin 2

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Asg		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chg	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chk	0	0		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chl	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cht	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dto	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Grb	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hee	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hep	0	0	0	0	0	0	0	0		0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hgp	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Htk	0	0	0	0	0	0	0	0	1	0		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan	0	0	0	0	0	0	0	0	1	0	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kmk	0	0	1	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kmy	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Krb	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0
Krg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0
Kwg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	1	0	0	0	0	0	0	0	0
Kwn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Lhm	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0		0	0	1	0	0	0	0	0	0
Moo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0		0	0	0	0	0	0	0	0
Mrk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0
Nak	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0		0	0	0	0	0	0
Ngr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
Nhk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0
Nms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0
Noi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0
Pet	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Plw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0

Kin 2F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0	0	0	0	0	0	0	0	0	0	0	0
Hep	0		1	1	0	0	0	0	0	0	0	0	0
Htk	0	1		1	0	0	0	0	0	0	0	0	0
Jan	0	1	1		0	0	0	0	0	0	0	0	0
Kmk	0	0	0	0		0	0	0	0	0	0	0	0
Kwg	0	0	0	0	0		0	0	0	0	0	0	0
Lhm	0	0	0	0	0	0		0	0	0	0	0	0
Mrk	0	0	0	0	0	0	0		0	0	0	0	0
Ngr	0	0	0	0	0	0	0	0		0	0	0	0
Nhk	0	0	0	0	0	0	0	0	0		0	0	0
Nms	0	0	0	0	0	0	0	0	0	0		0	0
Noi	0	0	0	0	0	0	0	0	0	0	0		0
Pet	0	0	0	0	0	0	0	0	0	0	0	0	

Kin 3

	Chg	Chk	Cht	Dto	Hee	Hep	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet
Chg		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chk	0		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cht	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dto	0	0	0		0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Hee	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hep	0	0	0	0	0		0	1	1	0	0	0	0	0	0	0	0	0	0	0
Hgp	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0
Htk	0	0	0	0	0	1	0		1	0	0	0	0	0	0	0	0	0	0	0
Jan	0	0	0	0	0	1	0	1		0	0	0	0	0	0	0	0	0	0	0
Kmk	0	1	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Kwg	0	0	0	0	0	0	0	0	0	0		0	1	0	0	0	0	0	0	0
Lhm	0	0	0	1	0	0	0	0	0	0	0		0	0	1	0	0	0	0	0
Moo	0	0	0	0	0	0	0	0	0	0	1	0		0	0	0	0	0	0	0
Mrk	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
Nak	0	0	0	1	0	0	0	0	0	0	0	1	0	0		0	0	0	0	0
Ngr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0
Nhk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0
Nms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Noi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0
Pet	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Kin 3F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0	0	0	0	0	0	0	0	0	0	0	0
Hep	0		1	1	0	0	0	0	0	0	0	0	0
Htk	0	1		1	0	0	0	0	0	0	0	0	0
Jan	0	1	1		0	0	0	0	0	0	0	0	0
Kmk	0	0	0	0		0	0	0	0	0	0	0	0
Kwg	0	0	0	0	0		0	0	0	0	0	0	0
Lhm	0	0	0	0	0	0		0	0	0	0	0	0
Mrk	0	0	0	0	0	0	0		0	0	0	0	0
Ngr	0	0	0	0	0	0	0	0		0	0	0	0
Nhk	0	0	0	0	0	0	0	0	0		0	0	0
Nms	0	0	0	0	0	0	0	0	0	0		0	0
Noi	0	0	0	0	0	0	0	0	0	0	0		0
Pet	0	0	0	0	0	0	0	0	0	0	0	0	

Similarity Matrices

User

	Asg	Chg	Chk	Chl	Cht	Dto	Fhn	Grb	Hee	Hep	Hgp	Hkr	Htk	Jan	Jsl	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Mgp	Moo	Mrk	Nak	Nee	Ngk	Ngr	Nhk	Nms	Noi	Pet	Pla	Plw	Poo	Som	Suy	Yak	Yng
Asg			1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0
Chg	1			1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0
Chk	1	1			1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0
Chl	1	1	1		1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Cht	1	1	1	1		1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Dto	1	1	1	1	1		0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	0	1	0	0	0	0	
Fhn	0	0	0	0	0	0		0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	
Grb	1	1	1	1	1	1	0		1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Hee	1	1	1	1	1	1	0	1		1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Hep	1	1	1	1	1	1	0	1	1		1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Hgp	1	1	1	1	1	1	0	1	1	1		0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	0	1	0	0	0	0	
Hkr	0	0	0	0	0	0	1	0	0	0	0		0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	
Htk	1	1	1	1	1	1	0	1	1	1	1	0		1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Jan	1	1	1	1	1	1	0	1	1	1	1	0	1		0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Jsl	0	0	0	0	0	0	1	0	0	0	0	1	0	0		0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	
Kmk	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0		1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Kmy	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1		1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Krb	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1		1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Krg	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1		1	1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Kwg	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1		1	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Kwn	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1		1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Lhm	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	0	1	1	1	1		0	1	1	1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Mgp	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0		0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1	1
Moo	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0		1	1	0	0	1	1	1	1	1	1	0	1	0	0	0	0	
Mrk	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1		1	0	0	1	1	1	1	1	0	1	0	0	0	0	
Nak	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	0	1	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	
Nee	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0		0	0	1	0	0	0	0	0	1	0	1	1	1	
Ngk	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1		0	0	0	0	0	1	0	1	1	1	1	
Ngr	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0		1	1	1	1	0	1	0	0	0	0	
Nhk	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1		1	1	1	0	1	0	0	0	0	
Nms	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1		1	1	1	0	1	0	0	0	0	
Noi	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1		1	1	0	1	0	0	0	0	
Pet	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1			0	1	0	0	0	0	
Pla	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0		0		1	1	1	1	
Plw	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0			0	0	0	0
Poo	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0		1	1	1
Som	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1
Suy	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	
Yak	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1
Yng	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1

User F

	Cht	Fhn	Hep	Hkr	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Nee	Ngk	Ngr	Nhk	Nms	Noi	Pet	Pla	Poo	Suy	Yng
Cht		0	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0
Fhn	0		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Hep	1	0		0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0
Hkr	0	1	0		0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1
Htk	1	0	1	0		1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0
Jan	1	0	1	0	1		1	1	1	1	0	0	1	1	1	1	1	0	0	0	0
Kmk	1	0	1	0	1	1		1	1	1	0	0	1	1	1	1	1	0	0	0	0
Kwg	1	0	1	0	1	1	1		1	1	0	0	1	1	1	1	1	0	0	0	0
Lhm	1	0	1	0	1	1	1	1		1	0	0	1	1	1	1	1	0	0	0	0
Mrk	1	0	1	0	1	1	1	1	1		0	0	1	1	1	1	1	0	0	0	0
Nee	0	1	0	1	0	0	0	0	0	0		1	0	0	0	0	0	1	1	1	1
Ngk	0	1	0	1	0	0	0	0	0	0	1		0	0	0	0	0	1	1	1	1
Ngr	1	0	1	0	1	1	1	1	1	1	0	0		1	1	1	1	0	0	0	0
Nhk	1	0	1	0	1	1	1	1	1	1	0	0	1		1	1	1	0	0	0	0
Nms	1	0	1	0	1	1	1	1	1	1	0	0	1	1		1	1	0	0	0	0
Noi	1	0	1	0	1	1	1	1	1	1	0	0	1	1	1		1	0	0	0	0
Pet	1	0	1	0	1	1	1	1	1	1	0	0	1	1	1	1		0	0	0	0
Pla	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0		1	1	1
Poo	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1		1	1
Suy	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1		1
Yng	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	

Time

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Asg		0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1
Chg	0		1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0
Chk	0	1		0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0
Chl	1	0	0		0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1
Cht	0	1	1	0		0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0
Dto	1	0	0	1	0		1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1
Grb	1	0	0	1	0	1		1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1
Hee	1	0	0	1	0	1	1		0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1
Hep	0	1	1	0	1	0	0	0		1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0
Hgp	0	1	1	0	1	0	0	0	1		1	0	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0
Htk	0	1	1	0	1	0	0	0	1	1		0	0	0	1	1	1	0	1	1	0	0	0	1	1	0	0	0
Jan	1	0	0	1	0	1	1	1	0	0	0		1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1
Kmk	1	0	0	1	0	1	1	1	0	0	0	1		1	0	0	0	1	0	0	1	1	1	0	0	1	1	1
Kmy	1	0	0	1	0	1	1	1	0	0	0	1	1		0	0	0	1	0	0	1	1	1	0	0	1	1	1
Krb	0	1	1	0	1	0	0	0	1	1	1	0	0	0		1	1	0	1	1	0	0	0	1	1	0	0	0
Krg	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1		1	0	1	1	0	0	0	1	1	0	0	0
Kwg	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1		0	1	1	0	0	0	1	1	0	0	0
Kwn	1	0	1	0	1	1	1	0	0	0	1	1	1	0	1	1	0		0	0	1	1	1	0	0	1	1	1
Lhm	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0		1	0	0	0	1	1	0	0	0
Moo	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1		0	0	0	1	1	0	0	0
Mrk	1	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0		1	1	0	0	1	1	1
Nak	1	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1		1	0	0	1	1	1
Ngr	1	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1		0	0	1	1	1
Nhk	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	0		1	0	0	0
Nms	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1		0	0	0
Noi	1	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0		1	1
Pet	1	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1		1
Plw	1	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	

Time F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		1	1	0	0	1	1	0	0	1	1	0	0
Hep	1		1	0	0	1	1	0	0	1	1	0	0
Htk	1	1		0	0	1	1	0	0	1	1	0	0
Jan	0	0	0		1	0	0	1	1	0	0	1	1
Kmk	0	0	0	1		0	0	1	1	0	0	1	1
Kwg	1	1	1	0	0		1	0	0	1	1	0	0
Lhm	1	1	1	0	0	1		0	0	1	1	0	0
Mrk	0	0	0	1	1	0	0		1	0	0	1	1
Ngr	0	0	0	1	1	0	0	1		0	0	1	1
Nhk	1	1	1	0	0	1	1	0	0		1	0	0
Nms	1	1	1	0	0	1	1	0	0	1		0	0
Noi	0	0	0	1	1	0	0	1	1	0	0		1
Pet	0	0	0	1	1	0	0	1	1	0	0	1	

Rate

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Asg		0	1	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Chg	0		0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1
Chk	1	0		0	1	1	0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Chl	0	1	0		0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1
Cht	1	0	1	0		1	0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Dto	1	0	1	0	1		0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Grb	0	1	0	1	0	0		1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1
Hee	0	1	0	1	0	0	1		0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1
Hep	1	0	1	0	1	1	0	0		1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Hgp	1	0	1	0	1	1	0	0	1		1	0	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Htk	1	0	1	0	1	1	0	0	1	1		0	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Jan	0	1	0	1	0	0	1	1	0	0	0		1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1
Kmk	0	1	0	1	0	0	1	1	0	0	0	1		0	0	0	1	0	0	0	1	1	1	1	0	1	1	1
Kmy	1	0	1	0	1	1	0	0	1	1	1	0	0		1	1	0	1	1	1	0	0	0	0	1	0	0	0
Krb	1	0	1	0	1	1	0	0	1	1	1	0	0	1		1	0	1	1	1	0	0	0	0	1	0	0	0
Krg	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1		0	1	1	1	0	0	0	0	1	0	0	0
Kwg	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0		0	0	0	1	1	1	1	0	1	1	1
Kwn	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	1	0		1	1	0	0	0	0	1	0	0	0
Lhm	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1		1	0	0	0	0	1	0	0	0
Moo	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1	1		0	0	0	0	1	0	0	0
Mrk	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0		1	1	1	0	1	1	1
Nak	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1		1	1	0	1	1	1
Ngr	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1		1	0	1	1	1
Nhk	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1		0	1	1	1
Nms	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0		0	0	0
Noi	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0		1	
Pet	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1		1
Plw	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	

Rate F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		1	1	0	0	0	1	0	0	0	1	0	0
Hep	1		1	0	0	0	1	0	0	0	1	0	0
Htk	1	1		0	0	0	1	0	0	0	1	0	0
Jan	0	0	0		1	1	0	1	1	1	0	1	1
Kmk	0	0	0	1		1	0	1	1	1	0	1	1
Kwg	0	0	0	1	1		0	1	1	1	0	1	1
Lhm	1	1	1	0	0	0		0	0	0	1	0	0
Mrk	0	0	0	1	1	1	0		1	1	0	1	1
Ngr	0	0	0	1	1	1	0	1		1	0	1	1
Nhk	0	0	0	1	1	1	0	1	1		0	1	1
Nms	1	1	1	0	0	0	1	0	0	0		0	0
Noi	0	0	0	1	1	1	0	1	1	1	0		1
Pet	0	0	0	1	1	1	0	1	1	1	0	1	

Edge

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Asg		0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1
Chg	0		1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Chk	0	1		0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Chl	1	0	0		1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1
Cht	1	0	0	1		1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1
Dto	1	0	0	1	1		1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1
Grb	1	0	0	1	1	1		1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1
Hee	1	0	0	1	1	1	1		0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1
Hep	0	1	1	0	0	0	0	0		1	1	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Hgp	0	1	1	0	0	0	0	0	1		1	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Htk	0	1	1	0	0	0	0	0	1	1		1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Jan	0	1	1	0	0	0	0	0	1	1	1		0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
Kmk	1	0	0	1	1	1	1	1	0	0	0	0		1	0	1	0	0	1	0	0	1	1	0	0	1	1	1
Kmy	1	0	0	1	1	1	1	1	0	0	0	0	1		0	1	0	0	1	0	0	1	1	0	0	1	1	1
Krb	0	1	1	0	0	0	0	0	1	1	1	1	0	0		0	1	1	0	1	1	0	0	1	1	0	0	0
Krg	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0		0	0	1	0	0	1	1	0	0	1	1	1
Kwg	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0		1	0	1	1	0	0	1	1	0	0	0
Kwn	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1		0	1	1	0	0	1	1	0	0	0
Lhm	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0		0	0	1	1	0	0	1	1	1
Moo	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0		1	0	0	1	1	0	0	0
Mrk	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	1		0	0	1	1	0	0	0
Nak	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0		1	0	0	1	1	1
Ngr	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1		0	0	1	1	1
Nhk	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	1	1	0	0		1	0	0	0
Nms	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	1	1	0	0	1		0	0	0
Noi	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0		1	1
Pet	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1		1
Plw	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	1	

Edge F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0	0	0	1	0	1	0	1	0	0	1	1
Hep	0		1	1	0	1	0	1	0	1	1	0	0
Htk	0	1		1	0	1	0	1	0	1	1	0	0
Jan	0	1	1		0	1	0	1	0	1	1	0	0
Kmk	1	0	0	0		0	1	0	1	0	0	1	1
Kwg	0	1	1	1	0		0	1	0	1	1	0	0
Lhm	1	0	0	0	1	0		0	1	0	0	1	1
Mrk	0	1	1	1	0	1	0		0	1	1	0	0
Ngr	1	0	0	0	1	0	1	0		0	0	1	1
Nhk	0	1	1	1	0	1	0	1	0		1	0	0
Nms	0	1	1	1	0	1	0	1	0	1		0	0
Noi	1	0	0	0	1	0	1	0	1	0	0		1
Pet	1	0	0	0	1	0	1	0	1	0	0	1	

Face

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Asg		1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1
Chg	1		0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1
Chk	0	0		1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Chl	0	0	1		0	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Cht	1	1	0	0		0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1
Dto	0	0	1	1	0		0	0	0	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Grb	1	1	0	0	1	0		1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1
Hee	1	1	0	0	1	0	1		1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1
Hep	1	1	0	0	1	0	1	1		0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1
Hgp	0	0	1	1	0	1	0	0	0		1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Htk	0	0	1	1	0	1	0	0	0	1		1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Jan	0	0	1	1	0	1	0	0	0	1	1		1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Kmk	0	0	1	1	0	1	0	0	0	1	1	1		0	0	0	1	0	1	1	0	1	0	1	1	1	0	0
Kmy	1	1	0	0	1	0	1	1	1	0	0	0	0		1	1	0	1	0	0	1	0	1	0	0	0	1	1
Krb	1	1	0	0	1	0	1	1	1	0	0	0	0	1		1	0	1	0	0	1	0	1	0	0	0	1	1
Krg	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1		0	1	0	0	1	0	1	0	0	0	1	1
Kwg	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0	0		0	1	1	0	1	0	1	1	1	0	0
Kwn	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0		0	0	1	0	1	0	0	0	1	1
Lhm	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0		1	0	1	0	1	1	1	0	0
Moo	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	1		0	1	0	1	1	1	0	0
Mrk	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0		0	1	0	0	0	1	1
Nak	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0		0	1	1	1	0	0
Ngr	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0		0	0	0	1	1
Nhk	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0	1	0		1	1	0	0
Nms	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1		1	0	0
Noi	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1		0	0
Pet	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0		1
Plw	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	

Face F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		1	0	0	0	0	0	1	1	0	0	0	1
Hep	1		0	0	0	0	0	1	1	0	0	0	1
Htk	0	0		1	1	1	1	0	0	1	1	1	0
Jan	0	0	1		1	1	1	0	0	1	1	1	0
Kmk	0	0	1	1		1	1	0	0	1	1	1	0
Kwg	0	0	1	1	1		1	0	0	1	1	1	0
Lhm	0	0	1	1	1	1		0	0	1	1	1	0
Mrk	1	1	0	0	0	0	0		1	0	0	0	1
Ngr	1	1	0	0	0	0	0	1		0	0	0	1
Nhk	0	0	1	1	1	1	1	0	0		1	1	0
Nms	0	0	1	1	1	1	1	0	0	1		1	0
Noi	0	0	1	1	1	1	1	0	0	1	1		0
Pet	1	1	0	0	0	0	0	1	1	0	0	0	

Unattached

	Asg	Chg	Chk	Chl	Cht	Dto	Grb	Hee	Hep	Hgp	Htk	Jan	Kmk	Kmy	Krb	Krg	Kwg	Kwn	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet	Plw
Asg		0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1
Chg	0		1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Chk	0	1		0	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Chl	1	0	0		0	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1
Cht	0	1	1	0		1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Dto	0	1	1	0	1		0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Grb	1	0	0	1	0	0		1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1
Hee	1	0	0	1	0	0	1		1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1
Hep	1	0	0	1	0	0	1	1		0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1
Hgp	0	1	1	0	1	1	0	0	0		1	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Htk	0	1	1	0	1	1	0	0	0	1		1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Jan	0	1	1	0	1	1	0	0	0	1	1		1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Kmk	0	1	1	0	1	1	0	0	0	1	1	1		0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
Kmy	1	0	0	1	0	0	1	1	1	0	0	0	0		0	1	0	1	0	0	0	0	1	0	0	1	1	1
Krb	0	1	1	0	1	1	0	0	0	1	1	1	1	0		0	1	0	1	1	1	1	0	1	1	0	0	0
Krg	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0		0	1	0	0	0	0	1	0	0	1	1	1
Kwg	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0		0	1	1	1	1	0	1	1	0	0	0
Kwn	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0		0	0	0	0	1	0	0	1	1	1
Lhm	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	0		1	1	1	0	1	1	0	0	0
Moo	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1		1	1	0	1	1	0	0	0
Mrk	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1		1	0	1	1	0	0	0
Nak	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1		0	1	1	0	0	0
Ngr	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0		0	0	1	1	1
Nhk	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0		1	0	0	0
Nms	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1		0	0	0
Noi	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0		1	1
Pet	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1		1
Plw	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	

Unattached F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		0	1	1	1	1	1	1	0	1	1	0	0
Hep	0		0	0	0	0	0	0	1	0	0	1	1
Htk	1	0		1	1	1	1	1	0	1	1	0	0
Jan	1	0	1		1	1	1	1	0	1	1	0	0
Kmk	1	0	1	1		1	1	1	0	1	1	0	0
Kwg	1	0	1	1	1		1	1	0	1	1	0	0
Lhm	1	0	1	1	1	1		1	0	1	1	0	0
Mrk	1	0	1	1	1	1	1		0	1	1	0	0
Ngr	0	1	0	0	0	0	0	0		0	0	1	1
Nhk	1	0	1	1	1	1	1	1	0		1	0	0
Nms	1	0	1	1	1	1	1	1	0	1		0	0
Noi	0	1	0	0	0	0	0	0	1	0	0		1
Pet	0	1	0	0	0	0	0	0	1	0	0	1	

Tool

	Chg	Chk	Cht	Dto	Hee	Hep	Hgp	Htk	Jan	Kmk	Kwg	Lhm	Moo	Mrk	Nak	Ngr	Nhk	Nms	Noi	Pet
Chg		1	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0
Chk	1		0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0
Cht	0	0		0	0	1	0	1	1	0	0	1	0	1	1	1	0	0	1	1
Dto	1	1	0		1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0
Hee	1	1	0	1		0	1	0	0	1	1	0	1	0	0	0	1	1	0	0
Hep	0	0	1	0	0		0	1	1	0	0	1	0	1	1	1	0	0	1	1
Hgp	1	1	0	1	1	0		0	0	1	1	0	1	0	0	0	1	1	0	0
Htk	0	0	1	0	0	1	0		1	0	0	1	0	1	1	1	0	0	1	1
Jan	0	0	1	0	0	1	0	1		0	0	1	0	1	1	1	0	0	1	1
Kmk	1	1	0	1	1	0	1	0	0		1	0	1	0	0	0	1	1	0	0
Kwg	1	1	0	1	1	0	1	0	0	1		0	1	0	0	0	1	1	0	0
Lhm	0	0	1	0	0	1	0	1	1	0	0		0	1	1	1	0	0	1	1
Moo	1	1	0	1	1	0	1	0	0	1	1	0		0	0	0	1	1	0	0
Mrk	0	0	1	0	0	1	0	1	1	0	0	1	0		1	1	0	0	1	1
Nak	0	0	1	0	0	1	0	1	1	0	0	1	0	1		1	0	0	1	1
Ngr	0	0	1	0	0	1	0	1	1	0	0	1	0	1	1		0	0	1	1
Nhk	1	1	0	1	1	0	1	0	0	1	1	0	1	0	0	0		1	0	0
Nms	1	1	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1		0	0
Noi	0	0	1	0	0	1	0	1	1	0	0	1	0	1	1	1	0	0		1
Pet	0	0	1	0	0	1	0	1	1	0	0	1	0	1	1	1	0	0	1	

Tool F

	Cht	Hep	Htk	Jan	Kmk	Kwg	Lhm	Mrk	Ngr	Nhk	Nms	Noi	Pet
Cht		1	1	1	0	0	1	1	1	0	0	1	1
Hep	1		1	1	0	0	1	1	1	0	0	1	1
Htk	1	1		1	0	0	1	1	1	0	0	1	1
Jan	1	1	1		0	0	1	1	1	0	0	1	1
Kmk	0	0	0	0		1	0	0	0	1	1	0	0
Kwg	0	0	0	0	1		0	0	0	1	1	0	0
Lhm	1	1	1	1	0	0		1	1	0	0	1	1
Mrk	1	1	1	1	0	0	1		1	0	0	1	1
Ngr	1	1	1	1	0	0	1	1		0	0	1	1
Nhk	0	0	0	0	1	1	0	0	0		1	0	0
Nms	0	0	0	0	1	1	0	0	0	1		0	0
Noi	1	1	1	1	0	0	1	1	1	0	0		1
Pet	1	1	1	1	0	0	1	1	1	0	0	1	