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SOCIAL LEARNING MECHANISMS OF CULTURAL EVOLUTION

by

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## ABSTRACT OF THE DISSERTATION

### SOCIAL LEARNING MECHANISMS OF CULTURAL EVOLUTION

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Human cultural traditions are accumulated bodies of knowledge that have been built over time through innovation coupled with social learning. An evolutionary approach to culture examines culture traits as aspects of an organism's phenotype that are inherited through social learning processes. This dissertation applies theory from the literature on cultural evolution to understand mechanisms and strategies of this learning process in humans, and consists of three projects from data generated by two studies. For both studies, I used a novel experimental task: participants were asked to build weight-bearing devices from a length of weaving reed and a portion of modeling clay.

In the first project, using an experimental microsociey design, I tested the hypothesis that imitation is required for cultural accumulation. By manipulating visual access to behavior, I found evidence of cultural accumulation only when participants were able to view others building devices. This result is consistent

with the hypothesis that imitation is required for cumulative cultural evolution. In the second project, I tested the hypothesis that learners are able to infer the success of models by using model-based biases. I found that participants were more likely to copy the device designs of others who had performed well, than they were to copy device designs of those who had performed poorly. This difference held only in conditions in which participants could witness others building devices, as predicted by the use of model-based biases such as skill bias. In the third project, I tested participants' flexibility in the use of asocial and social information, in order to understand the contribution of individual learning constraints to cultural evolution at a population level. Participants built weight-bearing devices in three phases: an asocial learning phase, and two social learning phases. I measured both the performance of the weight-bearing devices and the use of social information. My results indicate that participants adjusted the degree to which they copied others relative to changes in their performance between the asocial and social phases. These data suggest that cultural evolution may rely on learners who are flexible, rather than fixed, in their learning strategies.

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## Chapter 1: Introducing Elaborated Culture

One of the central traits of our species is a dependence on culture: people in every society learn skills and use technologies that are important for survival. As a result of our cultural inheritance, humans occupy an ecological range that is unsurpassed among terrestrial vertebrate species (Boyd, Richerson, and Henrich 2011). These traits are not (and could not be) genetically pre-determined, and they are not individually invented *de novo* in every individual. Instead, culture traits are socially learned. Culture, defined here as socially learned, shared information within a population, is of interest to evolutionists because it is a secondary system of inheritance that may lead to adaptive changes in behavior without corresponding genetic changes.

While many animal species exhibit culture, humans alone seem to have uniquely elaborated culture, which is the result of the accumulation of information over time. An important unanswered question is how this is possible – how are humans able to produce cultural accumulation, the central trait responsible for our success as a species, and a key defining feature of human behavior? This dissertation contributes data toward understanding the mechanisms of this process. Specifically, I investigated three questions: 1) how learning mechanisms enable cultural complexity, 2) how the dynamics of cultural evolution are produced within populations, and 3) how the traits of cultural models influence learning. This dissertation consists of three semi-independent papers: the initial paper describes results from a pilot study on individual variation in asocial and social information use, the second paper reports the central results

from a large experimental microsociey study on social learning mechanisms needed for cumulative cultural evolution, and the final paper details a secondary finding for model-based biases taken from the microsociey study data.

## 2. Learning

Learning is operationally defined as a change to an individual at one point in time that is detected, through a change in behavior, at a later time (Rescorla 1988). This definition restricts learning to behavioral outputs, yet learning (and all behavior) must be underpinned by a cognitive (i.e., information processing) mechanism, and a failure of performance does not preclude learning (Shettleworth 1998). Therefore, a broad definition of learning would include any change in state due to experience; Shettleworth (1998) notes that this definition, while including phenomena that are not learning, encompasses the varied forms of learning better than would a more-restrictive definition. Learning fulfills the basic function of enabling animals to associate events in time and space, and is phylogenetically widespread. The shared structure of the neuron across primitive as well as more advanced organisms is indicative of a conserved mechanism (at the most basic level) for detecting these contingencies (Papini 2002).

Learning is a type of phenotypic plasticity that has been selected for, so therefore it is at once an adaptive product of evolution and a process of ontogenetic adaptation (Johnston 1982). Learned behaviors are acquired during the course of an individual's lifetime and therefore allow animals to respond appropriately to current environmental conditions. Though it is incorrect to describe a behavior as exclusively genetic or exclusively learned, it is useful to

examine the function of behaviors at the ends of the range of the fixed-plastic continuum when thinking about the function of learning. In contrast to non-learned innate behaviors, which have been selected for due to their ancestral adaptive benefits, the need to generate a range of behaviors in different ecological circumstances produces selection pressure for cognitive flexibility in the form of learning. A capacity for learning is predicted to evolve to address problems that are stable between generations (e.g., need to find a mate), yet vary in terms of the specific information to be learned between generations (e.g., choice of specific mates) (Johnston 1982, Stephens 1991). The ability to acquire adaptive behaviors may insulate animals from genetic change relative to species unable to learn (Dukas 2009), or speed up evolution by allowing animals to exploit new niches (Huey, Hertz, and Sinervo 2003, Price, Qvarnström, and Irwin 2003).

## 2.1 Social and Asocial Learning

Animals incorporate information into their behavioral repertoires through social or asocial means. Laland and colleagues (1993) note that these categories are likely in practice to comprise a continuum rather than a dichotomy, since the social component in social learning can be as minimal as a change in attention due to the presence of other animals (which then must be followed by individual exploration). Similarly, Galef (1988) argues that individual benefit is required for any socially-learned behavior to be maintained – so while a behavior may be initially acquired through social contact, individual learning acts to maintain the behavior. Social learning denotes change to behavior that is

socially mediated, either as a result of direct interaction with others, or as a result of changes to the environment caused by others (Galef 1988). Social learning is important for many important adaptive decisions, including foraging, mating, and predator avoidance (see Galef and Laland 2005, Kendal et al. 2005 for reviews), and is taxonomically widespread. Thorough documentation of social learning exists for non-human vertebrates (Box and Gibson 1999, Danchin et al. 2004, Frigaszy and Perry 2003b, Heyes and Galef 1996, Zentall and Galef 1988) and some evidence of social learning has been found for invertebrate species, including bumblebees (Leadbeater and Chittka 2007), noncolonial insects (Coolen, Dangles, and Casas 2005), and non-insect invertebrates (Webster and Fiorito 2001).

Social learning allows animals to avoid the cost in terms of time and energy of trial-and-error learning. Trial-and-error learning is inefficient because it does not necessarily result in acquisition of locally adaptive behavior, and time spent learning is time not spent increasing one's fitness (Boyd and Richerson 1988). Since social learning divorces the learner from the direct acquisition of information from the environment, it is adaptive under intermediate rates of environmental change, when socially acquired information might provide pertinent information. In contrast, extreme environmental stability is likely to be accommodated with genetic adaptation, whereas extreme rates of environmental change could render social information outdated. Laland et al. (1993) suggest that these dynamics are altered by consideration of transmission modes (these modes were initially described by Cavalli-Sforza and Feldman (1981)). Vertical

(parent-offspring) transmission is likely to track slowly changing environments, and horizontal (within-generation) transmission may be more adaptive than individual learning when there is high within-generation variability. Using theoretical modeling, Boyd and Richerson (1988) find that social learning should be pursued over asocial learning when asocial learning is inaccurate or costly and when it is likely that models have experienced the same environment as the learner (because the environment is relatively stable and there is not a great deal of migration between different habitats).

## 2.2 Rogers' Model

Social learning allows animals to avoid the costs of individual learning, but is not always adaptive. An influential theoretical paper by Alan Rogers (1988) suggests that this is the case because a producer-scrounger dilemma exists between social and individual learners in a population. While social learners are able to avoid individual learning costs, as their proportion increases in a population their information becomes increasingly outdated. This problem arises because as the proportion of social learners climbs, social learners increasingly learn from other social learners. Because individual learning is more adaptive when social learners outnumber asocial learners, Rogers' model predicts that the population will eventually attain an equilibrium between learning types, in which social and asocial learners are equally fit. This result is paradoxical because the ubiquity of social learning implies an adaptive benefit. Boyd and Richerson (1995) suggest that social learning is so widespread because it does provide a benefit, either by increasing individual learning efficiency or by allowing the

accumulation of information such that social learners are able to acquire information that they could not learn asocially within a single lifetime.

### 2.3 Strategic Social Learning

Theoretical modeling work suggests that the efficiency of individual learning might be increased by the deployment of social learning strategies – rules about from whom and when to learn from others (Laland 2004). Rather than employing social learning indiscriminately, strategic social learning predicts that social learning decisions will be made on the basis of direct evaluation of the payoff of a particular solution, e.g. success based biases like pay-off bias (Kendal et al. 2009, Pike et al. 2010), or indirectly, through the assessment of attributes associated with effective solutions over evolutionary time, e.g. model based biases such as prestige bias (Henrich and Gil-White 2001). Many of these strategy types have not yet been evaluated empirically. An exception is Mesoudi's (2011b) experimental comparison of social learning strategies. Participants in this study first built “virtual arrowheads” by using a computer to select parameters for five attributes. Each arrowhead was subjected to a virtual hunt and information was provided about the number of calories attained by the arrowhead to the participant. Participants were assigned to either a unimodal environment (in which there is a single best arrowhead design) or a multimodal environment (in which there are multiple different good designs of varying payoffs). After creating an arrowhead design, participants were presented with the choice to instead utilize social information under the constraints of one of four social learning strategies: payoff-bias (copying the highest-scoring design),



random copying, conformity, or averaging. Mesoudi reports that most participants did not choose to use the available social information; of those who did utilize the social information, the majority selected the payoff-bias option. The most adaptive strategy depended on the shape of the adaptive landscape: when there was only a single optimal arrowhead design, asocial and social learners performed equally well since asocial learners were able to converge upon the best design without the use of social information. For participants assigned to the multimodal scenario, payoff bias was the most adaptive solution because it allowed participants to jump to the highest adaptive peak, rather than getting stuck on a lower, locally adaptive peak.

### 3. Culture

The benefit of social learning in terms of allowing accumulation is realized in human culture. Though culture is a central concept of the discipline and has been since its founding, anthropologists have famously yet to arrive at a common definition: Kroeber and Kluckhohn (1952) documented 164 definitions within the scholarly literature. In recent decades, cultural anthropology has shifted from the sort of theoretical coherence that would allow for a unified definition, focusing instead on individual and situational variation. Behavior is often described as situated, contested, deeply personal, and historically mediated. This focus on specificity precludes generalization between societies, as phenomena documented by the anthropologist cannot be separated from their particular contextual variables, including the construction of the anthropological narrative by a particular researcher (Spiro 1986). While many cultural anthropologists

have abandoned the quest for macro-level understanding, researchers in other disciplines, as well as science-oriented anthropologists, have made significant progress toward understanding culture (for a recent review see Mesoudi 2011a).

For those interested in the evolution of culture, definitions that are inclusive enough to allow comparison with behaviors of non-human animals are warranted. Exclusionist definitions suggest that culture requires traits exclusive to humans, such as norms, symbolic systems, or language (e.g. Hill 2007, Kroeber and Kluckohn 1952, Tuttle 2001, Washburn and Burton 1979), or restrict culture to information that is transmitted in a particular, taxonomically-restricted manner, such as imitation or teaching (Boyd and Richerson 1985, Galef 1992, Tomasello 1994). If a human-specific mechanism is required for culture, this implies that the socially transmitted behaviors of non-humans may only be analogues of human cultural behaviors (Galef 1992, Tomasello 1994). When culture is defined anthropocentrically, the culture-like behaviors of non-human species are referred to with terms such as traditions or proto-culture. This practice is problematic because it eliminates the umbrella term that acknowledges the commonalities of systems of learned, shared behavior across humans and non-humans, and within the cultural system of humans. For example, *culture* is not synonymous with *symbolic system*, though symbolic systems characterize human culture. Therefore, additional terms should be used to cover the elaborations of culture (e.g. traits requiring language) in the human case, rather than describing culture as those cultural forms which apparently only human minds are capable of producing. As Cronk (1995, 1999) explains, culture

and behavior are not synonymous, and conflation of culture with behavior prohibits using the culture concept as explanatory for behavior. Rather, culture is socially transmitted information that may or may not influence behavior (though when studying non-verbal animals it may be difficult to detect information that is not influencing behavior).

### 3.1 Cultural Evolution

Scholars working from an evolutionary perspective (e.g. Atran 2001, Boyd and Richerson 1985, Boyer 1998, Cavalli-Sforza and Feldman 1981, Durham 1991, Sperber 1996), have developed a body of literature examining culture as a secondary system of inheritance. The idea that cultures evolve has a long history that predates Darwin (Campbell 1965). Though the concept was considered periodically in the intervening years (e.g. Keller 1915), cultural evolution research in its present form began to take shape in the 1970s, following the larger theoretical shifts in behavioral biology that began to focus on the evolutionary function of animal (including human) behavior (see Laland and Brown 2011, Segerstråle 2000 for reviews). Early incorporation of culture as a topic of evolutionary analysis appeared in Blum (1963) and Campbell (1965), and was followed by influential works by Ruyle (1973), Cloak (1975), Dawkins (1976), Feldman and Cavalli-Sforza (1976), Richerson and Boyd (1978), Alexander (1979), Durham (1979) and Lumsden and Wilson (1981).

The conceptualization of culture as an evolving system independent of the genetic system of inheritance distinguished this theoretical direction from that of others in the sociobiology movement, who argued that it was not necessary to

evaluate culture (in addition to genes) as a separate influence on human behavior (e.g. Darlington 1969, Morris 1967) Two especially seminal publications that ushered in this modern era were Cavalli-Sforza and Feldman's *Cultural Transmission and Evolution: A Quantitative Approach*, in 1981, and Boyd and Richerson's *Culture and the Evolutionary Process*, in 1985.

Research in cultural evolution is based on the recognition that culture traits have the characteristics necessary for natural selection: variation, heritability, and competition. Culture traits vary due to random copying error or deliberate modification. They exhibit heritability because they are transmitted to others through social learning, and they are subject to competition for limited cognitive resources if there exist multiple “functionally equivalent solutions to specific problems” (Laland and Brown 2011:146). These three components, shared with genetically inherited traits, have spurred the interest of modelers in applying the quantitative methods of population biology toward understanding culture.

Mathematical models have been criticized as too reductionist to capture the complexity of human cultural systems (though they are too complex for non-quantitative thinkers to easily understand, prompting the publication of books such as *Mathematical models of social evolution : a guide for the perplexed* (McElreath and Boyd 2007)). Modeling has several advantages over verbal explanations for understanding how culture traits evolve. To begin with, manipulation of multiple, independently changing variables cannot be easily accomplished through verbal means alone (Richerson and Boyd 2008). By

simplifying complex phenomena into mathematical notations, non-obvious, testable hypotheses are generated. While many practitioners acknowledge that modeling is heavily dependent on assumptions that may not be accurate, the full integration of modeling and empirical work is an ongoing project (Laland and Kendal 2003). Increasingly, reports have included validation of the findings of models with empirical testing or attempt to develop models on the basis of experimental data (e.g. Caldwell and Millen 2010a, Caldwell and Millen 2010b, Efferson et al. 2008, Efferson et al. 2007, Kameda and Nakanishi 2002, Kameda and Nakanishi 2003, McElreath 2004, McElreath et al. 2008, McElreath et al. 2005, Mesoudi 2008b, Mesoudi 2011b).

It is necessary here to emphasize the contrast of cultural evolution theory of the recent past with that of the early evolutionary anthropologists (e.g. Morgan 1877, Tylor 1871). Unlike early evolutionists, cultural evolution theorists of the past 40-plus years have been interested in culture as a general phenomenon, and are not involved in ranking societies or attributing racial or genetic explanations for culture traits. Unlike 19<sup>th</sup>-century formulations of cultural evolution, modern theories of cultural evolution do not propose that societies will inevitably “progress” through predetermined stages. Evolution, whether biological or cultural, is not inherently progressive, though unfortunately this notion remains common among those unfamiliar with evolutionary theory (Mesoudi 2011a; though see Currie and Mace 2011 for a recent resuscitation of Spencerian ideas). Momentary consideration of morphological adaptations consisting of the loss of complex traits suggests that evolution lacks this singular

directedness (See Henrich 2004 for a discussion of the loss of complex culture traits in a human society).

Clearly, cultural evolution also differs from biological evolution in some important ways. Mesoudi (2011a) points out that cultural evolution is Darwinian, rather than neo-Darwinian. It is not particulate, it is subject to Lamarckian inheritance, and, unlike random mutation, cultural evolution has a teleological quality because it can be directed by conscious decision-making. Unlike the genetic system of inheritance, culture traits are transmitted via publically observable behavior (Sperber 1996). As described above, culture traits are distinct from behavior. Culture traits are equivalent to genotypes, while observable behavior that serves as a vehicle for culture traits is analogous to the phenotype (Mesoudi 2011a). Given that culture traits do not have readily identifiable boundaries, the appropriate level of resolution for culture traits is an important question for empirical work. Pocklington and Best (1997) argue that units of selection for culture traits should be those units large enough to be repeatedly transmitted, and therefore subject to selection.

Cultural evolution is also distinct from biological evolution in that cultural transmission provides a novel means of spreading genetically maladaptive traits, such as religious beliefs limiting reproduction. While a capacity for culture is broadly adaptive, specific culture traits may have deleterious fitness effects. A well-documented case of the maladaptive possibilities of culture occurred among the Fore peoples of Highland New Guinea in the mid-20<sup>th</sup> century. Facing a shortage of meat, Fore people began to cannibalize the bodies of their deceased,

unknowingly spreading a fatal neurodegenerative disease, *kuru*. In addition to access to an (apparently tasty) meat source to satisfy a protein shortage, Fore individuals held a pre-existing belief that consuming bodies conferred vitality (Durham 2008). Interestingly, the Fore did have an understanding of infectious disease, and considered the possibility that *kuru* was infectious, but rejected this hypothesis because of the delay of disease onset and patchy distribution of *kuru* relative to the practice of human flesh consumption (Lindenbaum 1979). Boyd and Richerson (1985) argue that the mode of transmission affects the interaction between culturally acquired traits and adaptation. Vertically transmitted culture traits, in particular those acquired very early in ontogeny, are likely to have beneficial fitness effects because their transmission mode is so similar to the genetic system of inheritance. In contrast, horizontally-transmitted traits may elude the natural selection that they would have encountered if they were inherited, since they are acquired from non-genetically related individuals and may be acquired after reproduction. Boyd and Richerson (2006) suggest that human minds transmit these maladaptive traits because our evolved psychological propensities favor credulity over resistance, since ready adoption allows us to take advantage of the population-level information available in culture (which over evolutionary time was fitness-enhancing).

#### 4. Microsociety Methods

Much of evolutionary culture theory has been developed via mathematical modeling; because of their precision, laboratory methods have been shown to be particularly useful in validating the hypotheses and assumptions of these models

with actual human actors (who often behave quite differently than modeling has predicted: see Mesoudi and Whiten 2008). Experimental microsociety (laboratory microculture) methods, in which participants are asked to complete a task under some sort of group influence, were first used empirically by Jacobs and Campbell (1961), in a social psychology study designed to examine the perpetuation of a “cultural fraud” (1961:656): experimentally-seeded social information transmitted in spite of being contradictory to participants’ own visual perceptions.

The replacement method, used for the central study of this dissertation, is one of several laboratory methods used to study cultural transmission processes (Mesoudi 2007, Mesoudi and Whiten 2008, Whiten and Mesoudi 2008). In the replacement method, a type of diffusion method, participants are added to and removed from the experimental group. The replacement method was pioneered by Gerard et al. (1956), and most prominently applied by Jacobs and Campbell (1961). More recently, the replacement method has appeared in studies designed to examine the processes of cultural evolution specifically (Baum et al. 2004, Caldwell and Millen 2008a, Caldwell and Millen 2009, Caldwell and Millen 2010a, Caldwell and Millen 2010b, Caldwell et al. in press)

There are several advantages to using microsociety methods in the study of cultural evolution: participants can be randomly assigned to different groups, variables of interest can be manipulated and extraneous variables controlled, and results can be replicated (Mesoudi 2007). The use of microsocieties for studying cumulative cultural evolution also enables researchers to compress time, making



it possible to observe the processes of cultural evolution that might take several generations to accomplish in real time (Caldwell and Millen 2008b, Mesoudi 2007, Mesoudi 2008c, Mesoudi and O'Brien 2008). Experimental methods in cultural evolution research are envisioned by practitioners as complementing (not replacing) ethnographic, historical, and mathematical approaches (Insko et al. 1980, Mesoudi and Whiten 2008, Mesoudi, Whiten, and Laland 2006b). Of note, Insko and colleagues (Insko et al. 1982, 1983, 1980) used the replacement method in a series of studies designed to test competing anthropological theories about the origin of certain forms of social organization in traditional societies.

#### 5. Culture in non-human species

Modeling work offers a general, supra-organismal conception of culture, in which cultural effects are observed following the manipulation of a handful of variables. A few species, such as fish, allow the direct testing of these conjectures because they are able to endure invasive experiments such as cross-fostering (Laland, Atton, and Webster 2011). In the wild, socially learned behavioral traditions have been reported in populations from a range of taxonomic groups, including primates species (bonobos: Hohmann and Fruth 2003, macaques: Leca, Gunst, and Huffman 2007, capuchins: Perry et al. 2003, orangutans: van Schaik et al. 2003, van Schaik et al. 2009, chimpanzees: Whiten et al. 1999), cetaceans (reviewed by Rendell and Whitehead 2001), New Caledonian crows (Hunt and Gray 2003), and black rats (Terkel 1996). I focus here on research with non-human primates because of their close evolutionary relationship to humans, and the evidence that several species have multiple

behaviors that may be cultural. In primates, cultural behaviors have been documented for four behavior realms: foraging, material culture, communication, and social interactions (Sapolsky 2006). In common with some human culture traits, some non-human primate cultural behaviors in the social realm appear arbitrary, without any obvious function (e.g. chimpanzee handclasp grooming: McGrew and Tutin 1978), and others seem maladaptive (e.g. white-faced capuchin grooming practices: Perry, et al. 2003).

### 5.1 The Exclusion Method

Cultural behaviors result from the social transmission of individually invented behaviors, and therefore isolated populations might be expected to show behavioral variation. The technique of recognizing culture by the presence of behavioral variation is referred to variously as the method of elimination (van Schaik 2003), the ethnographic method (Wrangham 1994), the geographic method (van Schaik et al. 2003), the group contrast method (Fragaszy and Perry 2003a), and, perhaps most popularly, the method of exclusion (Krützen, van Schaik, and Whiten 2007). *Exclusion* refers to the necessity of eliminating the possibility that ecological or genetic differences are responsible for inter-population differences. This method came to prominence with Whiten et al. (1999), who provided evidence of chimpanzee behavioral variants by comparing data provided by research at seven long-term field sites in Africa. The exclusion method is indirect because it does not measure social transmission, the central feature of culture (Fragaszy and Perry 2003a), but rather detects culture through variation.

While the presence of variants is useful for the detection of culture, variation is not a necessary component of culture, and therefore the exclusion method risks missing behaviors that are socially learned and invariant across groups (Dewar 2003, Perry and Manson 2003). McGrew (2010) also points out that the exclusion method is too stringent because it is impossible to rule out ecological variation as a cause of behavioral variation, and even clear ecological variation that co-varies with behavioral variation could conceal socially transmitted behavior. Similarly, Perry et al. (2003) suggest that the presence of inter-group genetic variation does not exclude the possibility that a trait is socially acquired. Indeed, a recent retrospective comparison of behavioral variation in chimpanzee groups found a positive correlation between behavioral and genetic dissimilarity between groups (Langergraber et al. 2011). Langergraber et al. (2011) argue that genetic variation cannot be ruled out as a cause of inter-group behavioral variation in chimpanzees, but also urge judicious use of findings from the exclusion method, pointing out that a strict application of the exclusion method would rule out many traits considered cultural in humans. Van Schaik et al. (van Schaik 2010, 2009) provide an extended discussion of causes of type I and type II errors in identifying cultural behaviors in the wild using the exclusion method.

## 5.2 Koshima Island Macaques

The initial discovery of culture in a non-human species illustrates the difficulty of establishing that a shared behavior is indeed the result of social transmission. During the summer of 1953, a Japanese macaque living on

Koshima Island, Japan, was observed by Kinji Imanishi's research team to be "washing" sand from a sweet potato. The washing behavior, consisting of dipping the potato in a stream and using the opposite hand to brush off sand, slowly spread to most others in the population (though some animals developed variants of the original "brushing" behavior) (Kawai 1965). The assertion that this behavior had been socially transmitted first appeared in the literature with Kawamura's (1954) paper, written in Japanese, and these results were made available to an English-speaking audience with Kawai's (1965) follow-up paper.

The existence of cultural or proto-cultural behaviors in the Koshima Island macaques has been challenged on the basis that the mechanism of transmission is unknown. Since no human observers were on hand to document the spread of the behavior, critics have suggested it may have been invented multiple times independently (Galef 1992, Tomasello and Call 1997, Visalberghi and Fragaszy 1990). Visalberghi and Fragaszy (1990) and Galef (1992) argue that the slow spread of the washing behavior is more consistent with individual invention than with social learning, since social learning is presumed to allow more rapid diffusion. In an experiment with crab-eating macaques, Visalberghi and Fragaszy (1990) found that when water was provided, anything the animals were holding was dunked – including a lizard. On this basis, Visalberghi and Fragaszy call into question whether the Japanese sweet potato washers were learning this behavior socially, since dunking (which might easily lead to purposeful food washing) appears to be a common exploratory behavior for macaques.

### 5.3 Learning Mechanisms

Historically, research on social learning has been approached from two different research paradigms, ethology – in which researchers focus on the adaptive benefit of socially transmitted behaviors – and comparative psychology, whose practitioners are interested in determining the mechanisms underlying social learning (Galef 1988, Laland, Richerson, and Boyd 1993, Zentall 2006). Psychologists, with the benefit of experimental control offered by laboratory work, have portioned types of social learning processes into categories called social learning mechanisms. Social learning mechanisms are typically discussed as belonging to a hierarchy of social influence, ranging from social facilitation (the presence of another animal changing motivational state, indirectly resulting in learning), to imitation, the acquisition of an observed behavior. Identification of the operation of a particular mechanism depends on exclusion of the lower mechanisms, requiring experimental control conditions to rule out the effects of the more simple processes.

Although research about social learning is burgeoning (Nielsen et al. in press), social learning mechanisms as they exist are problematic because they are not discrete and lack the distinguishing qualities of mechanisms, though several attempts to provide a unifying framework have been made (Galef 1988, Heyes 1994, Hoppitt and Laland 2008, Whiten and Ham 1992, Zentall 1996). As Heyes (1994) discusses, while asocial learning mechanisms have an accepted taxonomy reliant on changes to observable behavior given an observable stimulus (e.g., habituation after repeated exposure), some classes of social

learning mechanism are identified based on the outcome and source of learning (e.g., behavioral matching in imitation), whereas other classes include only the source of the learning (e.g., some environmental influence in stimulus enhancement). Therefore assignment of a behavioral change to a particular category in most cases involves inference of the mechanism using the stimulus alone, rather than the link between the stimulus and the behavioral change, as in asocial learning. Since social learning types in most cases do not specify the sort of change that is needed, the same behavioral change could be assigned to multiple different categories of social learning mechanism, making the categories non-exclusive. As Heyes (1994) and Galef (1988) argue, social learning categories are not truly mechanisms; the current coding scheme reveals that we do not yet understand the mechanisms underlying social learning.

#### 5.4 Imitation and Related Mechanisms

Imitation, replication of an observed behavior, has been a topic of research interest from the early days of experimental psychology, following Darwin (reviewed in Galef 1988), and has gained particular prominence as the mechanism thought to enable culture. Conceptualizations of imitation have undergone several vacillations in the literature: currently imitation is conceived of as a sophisticated mechanism that researchers are at pains to identify in any non-human species; at other times imitation has been assumed to be a simple, unsophisticated means of behavior transmission, which apes in particular were thought to practice regularly (e.g. Yerkes 1916, Yerkes and Yerkes 1929). In chimpanzees, a few studies have reported evidence of imitation using a do-as-I-

do paradigm, in which the animals are trained to produce behavior demonstrated by a human model (Carrasco, Posada, and Colell 2009, Custance, Whiten, and Bard 1995, Myowa-Yamakoshi and Matsuzawa 1999, Tomasello, Savage-Rumbaugh, and Kruger 1993). However, evidence for spontaneous imitation of a conspecific model is more mixed.

Two mechanisms, emulation and imitation, have been notoriously difficult to distinguish experimentally. Both emulation and imitation result from observing behavior and result in behavioral matching; while imitation involves behavioral matching of the process used to accomplish a goal, emulation involves duplication of the goal, without clear evidence of behavior copying. Tomasello and colleagues (1987) provided an initial description of this mechanism in chimpanzees but did not refer to it by name until 1990 (the term *emulation* appeared initially in Wood 1989). Tomasello et al. (1987) provided captive chimpanzees with a t-bar tool that could be used to rake in food. Animals who were present during a demonstration of the tool learned to use the tool, but did not replicate the method used by the demonstrator. Tomasello et al. interpreted this finding to mean that chimpanzees were not imitating, but had instead learned something about the usefulness of the rake as a tool. This finding was pivotal in the comparative study of imitation as it eventually led to a reevaluation of claims of imitative abilities in non-human primates for those studies that had not controlled for copying based on the effect of learning about the relationships between objects and their properties (e.g. Horner and Whiten 2005, Whiten 1998, Whiten 2002, Whiten et al. 1996). An alternative explanation for the

behavior noted by Tomasello et al. is low-fidelity imitation (Byrne 2002, Whiten et al. 2009), if imitation is conceived of as learning from an action and producing an action that is topographically similar.

Tomasello et al.'s (1987) report culminated in a research trajectory designed to clarify whether chimpanzees learn more readily from observing actions or from observing other information about the relationship between manipulanda. This work has necessitated the use of creative methods, most notably the experimental "ghost control" (for a review of ghost control studies see Hopper 2010). Experimental "ghost controls" are intended to parse the effects of imitation and emulation by moving apparatuses or tools without a visible actor (e.g., by fishing line). If there is no difference in performance between magically moving items compared with behavioral demonstrations, this would suggest that learners are able to learn from object movements alone. In the fraught taxonomy of social learning mechanisms, this sort of emulation is sometimes referred to as "object movement reenactment" (Custance, Whiten, and Fredman 1999), contrasted with copying the result or goal of a demonstration, referred to as "end-state emulation" (Whiten et al. 2004), though these sources are not always distinguished with control conditions in experimental work (Hopper 2010). A demonstration of learning from a ghost condition would provide evidence of emulation, and unlike Tomasello et al. 1987, this finding would not be subject to the "low-fidelity imitation" critique, since imitation would not be possible in a ghost control. In the ghost control condition of a comparative study of chimpanzees and children, for example, Hopper et al. (2008) used fishing line to slide the door



of an acrylic test box to the left or right. Both children and chimpanzees demonstrated copying of the direction of door movement when a model was observed receiving a reward after the door was opened, supporting the hypothesis that chimpanzees are able to emulate. Most studies employing ghost controls, however, have not found evidence for emulative learning in chimpanzees (Hopper et al. 2007, Subiaul et al. 2004, Tennie, Call, and Tomasello 2006). From the point of view of testing for emulative learning, these findings are puzzling because they appear to conflict with the chimpanzees-as-emulators hypothesis advanced by Tomasello et al. (1987).

The failure to find results with ghost control conditions may have to do more with the artifice of the condition than with learning abilities, however. Subiaul (2007) has argued that the disparity in response to ghost controls is due to the human proclivity to attribute intentionality to the (invisible) agent, which he argues is absent in the non-human species that have been tested. Children, who, since they are young humans, do have the ability to attribute intentions, readily learn from these demonstrations (Hopper et al. 2008, Huang and Charman 2005, Subiaul et al. 2007, Tennie, Call, and Tomasello 2006, Thompson and Russell 2004). Whiten et al. (2004, 2009) also quite reasonably point out that the distinction between object movements and the actions of a model on those objects are not distinguishable in practice. In general, dissection of social stimuli into increasingly minute fractions of the social information available to social learners out in the world is problematic because we risk understanding only experimental results and not the phenomena they were

designed to test. The finding that chimpanzees do not learn from ghost conditions suggests that they do not find a ghost condition informative, but it is premature to conclude from failed ghost conditions that they are not learning from object manipulations when viewing a full behavioral demonstration.

At present, research to establish that non-human primates display culture is characterized by a gap between abilities demonstrated in the laboratory and findings from the field (Whiten and Mesoudi 2008). We have evidence suggesting that non-human primates have population-level behavioral variants, that they are capable of producing replicative behavior, and that they learn from behavioral demonstrations. Recent work has also established that chimpanzees are capable of transmitting behavioral variants to multiple individuals in transmission chains (Bonnie et al. 2007, Horner et al. 2006, reviewed in Whiten and Mesoudi 2008, Whiten et al. 2007). Although it is difficult to establish that a particular behavior has been transmitted by social learning in a wild population, the ingredients for a cultural system are present, and therefore it is perhaps parsimonious to regard chimpanzees as having the capability for, and in some cases displaying, culture. Yet, these cultural behaviors, like those of other non-human species, seem to be less complex than the cultures transmitted by humans.

## 6.0 Cumulative Cultural Evolution

Humans in every society learn techniques (for subsistence, childcare, and communication) and use tools (for food acquisition and processing and construction of shelters and clothing), that have been modified over time. One

result of modification is that existing techniques or technologies are improved, in terms of efficiency or production (Boyd and Richerson 2005, Laland 2004, Marshall-Pescini and Whiten 2008, Tennie, Call, and Tomasello 2009). This cultural “ratchet effect” (Tomasello, Kruger, and Ratner 1993) enables the cross-generational transmission of accumulated information. As a result, humans learn information that any single individual could not invent in his or her lifetime. A prominent hypothesis (hereon: “imitation hypothesis”) is that high-fidelity transmission of information via imitation is needed to support the cultural accumulation that enables complexity (Boyd and Richerson 1985, Boyd and Richerson 1996, Tomasello 1999, Tomasello, Kruger, and Ratner 1993).

#### 6.1 Archaeological Evidence for Cultural Cumulation

The ability to progressively improve existing technologies is central to understanding our remarkable success as a species. The appearance of sophisticated tools in the archaeological record has led some researchers to suggest that cumulation has been possible since at least since the beginning of the Middle Stone Age, 250-300 kya (McBrearty and Brooks 2000, Richerson and Boyd 2005, Sterelny 2012). Prior to this time, tool technology appears remarkably conservative, while afterwards, during the Upper Paleolithic, technological advances seem to have accelerated.

The first stone tools in the archaeological record, dated from 2.6 mya, were technologically simple yet experimental work has demonstrated that they required mental capacities exceeding those of our primate relatives. Captive bonobos trained to produce stone tools for a reward are able to produce

functional flaked tools roughly resembling the earliest flaked tools, but comparison with Oldowan tools (including ones made by contemporary humans as well as those attributed to australopithecines) suggests that bonobos are less skilled at stone tool manufacture (Toth, Schick, and Semaw 2006). Tools made by bonobos are characterized by the presence of many more misplaced blows; while part of this haphazard appearance may be due to biomechanical differences between the species, Toth et al. (2006) suggest that cognitive advances in australopithecines may also be responsible. The remarkable conservatism of the Oldowan industry, which was maintained for 1.5 My (Toth and Schick 2009), suggests that there was some impediment to improvement of these tool manufacturing techniques.

The change in rate of improvement to technologies that characterizes the transition from the earliest tool industry to behavioral modernity (the Upper Paleolithic) suggests a fundamental shift in learning processes. This shift is characterized by increasing reliance on socially acquired information, which may have further selected for increasingly sophisticated social learning abilities. Boyd and Richerson (1996) have argued that improved cultural transmission cannot have been the original selection pressure for high-fidelity imitation if imitation is required for cultural cumulation. Overcoming the costs of evolving imitation would require a population that already has information worth learning socially – if imitation is needed to generate this information, the social advantages of imitation or its underlying components (e.g. theory of mind) would have been the original selective pressure. During the early stages of the Oldowan, the ability of

individuals to invent better stone tool manufacturing techniques was likely constrained by the limited cognitive power of the small-brained australopithecines. The overall conservatism of the Oldowan industry suggests that even if individuals were able to improve existing techniques that these improvements were not sustained.

Sterelny (2011, 2012) has argued that technological advancement requires both brains that are able to improve existing technologies, and the components of social information transmission: populations large enough to produce and sustain innovations and cognitive mechanisms for social learning. Demographic factors are implicated in maintaining culturally acquired information because cultural knowledge held by a few expert individuals may be easily lost if these individuals are not imitated or if their knowledge is not improved upon (Kline and Boyd 2010). Evidence from the Upper Paleolithic transition supports the hypothesis that population size is important for cumulative cultural evolution, since anatomical modernity (including brain size increase) precedes the change to behavioral modernity in some locations by roughly 150,000 years, while increased population size seems to be more closely followed by behavioral modernity. Powell et al. (2009) model the relationship between population density and accumulating cultural information, and using estimates of increased population densities from mtDNA data, show that their predicted dates for transition match or predate the timing of the transition based on archaeological materials at several sites. The discontinuous nature of advanced technology in the archaeological record also supports the demographic hypothesis for

cumulative cultural evolution. D'errico and Stringer (2011) evaluate the evidence for an alternative saltationist hypothesis, advanced by Klein (2009), that genetic mutation resulting in advantageous neurological change is responsible for modern behavior, finding instead that cultural artifacts of various forms appear and disappear over time. Proponents of the demographic explanation for cumulative cultural evolution (e.g. Powell, Shennan, and Thomas 2009) acknowledge that additional work is needed to establish the factors responsible for maintenance of critical population numbers.

If imitative abilities are needed to establish a system of cultural cumulation, once these have evolved and cumulation begins (perhaps during the Middle Stone Age, and accelerating once populations have reached a critical threshold), the selection pressure on social learning abilities and skills needed for disseminating information (teaching) would have increased. A system of cultural knowledge acquisition is a type of niche construction that likely had wide-ranging evolutionary implications. Cachel (1997:587) argues that the shift toward information stored at the population level, rather than generated anew by individual brains, has relaxed the selection pressure on individual intelligence, which may explain the decrease in cranial capacity among modern humans over the last 10,000 years. Developing high-fidelity imitation has meant that detailed behavioral information can be transmitted between generations without genetic changes to the particular cognitive means of acquiring these skills individually.

Csibra and Gergely (2011) have argued that communicative abilities necessary for teaching and being prepared to learn from teaching are specifically

human adaptations, part of what they have deemed “natural pedagogy” (Csibra and Gergely 2009). Individuals who are adapted to attain information from others through imitation are not only able to build their innovations on accumulated advances of past generations, but are able to acquire information that may have been quite difficult to learn individually, specifically because the relationship between the ends and the behavioral means is difficult or impossible to detect (Gergely and Csibra 2006, Shea 2009, Tennie, Call, and Tomasello 2009, Whiten et al. 2009). Several recent studies have reported that human subjects, in particular children, seem compelled to imitate demonstrated actions that appear superfluous for attaining the stated goal of experimental tasks (Call, Carpenter, and Tomasello 2005, Horner and Whiten 2005, Kenward 2012, Lyons et al. 2011, McGuigan 2012, Whiten et al. 1996); this tendency is referred to as over-imitation. Such an ability would enable children to learn the group-specific, arbitrary behaviors that characterize much of human cultural variation. Consistent with this hypothesis, Over and Carpenter (2012) argue that over-imitation appears when subjects are more motivated to pursue social (rather than functional) goals. This shift in learning and teaching skills may have been responsible for initiating the acceleration of cultural cumulation that has continued to date in many human populations.

## 6.2 CCE in Non-humans

In non-human species, few reports have been made of behaviors that appear to be the result of a ratcheting process. In New Caledonian crows, Hunt and Gray (2003) used the design of foraging tools the birds make from *Pandanus*

species tree leaves as evidence of a cumulative process. Though the tools do appear to be the result of a complex manufacturing process, Hunt and Gray (2003) do not provide evidence that this technique was socially acquired. Holzhaider et al. (2010) examined the ontogeny of *Pandanus* leaf tool manufacture in a population of wild New Caledonian crows, and provide evidence that young crows gradually acquire the technique and do so in proximity to their tool-manufacturing parents. Yet, as Holzhaider et al. (2010) acknowledge, these data do not allow the exclusion of the possibility that crows learn this behavior by trial-and-error. In wild chimpanzees, Sanz et al. (2009) have documented manufacture of termite-fishing tools with a design feature that improves efficiency, though the transmission mechanism is not yet known. The dearth of evidence for accumulating culture in non-human primates should not be taken as evidence for a lack of accumulating culture, however. Boesch and Tomasello (1998) argue that the accumulation of cultural elements in non-human animals may be hidden from researchers because this accumulation is not sufficiently fast or dramatic. Indeed, without longer-term documentation of behavioral change it is difficult to conclude from the past 50 years of field study with chimpanzees that no current behavior is an improved elaboration of previous practices.

Direct critiques of the imitation hypothesis have highlighted the need for additional processes or have questioned the need for a high-fidelity mechanism. Heyes (1993) has criticized the imitation hypothesis on the basis that there is no reason to expect that imitation would insulate information from additional



modification once it has been acquired. Similarly, Galef (1992, 1995) has suggested that while imitation may aid in the acquisition of cultural behavior, behaviors are maintained only when they benefit the individual. Cognitive anthropologists Claidiere and Sperber (2010) suggest that even with very high-fidelity imitation, socially acquired behaviors in a population would be expected to eventually erode in the direction of individual preferences in the absence of some additional process to maintain stability. These individual preferences are described in detail elsewhere as pre-existing cognitive representations (Atran 2001, Atran, Medin, and Ross 2005, Boyer 1998, Sperber 1996). In response to these critiques, Henrich and Boyd (2002) developed a model indicating that exact replication is not a necessary aspect of cultural stability because social learning, even if inaccurate, is not random: population-level stability can emerge from processes such as conformity (a tendency to follow the majority).

While these critiques of the imitation hypothesis have focused on the failure of imitation to account for stability, others have suggested that additional processes are necessary for cumulative culture. Laland (2004) argues that ratcheting requires individuals to determine whether an observed alternative behavior would yield a better outcome than would the current variant. In chimpanzees, some experimental work has suggested that this species is limited by failure to switch solutions once they are acquired. This trait, which has been referred to as “habit” or “conservatism,” has been documented in several recent studies (Hrubesch, Preuschoft, and van Schaik 2009, Marshall-Pescini and Whiten 2008, Price et al. 2009). Interestingly, in orangutans, Lehner et al. (2011)

have found evidence for cultural ratcheting, including strategy switching and improvement of acquired techniques, in an experiment with captive animals. Lehner et al. (2011) argue that orangutans have not been found to display cultural cumulation in the wild because they rarely display innovative behavior. In contrast, captive studies have documented a capacity for innovation in orangutans (Lehner, Burkart, and van Schaik 2010, Lehner, Burkart, and van Schaik 2011, Russon et al. 2009), which may be motivated by the presence of food rewards (Lehner et al. 2010). In terms of foraging, orangutans may be more likely to have innovatory capacities than chimpanzees due to their unique semi-solitary lifestyle: benefits of innovation might be transmitted directly to offspring through vertical transmission, whereas for chimpanzees more efficient foraging techniques that are transmitted to others might lead to increased food competition with unrelated individuals.

## 7. Organization of the Dissertation

The preceding review provides the background material for the questions addressed by this dissertation. I am interested in culture as a system of information transmission common to many species, and this comparative perspective requires understanding research on non-human primates as well as experimental work with humans. It is also necessary to understand the social learning abilities and cultural features of non-human primates in order to evaluate hypotheses about the uniqueness of human culture.

In Chapter Two, I address one of the prominent hypotheses for cumulative cultural evolution in humans: the imitation hypothesis. Though this claim was

initially broached nearly twenty-five years ago (Boyd and Richerson 1985), work to empirically evaluate the idea that imitation is needed for cumulative cultural evolution has only recently begun, and in the interim several other explanatory hypotheses have been proposed (as discussed above).

In Chapter Three, I investigate the use of a preference for copying successful individuals (model-based bias). Modeling work predicts the presence of biases designed to detect and copy strategies of successful individuals, but existing experimental work has approached this question using direct information about success (i.e., explicitly telling participants in a learning task which of the models' designs are best). Instead, I tested whether participants demonstrate evidence of being able to infer this information themselves.

In Chapter Four, I examine the use of social and asocial information within individuals. At a population level, cultural evolution requires both social and asocial information use, and here I was interested in testing whether this effect appears to be the result of strategy switching or stable strategy use and assortment.

## Chapter 2: Social Learning Mechanisms of Cumulative Cultural Evolution

### 1. Introduction

Socially learned information can be an important source of adaptive behavior for animals in many taxa (Galef and Laland 2005). Humans have especially complex shared behavioral traditions, or *culture*, which have allowed extensive modification of the natural environment and consequently expansion into a wide variety of habitats (Boyd and Richerson 1995, Mithen 1996, Tomasello 1999). Human cultural complexity is enabled by an additive process of individual innovation, coupled with transfer of this information to others in the population via social learning. This additive process is termed *Cumulative Cultural Evolution* (CCE) (Boyd and Richerson 1996).

Among animal species, humans have uniquely complex culture. Due to the additive nature of human cultural traditions, the socially learned body of information that humans acquire vastly exceeds what any individual could invent in his or her lifetime. In other animal species, however, the degree to which socially learned information exhibits this additive quality seems relatively limited, and the difference between what may be acquired by individual and social learning less pronounced. One hypothesis is that imitation is required for human-like cultural complexity (Boyd and Richerson 1985, Boyd and Richerson 1996, Tomasello 1999, Tomasello, Kruger, and Ratner 1993). Imitation, which is defined as behavioral replication in an observer following the witnessing of that behavior in a demonstrator, is proposed to be especially important for the accumulation of cultural information because it allows high-fidelity information

transfer between individuals. Without a high-fidelity transmission mechanism, information is likely to be lost; individual modifications will not be socially acquired and therefore not be subject to the additional modification which enables cultural complexity (see Galef 1988, Heyes 1993 for alternative views).

Recent modeling results suggest that small increases in fidelity can result in longer-lived traditions and therefore greater opportunities for cultural accumulation through diffusion and modification of existing practices (Enquist et al. 2010). Yet, whether imitation produces higher-fidelity information transfer than other social learning mechanisms is itself an open question (Laland and Hoppitt 2003).

The contention that imitation is producing the conditions necessary for accumulation is corroborated by the lack of evidence for cultural accumulation in wild non-human populations, among which no clear evidence of imitative learning of traditions has been collected to date due to the difficulty of testing particular social learning mechanisms under field conditions (Whiten 2011). Interestingly, however, cultural transmission studies with chimpanzees have provided evidence of diffusion of experimentally seeded behaviors across several individuals (Bonnie et al. 2007, Horner et al. 2006, Whiten, Horner, and de Waal 2005, Whiten et al. 2007), complicating the argument that differences in transmission fidelity are responsible for the relative lack of complexity in non-human cultural behaviors. Of particular relevance to the current study is the diffusion chain research conducted by Horner et al. (2006). In this study, a single chimpanzee in three groups was trained to open an artificial fruit using one of two techniques.

One individual was then allowed to observe the model, and after acquiring the behavior the observer individual served as a demonstrator for another observing individual, who in turn acted as a demonstrator for an additional individual. Horner et al. (2006) report that the alternative techniques demonstrated were reliably transmitted across chains of six and five individuals, suggesting that chimpanzees are capable of some degree of transmission fidelity. While these data are consistent with social learning of behaviors, the naturalistic study design was not intended to distinguish the social learning mechanisms underlying the transmission events.

Among studies which have been designed to capture this level of mechanistic detail, findings for imitation in chimpanzees is mixed, with the central debate surrounding the differentiation of imitation from a related mechanism termed *emulation*. Emulation, in contrast to imitation, involves learning from the *products* of behavior, e.g., a completed tool, rather than the behavior itself, e.g. the action of tool making (for a review see Whiten et al. 2009). In order for imitative learning to be positively identified, the possibility that the performance resulted from emulative learning must be eliminated. Among the studies which have controlled for emulation, there is some evidence that chimpanzees learn from actions (Hopper et al. 2007). Yet, comparative research suggests that imitation in apes does not involve the degree of bodily action matching that characterizes human imitation (Horner and Whiten 2005, Nagell, Olguin, and Tomasello 1993, Tennie et al. 2010). In sum, chimpanzees are capable of transmission fidelity at least at the level required to sustain shared behaviors

recognizable at the population level, but do not demonstrate the sort of high-fidelity behavioral replication thought to be required for CCE.

A recent study, Dean et al. (2012), found that, in children, performance in solving a puzzlebox equipped with sequential challenges covaried with a suite of abilities including imitative performance, consistent with the imitation hypothesis for CCE. Capuchins and chimpanzees, in contrast, showed little evidence of utilizing these social skills in solving the task, and underperformed relative to human children. To date, the only published report to explicitly test the imitation hypothesis for CCE in adults, Caldwell and Millen's (2009) experimental microsociey study, found no evidence of a superior effect of imitation over related social learning mechanisms in generating CCE. The current study was designed to elaborate on Caldwell and Millen's (2009) work, using the same basic experimental microsociey design with a novel task. Experimental microsocieys approximate cultural dynamics within a laboratory setting by examining the flow of information in groups of participants as they complete an experimental task (see Mesoudi and Whiten 2008 for a review). The addition and removal of group members is intended to simulate cultural generations. After validating their microsociey design in an earlier study (2008), Caldwell and Millen (2009) asked participants to build and fly paper airplanes as part of a transmission chain. In their design, each member of the group had a start time for building his or her plane which was slightly staggered, allowing for some overlap in cultural generations and therefore opportunity for social learning. Each group of participants was randomly assigned to one of seven experimental

conditions, each with various degrees of social information access. Groups in the action conditions were allowed to observe other group members building airplanes, allowing potential learning via imitation. Groups in the results conditions were able to examine completed planes and their flight distances, providing opportunity for emulative learning. Caldwell and Millen found evidence of cultural accumulation in all seven conditions tested, and found no superiority in performance of groups with access to action information compared to those without access to action information. Caldwell and Millen interpret these results to mean that emulation may be sufficient for CCE. Yet, as these authors acknowledge, the nature of the task may not be appropriate for generalization to the transmission processes for other cultural behaviors, which, due to their complexity, may require imitation to generate cumulation (2009:1482).

Tasks may be complex for several reasons, including uncertainty about behaviors that might be used to replicate outcomes. In this sense, paper airplane construction is a relatively simple task because it typically consists of executing a series of proscribed steps. This characteristic of the task means that even in the emulation condition of Caldwell and Millen's study (2009) it might have been possible for participants to infer the behavioral means used to create the airplanes (and improve upon them), in part due to prior experience with paper airplane building. Therefore, the demonstration of CCE in the emulation condition might be characteristic of tasks that allow reverse engineering of behavior from outcome. As Caldwell and Millen (2009) note, when behaviors cannot be readily inferred from outcomes, the use of imitation might be required



to generate CCE. The current study task was designed to be novel for most participants, making it likely that participants had to rely upon the available information in each condition (rather than prior knowledge) to solve the task. The number of behavioral steps required to produce a particular outcome is also likely to affect the degree to which participants are able to infer behavior from end-product, and the current task was also designed to incorporate this type of complexity.

In the current study, participants were assigned to micro-society groups and asked to build devices from a length of weaving reed and a portion of modeling clay. Research staff assessed the success of these devices by measuring the number of weights held by each device while it was being suspended from a wooden stand. The primary goal of the research was to test the imitation hypothesis for CCE using a complex, naturalistic task. It was predicted that in light of the complexity and unfamiliarity of this task, successive improvement to the reed and clay devices would occur in the presence of behavioral information, but not when behavioral information was not available.

Participant groups were assigned to one of three social conditions or one non-social control condition. In the social conditions, participants had visual access to either the completed devices others on their team had created, the building behaviors used to create devices, or both. When behavioral information was available, imitation would be a possible social learning strategy. When only information about completed devices was available, participants may have relied on other learning mechanisms, such as emulation. In the non-social control

condition, participants saw neither the completed devices of others, nor their behaviors.

## 2. Methods

### 2.1 Participants

Participants were recruited from the local community and the campus of Rutgers University. 604 subjects (349 females and 255 males) took part in the study. The mean age for subjects was 21 years (S.D. 4.80, range 18-60). The testing took place in central New Jersey between October, 2010, and April, 2011. All applicable human subjects protection protocol were followed and permission to do the study was granted by Rutgers University Institutional Review Board.

### 2.2 Materials

Each subject was provided a 160-cm length of 6.35-mm ( $\frac{1}{4}$ -in) flat weaving reed and 75-g of modeling clay. Participants also had access to a wooden stand with a 12.5-cm diameter hole (figure 1.1). These materials were distributed to each team at the beginning of the task, but participants were instructed that they were not allowed to touch the materials until instructed to begin building their devices. All instructions were given to participants both orally and in writing.



Figure 1.1: Materials: wooden stand, clay, and reed

### 2.3 Procedure

Once seated, participants were told that they were part of a team trying to build devices to hold as much weight as possible. During this instructional period, participants were shown the weights and the weight-adding process: a research staff member showed participants an example weight, and, using a stand and a weight, repeatedly demonstrated the weight-adding process by dropping weights through the center of the hole in the stand. This demonstration was made to every two participants in the row to ensure all participants were able to view it, and research staff assessed attention to the demonstration by observing eye contact with the stand. If any participants appeared not to be

paying attention, the group was reminded to watch the demonstration, until all participants had been observed to gaze at the stand.

In all conditions, participants were instructed that at some points in time they might be able to watch what others were doing, or see the completed devices of others. Participants were instructed that looking at others or their completed devices was permitted, but that talking to one another was not permitted. Following Caldwell and Millen (2008), building start times of each participant were staggered. In every condition, the third participant waited an additional five minutes to begin building his device following the start time of the second participant. By waiting, the third participant in the device-only condition had access to the completed device of the second participant five minutes earlier. Thus, the third participant in the device-only condition was not unduly disadvantaged relative to the third participant in the behavior-only condition. Each participant spent a period of time waiting to begin building, and 15 minutes building. Participants were provided with a timer showing two times simultaneously counting down, and were instructed that the number on top was the “waiting time” while the bottom number was the “building time.” Each timer was programmed to ring twice, to indicate the start and end of the building period. Participants were told that they could begin building as soon as they heard the timer chime initially.

While waiting, participants were unable to see others building devices, or their completed devices. Participants were instructed that during the waiting period they were not permitted to wear headphones, to use cell phones for any

purpose, or to use a computer. These activities were prohibited due to their potential to disturb other participants or distract participants from beginning the task on time, due to failure to hear the timer chime. Waiting times were equal across the conditions for a given position in the chain, because participants may have used the available time to strategize how to complete their devices. The asocial control condition was included in order to control for the possibility that individuals later in the chain were better able to make devices due to longer time spent planning. See figure 1.2 for group composition.

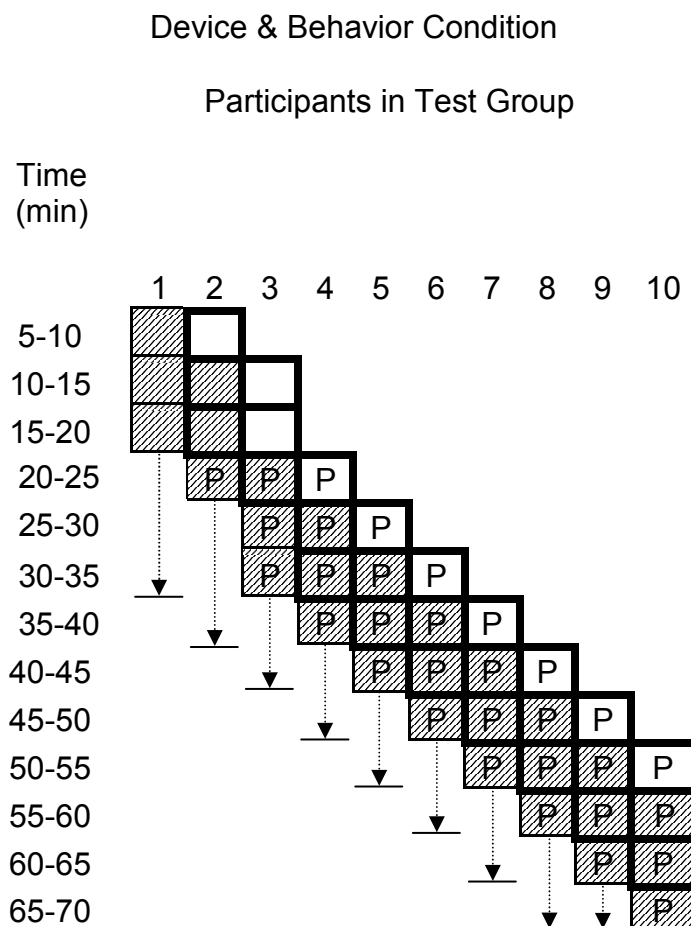


Figure 1.2: Microsociety Design Schematic

(following Caldwell and Millen 2008).

This schematic indicates the role of each participant during any one trial for the device and behavior condition. In the device-only condition, no behavioral information was available. In the behavior-only condition, no device information was available. In the asocial condition, no device or behavioral information was available.

Key for Microsociety Design Schematic

- = building behavior of previous participant(s) in chain visible
- = building device
- P = completed device of previous participant(s) in chain visible
- = completed device of participant visible to others in the chain (line indicates when device was removed from view)

Following completion of the device or expiration of the 15-minute build time, 50.6-g weights were added to the device by a research assistant, one at a time, until a weight slipped off the stand or the device fell or broke. If a weight slipped off the stand but the device did not fall or break, the weights were added again in order to control for variation in the adding process. If weights were added again, the higher number was recorded as the number of weights held. The higher number, rather than the mean, was chosen as the measure of success because bias in the adding process is more likely to negatively affect the number of weights than to artificially increase the number of weights held, given the physical limitations of the clay and reed devices. Therefore, the higher number was conceived of as more accurately representing the true capability of the device than the mean of a higher and lower score.

Information about the success of devices was not provided to observers. The success of team members was not made available to mimic conditions of uncertainty in the real world: frequently, directly ascertaining the payoff of observed behaviors or end-products is not possible, in particular during the initial period of observation for a novel behavior. When social learners do not have direct access to information about the success of a strategy, other available content and context cues are expected to inform decisions about when and whom to copy (Laland 2004, Rendell et al. 2011). Participants were not rewarded for performance. Following the weight-adding process, participants left the testing area.

Visual access to participants and their devices was manipulated by adding and removing lightweight barriers between participants. In conditions for which device information was available (device-only condition, and device and behavior condition), completed devices were placed on a display table 1.25M in front of the line of participants, and this display table was shifted to give visual access to successive groups of participants. Barriers between participants and a barrier on the right-hand side of the display table prevented visual access to participants farther down the transmission chain. A maximum of two devices was placed on the display table at a time. As each participant completed his or her device, it was placed on the left portion of the display table, and any device(s) currently on the display table were shifted to the right. At this time, the right-most device on the display table was removed from the participants' view. The display table was shifted toward the end of the chain of participants every 5 minutes by aligning the barrier of the display table with the right-hand barrier of the next participant in the chain (see figures 1.2 and 1.3 for details). The display table began each trial with its barrier aligned with the right-hand barrier of participant 4. In order to maintain experimental control over the devices in view, participants were asked not to stand up in attempt to view the devices. See figure 1.3 for details of the experimental setup at minutes 30-35.



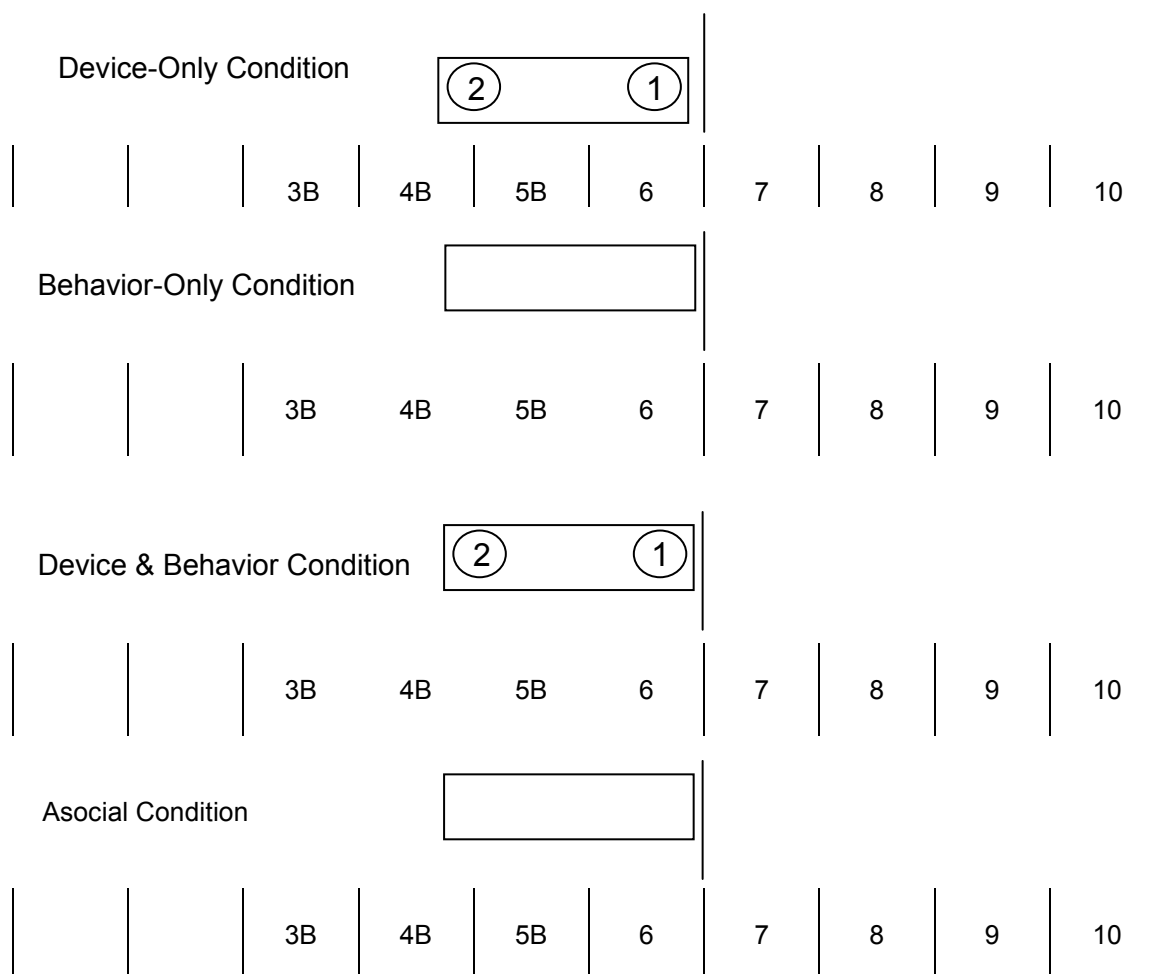
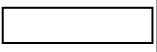



Figure 1.3: Participant Activities at Minutes 30-35

At minute 30, participants 1 and 2 have left the testing area. Participants 6-10 are waiting to begin building. Participants 3-5 are building. In the device conditions (device-only and device & behavior), participants in positions 3-6 are able to view completed devices of participants 1 & 2. In the behavior conditions (behavior-only and device & behavior) participants 3-6 are able to watch one another building devices.

Key for Figure 1.3 Participant Activities at Minutes 30-35

 = Display table where devices were placed following completion.

 = Completed device (x denotes position of participant who created device)

 = Barrier blocking visual access between participants

B = Building device

### 3. Results

The mean number of weights held by a device in any condition was 6.68 (S.D. 9.11), and number of weights held ranged from 0-66. Figure 1.4 shows the mean number of weights held per device in positions 1-6, for groups of size six or greater ( $k=61$ ,  $n=366$ ). The group size has been restricted to groups of the same size because of group size variation due to no-show participants. The supplementary material includes descriptive statistics for the performance of conditions based on various chain lengths (table S1.1), photos of selected devices (figure S1.1).

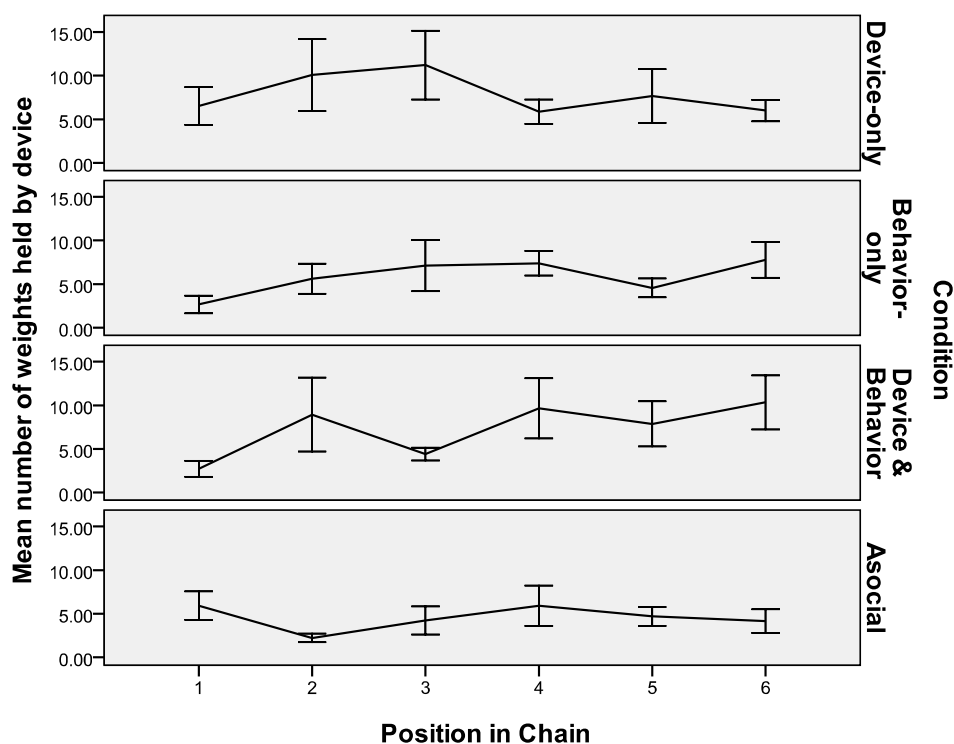


Figure 1.4: Measures of success of clay and reed devices over generations, for groups of six or greater. Error bars indicate  $\pm$ S.E.M.

Cultural accumulation would predict successive improvement in each experimental generation, such that each position does better than the one preceding it ( $10 > 9 > 8$ , etc.). In order to test this explicitly, a Page's  $L$  trend test was used (Page 1963). Page's  $L$  trend test is a repeated-measures ranking test similar to Friedman's test that is used when the analysis requires a specific hypothesized rank order. Due to variation in group sizes from no-show participants, the results reported here are for participants in groups of at least six participants, truncating the group at position six ( $k=61$ ,  $n=366$ ). The  $L$  in both behavior conditions reached the critical value for significance ( $p < .05$ ), indicating that there is a significant trend of improvement in both behavior conditions (behavior-only condition and device & behavior condition). No trend of improvement in the device-only condition or the asocial control condition was detected. See table 1.1.

Table 1.1: Summary of Cultural Accumulation Results: Page's  $L$  Trend Test

Condition	$L$	$p$
Device-only ( $k = 15$ , $n = 6$ )	1106	.454
Behavior-only ( $k = 18$ , $n = 6$ )	1395	.015
Device & Behavior ( $k = 15$ , $n = 6$ )	1167	.017
Asocial ( $k = 13$ , $n = 6$ )	962	.409

In order to examine the effect of truncating the group size at six participants, the Page's  $L$  values were also determined for chains of size 3-10 (truncating at the third through the tenth participant, respectively). It should be noted that these truncation points create nested data (i.e., a group of five or greater contains five-participant chains, as well as chains with original lengths 6-10 which have been truncated at position five). The overall pattern of Page's  $L$  scores from the full data set for chains of at least three participants mirrors the findings of the six-person chains: no chain length in the asocial or device-only condition reached the critical  $L$ , so no evidence for cumulation was found for groups not allowed access to behavior, regardless of truncation point. In contrast, of the behavior-condition truncation points (chains of 3-10), 11 of 16 reached the critical  $L$ . Two additional groups were within one and two points of reaching critical  $L$  status, respectively. The full set of trend test results for groups of size 3-10 may be found in the supplementary material (table S1.2).

As a measure of cumulation in each chain, Spearman correlation coefficients were derived per chain, and transformed using Fisher's  $z$ -transformation. See Table 1.2 for details of the correlation results. To determine whether there was a significant difference in performance between the conditions depending on the presence of behavior, a two-way ANOVA was calculated on the Fisher's  $z$ -transformed correlation coefficients for behavior conditions (behavior-only and device & behavior) and non-behavior conditions (device-only and asocial). This analysis included chains of at least 6 participants ( $k=61$ ,  $n=466$ ). The ANOVA results revealed a significant main effect of behavior

[ $F(1,57)=10.563$ ,  $p=.002$ ], but not of device [ $F(1,57)=0.001$ ,  $p=.973$ ] and there was no interaction effect [ $F(1,57)=0.835$ ,  $p=.365$ ]. The behavior conditions therefore show superior cumulative effects relative to the non-behavior conditions. When the asocial condition was removed from the analysis so that the behavior conditions could be compared against the device condition alone, this ANOVA also showed a significant main effect of behavior [ $F(1,57)=9.616$ ,  $p=.003$ ].

Table 1.2: Mean Correlation Results Per Condition

Condition	$r$ (z-transformed values)
Device-only ( $k = 15$ , $n \geq 6$ )	-0.164
Behavior-only ( $k = 18$ , $n \geq 6$ )	0.197
Device & Behavior ( $k = 15$ , $n \geq 6$ )	0.284
Asocial ( $k = 13$ , $n \geq 6$ )	-0.054

Since no evidence of cultural accumulation was found in the device-only condition, it might be possible that participants in this condition were not learning socially at all. In order to test this hypothesis, a comparison of the zero scores in each condition was conducted (see Table 1.3). Zero scores indicate that the participant's device held no weight at all. Since those in the first position in the chain would be expected to have randomly-distributed scores, position one

scores have been excluded for this analysis. A Pearson's chi-square test showed a significant difference between the number of zero scores in each condition  $\chi^2 (3, n = 305) = 8.72, p = .033$ . In addition, comparison of the zero scores in the device-only condition and the asocial condition were significantly different, suggesting that those in the device-only condition are learning socially  $\chi^2 (1, n = 140) = 6.57, p = .010$ .

Table 1.3: Zero Scores Distribution

	Device-only	Behavior-only	Device & Behavior	Asocial
Observed Count	5	9	7	14
Expected Count	8.6	10.3	8.6	7.5
Std. Residual	-1.2	-0.4	-0.5	2.4
% Within Condition	6.7	10	9.3	21.5

#### 4. Discussion

When behavioral information was available, participants demonstrated evidence of cumulative culture, improving their device performance for each participant in the chain. Comparison of performance between behavior and non-behavior conditions indicates that behavior is required to generate CCE in this task. This result is in accordance with the hypothesis that imitation is required for cumulative cultural evolution. The distribution of completely non-successful devices between conditions suggests the null result in the device-only condition is not due to failure to attend to the completed devices (or other experimental contingencies). That is, while participants in the device-only condition seem to be gaining some information from observation of completed devices in this condition, they were unable to improve their device designs. This lack of improvement in the device-only condition, in contrast to the improvement demonstrated in the behavioral conditions, implies that participants extracted (and improved upon) some specific information about building techniques from the observed demonstrations. Apparently the information contained in completed devices was insufficient to convey how to improve one's device. Although they were unable to improve their devices after observing completed devices, it is unclear whether participants were also unable to ascertain the behaviors used to create the devices. It would seem that replication of the building behaviors would be a minimal component of technique improvement. These two possibilities might be distinguished in future studies by asking participants explicitly to re-create the behaviors used to create an observed device. This question is also

interesting because one implication of the imitation hypothesis for CCE is that improvement is possible when behavioral techniques are replicated, yet behavioral information could provide some additional information that allows for improvement of devices which simple replication does not.

In contrast to Caldwell and Millen (2009), evidence for CCE was not found for the device-only condition of the current study. One explanation for these conflicting results is a difference in the degree of difficulty in the tasks: while performance on Caldwell and Millen's task may have been enhanced via emulative learning alone, participants in the current study may have needed the additional information provided by behavior in order to improve their device designs. That is, participants in the current study may not have been able to infer how to replicate (or improve upon) the devices that they saw only as finished products, because they could not readily infer the required behavioral steps. The creation of complex artifacts in human evolutionary history may have involved a similar problem in terms of "opacity" of the relationship between end-product and means, which Gergely and Csibra (2005) have argued may have selected for enhanced imitative abilities in the human lineage. The task used for the present study also may have been relatively less circumscribed in terms of the behavioral possibilities that might be used to enhance observed end products. As Whiten and Ham (1992) suggest, when there are fewer behavioral options for creating a device with similar design features, it may be the case that behavioral replication can be produced even in the absence of observing behaviors. For an evaluation of the imitation hypothesis for CCE, tasks should



be designed such that some improvement with imitation might be expected (e.g., an advantage associated with particular techniques). In the current study, the ability to view building behaviors, by providing additional information about the techniques needed to produce particular designs, may have provided this advantage. An alternative explanation is that because in the current study participants were not apprised of the success of other members of their team, participants in the device condition may not have known whom to emulate. This explanation bears further testing, as does the hypothesis that model-based biases contributed to the performance improvement noted in the behavior conditions.

While these results support the imitation hypothesis for cumulative cultural evolution, further studies with carefully designed control conditions are needed to clarify which social learning mechanisms are in use. The availability of behavioral information cannot be taken as evidence of imitation, as the critique of experimental research on non-human animal imitation amply illustrates. Instead, future studies should exclude related mechanisms through exacting control conditions. In addition, future research efforts might be directed toward understanding the threshold at which artifacts become too complex to reproduce via emulative means alone. Experimental microsocieties allow this required degree of experimental control, and the development of appropriately complex and naturalistic tasks will go some way toward accomplishing the goal of developing a synthetic theory of the evolution of culture that complements findings from mathematical and ethnographic approaches (Insko et al. 1980,

Mesoudi 2008a, Mesoudi 2011a, Mesoudi and Whiten 2008, Mesoudi, Whiten,  
and Laland 2006a)

## 6.0 Supplementary Tables and Figures

Table S1.1: Summary of Device Performance Per Generation. The N-values indicate where the chain has been truncated. Continued on following page.

Condition	Replicates and Group size	Mean Number of Weights Held by Device					
		First Generation (Position 1) M (S.D.)	Second Generation (Position 2) M (S.D.)	Third Generation (Position 3) M (S.D.)	Fourth Generation (Position 4) M (S.D.)	Fifth Generation (Position 5) M (S.D.)	Last Generation (Positions 6 -10) M (S.D.)
Device-only	k = 15, n = 6	6.53 (8.37)	10.07 (16.01)	11.20 (15.21)	5.87 (5.41)	7.67 (11.93)	6.00 (4.77)
	k = 12, n = 7	7.67 (9.05)	12.25 (17.32)	10.17 (14.49)	5.92 (5.79)	7.92 (13.34)	5.17 (6.28)
	k = 8, n = 8	6.38 (3.89)	14.50 (20.54)	14.00 (16.54)	4.88 (3.56)	5.63 (5.88)	4.38 (3.78)
	k = 5, n = 9	6.80 (3.11)	12.80 (18.13)	20.80 (17.99)	4.20 (1.48)	7.20 (7.19)	2.60 (2.61)
	k = 3, n = 10	7.00 (2.65)	19.33 (22.28)	14.33 (18.93)	4.00 (2.00)	5.00 (3.61)	1.33 (0.58)
Behavior-only	k = 18, n = 6	2.67 (4.24)	5.61 (7.29)	7.11 (12.42)	7.39 (6.02)	4.56 (4.61)	7.78 (8.72)
	k = 12, n = 7	2.17 (3.13)	4.83 (6.66)	8.83 (14.65)	9.25 (6.41)	5.50 (5.25)	6.00 (6.48)
	k = 10, n = 8	2.40 (3.37)	5.50 (7.12)	10.10 (15.84)	7.40 (4.79)	6.10 (5.55)	5.20 (6.41)
	k = 5, n = 9	0.20 (0.48)	3.00 (2.65)	15.80 (21.58)	8.40 (6.23)	5.40 (3.91)	11.40 (12.30)
	k = 4, n = 10	0.25 (0.50)	2.00 (1.63)	8.00 (14.67)	7.75 (6.99)	6.00 (4.24)	2.75 (1.71)
Device & Behavior	k = 15, n = 6	2.73 (3.54)	8.93 (16.43)	4.40 (2.82)	9.67 (13.37)	7.87 (10.00)	10.33 (11.95)
	k = 13, n = 7	2.92 (3.77)	10.23 (17.36)	4.62 (2.96)	11.08 (13.87)	8.62 (10.56)	12.00 (11.16)
	k = 9, n = 8	3.56 (4.39)	10.89 (20.82)	4.56 (2.83)	8.56 (2.83)	5.67 (5.98)	6.89 (2.76)
	k = 6, n = 9	4.50 (4.93)	14.17 (25.50)	4.67 (3.45)	8.50 (13.11)	3.50 (1.98)	5.50 (3.56)
	k = 4, n = 10	2.75 (3.40)	20.00 (30.78)	4.75 (4.27)	2.75 (4.86)	3.25 (1.89)	2.00 (1.83)

Condition	Replicates and Group size	First Generation (Position 1) M (S.D.)	Second Generation (Position 2) M (S.D.)	Third Generation (Position 3) M (S.D.)	Fourth Generation (Position 4) M (S.D.)	Fifth Generation (Position 5) M (S.D.)	Last Generation (Positions 6 -10) M (S.D.)
Asocial	$k = 13, n = 6$	5.92 (5.89)	2.23 (1.83)	4.23 (5.86)	5.92 (8.35)	4.69 (3.88)	4.15 (4.91)
	$k = 3, n = 7$	8.00 (10.39)	2.00 (1.73)	6.00 (6.00)	13.67 (15.14)	4.33 (4.16)	2.00 (2.00)
	$k = 2, n = 8$	11.00 (12.73)	1.50 (2.12)	9.00 (4.24)	17.00 (19.80)	5.00 (5.66)	10.00 (0.0)
	$k = 2, n = 9$	11.00 (12.73)	1.50 (2.12)	9.00 (4.24)	17.00 (19.80)	5.00 (5.66)	2.00 (0.0)
	$k = 2, n = 10$	11.00 (12.73)	1.50 (2.12)	9.00 (4.24)	17.00 (19.80)	5.00 (5.66)	8.50 (9.19)

Table S1.1: Summary of Device Performance Per Generation. The N-values indicate where the chain has been truncated (continued from previous page).

Figure S1.1: Examples of Devices

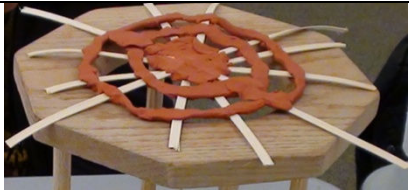


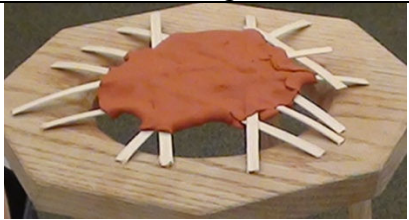
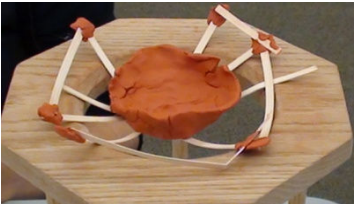
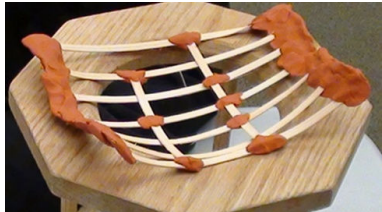
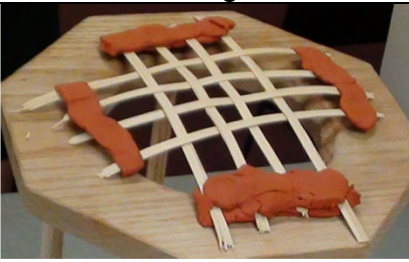


Highly Successful Devices (> 95 <sup>th</sup> percentile)	Average Devices (held 6 weights)	Unsuccessful Devices (no weights held)
 47 weights		
 32 weights		
 41 weights		

Table S1.2: Cultural Accumulation Results for Groups of Size 3-10: Page's L Trend Test  
(continued on following page)

	Condition	Number of Chains	$L$	Critical $L$	$p$
Groups of 3 or greater	Device-only	$k = 23$	284	288	.119
	Behavior-only	$k = 22$	270	275	.183
	Device & Behavior	$k = 21$	262	263	.061
	Asocial	$k = 26$	310	324	.390
Groups of 4 or greater	Device-only	$k = 21$	534	547	.248
	Behavior-only	$k = 22$	578	573	.019
	Device & Behavior	$k = 20$	532	522	.006
	Asocial	$k = 21$	532	547	.298
Groups of 5 or greater	Device-only	$k = 18$	822	846	.286
	Behavior-only	$k = 20$	947	937	.018
	Device & Behavior	$k = 17$	808	800	.019
	Asocial	$k = 17$	775	800	.314
Groups of 6 or greater	Device-only	$k = 15$	1106	1153	.454
	Behavior-only	$k = 18$	1395	1378	.015
	Device & Behavior	$k = 15$	1167	1153	.017
	Asocial	$k = 13$	962	1003	.409
Groups of 7 or greater	Device-only	$k = 12$	1330	1410	.362
	Behavior-only	$k = 12$	1407	1410	.056
	Device & Behavior	$k = 13$	1557	1525	.007
	Asocial	$k = 3$	337	370	.480
Groups of 8 or greater	Device-only	$k = 8$	1257	1371	.193
	Behavior-only	$k = 10$	1649	1703	.282
	Device & Behavior	$k = 9$	1563	1537	.014
	Asocial	$k = 2$	336	362	.297

	Condition	Number of Chains	$L$	Critical $L$	$p$
Groups of 9 or greater	Device-only	$k = 5$	1011	1204	.984
	Behavior-only	$k = 5$	1228	1204	.015
	Device & Behavior	$k = 6$	1449	1436	.028
	Asocial	$k = 2$	442	500	.395
Groups of 10 or greater	Device-only	$k = 3$	767	987	.997
	Behavior-only	$k = 4$	1318	1301	.025
	Device & Behavior	$k = 4$	1247	1301	.251
	Asocial	$k = 2$	594	670	.389

Table S1.2: Cultural Accumulation Results for Groups of Size 3-10: Page's  $L$  Trend Test (continued from previous page)

### Chapter 3: Indirect Information Use under Conditions of Uncertainty

#### 1. Introduction

All behavioral decision-making involves a fundamental problem in terms of the management of uncertainty. The effects of behavioral decisions on fitness are uncertain because environmental variables cannot be fully anticipated by the individual decision-maker (Dall et al. 2005). Social information reduces uncertainty by allowing animals to better predict outcomes of their own behavior under similar environmental circumstances (Danchin et al. 2004, Valone 2007). In particular, animals are attuned to gather information about the success of observed others. Since the animals from whom one learns are themselves adapted to behave in fitness-maximizing ways, success may be assessed indirectly by monitoring the decisions made by others, in the form of social cues, or directly, by monitoring information about performance (public information) (Danchin et al. 2004). For example, Giraldeau et al. (2002) describe the information about patch quality available for observers of a foraging bird: the appearance of food in the beak generates public, direct information, and consequent behavioral decisions (additional probing or flying away) provide indirect information in the form of social cues. If the direct information informing decisions is not available, copying decisions can lead to maladaptive information cascades (Bikhchandani, Hirshleifer, and Welch 1992), and therefore Giraldeau et al. (2002) argue that animals prefer to use public information rather than social cues. To compare the use of public information and social cues, Coolen et al. (2005) examined nine-spine stickleback feeding preference when public



information about feeding patch quality (feeding rate) conflicted with social cues (presence at a patch). Coolen et al. report that fish preferred to utilize the rich, poorly-attended feeding patch over the resource-poor patch that had been experimentally manipulated to seem more popular, providing support for the hypothesis that, when available, cues about quality of a resource are preferred over the decisions of other individuals.

In the few studies to have explicitly compared social learning strategies in human learners, copying the strategy used by the most successful individuals (payoff-bias) appears to be preferred to choosing the most popular variant (conformity) (McElreath et al. 2008, Mesoudi 2011b) and to averaging and random copying (Mesoudi 2011b). In the experimental paradigms used by Mesoudi (2011) and McElreath et al. (2008), participants completed a task via computer and were directly provided with information about the performance of other individuals. In comparison to payoff bias, strategies like conformity bias are indirect. Conformity bias is useful because others are expected to behave adaptively, and therefore the most popular strategy is likely to be correct. Excluding any additional social benefits (e.g. social coordination) of copying behavior (Carpenter 2006, de Waal 2001), however, learners prefer to directly acquire the information that conformity bias is designed to indirectly assess. In real life, learners may not always have direct access to information about payoffs. For example, past reproductive success of a particular individual may not be clear at the time a mate choice decision is made. In addition, models who are potential competitors may wish to conceal their successes (Mesoudi 2008b).

When outcome information is not provided explicitly, learners should utilize model-based biases (Richerson and Boyd 2005) to decide whom to copy. Model-based biases are strategies of “copy-successful-individuals” (Laland 2004). Model-based biases include preferential copying based on age, skill, prestige, or perceived self-similarity (see Mesoudi 2009 for a review). Traits used to index success may be more or less related to a given target outcome; Boyd and Richerson (1985) indicate that the utility of a trait is related to how closely it tracks success. Mesoudi (2009, 2011a) illustrates this principle, cultural hitchhiking, with the Tiger Woods effect: those wishing to emulate Tiger’s golf prowess may copy his clothing choices as well as his swing, though only replicating Wood’s swing is more likely to result in a better golf game. Participants in Mesoudi and O’Brien’s (2008) virtual arrowhead design study, for example, copied functional traits of arrowheads along with neutral traits which had no bearing on performance. While no published reports have examined the ability to infer success in the context of an experimental microsociey, a recent study (Caldwell and Millen 2010a) examined performance effects in the presence and absence of outcome information.

Caldwell and Millen (2010a) explicitly tested the effects of providing outcome information to experimental microsociey groups in a transmission chain paradigm. Participants were tasked with building an uncooked-spaghetti-and-clay tower as high as possible under two information conditions. In the immediate-information condition, participants were apprised of their own performance immediately. In the delayed-information condition, participants

were apprised of their performance only after a 5-minute delay. Each tower was measured twice: immediately following the construction period and after a five-minute delay; however, in the immediate-information condition the second measurement took place after the experiment via video analysis, as did the first measurement for the delayed-information condition. Caldwell and Millen report greater within-group design similarity in the delayed-information condition than in the immediate-information condition, consistent with the hypothesis that uncertainty increases reliance on social information (Boyd and Richerson 1988, Laland 2004). While participants in both conditions were asked to create as high a tower as possible, in the delayed-information condition participants were also informed that their towers would be measured following being subjected to “wind” created by the fan, while those in the immediate-information condition were not made aware of this second measurement. Despite this difference, immediate-information groups demonstrated cumulative effects (increasing scores across the transmission chain) for both immediate and delayed performance. Interestingly, groups in the delayed-information condition did not demonstrate cumulative improvement following the five-minute delay, while they did demonstrate cumulative effects for immediate performance. This difference in performance suggests that outcome information assisted participants in building increasingly effective devices, even when the task requirements were not made salient (immediate-information, delayed measurement), and that the delay in outcome information handicapped cumulative performance even when task

requirements were made salient (delayed-information, delayed measurement).  
See table 2.1 for a summary.

Table 2.1 Summary of Caldwell and Millen (2010) Conditions and Results

Condition	Measurement	
	Immediate Task	Delayed Task
Immediate-information (immediate measurement salient)	Cumulation	Cumulation
Delayed-information (delayed measurement salient)	Cumulation	No cumulation

While Caldwell and Millen report a between-condition difference in cumulation, they report no overall performance difference between the two conditions. This result suggests that outcome information is specifically important for the regular generational improvements diagnostic of ratcheting. Specifically, ratcheting appears to be inhibited by the dissociation between behavior and outcome introduced by the delay. In the delayed task for the delayed-information condition, participants were presented with cues of performance generated during behavior, as well as direct information about performance of towers, but both pieces of information were not provided for any one individual. Therefore these participants were faced with known performance of a design in the absence of behavior used to create that design, and known behavior without information about performance. The finding that no cumulation

is generated when behavior is not presented with outcome is difficult to interpret as directly due to the absence of outcome information, however, since we do not know how participants would have performed in the complete absence of outcome information. In the current design, it is impossible to eliminate the possibility that the availability of outcome information paired with end-product information distracted from the use of available performance cues in behavior, and inhibited the use of these cues. It is reasonable to expect that direct information about performance would be weighed more heavily by observers than behavior information without performance cues. However, the data also suggest that participants were unable to understand exactly how to improve upon high-scoring designs without watching the building process, consistent with the imitation hypothesis for cumulative cultural evolution, and in contrast to Caldwell and Millen's earlier finding with a paper airplane building task (2009).

While this result is consistent with the idea that outcome information is important for cumulation, it is also important to determine how participants perform in the absence of any direct information about performance. In the current study, participants were asked to build a weight-bearing device from a length of flat weaving reed and a portion of modeling clay. Participants were assigned to experimental microsociety groups using the replacement method pioneered by Jacobs and Campbell (1961) and applied to the study of cultural evolution most recently by Baum et al. (2004) and by Caldwell and Millen (2008a, 2009, 2010a, 2010b, in press).

Participant groups were randomly assigned to one of four learning conditions, under which various information about social behavior was available. In the asocial condition, participants had no access to any social information. In the behavior-only condition, participants were able to watch others building devices, but were not able to see the completed devices. In the device-only condition, participants were able to observe completed devices of other individuals but not their building behaviors. In the final, social condition, participants were able to see both completed devices and behaviors. Initial findings (reported above, in Chapter Two) indicated the presence of cumulative effects in behavior conditions but not in the non-behavior conditions. No performance information was provided to participants in any condition, which allowed evaluation of the possibility that cumulative effects could be due to the use of context cues that convey success at the task.

If participants utilized context cues related to performance in making copying decisions, they are predicted to copy the device designs of participants who scored better more often than they copy designs of participants who did not score well. Further, if participants utilized context cues related to performance in making copying decisions, this effect is predicted to hold in behavior conditions but not in non-behavior conditions. Alternatively, if participants copied device designs on some other basis without the use of performance-based cues (e.g. random copying), they are not be expected to show greater copying of high-performing versus low-performing devices.

## 2. Methods

### 2.1 Participants

Participants were recruited from central New Jersey. 604 subjects (349 females and 255 males) took part. Their mean age was 21 years (S.D. 4.80, range 18-60). The testing took place in central New Jersey between October, 2010, and April, 2011. All appropriate human subjects protection protocol were followed and permission to do the study was granted by Rutgers University Institutional Review Board. Participants were compensated for their time (US\$20) but were not rewarded for performance.

### 2.2 Materials

Participants were provided with 160-cm length of 6.35-mm (1/4-in) flat weaving reed and 75-g of modeling clay. They were also provided with a wooden stand with a 12.5-cm diameter hole, supported on 20-cm high wooden dowels. See figure 1.1 for materials. Materials were distributed to each team at the beginning of the task, but participants were instructed that they were not allowed to touch the materials until instructed to begin building their devices. All instructions were given to participants both orally and in writing.

### 2.3 Apparatus

Participant testing was recorded using Sony HDR-CX150 camcorders, which were also used to create a photograph of each device. Participants were seated in a straight row of ten tables and chairs, with chairs facing the same direction. Lightweight foam board barriers were added and removed between participants to manipulate visual access between adjacent participants and their devices. A

stand was placed 1.25M in front of the row of participants, where completed devices were placed for those conditions that included visual access to devices (device-only and device & behavior). This stand was shifted to give access to successive groups of participants. Full details of the testing procedure are provided in Chapter Two.

## 2.4 Procedure

Once seated, participants were told that they were part of a team trying to build devices to hold as much weight as possible. The weight-adding process was demonstrated using a stand and a weight. All participants were instructed that they might be able to view others or their completed devices at certain points in time, and that they could feel free to observe these items if they became visible.

Participant start times were staggered in order to simulate cultural generations, following Caldwell and Millen (2008a). Each participant spent some portion of time waiting to begin building, and 15 minutes building his device. See figure 1.2 for details. To measure performance, following the 15-minute building time, 50.6-g weights (construction nuts) were added to the center of the hole in the stand until a weight slipped off or the device broke. Regardless of the placement of the device materials, each weight was released to the center of the hole in the stand from approximately 5-cm above the top surface of the stand.

## 2.5 Device Coding

A device-design coding scheme was developed that enabled a single design code to be assigned to each device. The code assigned to a particular



device was derived by answering a series of yes/no questions about major design features of the device. See Appendix One for the coding scheme. Codes were assigned to devices by a coder, who was blind to the experimental hypotheses, using photos of completed devices taken prior to the weight-adding process.

To assess whether participants were able to differentiate successful from non-successful devices, a measure of design copying was derived by examining repeated device designs within a single group. In order for a device (the target's device) to be considered as a possible copy of a previous device (the model's device), the repeated design type had to be created by a target individual with social access to the model. That is, participants who would not have been able to see the model's design because of timing of the experiment would not have been considered as possibly copying the model. The ability to access social information was slightly different per each position in the chain between the social conditions. For example, a participant in position 5 in the device-only condition was able to view completed devices built by participants 1, 2, and 3, whereas a participant in position 5 in the behavior-only condition would have been able to observe behavior of participants 3 and 4. The difference in these conditions in terms of who could see whom therefore generate different "rules" about when copying is possible. Of those participants who were able to view previous devices (i.e., participants in positions  $> 1$ ), each device was scored as repeating or not repeating a previously-occurring device design to which the target individual had visual access.

In order to compare copying of successful device designs with failing device designs, examination of repeated device designs was conducted for the high and low scoring devices separately. For comparative purposes, two groups of equal size were needed. Since 12.4% of the sample had built a device that held no weight at all, devices that had scored in the top 12.4% of device scores, holding 14 or more weights, were designated as the successful comparison group. The 14-weight designation was the lowest score possible for a device to be part of the top 12.4% of device scores.

Target devices within a single group were coded as having repeated an existing successful or non-successful device design if 1) the target's and model's device types were the same, 2) the target individual would have been able to see the model's device, and 3) the model's device occurred in a position earlier in the chain. When repeated device designs occurred in succession, the target device was coded as repeating the model's design only if the last available device was one of the category members (either failing or successful). For example, if participants in positions 1, 2, and 3 created identical designs but only the first design was successful (>13 weights held), the device of the second participant would be coded as repeating, whereas the device of the third participant would be left out of the analysis because it is unclear whether participant three's device was a copy of the first or of the second device. The index of repeated high or low device designs is therefore conservative and is different from the overall repeated designs index (which was calculated by simply comparing repeated

device designs relative to maximum possible number of repeated device designs for a group of a particular size).

The asocial control condition does not involve participants having any social access to existing devices. Therefore, this condition was coded using device-only and behavior-only “rules” in terms of who was able to see whom. For successful devices, coding repeated designs as if they had occurred in the device condition or in the behavior condition did not matter. For failing devices, however, using device-only or behavior-only rules did change the results for the asocial control, and therefore any comparisons between behavior conditions have used the asocial results coded as if they occurred in the behavior condition, whereas comparisons between the device-only condition and the asocial condition were coded as if the asocial condition had happened under device-only social access.

Histograms depicting the status and fate of each device design type in terms of copying, by number of weights held, may be found in the supplementary material, figure S2.1.

### 3. Results

Participants in the two behavior conditions built significantly more repeated successful than repeated failing device designs. See Table 2.2.

Table 2.2: Repeated Designs Index of Failing and Successful Devices. Chi-square results generated from repeated designs indices comparison.

Repeated Designs Index					
Condition	Successful Designs	Failing Designs	Chi-Square Results	Mean Number of Weights Held	
				Repeated Successful Design	Repeated Failing Design
Device-only	28%	11%	(1, n=56) = 2.78, p = .095	6.91	5.00
Behavior-only	37%	21%	(1, n=62) = 3.92, p = .048	8.36	4.29
Device & behavior	40%	14%	(1, n=72) = 11.57, p = .001	9.42	2.17
Asocial (control) Behavior "rules"	22%	12%	(1, n=59) = 1.69, p = .194	8.75	0.80
Asocial (control) Device "rules"	22%	16%	(1, n=69) = .581, p = .446	8.75	1.13

Repeated designs index is derived from the number of repeated designs within a single group, as a percentage of the total possible repeated designs.

While these results are consistent with the hypothesis that participants were more likely to copy successful than failing device designs, it might also be the case that successful designs were simply more popular and co-occurred in a group by chance. To test the possibility that successful designs were simply more popular regardless of available social information, the index of repeated successful device designs was compared between the social conditions and the asocial control condition. This analysis revealed that the rate at which successful

designs were repeated in a single group was significantly different from chance in the behavior conditions (behavior-only and device & behavior), but not in the device-only condition [behavior-only condition:  $\chi^2 (1, n=47) = 7.60, p=.006$ ; device & behavior condition:  $\chi^2 (1, n=48) = 9.60, p=.002$ ; device-only condition:  $\chi^2 (1, n=56) = 2.96, p=.085$ ]. That is, participants in the behavior conditions built significantly more repeated successful designs than the baseline rate of successful device design building demonstrated in the asocial condition. This result supports the hypothesis that participants in the behavior conditions may have been copying the successful designs of others in their group.

An alternative explanation for the preceding results is that rather than preferentially copying device designs of those who were highly successful, participants may have simply avoided copying device designs of those who were unsuccessful. Perhaps the elevation of repeated designs index for behavior conditions is because behavior is needed to replicate a device design, and the difference between the repeated designs index for successful and unsuccessful designs is due to a depression of copying of very poor designs. If this were the case, the repeated designs index for failing devices would be significantly lower in the social conditions versus the asocial control, since participants would have needed to see social information to avoid copying designs that were failing. However, there was no significant difference between the asocial control and the social conditions in terms of the repeated designs index for failing devices, supporting the previously-proposed suggestion that the indices of repeated designs for successful and failing designs are different due to increased copying

of successful designs. [Chi-square, behavior-only condition:  $\chi^2 (1, n=74) = 3.64$ ,  $p=.056$ ); device & behavior condition:  $\chi^2 (1, n=94) = .039$ ,  $p=.844$ ); device-only condition:  $\chi^2 (1, n=70) = .253$ ,  $p=.615$ ].

Table 2.3 Overall Repeated Designs Index per Condition

Condition	Repeated Designs Index (co-occurring designs as a percentage of total possible)	Mean Number of Weights Held	
		Repeated design	Did not repeat design
Device-only	59%	7.57	6.33
Behavior-only	44%	6.57	6.49
Device & behavior	54%	9.23	7.88
Asocial (control)	39%	6.34	8.30

These results raise the question of why participants in the device-only condition did not copy successful device designs at better-than-chance levels. There are at least two possibilities: 1) it may be the case that participants in the device-only condition were unable to copy modeled device designs in the absence of behavioral information; 2) alternatively, those in the device-only condition could copy modeled device designs but were unable to utilize available context cues, such as skill bias, in their decision to copy, and this hindered their ability to choose proper models. To rule out the hypothesis that participants in

the device-only condition did not show copying of the successful device designs because they could not copy them very well at all, the overall repeated designs index was compared between device-only and behavior-only conditions. A Pearson's chi-square performed on the overall repeated designs indices of the device-only and the behavior-only conditions revealed a statistically significant difference between device-only and behavior-only overall repeated designs indices,  $\chi^2(1, n=264) = 6.146, p=.014$ ), with device-only participants showing more repeated designs than behavior-only participants. This result suggests that the failure of participants in the device-only condition to copy successful designs more than unsuccessful designs was not because they were generally less able to copy device designs of others in their group than were participants in other conditions.

#### 4. Discussion

The current study indicates that learners are capable of inferring success information on the basis of behavior alone. Participants in an experimental microsociey repeated device designs of successful devices significantly more than they repeated device designs of failing devices, and this effect held only when behavior was observable. This result is consistent with the operation of model-based biases which allow individuals to infer success.

The current results raise an interesting question about the role of providing performance information that is not in synchrony with the available behavioral information. In Caldwell and Millen's (2010) study, only participants who were confronted with delayed information about performance and delayed

measurement of performance did not demonstrate cumulation. These participants were confronted with both known outcomes and known behavior, and therefore needed to weigh the usefulness of copying behavior without knowing outcome or attempting to figure out how to replicate an observed device design that had performed well. These same participants demonstrated cumulative effects when information about outcomes and behavior was presented in synchrony (even though this measurement, the immediate measurement, had not been made salient). In the current study, in contrast, no information was provided about performance to participants in any condition, yet ratcheting was demonstrated, on average, in chains that were able to observe behavior. If learning from payoff is the preferred strategy in humans, providing this information directly may have distracted participants in Caldwell and Millen's study from utilizing available context cues.

Future research efforts might be directed toward establishing the specific mechanisms underlying the ability to infer performance, evident in the current results. Model-based biases that have been proposed include a preference for copying based on age, skill, prestige, or familiarity. Existing data from the current study do not allow evaluation of prestige or familiarity hypotheses, and there is no evidence that age affected performance. Boyd and Richerson (1985) argue that these mechanisms are increasingly adaptive relative to their potential for allowing accurate prediction of performance, consistent with the idea that it is skill at the current task that participants are utilizing to inform their copying decisions.



The current study is an initial attempt to evaluate the use of model-based cues in social learning. Because this study was not designed to test these hypotheses, future work will be needed to clarify how participants are able to evaluate success. Using existing video, one might ask blind raters to rank perceived performance of individuals, as well as various attributes thought to be important for model-based biases. Another method of determining the cues used for these model-based biases would be to interview participants about the cues they perceive as being important for their use of particular models. Additional work might also add a nuanced understanding of the threshold at which devices are perceived as being successful or unsuccessful. For example, are participants able to differentiate moderately successful from highly-successful individuals? In addition, to what extent do cues accurately predict success? Are some cues more predictive than others? Are certain individuals better at detecting these cues?

An additional set of questions has to do with who is copied, separate from perceived skillfulness – perhaps the current results are explained by a difference in ease of copying, with those who are skillful being easier to copy relative to those who are having real trouble with the task. While verbal communication was not permitted in this study, the well-established human proclivity for purposes of teaching (“natural pedagogy” (Csibra and Gergely 2011)) may have been responsible for modifying behaviors to maximize these communicative effects. The current design could be modified to include the possibility of teaching by asking participants to teach others, perhaps allowing verbal

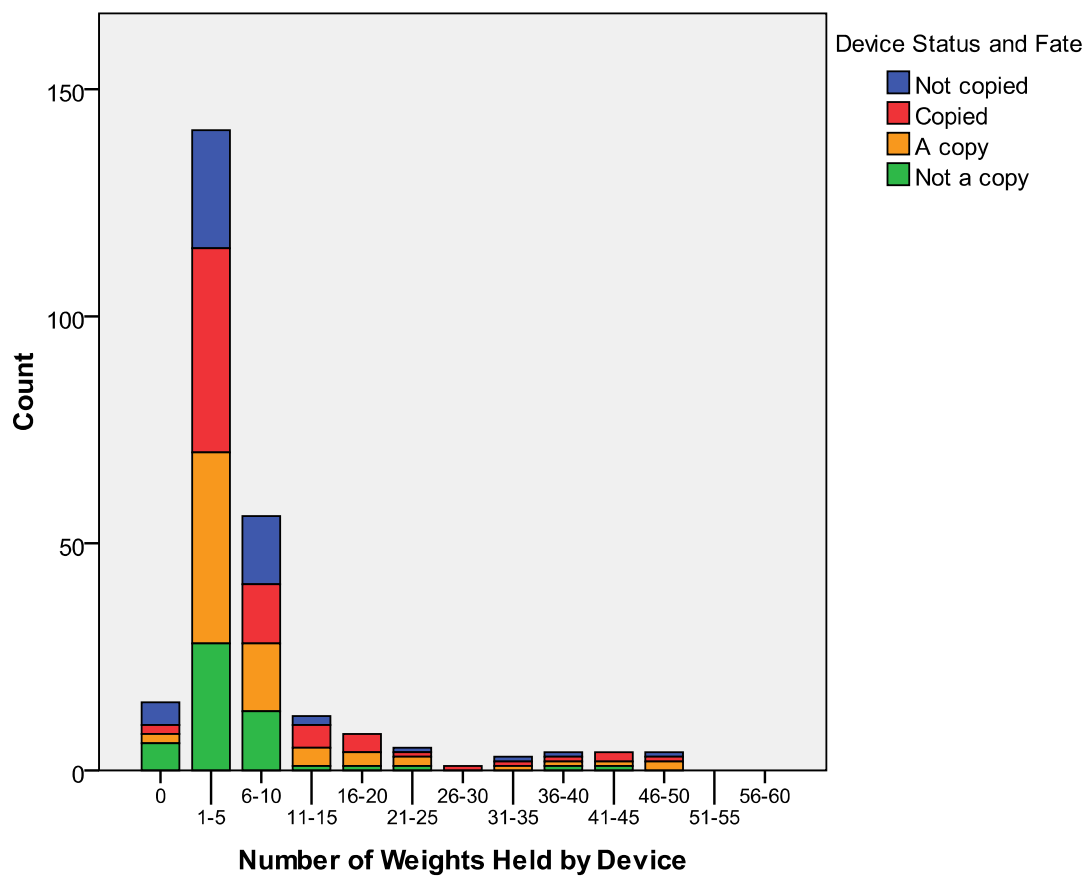
communication; comparison with the existing results would allow evaluation of the hypothesis that natural pedagogy evolved prior to language (Csibra and Gergely 2011).

In contrast to existing comparisons of social learning strategies, the current study did not provide explicit information about outcomes to participants. Payoff information is direct information about the performance of other individuals that appears to be preferred to indirect information. Future experimental comparisons of social learning strategies might test indirect information use by comparing the effect of model-based cues of success with other indirect social learning strategies such as conformity. Finally, as empirical research takes up the mantle of testing hypotheses generated from mathematical modeling, it is important to interpret microsociey results with the knowledge that behavior provides more than input for copying. As these results demonstrate, any discussion of different performance between behavior and non-behavior conditions should also acknowledge that model-based biases are a potential contributor to cumulative performance that will not be found in conditions designed to test emulation.

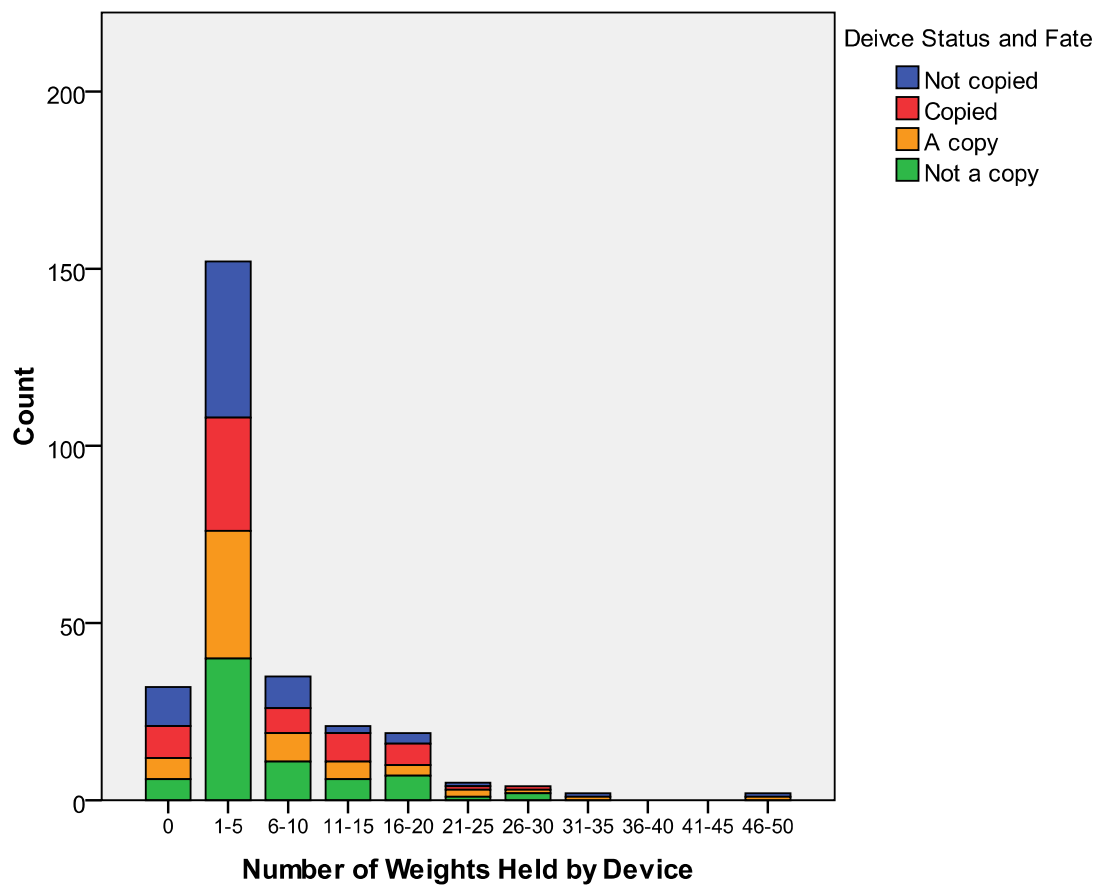
## 5.0 Supplementary Figures

Figure S2.1 Device Design Status and Fate in Terms of Copying, by Number of Weights Held and Condition

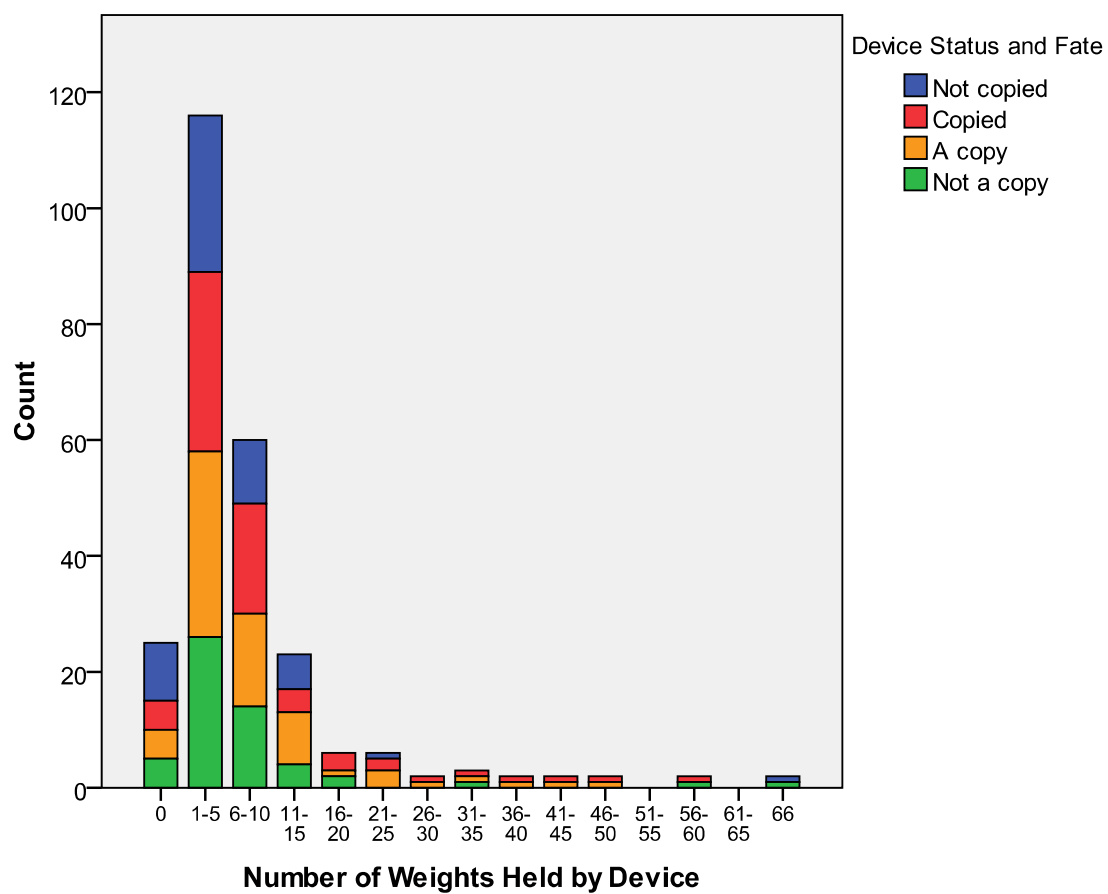
Device-Only Condition



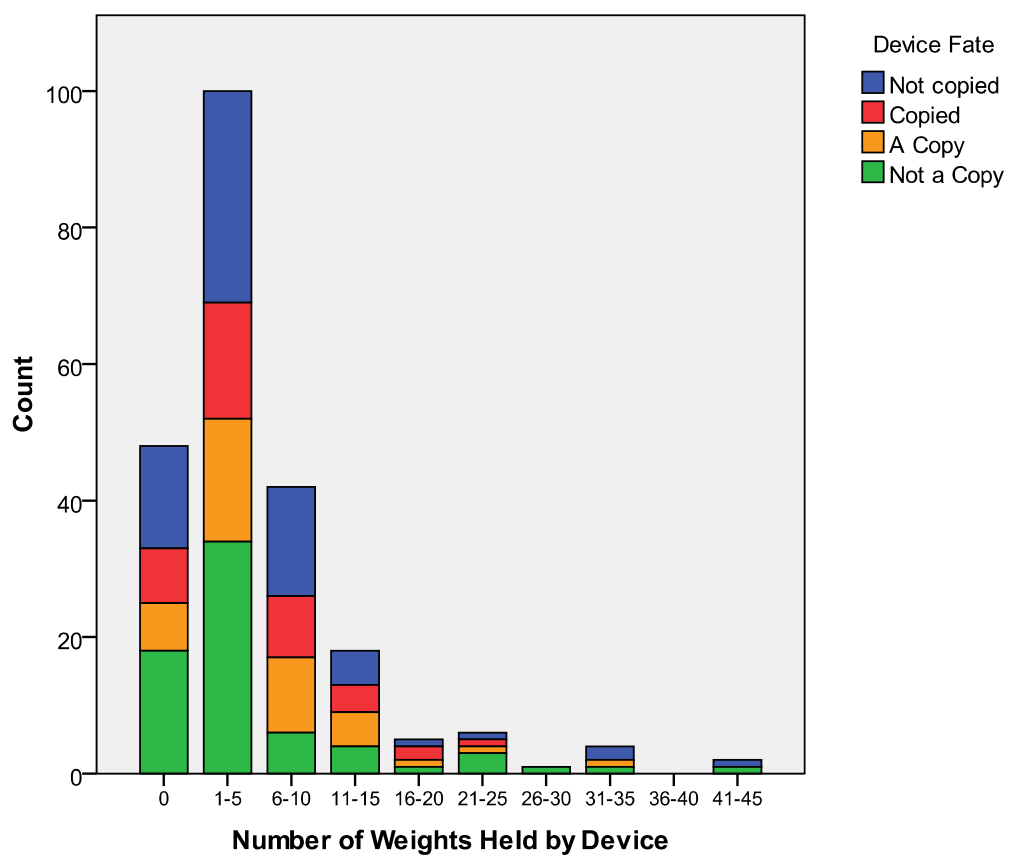
## Behavior-only Condition



## Device &amp; Behavior Condition



## Asocial Condition



## Chapter 4: Evidence for Facultative Adjustment of Social Information Use in a Functional Task

### 1. Introduction

Animals acquire information about the environment through asocial or social learning. Both of these processes are important for the development of cultural information systems, and much of the theory about why culture confers an adaptive advantage in a changing environment involves defining the conditions under which individuals learn socially or asocially (Rogers 1988). Existing models have looked at how conditions that are external to the actors affect the net fitness of social learners at equilibrium, in reference to Alan Rogers' seminal work. Rogers' model describes an apparent paradox that results from costliness of learning socially (potentially receiving outdated information) and the costliness of asocial learning (relatively greater time investment, potential for error that might be avoided with the use of environmentally current socially-acquired information). Learners in Rogers' model scrounge social information to avoid the costs of asocial learning, but as social learners increase in a population, learning individually is comparatively more adaptive. Social learning becomes increasingly less adaptive as it increases in frequency because, in a changing environment, social learners are increasingly likely to acquire outdated information from other social learners. The result is a balanced polymorphism of asocial and social learners. Since the proportion of social learners does not affect the payoff for asocial learners, individuals in a population at equilibrium

have the same net fitness as those in a population composed solely of asocial learners.

Analytical solutions to Rogers' model include flexible use of social and asocial learning by individuals (Boyd and Richerson 1995, Kameda and Nakanishi 2003, Rendell, Fogarty, and Laland 2010), such as a bias to learn socially only when asocial information is not satisfactory (Boyd and Richerson 1995), or a preference to use social learning, switching to asocial learning when social learning is not satisfactory (Enquist, Eriksson, and Ghirlanda 2007). Experimental results have also suggested that this facultative adjustment is important for understanding how culture is adaptive. Kameda and Nakanishi (2003) report that an experimental population able to switch between asocial and social learning outperforms a purely acultural population, because socially acquired information has an uncertainty-reduction function. That is, asocial agents facing a moderately imperfect match between the true state of the environment and the signals generated by that environment ("noise"), benefit by switching to social information as uncertainty about signal strength increases. Therefore, the social information in this population of flexible learners represents the true environmental state more accurately than does information generated by a population of learners who are making learning decisions irrespective of the effect of noise. In a virtual arrowhead design task, Mesoudi (2008b) found that participants were more likely to rely on social information when their device designs did not perform well, as measured in virtual calories attained. This polymorphic information use strategy resulted in greater caloric benefit relative to



a hypothetical population of pure social and asocial information users, who would be expected to encounter the negative effects of scrounging described by Rogers.

While there is some experimental evidence that human participants use social and asocial information sources facultatively, other work indicates that individuals pursue strategies that are suboptimal with respect to theoretical modeling. McElreath et al. (2005) report a wide range in variability of the use of social information in an experimental micro-society virtual crop-planting experiment, with 36% of the experimental population choosing to access social information about crop planting decisions “never or very rarely” (498). Similarly, Efferson et al. (2007) report that economic game-playing participants in the Bolivian highlands relied more on asocial information than on imitation, although imitation would have been the more successful strategy. In a recent iteration of the virtual arrowhead task, Mesoudi (2011b) found that the majority of participants under-utilized social information even when its use would have been adaptive. So, while social information provides an advantage in theoretical models and within the constructs of laboratory games, we know little about the factors triggering the sub-optimal use of social information. One possibility is that individuals vary in ability to access and use asocial or social information. Limitations in this capacity could be expressed at the individual level through learned, developmental or genetic constraints. Within the cultural evolution literature, imitation has received much research attention because it could provide a mechanism for inducing or perhaps maintaining behavioral similarity

between individuals. However, cultural evolution also requires the introduction, via innovation (innovation "sensu process" Reader and Laland 2003) of new behavioral variants through individual modification of existing socially transmitted information. If avoidance of social learning allows specialization in asocial learning, in particular innovation, we might expect these capacities to be traded off (Kendal et al. 2005). To date, studies that explicitly define the relationship between social learning and innovation within individuals have been limited to pigeons (Bouchard, Goodyer, and Lefebvre 2007), common marmosets (Burkart, Strasser, and Foglia 2009), and neotropical raptors (Biondi, Bo, and Vassallo 2010).

The relationship between social and asocial learning abilities is relevant to considerations of the evolution of cognition and sociality generally. Social intelligence hypotheses posit that primate cognitive evolution is a result of selection pressure for the abilities necessary to negotiate social complexity (Byrne and Whiten 1988, Dunbar 1998, Jolly 1966). The legacy of this selection pressure is predicted to be differential development of social abilities relative to skills needed to address foraging problems. Evidence that traits displayed while solving problems in these realms are independent within individuals would support the idea of domain-specific modularity, implying that specialization is the adaptive solution to these selection pressures. Alternatively, trade-offs within individuals might be due to functional specialization in terms of cognitive processing, such as allocation of attention (Burkart, Hrdy, and van Schaik 2009). If trade-offs are evident, they may be associated with particular social systems,

like cooperative breeding, that allow individuals to minimize the costs of specialization (Burkart, Hrdy, and van Schaik 2009, Hrdy 2009). If individuals living in cultural systems do have stable strategies, it is necessary to determine how these individuals assort to produce the conditions necessary for cultural evolution (Efferson et al. 2008).

Alternatively, the selection pressures that promoted increased cognitive abilities in the primate lineage may have resulted in skills that are not easily allotted to independent domains of knowledge (Galef 1992, Heyes 1994). There are several possible causes for this lack of separability. The cultural intelligence hypothesis suggests that social and asocial learning have coevolved, with social learning enhancement increasing individual learning abilities (van Schaik and Burkart 2011, Whiten and van Schaik 2007). Another possibility is that findings of correlated performance on tests of these domains result from a cognitive solution to these hypothesized selection pressures as an increase in overall, generalized intelligence. Reader et al. (2011) analyzed cognitive measures from non-social and social domains in 62 primate species, and report that these performance measures are highly correlated, suggesting that social and asocial cognition are not supported by independently evolved modules.

The current study was designed to distinguish between two hypotheses: 1) that individuals show inflexible use of social and asocial learning, or 2) that individuals show flexible use of social and asocial learning. Data were collected about performance on social and asocial tasks, as well as the degree to which participants imitated available social information. It was predicted that if inflexible

strategies are in use, performance on the asocial and social learning tasks should be consistently traded off within individuals. That is, there should be an inverse relationship between performance on the asocial and social portions of the study. Specifically, participants who do very well at the asocial task will decide not to utilize social information when it is available, and when social information use is mandatory they will demonstrate sub-par imitation skills. The use of flexible strategies, in contrast, would predict no relationship between performance on the social or asocial tasks, or a positive relationship if the skills needed are underpinned by a general factor of intelligence.

## 2. Methods

### 2.1 Participants

Participants were 50 individuals (27 females, 23 males) recruited at Rutgers University. The mean age of participants was 26.1 years (S.D. 7.05, range 18-55).

All participants gave written consent for participation and were compensated US\$15 for participating. Permission for the study was granted by Rutgers Institutional Review Board.

### 2.2 Experimental Task

In order to assess social and asocial learning skill, participants built functional devices capable of holding weight, in the form of U.S. quarter dollar coins. Participants constructed devices out of a 160cm length of 6.35mm flat (¼in) weaving reed and 75g of modeling clay (see figure 1.1 for materials), and were provided with a wooden stand that included a 12.7cm round opening

located on dowels 20cm above the base of the stand. Participants built three devices, one in each of three trials, and were given new materials with which to make each device. Each participant had 15 minutes to build each device. Participants were instructed to build their devices to hold the maximum amount of weight possible, in the form of U.S. quarter dollar coins (“quarters”). Participants were instructed that the weight would be dropped through the center of the hole in the stand, and a demonstration of the weight-adding process was given by the experimenter prior to the start of the first trial using a stand and quarter. The instructions given to participants explicitly stated that the task would be over once a quarter dropped onto the table or floor, but the design of the device was left up to participants. For example, when participants inquired about whether the device was to “cover the hole” they were told that the design was “up to them,” and the goal of supporting as many quarters as possible was reiterated. Participants were instructed that they should not attach their devices to the stand, nor should they allow the device to touch the table or the base of the stand. Instructions for the building task were given orally and in writing. Task timing and additional instructions were provided via computer using Superlab 4.0. Participants were not able to see one another and were instructed not to communicate with each other.

Social information was provided via a demonstration of device-building completed by a videotaped experimental confederate. The confederate’s identity was masked by displaying only the torso and arms of the individual. No

information was provided regarding the success of the confederate's device. Following the completion of each of the three devices, devices created by participants were tested in the following manner: quarters were released one-at-a-time, from approximately 5cm above the top surface of the stand, to the center of the hole in the stand. The success of the device was measured in terms of maximum number of quarters held. If at any point the device fell from the stand or broke, any quarter that had already been added to the device was counted, but the task was over. If a quarter slipped from the device, all quarters were removed and re-added for a second trial. Performance on the task was scored as the greater of the two trials. The higher number was used, rather than the mean, because the risk of an inaccurate undercount was deemed more likely than inaccurate overcount. For example, it is easy to imagine how a quarter might be added in such a way that it rolls off the device onto the floor even though the device is capable of holding that quarter; however, it is difficult to imagine a situation in which a device held more quarters than it was truly capable of due to some error in the adding process. Participants were present for the testing process.

### 2.3 Experimental Conditions

Participants engaged in 3 device building tasks (see figure 2.1 for details). To establish a baseline for individual skill at device building, in the initial condition participants built devices with no social information (phase 1, asocial). Following the first task, a prompt appeared asking the participant whether he or she would like to watch a video of someone else engaged in device building. This was

done in order to assess proclivity for social information use. Most participants (83%) elected to watch the video. All participants, regardless of their selection, next watched the video of the experimental confederate constructing a device. The start of the second 15-minute building session (phase 2, imitation optional) coincided with the beginning of the video (cued via keyboard input from the participant).

Finally, participants were randomly assigned to one of two experimental conditions for building a third device (phase 3): in the imitation-requested condition (phase 3, imitation requested), the computer displayed the following text: “The goal of the next exercise is to imitate what you see the person on the video doing, as closely as you can.” Participants randomly assigned to the imitation-optional condition (phase 3, imitation optional) were shown the following text: “Next, you will see a video. The person shown in the video is making a device. This person has received the same instructions you have.” Following keyboard input, all participants were then presented with the same video of the experimental confederate that they had seen during the second device-building task, and were prompted by the display to begin building their third devices.

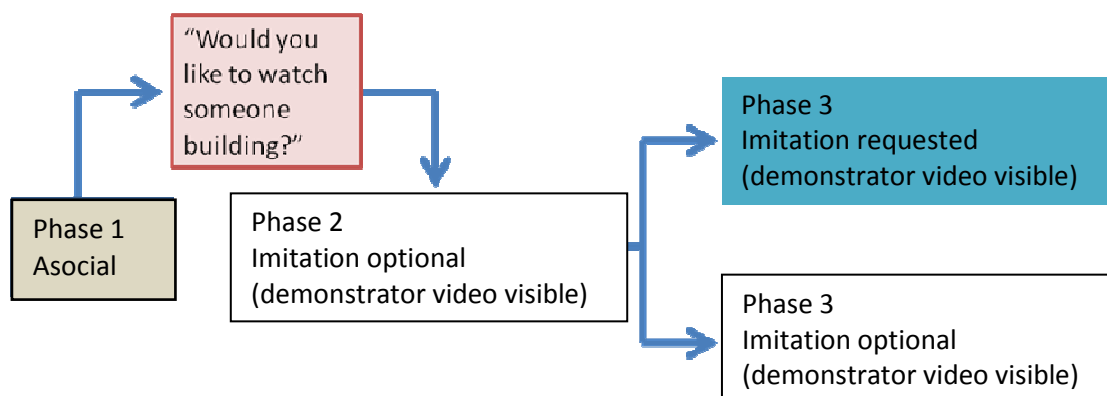


Figure 2.1: Schematic of Experimental Design

### 3. Results

#### 3.1 Video Coding

In order to determine the degree to which the participants appeared to be imitating the performance of the confederate, the behaviors of the confederate were coded by a research assistant blind to the study hypotheses and experimental condition of the participants. The codes developed were functional units of behavior, e.g. “use stand to measure reed ring.” Video of the research participants was then scored according to the degree to which each behavior demonstrated by the confederate was matched by the participant, using a 5-point scale: 1: Ignored step or skipped over it; 2: Did something but it’s unrecognizable; 3: Attempted step but not perfect; 4: Almost accurate 5: Completely accurate. The order in which participants completed steps in comparison to the confederate was not considered, therefore maximizing the recognition of any possible imitative efforts by the participants. From these scores, a composite score consisting of the sum of all the imitation scores was generated.



### 3.2 Analysis

Three participants were excluded from the analysis due to failure to press the space bar to begin the video when instructed during phase 2 (imitation optional), thus resulting in lack of social information during the second building task. Nonparametric statistics were used for the data of the remaining 47 participants because the data were not normally distributed.

The first question of interest was whether performance on phase 1 (asocial) might be used to predict imitative performance. A negative relationship between these scores would be consistent with the idea that individuals assort into stable asocial/social information use types, whereas a positive or no relationship between performance on these two measures would suggest that they are not separable performance domains (and therefore could be used flexibly). This analysis did not reveal any relationship between performance (number of quarters held) on the first phase and the utilization of imitation in the second phase, when imitation became available as an option ( $r_{\tau}(47) = -0.031$ ,  $p$  (two-tailed) = .771). Next, performance on phase 1 (asocial) was compared to imitation on the imitation-mandatory condition of phase 3. Again, there was no statistically significant relationship between performance on the first phase and the degree of imitation on the imitation-mandated phase ( $r_{\tau}(26) = -0.083$ ,  $p$  (two-tailed) = .564).

While phase 1 (asocial) task performance did not seem predictive of later imitation, it was of interest to determine whether participants might be using stable imitation strategies. To test for stable imitation strategies, phase 2

(imitation optional) ( $M = 12.05$ ,  $SD = 9.43$ ) and phase 3 (imitation optional) ( $M = 10.53$ ,  $SD = 10.22$ ) composite imitation scores were compared. The analysis of these scores showed no statistically significant difference between these scores, ( $z = -0.512$ ,  $p = .609$  two-tailed), which is consistent with a stable demonstration of the use of social information within subjects. Plotting the change in imitation scores from phase 2 to phase 3 (Figure 2.2, Figure 2.3) suggested that those participants in the imitation-optional phase who did substantially change the degree of imitation from the previous phase tended to imitate less.

Figure 2.2: Change in imitation composite score per individual from phase 2 to phase 3. Lines represent individual participant imitation composite scores.

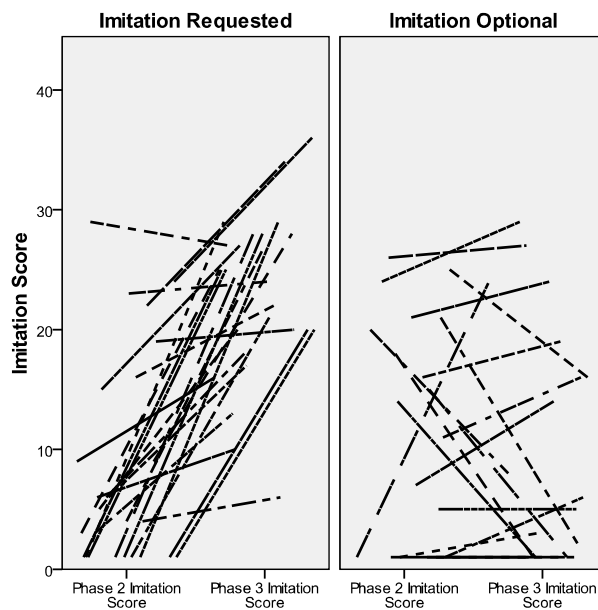
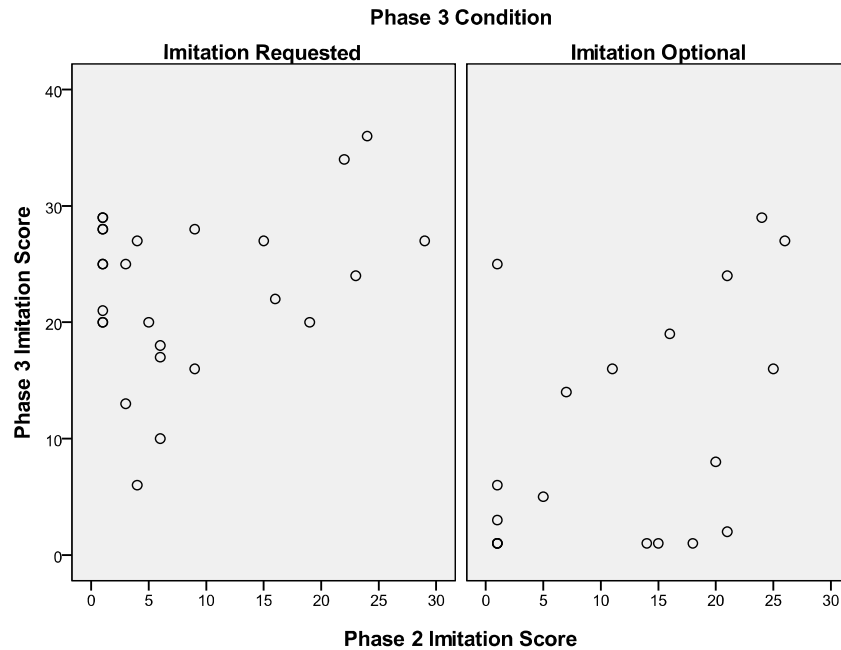


Figure 2.3: Phase 2 imitation composite score relative to phase 3 imitation composite score. Dots represent individual participant imitation composite scores.



Copying the technique of the model was a beneficial strategy in terms of number of weights held by devices, as performance on phase 3 was highly significantly correlated with imitation degree when imitation was requested, as depicted in figure 2.4 ( $r_r(24) = 0.507$ ,  $p$  (two-tailed)  $< .001$ ). Given the potential benefit of imitation, it is somewhat surprising that so many participants decided not to imitate: 34% of participants did not imitate in any discernible way when imitation was optional in phase 2. Likewise, in the imitation-optional condition of phase 3, 32% of participants did not imitate in any discernible way. Comparison of the imitation-requested condition with the imitation-optional condition supported the conclusion that participants were imitating less than was possible.

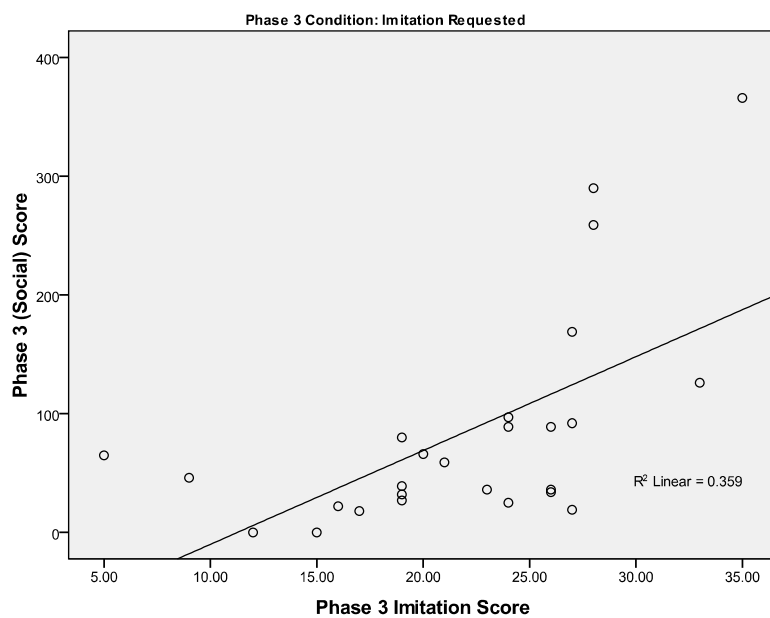
In the imitation-requested condition (phase 3), participants imitated significantly more than did participants in the imitation-optional condition (phase 3) ( $U = 85.00$ ,  $z = -3.73$ ,  $p < .001$ ). Participants in the imitation-requested condition also imitated significantly more than they had in phase 2, when imitation was also optional ( $z = -4.37$ ,  $p < .001$ ). Comparing participants in phase 2 prior to their random assignment to one of the two conditions for phase 3 yielded no significant difference in their degree of imitation for each of the two conditions of phase 3: ( $U = 197.00$ ,  $z = -1.17$ ,  $p = .241$ ).

Of the participants who did not imitate at all in phase 2 and who were randomly assigned to the imitation-optional condition of phase 3 ( $n = 6$ ), 3 participants continued to not imitate at all in phase 3. These imitation-averse individuals did not appear to be different from other participants in terms of age, phase 1 score, or phase 2 score. Lack of imitation in phase 2, when imitation first became available as a strategy, did not seem to be due to lack of imitation skill, as those who did not imitate when it was optional in phase 2 and subsequently were in the mandated imitation condition in phase 3 were not significantly different in terms of phase 3 (imitation-requested) imitation compared with participants who did imitate in phase 2: ( $z = -1.38$ ,  $p = .181$ ). In addition, the lack of imitation in phase 2 did not seem to be connected to lack of skill at producing beneficial outcomes from imitation, as participants who did not imitate in phase 2 did not fare significantly worse on phase 3 (imitate-requested) than those who did imitate in phase 2 (Mann-Whitney  $U = 62.50$ ,  $z = -0.755$ ,  $p =$

.458). The analysis therefore did not produce evidence that imitative skill was determining imitative decisions.

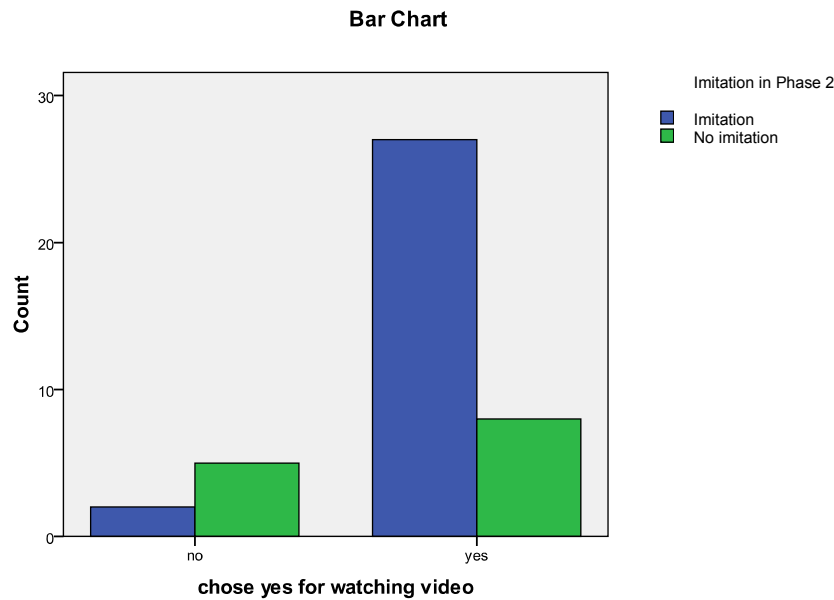
There was some evidence that interest in the social information provided was related to imitative decisions: those who chose yes for watching the video showed a significant difference in terms of imitative versus non-imitative performance in phase 2 (see figure 2.5) ( $c^2(1, n = 42) = 6.44, p = .011$ ). However, this effect did not extend to the degree of imitation: participants who preferred to watch the video when asked were not different from those who preferred not to watch the video in terms of the degree to which they imitated during either phase 2 or phase 3 (phase 2:  $U = 80.50, z = -1.43, p = .160$ ; phase 3, imitation-requested:  $U = 65, z = -1.95, p = .053$ ; phase 3, imitation-optional:  $U = 2.00, z = -1.30, p = .316$ ).

Figure 2.4: Phase 3 imitation composite score relative to phase 3 number of weights held, for participants in the imitation-requested condition of phase 3.



Dots represent individual participant scores.

Figure 2.5: Imitators versus non-imitators on phase 2, relative to selection for watching video.



One explanation for this result is that although imitation was a beneficial strategy, it was not the sole strategy for doing well. The benefit of imitation effect did not hold when imitation was optional in phase 3  $r_{\tau}(17) = 0.227$ ,  $p$  (two-tailed) = .187, or phase 2:  $r_{\tau}(45) = -0.107$ ,  $p$  (two-tailed) = .311. This result suggests that some participants did very well even though they did not imitate.

Since imitating is linked with performance in phase 3 (imitation requested), the alternative, that some participants imitated a great deal and yet did not fare well, does not seem to be a logically tenable conclusion (though the possibility that some aspect about being asked to imitate enhances performance through some extra-imitative means remains to be tested). The finding that participants in the imitation-requested condition overall did no better than those in the

imitation-optional condition – even though imitation was linked with better performance – also supports the initial interpretation. The median imitation-requested score was 52.5, whereas the median imitation-optional score was 46.00. This difference was not significant:  $U = 219.5$ ,  $z = -0.632$ ,  $p = .527$ .

This lack of imitation in phases 2 and 3 (imitation optional) may be due to the study design, as participants were not provided information about the success of the model's device design. Although participants were not apprised of the model's success in the task, the model's device held more quarters (359) than all but one of the participants' devices in any of the 3 tasks. The most successful participant device held 366 quarters in the imitation-requested phase 3 (Imitation-requested phase  $M = 83.88$ ,  $SD = 91.59$ ). It also may be the case that individuals extracted information from the confederate's performance and increased their own performances without imitation. This theory is supported by the finding that the availability of social information in phase 2 increased performance over asocial task performance in phase 1, yet task 2 task performance was not linked with imitation. The study design did not allow for control of learning effects due to repeated task performance, yet if experiential effects alone were responsible for the increase in scores from phase 1 to phase 2, a consistent increase in score performance for each of the three tasks would be expected. The lack of difference between performance on phases 2 and 3 in the imitation-optional phase 3, however, hints that the difference between performance on phases 1 and 2 is due to the new availability of social

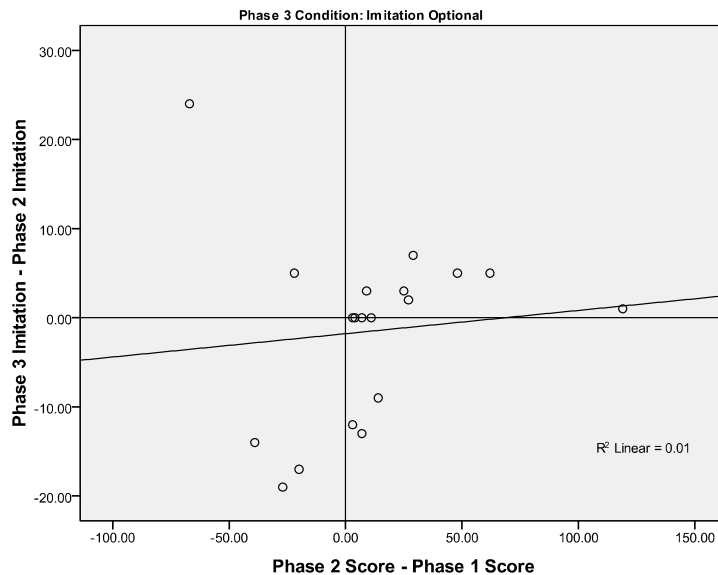


information (or, alternatively, some differential increase with the second performance of a task, or a differential effect of boredom with the third repetition).

In order to test for adjustment of social information use based on task performance, a difference score was calculated for performance on the imitation optional learning phase (2) and the asocial learning phase (1). Then, a difference score was calculated for the degree of imitation demonstrated in the two social phases (2 & 3), for the imitation-optional third phase. Both difference scores consist of the result from taking the difference of these two scores. This analysis indicated a statistically significant positive correlation between these measures:  $r_r(17) = 0.346$ ,  $p$  (two-tailed) = .044. It appears that participants adjusted the degree to which they imitated in the third phase based upon whether performance improved between phase 2 and phase 1 (see figure 2.6). When performance in the first social learning phase was better than performance in the asocial phase, participants increased the amount they imitated in the following phase. When performance between the asocial and first social phase decreased, participants subsequently decreased their imitative behavior. In order to better understand this effect, it was necessary to examine whether a relationship between performance in the asocial phase and the degree of imitation on the second phase might be responsible for the apparent adjustment of strategy noted. Performance on the asocial task alone did not appear to affect the degree to which participants imitated during phase 2 in any linear way:  $r_r(45) = -0.031$ ,  $p$  (two-tailed) = .771, and those who imitated on phase 2 versus those who did not were not significantly different in terms of phase 1 score: mean rank

of imitators: 23.52, mean rank of non-imitators: 24.94 ( $U = 233.00$ ,  $z = -0.337$ ,  $p = .736$ ). Since imitative behavior did not increase significantly from phase 2 to phase 3 (imitation optional), the notion that increasing exposure to social information alone increases imitation is not well supported. In sum, the adjustment of imitative strategy seems to be based on performance differences between the first and second phases rather than an effect of performance of phase 1 on imitation in phase 2, or a progressive increase in imitation due to social exposure.

Figure 2.6: Difference in phase 2 score and phase 1 score relative to difference in phase 3 imitation composite score and phase 2 imitation composite score.



Dots represent individual participant difference scores

#### 4. Discussion

These data suggest that individuals flexibly adjusted the degree to which they relied on imitative behavior based upon comparing task performance outcomes under asocial and social conditions. This is experimental evidence of the sort of facultative adjustment of behavioral strategy that theoretical modeling has suggested is necessary for the adaptive benefit of culture. These results are related to the strategy documented by Mesoudi (2008b): “copy successful individuals when behavior is unproductive,” with the added element of relative performance tracking. This result raises the possibility that participants thought of their performance as causally linked with imitation. Yet another possibility is that this result is due to non-imitative convergence to optimal solutions. That is, the increase in apparent imitative behavior may be due to the existence of optimal solutions for this task, which participants discovered independently over multiple runs through trial and error. Future studies might include repeated asocial phases to differentiate between these explanations.

Although imitation was related to increased success, a substantial portion (34%) of the sample chose not to imitate when social information became available in phase 2. This result suggests that some participants continued to gather asocial information, echoing the findings of previous studies (e.g. Efferson et al. 2007, McElreath et al. 2005). This under-utilization of social information is perhaps related to the characteristics of the particular subject population. In common with McElreath et al. (2005), participants in this study were recruited on a college campus, making them members of a study population that Henrich et

al. (2010) deem outliers relative to the rest of humanity. Henrich et al. (2010) argue that members of Western, Educated, Industrialized, Rich, and Democratic societies should not be assumed to be representative of humans at large – that in fact, these subjects are “WEIRD” because these characteristics are in fact rather unusual considering the distribution of societal variation around the world. While this critique is certainly applicable in some respects to the current sample (students in college or graduate school are “educated”), 50% of the sample were graduate students, one quarter of whom, on this campus, are relatively recent arrivals to the United States (foreign students) (Office of Institutional Research and Academic Planning, Rutgers University 2012). Of the foreign students enrolled in graduate school at Rutgers-New Brunswick, roughly half are from East or South Asia. Therefore the conclusion that these participants are necessarily from Western, rich, or democratic societies is not necessarily warranted (though I did not collect specific data regarding country of origin from these participants). It is important to note, however, that as students in the United States some societal influence should be expected, even among those students who are foreign-born. As Henrich et al. (2010) note, many studies have found that American society is the most individualistic in the world. This particular characteristic might explain the under-utilization of social information found in the current study, as participants may have wanted to use their own means of solving the task, rather than relying on the available social information. In an educational setting, participants also may have held pre-existing notions about the value of “thinking for themselves” and could have seen using social

information in this particular setting as a form of cheating. Validation of these results cross-culturally will be needed to establish whether this finding is particular to WEIRD societies.

Although the presence of uncertainty predicts that individuals should rely on social information, in the current study individual information was provided first. Therefore, participants had some idea about their ability to complete the task prior to the exposure to social information and could therefore weigh the benefit of copying the model. It is also important to note that behavioral observation provides several different sources of information. Call and Carpenter (2002) suggest that these information sources include demonstrator actions, results, and goals. In turn, an array of potential learning outcomes may be generated from these information sources, including emulation, imitation, and stimulus enhancement. Therefore, in the social phases participants may have observed video and extracted useful information even when they did not produce imitative behavior. When this social extraction led to increased performance, participants may have been prompted to ratchet up their imitation. Additional work might include the use of gaze tracking or cognitive testing to disentangle the roles of social information use and behavioral responses.

## Chapter 5: Conclusion

Culture has historically been considered a trait that is exclusive to humans. For some, the idea that other creatures have culture threatens to destroy the closely-held claim that we have somehow overcome the fact that we are biological organisms. The extreme cultural determinist position is misguided: it misrepresents both biology (by conflation with genetic determinism) and culture (with the assumption that culture operates outside of biological constraints). The realization that other animals have socially learned, shared behavioral practices does not diminish the achievements of human culture, however. Instead, comparative work reveals how and why we are different. That is, understanding culture as information reveals that humans have a highly complex, elaborated system of information transmission that allows us to in some ways supplant the genetic system. Human cultural transmission mechanisms likely have multiple sources that include genetic predispositions for certain learning mechanisms (e.g. high-fidelity imitation), preferences (e.g. learning from successful models), and traits (e.g. flexible use of learning strategies).

In this dissertation, I have contributed data in service of discovering how learning mechanisms produce culture. The three studies that comprise this dissertation contribute toward the goal of developing a unified, evolutionary science of culture (Mesoudi 2010, Mesoudi 2011a, Mesoudi, Whiten, and Laland 2006b, Whiten and Mesoudi 2008). The chapter on social learning mechanisms of cumulative cultural evolution contributes toward a growing body of research on social learning and cultural transmission (Caldwell and Millen 2008b). My

additional analysis of these data in Chapter Two contributes toward understanding the use of learning strategies (Laland 2004), and the novel experimental task that I used in both studies adds to experimental research methodology for microsociety work, which has not often considered the transmission process of material items (Schönpflug 2008).

In the first study of this dissertation, I found support for the hypothesis that cumulative cultural evolution requires imitation (Boyd and Richerson 1985, Boyd and Richerson 1996, Tomasello 1999, Tomasello, Kruger, and Ratner 1993). These results are in opposition to those reported by the sole existing study of social learning mechanisms of cumulative culture in adult humans (Caldwell and Millen 2009), who report no difference between conditions. As I argue above, this is likely due to a difference in task difficulty; while my study utilized reed and clay device building, Caldwell and Millen asked participants to create paper airplanes. Because paper airplane building is highly familiar to most adults in the UK, it is possible that even when imitation was not possible participants were easily able to reverse-engineer planes. The imitation hypothesis specifies that details of behavior that allow improvement are lost in the absence of observation. If there is behavioral script available to be activated, however, there is little reason to expect that learners would require observation of the details of a demonstration to produce improvements. In one sense, Caldwell and Millen's results do support the imitation hypothesis, because the behavioral means for creating a plane are a known entity, and therefore behavioral observation becomes redundant. I would argue, however, that imitative *learning* is typically,

and perhaps necessarily, employed precisely when behavioral means are not known. Children learning to construct paper airplanes do so through imitation, and only once that skill has been attained will learners be able to use end-products as an inspiration for future modifications of known behavioral repertoires.

From a purely functional perspective, the finding that 12% of participants built a device that held no weight at all is somewhat puzzling. If the task requires only application of the principles of physical causality that are proposed to emerge early in ontogeny (“folk physics”), this finding might be used to call into question participants’ motivation. Anecdotal review of the device photos suggests that a few of the participants who built failing devices appear to have created devices that are designed to achieve aesthetic, rather than functional, goals. Rather than implying a lack of understanding of folk physics, these devices may have been efforts to signal artistic talent. Follow-up work might be pursued to examine the social conditions eliciting these solely artistic devices, e.g., whether they appear more in males in mixed-sex groups (implying effort to signal creativity or artistry to females). Some participants may have felt that they could not “solve” the task and were instead interested to see what else they might accomplish with these crafts materials, which may have been last encountered in art class. Because I did not reward participants based on task performance, for this subset of participants the motivation to create a weight-bearing device may have not outweighed the desire to demonstrate artistic talent. Of course, I also cannot eliminate the possibility that some participants did not



understand the directions. For most of the participants who built failing devices, I would suggest, however, that the directions were understood and that building a failing device was unintentional. The presence of failing devices demonstrates that the task requires more than application of the universal principles of folk physics. My impression from watching 754 clay and reed device building trials is that overall participants were interested in how well they had done, and in particular learning how well they had done relative to other individuals. Young men seemed particularly likely to inquire about how well they had done relative to others, and quite a few times after adding the weights to a device I was asked by a hopeful young man, "Is that the highest score?" In actuality, the highest-scoring device was created by a woman, who was utterly indifferent when I told her she had outscored hundreds of other people. I acknowledge that additional research will be needed to verify these personal impressions.

In contrast to the studies providing design inspiration for the current research (Caldwell and Millen 2009, Caldwell and Millen 2010a), in my studies participants were not rewarded based on performance. This decision was strategic: the addition of a monetary performance reward introduces a potential additional uncontrolled variable because participants may differ in the degree to which they are motivated by money, and the motivation to pursue the monetary reward may be different from the motivation to perform well at the task. Instead, within my results performance on the task itself is the motivating factor. While this difference may compromise the current generalizability of these results, I suggest that future research should adopt this technique as my data illustrate

that participants are sufficiently motivated to perform well on microsociey tasks even without monetary rewards.

Drawing from the data provided by the central study of the dissertation, in Chapter Three I examine whether participants are able to infer success based on behavior, as predicted from the theory on model-based biases (Richerson and Boyd 2005). Because I did not provide information about how well others had done to participants in any condition of the first study, I was then able to compare participants' use of device designs from unsuccessful and successful models. I found that participants much more often copied the device designs of those who were successful versus those who were unsuccessful, and that this difference held only when behavior was visible. I was able to reject the hypothesis that this difference was just to the higher popularity of successful designs, because I show that more successful designs appear in the social conditions than in the asocial control. From my review of the literature, this appears to be the first study to explicitly test success-based biases in human learners using inference of success.

In Chapter Four, I examined the use of social and asocial information within individual learners. This study was inspired by findings that seemed to suggest that learners were pursuing relatively fixed strategies (Efferson et al. 2008, Efferson et al. 2007, McElreath et al. 2005, Toelch et al. 2009) which appeared to be in conflict with the assertion from modeling work that individuals should use flexible social learning strategies (Boyd and Richerson 1995, Kameda and Nakanishi 2003, Rendell, Fogarty, and Laland 2010). I found that

participants appear to be switching strategies, from social to asocial information use, depending on the usefulness of this information, and I found no evidence to suggest that learners had stable information use strategies.

The device-building task used in these studies provides an important new means of testing social transmission of culture traits. Within this task, the vehicles of transmission are the physical components of devices. Features of devices that are replicated may be analyzed as a means of examining the transmission of culture traits. The units of selection are the ideational units needed to create those device components. Here, ideational units might be steps for creating a similar device feature, as part of a cultural recipe (Mesoudi and O'Brien 2008). Because it is probable that components of devices, e.g., woven reed, have separable evolutionary trajectories from other traits, additional analyses will be needed to untangle the carving joints for these culture traits.

Taken together, these three papers offer an enhanced understanding of some of the important dynamics of human culture. The modern evolutionary analysis of cultural change is relatively young, and laboratory study of culture traits needs to be supplemented by ethnographic work (e.g. Henrich and Broesch 2011), in order to confirm that our simplifying assumptions are correct, and to test the hypothesis that cultural dynamics are cross-cultural. Experimental work would also benefit from increased collaboration with those doing field research. Boesch (1993) argues that tasks used to test cultural learning abilities must employ traits actually thought to be socially acquired in the wild: whether or not a chimpanzee imitates the use of a reaching stick in the laboratory is not

informative about the transmission of, e.g., nut cracking in the wild. This point might also be applied to humans, as cultural learning mechanisms would not be expected to operate in all situations and for all tasks – on the contrary, theory predicts that learners should be selective, both in the use of social learning and in the choice of model. Tasks that are easily acquired through individual learning, and for which there are few deleterious fitness consequences to making a poor decision, might not typically be learned socially.

Humans, like all other creatures on earth, are animals who are adapted to produce behavior that enables the propagation of genetic material. The ability to learn is an adaptation enabling the incorporation of information into a behavioral repertoire. The ability to learn socially allows the transmission of information between unrelated individuals, including the individual innovations that make up culture. Understanding culture at the level of information transmission provides a means of moving beyond the morass of simply describing culture traits. The scientific paradigm, and specifically a Darwinian framework, provide tools to pursue these goals.

## Appendix One: Coding Scheme For Device Designs

Number in parentheses is the design code assigned.

1. Is it Complete (device is placed on the stand)?

Yes- Question 2

No- Incomplete (11)

2. Does it catch under the circle (the catching mechanism catches weights directly below the hole in the stand)?

Yes- Question 9

No- Question 3

3. Does it cover the whole entire circle (none or barely-visible pores not large enough for a pencil to go through)?

Yes- Full Coverup (1)

No- Question 4

4. Is the shape just one linear direction across from one side of the stand to the other with no points of intersection?

Yes- Linear Bridge (2)

No- Question 5

5. Does it have symmetry (if split in half, will both sides reflect to be the same or very similar)?

Yes- Question 6

No- Question 8

6. Are there spokes / central focal point that will branch out to the sides (6+ points in different directions need to branch out to be considered)?

Yes- Question 7

No- Crossy / X (does not have to be perpendicular. It has to resemble a general X-shape) (3)

7. Is the device a flat planar surface (with no curves)?

Yes- Flat Symmetry (if split in half, both sides reflect to be the same or very similar) (4)

No- Above Surface / Dome symmetry (has some curve element that is symmetrical when folded in half) (5)

8. Does it have nesting attributes (resembles a typical bird's nest that's not uniform or woven in sloppy manner or not stacked in a uniform way)?

Yes- Nesters (6)

No- Disorganized Top Catcher(7)

9. Does it touch the base of the stand?

Yes- Bottom Dweller (8)

No- Question 10

10. Is there a bowl (something with flaring sides above a flat surface) on the device?

Yes- Hanging Bowl Below (suspended structure that has a bowl to catch weights) (9)

No- Settle Under Collector (suspended structure that has planar surface to collect weights) (10)

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