RETHINKING BEHAVIORAL EVOLUTION

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Introduction

The emerging discipline of evolutionary developmental biology (also known as evo-devo) has been driven, in part, by evidence demonstrating the existence of non-genetic forms of inheritance that are developmentally derived—in particular epigenetics or cell memory (Hall, 2003; Müller, 2008).[1] Where earlier theorists had supposed that evolution results only from natural selection acting on variation that is both produced and transmitted via genetic mechanisms, proponents of evo-devo argue that non-genetic developmental mechanisms can also contribute importantly to changes in the distribution of phenotypes in populations over time. Non-genetic inheritance provides important support for this claim.

Uptake of this new perspective has been uneven, however. Some areas of evolutionary study have seen vigorous engagement with the broad conceptual framework offered by evo-devo—the study of the evolution of morphological traits is a notable example. In contrast, those who work on the evolution of behavioral traits—especially workers in the fields of animal behavior, behavioral ecology and ethology—have shown scarcely any substantial engagement with the theoretical framework presented by evolutionary developmental biology (Ghalambor et al., 2010: 90; Bertossa, 2011: 2056-57).[2]

One reason for the lack of engagement with evo-devo in behavioral biology may be the perception that evo-devo is concerned solely with understanding the role development plays in morphological evolution. Evo-devo has its roots in the evolutionary embryology of the 19th century, a field focused on the embryonic

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[1] There are other threads of evidence supportive of an evo-devo research program besides evidence for non-genetic inter-generational inheritance that is developmentally derived. For example, the growing body of work on developmental constraint and the origins of body plans. Müller, 2008 provides a nice overview of the many conceptual foundations of evo-devo that makes these different threads of evidence clear.

[2] There are some notable exceptions to this general trend. For example; Carroll and Corneli, 1999; Gottlieb, 2001; Sih et al., 2004a; Sih et al., 2004b; Laland et al., 2008; Dingemanse et al., 2010; Ghalambor et al., 2010; Mery and Burns, 2010; Bertossa, 2011: 2056-57.

foundations of morphology and body plans (Hall, 2000; Müller, 2008). These origins are still reflected in the way evo-devo is most often discussed today. Many key proponents of evo-devo still describe its explanatory focus as being the "origins of organismal form" and discuss key evo-devo concepts such as innovation and novelty in terms peculiar to morphology (for example, Müller and Newman, 2005; Müller, 2007; Müller, 2008; Müller, 2010). This focus upon morphological evolution gives the appearance that evo-devo could only ever be concerned with morphology, but the appearance is deceptive. Evo-devo at its heart is a science concerned with the relationship between development and evolution in general, not just morphological development and morphological evolution. Though much of the empirical work that has moved the field forward has focused on morphological cases, at a theoretical and conceptual level evo-devo is simply concerned with the influence of development upon phenotypic variation, regardless of the traits in question. Thus, if it can be shown that developmental processes play a role in the evolution of behavioral traits, just as they do for some morphological traits, then the existing conceptual framework offered by evo-devo is the obvious starting point for researchers wishing to understand behavior in light of this evidence.

In this paper I seek to motivate those working in behavioral biology to engage with evo-devo, by pointing out some evidence demonstrating that developmental processes can play a role in the evolution of behavior. I begin the paper with an overview of evo-devo, focusing on the relationship between the emerging conceptual framework it represents and the status quo within evolutionary biology—the "received" view or Modern Synthesis (this being the most prevalent account of evolutionary biology within behavioral ecology, ethology and animal behavior). I then show how non-genetic inter-generational forms of inheritance lend support to the evo-devo approach, using chromatin marking (a developmentally-derived form of epigenetic inheritance) as an example. In the second part of the paper, I argue that a type of behavioral inheritance—social learning—presents a challenge to the Modern Synthesis analogous to that provided by epigenetics. Like chromatin marking, social learning is a non-genetic inheritance channel. It is a developmental process via which behavioral traits acquired during the lifetime of the parent can be transmitted to their offspring and subsequent generations, thus contributing to evolution. This interplay between the evolution and the developmental process of social learning is important to explaining the evolution of behavior in numerous species and thereby justifies the application of the evo-devo research approach to the behavioral domain.

1. Evo-devo: Moving away from the Modern Synthesis

1.1 What is the Modern Synthesis?

Since the mid-twentieth century the dominant theory within evolutionary biology regarding how the requirements for selection are satisfied has been the Modern Synthesis (or "received view"). The Modern Synthesis is a general theory of evolution and includes claims both about the conditions that are necessary in principle for evolution by natural selection to take place, and about how these are actually instantiated.

In the simplest case, three necessary conditions must hold within a population for it to undergo evolution by natural selection—(I) phenotypic variation, (II) heritability of phenotype and (III) differential survival and reproduction. When these three conditions hold in any population of entities, evolution by natural selection is highly likely (Lewontin, 1970: 76; Godfrey-Smith, 2008). A fourth condition, (IV) cumulative selection, is required for the evolution of complex adaptations (Sterelny and Griffiths, 1999). This requires that inheritance be stable over many generations. Without such stability of inheritance, the accumulation of beneficial mutations necessary for complex adaptation is not possible.

One key empirical claim of the Modern Synthesis is that the underlying biological structures enabling evolution by natural selection to occur are predominantly genetic (Huxley, 2010; Mayr, 1982: 542-46; Dobzhansky, 1937: 26; Fisher and Bennett, 1999). In other words, genes are the major channel of inheritance for traits, and it is genetic mutation and recombination that provide heritable phenotypic variation within populations. Furthermore, the supply of variation generated by these mechanisms is taken to be largely isotropic (uniform in all directions) and thus unbiased with respect to adaptive value. A further conclusion is generally accepted along with these claims: that the large-scale evolutionary events in the tree of life (such as the emergence of novel capacities or morphological features) are simply the outcome of the accumulation of a series of small-scale events at the genetic level (Jablonka and Lamb, 2005; Bonduriansky and Day, 2009). But this is not (as the others are) an empirical claim; it is a simplifying assumption or idealization that allows evolutionary biologists to ignore features of the world which, according to proponents of the Modern Synthesis, are not of evolutionary significance on a large scale (Mayr, 1982: 832). To illustrate—the

Modern Synthesis is only committed to the empirical claim that the underlying biological structures enabling natural selection to occur are predominantly genetic, not that they are exclusively so. Proponents of the Synthesis do not deny that non-genetic structures capable of sustaining selection exist, nor that evolution via these routes of inheritance may occur. For example, Richard Dawkins (a prominent advocate of the Modern Synthesis) takes seriously the possibility that human culture can evolve by natural selection in his discussion of memetic evolution (Dawkins, 1976). That non-genetic structures capable of sustaining selection are widespread enough to contribute to evolution beyond a few special contexts, however, is denied. The transmission of behavior via human culture is thus not included as a source of heritable phenotypic variation in the general account of evolution presented by the Modern Synthesis, because it is considered relevant only to a "special" and restricted class of species (i.e. humans and other higher primates) (Tomasello, 1999a; Tomasello, 1999b; Dawkins, 2004). This idealization is a very strong one. Advocates of the Modern Synthesis are claiming that we need look only to natural selection and gene frequency change over time in order to explain the vast majority of evolution—nothing else is relevant to this task (Stebbins and Ayala, 1981; Charlesworth, 1996; Dawkins, 2004; Mayr, 1993).

One consequence of this idealized view of the evolutionary process is that proponents of the Modern Synthesis "bracket off" the study of development and ontogeny from the study of evolution (Sterelny, 2000; Müller, 2007; Jablonka and Lamb, 2005; Gilbert et al., 1996). This key aspect of the Modern Synthesis is best represented by Ernst Mayr's widely-accepted proximate-ultimate distinction (Mayr, 1961; Beatty, 1994). According to Mayr (a key architect of the Modern Synthesis) when we look at the types of questions asked in biology we are able to identify two domains of enquiry—functional biology and evolutionary biology. Research in functional biology is fundamentally concerned with "how" questions, such as "how does a bat wing develop?" and "how does the bat wing work?" Mayr claims that answering these questions requires the functional biologist to uncover a particular type of cause—a proximate cause. Proximate causes "govern the responses of the individual (and his organs) to immediate factors of the environment" and include development, ontogeny, and agency (Mayr, 1961: 1503). Research in evolutionary biology, on the other hand, concerns an entirely different set of questions—"why" questions, such as "why does the bat have wings?" and "why do bats and birds both have wings?" According to Mayr, answering "why" questions requires that the evolutionary biologist look to a different type of cause—an ultimate cause. Ultimate

causes "are responsible for the evolution of a particular DNA code of information with which every individual of every species is endowed" (Mayr, 1961: 1503). Natural selection is—unsurprisingly—the central ultimate cause. According to Mayr these two domains of enquiry (functional biology and evolutionary biology) are largely causally independent—they are concerned with answering fundamentally different questions; they answer them by appeal to different sets of causes; and the research within each of those domains can provide little (if any) explanatory traction upon the questions of the other. Thus, biologists who conflate these two classes of questions—for example, by attempting to respond to ultimate questions by considering development, or by attempting to respond to proximate questions by considering adaptation—are making a serious category mistake.

Mayr's view makes excellent sense within the context of the gene-focused view he advocated. If, as the Modern Synthesis assumes, the sole inheritance channel is the transmission of DNA in the germ-line cells, it follows that only traits and variants that arise from genetic mutation and recombination in the germ line can contribute to natural selection. Any other traits or variants that arise (for example those acquired via developmental or environmental processes) are not important in the evolutionary context, as they are assumed not to be heritable: while selection may act upon them, no evolutionary change can result. In this context the bracketing-off of developmental biology from evolutionary biology is entirely reasonable. If proponents of the Modern Synthesis are correct to presume that genetic inheritance is the only kind there is, then developmental processes are indeed causally independent from evolutionary processes and irrelevant to them.

1.2 Enter evolutionary developmental biology

Evolutionary developmental biology (or evo-devo) challenges this aspect of the Modern Synthesis, for its subject matter is precisely the relationship between the developmental processes within individuals and evolutionary processes within populations (Hall, 1999; Müller and Newman, 2005).[3] Proponents of evo-devo take seriously the potential for so-called proximate causes (in particular, developmental processes) to inform our understanding of evolutionary "why?" questions. They

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[3] This is itself an oversimplification. Evo-devo is a broad church. There are many ways in which evo-devo can be said to challenge or disagree with the Modern Synthesis, I present but one here. The true extent and nature of the challenge evo-devo presents to the Modern Synthesis is as yet unresolved (Hall, 2000; Laubichler, 2009; Minelli, 2009; Craig, 2009, 2010a, 2010b; Müller and Pigliucci, 2010).

thus challenge Mayr's supposition that functional and evolutionary biology are effectively independent.

In particular, evolutionary developmental biologists investigate the potential for developmental mechanisms to contribute to and influence the supply of variation to natural selection. Key issues within evo-devo such as plasticity, novelty, innovation, and evolvability relate to the mechanisms supplying phenotypic variation to selection and the nature of that supply (Müller and Newman, 2005). By incorporating both proximate and ultimate causes into their investigations, evolutionary developmental biologists make it possible to entertain a picture of evolution that includes both developmental processes and natural selection (Hall, 1999; Müller and Newman, 2005).

Proponents of evo-devo thus reject Mayr's sharp dichotomy, but most of them do so in a reformist rather than a revolutionary spirit, regarding the account of the evolutionary process provided by the Modern Synthesis as overly simplified rather than eschewing it altogether (Laland et al., 2012). In particular, the presumption that genes provide the sole route for phenotypic inheritance and that development therefore has no place in evolution is seen as the consequence of a view of the nature of evolution that is overly simplified rather than wholly mistaken. Proponents of evo-devo argue that developmental processes are important in structuring the supply of phenotypic variation to selection and thus can explain disparity in the tree of life: biases in the available variation can drive different populations' evolutionary trajectories in different directions (Müller, 2008). They also claim that there are there are extra-genetic channels of inheritance that come into play during development and are not captured if we simply focus upon gene frequency change over time in populations (Jablonka and Lamb, 2005). Thus, because it "brackets off" developmental processes from the processes of evolution, the Modern Synthesis cannot adequately capture the true nature of evolution and the actual role of natural selection in shaping the tree of life as we see it today (Pigliucci, 2007, 2008, 2009; Pigliucci and Muller, 2010). One key piece of evidence supporting this assessment of the Modern Synthesis by advocates of evo-devo comes from the study of epigenetics—the functioning of extra-genetic cellular entities that are heritable and apparently widespread (Hall, 2003; Raff, 1998; Müller, 2007; Müller, 2008).

1.3 Epigenetics

The science of epigenetics or "cell memory" is the study of changes in phenotype or gene expression that are not generated by changes in the DNA of the cell (Hall, 2011). A simple example of an epigenetic effect is seen during growth in our own bodies. As our bodies develop, the cells in our body (despite carrying the same DNA) change in morphology and physiology according to the role they are playing in the body. For instance, bone cells, brain cells, and skin cells all differ in appearance and action despite containing the same complement of DNA. Variation in the appearance and action of these cells is due to the differential activation of gene expression in the cells during development. Importantly for our purposes here, when such differentiated cells divide during growth, each daughter cell has the same activation pattern as its parent cell. The inheritance of the activation pattern from parent to daughter cell is not solely caused by the transmission of genetic material from parent cell to daughter cells. Epigenetic material—non-genetic cellular factors—must be transmitted as well. For our purposes what is important is that such mechanisms are widespread and, in some cases, have been shown to be capable of facilitating the type of cell-to-cell inheritance needed to satisfy the heredity requirement for natural selection (Grant-Downton and Dickinson, 2006; Richards, 2006; Jablonka and Lamb, 2008; Jablonka and Raz, 2009; Gilbert and Epel, 2009; Richards et al., 2010). One example of this is chromatin marking.

Chromatin is the material that makes up chromosomes. In addition to DNA this includes non-genetic molecules such as RNA, proteins, and other molecules. The way that these non-genetic factors within the chromatin are distributed along the DNA making up any given chromosome is known as "chromatin marking". Crucially, this marking influences which genes on each chromosome are expressed and when. In other words, these non-genetic factors determine how the genetic code is read and interpreted. Some of these marks and the gene expression patterns they control have been shown to be heritable. The best studied of these is DNA methylation patterns.

DNA methylation is the attachment of a methyl group to the DNA within the chromosome. It is seen in all vertebrates and plants, and in some invertebrates, fungi, and bacteria (Jablonka and Lamb, 2005). Methylation affects gene expression; the presence or absence of these methyl groups, and their density in a region of DNA, alters the likelihood of that region of DNA being transcribed. The transgenerational inheritance of methylation patterns and their phenotypic effects has been shown in asexual plants and single-celled organisms (Chong and Whitelaw, 2004; Richards, 2006; Hauser et al., 2011; Youngson and Whitelaw, 2008)

and amongst eukaryotes (Morgan et al., 1999; Rakyan et al., 2001; Crews et al., 2007; Anway and Skinner, 2006; Cropley et al., 2006; Cuzin et al., 2008; Youngson and Whitelaw, 2008).

In single-celled and asexually budding organisms the primary mode of inheritance for methylation patterns, known as structural inheritance, involves the transfer of elements of the parental cells to offspring during mitotic reproduction or binary fission (Jablonka and Raz, 2009). In particular, when cells reproduce via meiosis, mitosis, or fission, the parent cell is cleaved into a number of daughter cells. In this process the parent cell is lost, but elements of its structural properties are conserved in the daughter cells. One such conserved structure is methylation patterns in the DNA. The conservation of these patterns results in the replication of phenotypic effects seen in the parent cells, in the offspring cells.

In sexually-reproducing multi-cellular organisms like mammals, the mechanisms of inheritance are less well understood. In these organisms many of the chromatin markings of cells in the offspring are "reprogrammed" rather than maintaining the parental state during reproduction and early embryonic development (Reik et al., 2001). While originally it was thought that this reprogramming completely ruled out the inheritance of epigenetic factors in sexual organisms, more recent research has shown that the erasure of methylation patterns is incomplete, at least with respect to the maternal alleles (Morgan et al., 1999; Chong and Whitelaw, 2004; Blewitt et al., 2006). The agouti viable yellow mouse allele provides the most famous example of this type of inheritance in mammals.

Fig. 1: Genetically identical (but epigenetically different) mice

These mice represent the continuum of phenotypes ranging from yellow on the left to agouti on the right depending on the level of activation of the agouti viable yellow (A^{vy}) allele.

(Source: Morgan et al., 1999)

The mice in the picture above are genetically identical. They all carry two alleles at a genetic locus for wild-type coat colour: A^{vy} and a. What differs between them is the amount of folic acid consumed by mouse dams during pregnancy. The smaller brown mice on the right had mothers who were fed folic acid. The larger mice on the left, did not (Wolff et al., 1998). The different diets of the two dams has led to the generation of different methylation patterns on the chromosomes of the embryos developing within them and thus different phenotypes. In particular, the presence or absence of folate in the maternal environment induces changes to the DNA methylation patterns and this alters whether the dominant "agouti viable yellow " allele (A^{vy}) within that embryo is "activated" or "inactive." The phenotype of Avy/a mice pups is thus dependent on the level of activity of the Avy allele and ranging from yellow (Avy is strongly activated) through to agouti (A^{vy} is not active).[4]

The phenotypic effects of methylation at the A^{vy} allele are transgenerational. All Avy/a mice are genotypically identical at the A^{vy} allele, yet within this class, agouti dams are more likely than yellow dams to have agouti pups, and vice versa (Wolff et al., 1998; Morgan et al., 1999; Blewitt et al., 2006). It is clear that the inheritance of the phenotype from dam to pup results from the incomplete erasure of the epigenetic modification in the germ line cells (Cropley et al., 2006; Waterland et al., 2007), but the exact mechanism of inheritance is unclear. Although the methylation patterns that influence the expression of the A^{vy} allele in the dam are replicated in the juvenile offspring, those patterns are not seen in the offspring at the blastocyst stage of development, which is good evidence that the methylation patterns themselves are not being retained during cell reprogramming. Some other epigenetic element appears to be underwriting the inheritance here but it is not clear what it is (Blewitt et al., 2006). This problem is not restricted to the agouti viable yellow mouse allele; broader studies suggest that although the DNA methylation patterns are clearly important to the inheritance of the phenotype in a

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[4] Note that A^{vy}/a agouti mice are often described as "pseudoagouti" so as to distinguish them from mice that lack the silent A^{vy} allele but also have the agouti phenotype (i.e. a/a agouti mice). Assume all agouti mice discussed here are A^{vy}/a mice.

number of cases, some other element is also required for transmission (Daxinger and Whitelaw, 2010; Jablonka and Raz, 2009).

1.4 Lessons from chromatin marking

Chromatin marking challenges some key assumptions of the Modern Synthesis regarding the supply of phenotypic variation to selection—in particular, the assumption that phenotypic variation to selection is exclusively supplied by genetic mechanisms and that the supply itself is isotropic. First, chromatin marking is a route of inheritance that is not genetic—while genes are necessary in such circumstances, they are not sufficient for the expression of the traits in question in the parent and their reiteration in further offspring; the particular chromatin marking patterns are also required. Furthermore, traits underwritten by chromatin marking are stable within lineages over multiple generations (Crews et al., 2007; Anway and Skinner, 2006) and potentially widespread—chromatin marking is found in all cells with chromosomes. Chromatin marking thus presents a source of variation that is heritable and potentially capable of contributing to cumulative selection, challenging the assumption that the only evolutionarily significant source of phenotypic variation to selection is via genetic mutation and recombination. In addition, the supply of variation via chromatin marking is not isotropic. Because chromatin marking arises via the interaction between the organism and the environment, it offers a route via which the environment can potentially bias the supply of variation to selection (though not necessarily towards adaptive benefit). Chromatin marking therefore can potentially help to explain the divergent evolutionary trajectories that create disparity in the tree of life.

There are still many questions surrounding chromatin marking, however. First, just how widespread is inter-generational inheritance via the transmission of chromatin marking? Although chromatin marking is clearly heritable across generations within many single-celled organisms, it is not clear how widespread its inheritance is in multicellular organisms. If it turns out to be very rare, then the gene-centrism of the Modern Synthesis would be justified. A second question relates to the stability and fidelity of the inheritance that chromatin marking offers. While it might be capable of maintaining selected traits over generations, can chromatin marking underwrite their persistence over the tens and hundreds of generations required for cumulative evolution and thus for the evolution of complex adaptations? If the evolutionary reach of chromatin marking is only very shallow, perhaps it can still be justifiably partitioned off from general evolutionary

theory. These concerns cannot be ignored, but they alone do not threaten the science of evo-devo. Chromatin marking (like other epigenetic mechanisms) presents a potential alternative to genetic inheritance, and thus gives reason to question the idealizations of the Modern Synthesis even though at this time it does not conclusively discredit them. Epigenetic inheritance reveals the need for further research into the role of developmental factors in evolution and thus provides important motivation for the evo-devo research program (Müller, 2008).

2. Rethinking Behavioural Evolution

Epigenetic chromatin marking has been shown to underwrite both morphological and behavioral traits, and thus motivates the application of the evo-devo approach across a broad range of contexts (Jablonka and Raz, 2009; Bonduriansky and Day, 2009). While this alone could be seen as sufficient to motivate an evo-devo of behaviour (Jablonka & Lamb, 2005), research in the behavioral domain also offers distinctive motivations of its own. In particular, as I will argue, social learning is a widespread and evolutionarily efficacious route of inheritance for behavioral traits; an extra-genetic channel of inheritance for characters acquired during development. It is also potentially a source of bias in the supply of variation. Thus, I claim, understanding the role that social learning plays in evolution requires us to focus upon the interplay between the developmental processes within individuals (in particular, those that are affected by social learning) and the evolution of populations over many generations— i.e. upon the subject matter of evo-devo. Evidence that social learning acts as a route of behavioral inheritance thereby motivates the extension of the evo-devo research approach to the behavioral domain, while the distinctive features of social learning as a form of inheritance raise new questions for that approach.

I begin by discussing the view of social learning and evolution that is standard within behavioral biology—that inter-generational inheritance of behavioral traits via social learning sufficient to satisfy the requirements for cumulative selection is limited to only a few special cases in the animal kingdom. I then give an overview of the evidence demonstrating the widespread existence of animal traditions. Such traditions, I argue, represent a feasible source of non-genetic inter-generational inheritance of behavioral traits that is widespread and stable enough to bring behavioral evolution within the ambit of evo-devo.

2.1 Social learning – the traditional view

Within behavioral ecology, animal behavior, and ethology there has been little to no engagement with evolutionary developmental biology (Ghalambor et al., 2010: 90; Bertossa, 2011: 2056-57). Rather, the Modern Synthesis, and the approach to development and evolution it advocates, is the norm. This is demonstrated clearly by the central role accorded to Mayr's proximate-ultimate distinction and Niko Tinbergen's related "four questions" of ethology in these fields (Tinbergen, 1951; Tinbergen, 1963; Griffiths, 2008; Manning, 2005). Tinbergen argued that behavioral biology is best understood as responding to four interrelated problems or questions —Causation, Ontogeny, Survival Value and Evolution (Fig. 2)—each of which corresponds to a different aspect of the question "Why is behavior x as it is?" Tinbergen's taxonomy established a set of principles that have defined research in behavioral biology for more than half a century.

1. Causation:	2. Ontogeny:
How does it work?	How did it develop?
3. Survival value:	**4. Evolution:**
What is it for?	Why did it evolve?

Fig. 2: Tinbergen's Four Problems

Textbooks and collections of papers on the foundations of animal behavior (Houck and Drickamer, 1996); methodology in the studying of animal behavior (Martin and Bateson, 2007; Lehner, 1998; Manning and Dawkins, 1998); behavioral evolution (Slater and Halliday, 1994); behavioral ecology (Krebs and Davies, 1997); cognitive evolution (Shettleworth, 2010); and cognitive ethology (Allen and Bekoff, 1999), not to mention hundreds of journal articles published across these fields, all refer to Tinbergen's "four questions." Most of them explicitly combine them with Mayr's distinction as in Fig. 3 (for example, Martin and Bateson, 2007).[5]

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[5] Note that Tinbergen never presented his questions in this manner. This (now prevailing) presentation of the four problems is thought to be originally due to Klopfer & Hailman (1972) and Alcock (1975) (Dewsbury, 1999).

Proximate "How questions"	1. Causation: How does it work?	3. Ontogeny: How did it develop?
Ultimate "Why questions"	2. Survival value: What is it for?	4. Evolution: Why did it evolve?

Fig. 3: Tinbergen's Four Problems as questions with Mayr's proximate-ultimate distinction

Social learning—learning that involves the use of information gained from other individuals such as the location of food sources or successful behavioral patterns—encompasses a range of different learning processes ranging from true imitation to stimulus enhancement (see Brown and Laland, 2003: Table 1 for a summary). It is accepted that such learning is widespread in the animal kingdom, in species from insects (Leadbeater and Chittka, 2007) to complex vertebrates (Galef Jr and Laland, 2005). What is less accepted is that such learning is a route via which behavioral traits can be inherited over multiple generations and thus contribute to the outcomes of evolution. Rather, those interested in the evolution of animal behavior generally assume that the intergenerational inheritance of behavior within animal lineages is solely genetic. This is unsurprising given the widespread acceptance of the Modern Synthesis within behavioral biology.

Yet social learning obviously constitutes a channel through which behavioral patterns can be transmitted from one individual to another; a sort of inheritance. Why omit it from the evolutionary picture? Several widely-accepted assumptions about social learning are commonly invoked to justify this omission. To begin with, it is often argued that most social learning processes lack the fidelity and stability required to underpin the persistence of traits required for the evolution of cumulative and complex behaviors via natural selection; that only true imitation—the explicit copying of the behavior of others—and teaching can support the persistence of traits long enough for cultures or traditions to evolve (Tomasello, 1999a; Tomasello, 1999b). Such imitation, it is then claimed, is cognitively demanding and thus limited to a few "special cases"—the few species that possess what are thought to be the appropriate cognitive capacities, such as humans and primates (e.g. Galef, 1992). The assumption is thus that evolutionarily efficacious inheritance of behaviors by social learning is the rare exception, not the rule (Jablonka and Lamb, 2005; Laland and Janik, 2006; Avital and Jablonka, 2000).

Recent evidence of social learning and animal traditions beyond primates challenges this assumption, calling into question the exclusive focus upon genetic inheritance and the bracketing-off of development by those interested in the evolution of behavioral traits.

2.2 Social learning – challenging the traditional view

Two types of evidence support the view that the inheritance of behaviors via social learning is both widespread and evolutionarily significant: first, evidence of the existence of culture and traditions beyond the primate lineage; second, evidence that culture and traditions can be generated by relatively simple learning mechanisms.

Evidence of culture and traditions in non-human animals comes several sources. What is important is demonstrating that behavior is being transferred from one generation to the next via learning rather than via genes. A few different types of evidence are relevant here (in part due to Laland and Janik, 2006):

- The speed at which behaviors infiltrate a population: Behaviors that are produced by genetic mutation are generally slow to invade populations because, even when under very strong selection, they are transferred between individuals only during reproduction. If behaviors are heritable by social learning, however, they can feasibly invade entire populations within a generation.

- The speed at which behaviors are lost from populations: Socially learned behaviors are more likely to suffer a rapid decline than genetically heritable behaviors. This is because the persistence of socially learned behaviors in populations is much more contingent on the environment and random events. In particular, there is no silent transmission of behavioral traits—if a trait is not expressed it cannot be learned by others. This contrasts with genetic traits, which can be recessive and skip generations.

- The arbitrariness of persistent behavioral traits: That arbitrary or maladaptive differences in behavior take hold in populations and persist is a good indicator of the social transmission of behavior between individuals, as via genetic inheritance alone we would not expect the traits to reach fixation because they play no adaptive role (Tomasello, 1994: 274-75). Persistent variations between groups or

geographic "clines" in behavior within spatially distributed groups that are not explicable by differences in environment are usually used as an indicator of arbitrariness.

- The outcomes of "cross-fostering" experiments: This type of experiment gives us information about the extent to which differences in behavior are due to maternal environment or to genetics. To illustrate, imagine two populations of the same species in very similar environments. The majority of individuals in one of those populations exhibit a foraging technique not seen in the other population—in this case, nut cracking. Furthermore the technique is known to have persisted in the population over multiple generations. We might want to test whether the variation in nut cracking capacity between the populations is the product of a genetic difference or a difference in "culture". One way to do this is to look into the inheritance of the nut cracking behavior by doing cross fostering experiments (i.e. fostering the offspring of non-nut-cracking mothers with nut-cracking mothers and vice versa). If the nut cracking behavior is largely genetically inherited, we should not see it in those individuals taken from the non-nut-cracking population and raised in the nut-cracking population. This is because they should lack the appropriate genes. Conversely if the nut cracking behavior is inherited via some social means we should see it only those individuals raised in the nut-cracking population. Those raised in the non-nut-cracking population will lack the technique because the appropriate social stimulus is unavailable to them in that environment.

It is generally accepted that these types of evidence exist for some primates, particularly chimpanzees, Pan troglodytes (Whiten et al., 1999; Whiten, 2005). What is less accepted is the idea that some or all of the characteristics of culture and traditions are seen in other species, even those very far removed phylogenetically from primates. Among the most famous challenges to this view is the tool use of the New Caledonian crow (Corvus menuloides).

New Caledonian crows manufacture and use stick- and leaf-based tools for foraging. These tools are complex and their successful use requires skill. There is strong evidence that a significant portion of tool use and manufacture in New Caledonian crows is maintained in populations via social learning and that the complexity of the tools is a product of cultural evolution. First, there is evidence of

geographic clines in tool design and manufacture (Hunt and Gray, 2003; Hunt and Gray, 2007). Second, there is evidence of the relatively fast transmission of innovative behaviors within groups (Holzhaider et al., 2010). Third, there is evidence that social learning plays an important role in the development of the tool use and manufacture behaviors in juvenile crows similar to that played in the development of stick-fishing and nut-cracking technologies in chimpanzees (Holzhaider et al., 2010; Kenward et al., 2006).

While the crow case is particularly impressive for the cultural complexity involved and demonstrates that the cultural achievements of primates are not unique, it is not a demonstration that animal culture is widespread across different taxa. Simpler animal cultures and traditions have been more widely observed however. The multi-generational transmission of elements of songs and vocalizations via social learning is observed in birds (Kroodsma, 1980; Podos and Warren, 2007; Mundinger, 1982) and whales (Deecke et al., 2000; Yurk et al., 2002). Similarly, simple foraging techniques and innovations have been shown to persist within populations and be transmitted between generations via social learning in rodents (Aisner & Terkel, 1992), various birds (Lefebvre and Bouchard, 2003), and even fish (Laland et al., 2003; Brown and Laland, 2003). These cases give grounds for thinking that animal cultures could be widespread. They also give grounds for questioning the supposition that behavioral inheritance via social learning is limited to cases of imitation and teaching. Fish provide a particularly good example of this.

Fish are traditionally thought to be fairly cognitively limited organisms, but recent studies have shown that fish are able to recognise and remember their shoal-mates, foraging and nest locations, and navigational routes. There is also evidence that fish learn via stimulus enhancement and social exposure —relatively cognitively simple processes (see Laland et al., 2003 and Brown and Laland, 2003 for a review of the evidence in both cases). In some fish, researchers suggest that this evidence is sufficient to demonstrate the existence of traditions that persist across many generations. A good example of social learning in fish is seen in the bluehead wrasse (Thalassoma bifasciatum). In this species, information about the location of arbitrarily determined mating sites and how to get to them is transmitted from older to younger fish via simple learning mechanisms. Individuals learn the location of traditional mating sites by observing and following others rather than via more cognitively demanding means of social transmission such as explicit copying or "true" imitation. The use of such sites is determined not by genes

but by the maintenance of information about those sites in the lineage via social learning, and there is evidence that the use of such sites can span several generations (Laland and Janik, 2006). Similar mechanisms have been shown to maintain foraging behaviors in other species, such as milk-bottle opening in some birds (Sherry and Galef, 1984; Sherry and Galef, 1990; Lefebvre and Bouchard, 2003). These cases suggest that social learning is widespread, and can be underpinned by simple mechanisms. This lowers the bar for achieving inheritance via social learning considerably.

2.3 Stable inheritance via social learning

One challenge to the picture I have presented here concerns the fidelity and stability of social learning as a channel of inheritance. It is clear that behavior can be transferred between individuals via social learning over multiple generations, but what evidence is there that this route of inheritance provides sufficient fidelity of transfer or stability over multiple generations to satisfy the requirements for cumulative selection?

Some features of social learning seem likely to undermine its ability to serve as an evolutionarily-significant channel of inheritance. First, unlike genetic inheritance, the inheritance of behavior via social learning cannot be silent: behavioral traits must be expressed in order to be transmitted. This makes the persistence of the traits far more fragile or sensitive to changes in the environment than in the case of genetic inheritance. Second, copying fidelity is crucial. Although copying failure is a potential source of novel behavioral variation in populations, it can also swamp out the effects of selection. This is a potential problem for genetic inheritance as well (a species with a very high mutation rate could not undergo cumulative selection), but simple social learning mechanisms such as stimulus enhancement appear particularly prone to copying error. Although these concerns are legitimate, they are not conclusive. Considering the role of niche construction may reveal mechanisms by which social learning can achieve robustness and high fidelity without the need for cognitively-demanding forms of imitation.

Niche construction refers to the ability of organisms to define, alter and build their own environments (Odling-Smee et al., 2003). The effects of niche construction can endure or accumulate over many generations, so that organisms inherit not just genetic information but features of their selective environment in what is known as "ecological inheritance." Proponents argue that niche construction can have important evolutionary impacts, altering the course of the evolution for

niche-constructing species (and for other species with which they interact) by generating long-term changes to the environmental elements of the selective regime. Examples of niche construction include the manufacture of nests, burrows and webs by animals, the alteration of atmospheric gases by plants, and the fixation of nutrients by bacteria.

Niche construction has the potential to increase the robustness and fidelity of social inheritance. Niche construction in this context is best thought of as "scaffolding" for inheritance, capable of buffering social inheritance mechanisms from changes in the environment. It aids social inheritance, for example, by reducing the likelihood of losing cues or materials required for the transfer of traits. Niche construction can also increase the likelihood of high-fidelity transfer by adding redundancy to the system. Niche construction coupled with social learning can thus provide a more effective route of inheritance. A good example of both these outcomes is seen in the New Caledonian Crow case.

We've noted already that New Caledonian Crow tool use is a particularly good example of animal culture outside the primate lineage. One way in which juvenile New Caledonian Crows learn to use tools is by interacting with the discarded tools of adult crows. Juvenile crows are naturally interested in the tools. They pick them up and carry them about. They also use them to mimic adults' use of them (Holzhaider et al., 2010; Kenward et al., 2006). By interacting with their environment, New Caledonian Crows have set up a situation (unintentionally, of course) in which juvenile crows are able to gain familiarity with tool structure and manipulation before they even begin to make tools themselves. In this way, the discarded tools of adult crows provide a type of ecological scaffolding for the development of tool use in subsequent generations—i.e. the simple addition of discarded tools to the developmental environment of juveniles makes the effective transmission of tool use and manufacture via social learning more likely, increasing both the fidelity and the robustness of the transfer. It is worth noting that a similar phenomenon is observed in chimpanzee troops that engage in tool use (Tomasello, 1994).

The role of niche construction in structuring the environment so as to facilitate the transfer of learned behaviors is not limited to cognitively complex species. Meerkats (Suricata suricatta) exhibit a type of niche construction in the transmission of foraging techniques. Meerkats eat scorpions. While they are a good source of protein, scorpions are also a potentially very costly prey because of their sting (which carries enough neurotoxin to kill an adult meerkat). Meerkats use

particular predation techniques for scorpions that involve disabling the sting. Interestingly—given the high costs of failure—these foraging techniques are learned. A form of niche construction scaffolds this learning. Adult meerkats modify the juvenile learning environment by presenting their offspring with live scorpions from which the adults have removed the stings. This is enables the naive foragers to learn from adults how to catch and disable scorpions, without the risk of a high cost sting (Thornton and McAuliffe, 2006). Once again, niche construction here increases the robustness and fidelity of transmission of behaviors between generations. The stability of the transfer of behaviors via social learning is sensitive to the costs of failure or transfer error—if a behavior is only transferrable via a costly or dangerous learning situation its persistence in a population is fragile. Scaffolding the juvenile learning environment via the provision of "safe" prey items reduces the costs of learning in the meerkat, at least during the initial learning phase, and thus increases the effectiveness of social learning as a form of inheritance.

Though the exact extent of social learning and its evolutionary reach remain unclear, niche construction provides a potential source of stability for social learning as a route of inheritance. Overall, the cases I have described provide good grounds for rethinking the relationship between development and selection in evolution. There is reason to question the standing assumption in behavioral biology that inheritance via social learning plays little role in the evolution of behavioral traits. This evidence, like that of epigenetic inheritance, undermines the "bracketing-off" of development from studies of behavioral evolution. As with epigenetics, inheritance via social learning is developmentally derived—it is the consequence of experience rather than the transfer of genetic material from parent to offspring. It is thus a form of inheritance that is not captured if development is ignored in evolutionary biology. Social learning is also like epigenetics in that it is not totally understood. While there is evidence that social learning could be an important channel of inheritance it is not clear how important it actually is. More research is required to establish how widespread inheritance via social learning is, and to determine its "evolutionary reach." Evo-devo is a science concerned with the relationship between the developmental processes within individuals and evolutionary processes within populations, and thus, research considering the relationship between the developmental process of social learning and evolution falls broadly within its purview. It is in this sense that we should be asking why social learning has not motivated an evo-devo approach to behavior if epigenetic

research motivates the application of evo-devo principles elsewhere in evolutionary biology.

3. Conclusion

In this paper I have argued that, like chromatin marking, social learning presents an important challenge to the bracketing off of development from evolution in the Modern Synthesis by being an example of a non-genetic inheritance route which is active during development. In doing this I have shown that there is clear motivation for the application of the evo-devo research framework in the behavioral domain. We already know that behavioral traits can be transferred over multiple generations via chromatin marking. This alone might be considered sufficient to motivate a reintegration of the study of behavioral development and behavioral evolution. Showing, in addition, that behavioral traits can also be transferred over multiple generations via social learning adds support to the claim that those interested in behavioral evolution should take seriously the interplay between development and evolution. Evo-devo, as a science that does take this interplay seriously, is the obvious place for behavioral biologists to begin the study of the evolutionary developmental biology of behavior.

Moving to an evo-devo of behavior will require openness to change amongst both behavioral biologists and evolutionary developmental biologists. For behavioral biology it means thinking more about the developmental systems underpinning behaviors and the ways in which this could influence evolution. This will require untangling the messy interplay between genetics, development and the environment and a new way of looking at the proximate-ultimate questions of behavioral biology (Laland et al., 2012). This will be challenging, both conceptually and methodologically.

For evo-devo there will also be challenges. The focus of evo-devo research to date has been upon morphological traits and their evolution. Because of this, many key terms and concepts used in evo-devo are tailored to suit this agenda and

thus are not directly applicable to behavior. For example, the concepts of novelty and innovation in evo-devo are standardly defined in a manner that explicitly makes reference to variation in morphological features such as the metazoan body plan or anatomy (e.g. Müller, 2010; Table 12.1). Such concepts are not directly applicable to behavioral traits. New evo-devo concepts that are either more general or designed specifically with behavior in mind will be needed.

While these challenges are real barriers to the use of the evo-devo research framework in the behavioral domain, the benefits of moving away from the standard approaches to behavioral biology towards an approach that integrates our understanding of development and evolution are potentially very large. For example, not only does social learning present a route of inheritance that is developmental; it is also a route of inheritance that is very often biased to adaptive value. Learning is dependent upon the perceived benefit of the behavior being learned by the organism. Learned behaviors that are beneficial are maintained during the lifetime of the organism and behaviors that fail to be beneficial or lose their value tend to be lost. Unlike genetic inheritance that is blind to adaptive value, social learning is consequently a potential source of bias in the supply of variation to selection. It may increase the rate at which adaptations evolve (for example) and thus drive the emergence of disparity in behavior in the tree of life. Thus, taking into account a role for social learning as a route of inheritance may help to explain many aspects of behavioral evolution, including the persistence of behavioral traits in populations, the rapid loss of behaviors in populations, differences in the rates of behavioral evolution between lineages and differences in extinction rates.

Acknowledgements

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