

Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns

Todd M. Freeberg

Departments of Audiology and Speech Sciences and Biological Sciences, Heavilon Hall, Purdue University, West Lafayette, IN 47907, USA

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Abstract

Female and male animals often choose mates based upon the complementarity of their courtship behaviours and preferences. The importance of this fact on the evolutionary dynamics of populations has long been appreciated. What has not been appreciated is the role that social learning might play in the transmission of systems of courtship behaviour across generations. This paper addresses the social transmission of courtship behavioural traditions in vertebrates. It discusses views of culture in the context of behavioural signals and preferences in courtship. It then reviews empirical evidence for culture-like processes affecting courtship behaviour, focusing on studies of song learning in passerine birds and work on social learning of mating preferences. The paper concludes with potential future directions for research on social traditions in systems of courtship behaviour, including determining mechanisms of transmission, genetic and non-social environmental effects, and selective factors influencing the stability of behavioural traditions over time. By integrating proximate and ultimate questions for the transmission of courtship systems, this work would increase our understanding of the ways individual development, cultural processes, and population evolution influence, and are in turn influenced by, one another. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

This paper addresses the social transmission of behavioural traditions in courtship in vertebrate animals. Since communicative signals and prefer-

ences for signals are some of the fundamental components of courtship systems (Mayr, 1963; Paterson, 1993; Hauser, 1996), I will focus on evidence for social learning in communication. First, the paper examines the idea of non-human animal ‘culture’, and offers a definition of a communicative culture for thinking about the social transmission of systems of courtship behaviour.

E-mail address: freeberg@bilbo.bio.purdue.edu (T.M. Freeberg).

Next, the paper reviews empirical evidence for social learning in courtship signals, mating preferences, and patterns of pairing and mating in animals. This evidence largely comes from studies of the learning of songs in birds, and from work on the influences of social traditions on mating preferences. The paper concludes with some suggested future areas of research that may bring a greater understanding of the influences of communicative cultures on courtship and mating patterns in animals, and of the implications of these influences to our thinking about behavioural ontogeny and evolution.

The question of social traditions in relation to systems of courtship behaviour is important to the theme of this special issue of *Behavioural Processes*: proximate causes and ultimate functions of behaviour in the mating systems of vertebrates. Indeed, there recently has been a greater call for synthetic research approaches that link the proximate and ultimate (Real, 1994; Drickamer, 1998; Bolhuis, 1999); ‘culture’ in systems of courtship behaviour provides a powerful way of doing this. ‘Culture’ (defined below) can influence the ontogeny of the courtship behaviours, and can act as an evolutionary force, in that behaviours are socially generated, selected, and transmitted in a population (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Laland et al., 1993). Furthermore, the social transmission of courtship behaviours makes the proximate-ultimate link perhaps more explicit than other studies of social traditions (such as foraging preferences). This is because courtship behaviours represent traits that can spread through populations, and that themselves serve as strong selective agents because they have a direct influence on reproductive success (see Kirkpatrick and Dugatkin, 1994; Laland, 1994a,b).

2. Communicative culture and systems of courtship behaviour

2.1. Culture defined and the question of animal culture

‘Culture’ and ‘cultural transmission’ are terms used frequently in studies of behavioural traditions

in animals. Culture is often viewed as a pattern or system of behaviours, and cultural transmission as the process by which it comes about and is maintained (this pattern/process distinction will be central to the discussion below of a problem with these terms). Cavalli-Sforza and Feldman (1981, p. 10), define culture as ‘those aspects of thought, speech, action [meaning behavior], and artifacts which can be learned and transmitted’. For Boyd and Richerson (1985, p. 33), culture is ‘information capable of affecting individuals’ phenotypes which they acquire from other conspecifics by teaching or imitation’.

Taking these and related ideas together, we might define culture in non-human animals, very simply, as behavioural traditions of a population that are socially learned and transmitted. The ‘behavioural traditions’ part of the definition is important in that if the behavioural variants in a population are highly variable and change considerably over short periods of time, they would not represent the rather conservative nature of a culture. As traditions, culture-like patterns must be fairly stable across time, which means that some selective process must be operating to maintain those patterns over time or space (Durham, 1976; Mainardi, 1980; Heyes, 1993; Galef, 1995; Giraldeau, 1997). The ‘of a population’ part of the definition stresses that culture is a population-level phenomenon, and not a characteristic of individuals alone (Mainardi, 1980; Boyd and Richerson, 1985). The ‘socially learned’ part of the definition is essential in that a culturally-transmitted behaviour requires social interaction — often teaching and/or imitation — between an individual possessing that behaviour and a naive individual, for that behaviour to develop in the naive individual (Galef, 1976, 1990, 1995). Congenital behaviours (present from birth or hatching) and behaviours acquired by an individual through strict trial-and-error learning (‘asocial learning’ in Heyes, 1994) do not represent cultural patterns or processes.

Culture defined in this manner would provide a way of approaching the question of behavioural variants in populations and how they are transmitted across generations for both humans and non-human animals. However, culture defined in

this manner is problematic. The problem stems from the processes by which culture-like phenomena are generated and transmitted. By using ‘culture’ broadly to refer to languages and systems of rules for behaviour in humans and to tool use in primates or song traditions in birds, we may be suggesting to readers that those social learning processes are the same for our species as for other taxa. As Galef (1992) has pointed out, however, it is highly unlikely that the social learning processes giving rise to behavioural traditions in non-human animals are homologous to those in our own species. Evidence of true imitation in non-human animals (outside of bird song learning; see below) is much rarer than typically believed, with cases of ‘imitation’ often explainable by simpler mechanisms (Galef, 1988, 1990; Whiten and Ham, 1992). Furthermore, evidence of actual teaching, or active information donation (King, 1994), in non-human animals is virtually non-existent (Galef, 1992; Tomasello et al., 1993; but see Caro and Hauser, 1992). Thus, we must take considerable care to make explicit what we mean by social traditions, culture, or cultural transmission in our work and writing.

2.2. Communicative culture and criteria for establishing it experimentally

Human cultures exhibit accumulation and progressive change: changes made and adopted by a group are added to changes that had been adopted earlier by the group in a generally progressive manner (see Heyes, 1993; Tomasello et al., 1993; Flinn, 1997; Henrich and Boyd, 1998). While there may be no true equivalent to accumulation and progressive change in non-human species, there is some evidence of semi-cumulative change in the vocal signals of passerine birds, which suggests the possibility of conservative traditions in communication (Mundinger, 1980; Baker and Cunningham, 1985; Boyd and Richerson, 1996; Payne, 1996; see Whiten et al., 1999, for evidence of culture in the form of perceptual-motor behavioural traditions in chimpanzees, *Pan troglodytes*). For the development of communicative signals and the preferences for those signals, a ‘communicative culture’ will act as a

constraint: individuals born into a given population will tend to develop the signals and preferences characteristic of that population and not some other population. These signals and preferences will likely be shaped in the population by selective factors in the physical and social environment (discussed in more detail in Section 5 below). As these selective forces will change somewhat over generational time, the signals and preferences of the ‘communicative culture’ will exhibit a change over time. New, possibly favorable, variants will be added into the population’s communicative tradition — perhaps due to copying errors during learning or immigration of potential social models possessing novel variants (see Jenkins, 1977; Goodfellow and Slater, 1986) — while unfavorable variants may be lost. Unlike the case in our own species, however, there is no mechanism for the recall of a lost variant within a population other than it re-arising *de novo* (thus, in a strict sense, even a communicative culture is not truly cumulative in the long term).

In light of the discussion above, we might define a communicative culture in animals as a population-specific, co-adapted set of behavioural signals, responses to those signals, and preferences for whom those signals and responses are directed, that is socially learned and transmitted across generations. It may be argued that simply adding the term ‘communicative’ to ‘culture’ is insufficient to address the problematic aspects of non-human culture addressed above. Communicative culture, on the other hand, is a more explicit description of what these traditions, and the processes by which they arise and are maintained, might be (and what they are not, such as material cultures; see McGrew, 1992). As is the case with the broadly used term, ‘learning’, however, calling something a communicative culture would require that it be explained, and would not be an explanation itself (Galef, 1976; West and King, 1996; Giraldeau, 1997). While this idea of a communicative culture can potentially apply to any system of signaling and response behaviour, such as alarm calling (Slobodchikoff and Coast, 1980; Macedonia and Evans, 1993; Owings and

Morton, 1998), here we will focus on the behaviours and preferences of courtship systems.

Demonstrating a communicative culture requires both long-term analyses of the consequences of different social traditions in populations and intensive, longitudinal analyses of behavioural development in individuals (fitting again with the proximate-ultimate theme in vertebrate mating systems). To demonstrate experimentally that the courtship behaviours and preferences in animal species represent a communicative culture, three minimal criteria should be met (see also Galef, 1976, 1990; McGrew 1992; Galef and Allen, 1995; Flinn, 1997; other important considerations are discussed in Section 5 below).

1. In the populations being studied, the behaviours or preferences must represent traditions: they must be fairly stable once attained within an individual and across generational time and, ideally, they will be demonstrably distinct across different populations.
2. Young animals must be able to learn elements of their courtship systems by interacting with older and more experienced conspecifics. Further, it is important to try to document the specific social learning mechanisms that facilitate and maintain those behaviours, since a communicative culture is both the pattern of behaviours and the process by which those behaviours develop and are transmitted (Galef, 1976, 1988; Flinn and Alexander, 1982; Whiten and Ham, 1992; King, 1994).
3. The courtship variants developed by those young animals must in turn be transmittable to another generation of young animals, and in the absence of the original adult social models. Documenting the origin, maintenance, change, and loss of variants over several 'cultural' generations would prove helpful to our understanding of how communicative cultures evolve.

Numerous studies have provided strong evidence of social learning in elements of vertebrate courtship systems. Two primary areas of research have addressed whether culture-like processes may influence the development and potentially transmission of systems of courtship behaviour.

These include studies of song traditions in passerine birds and of the social learning of mating preferences and courtship patterns. These areas of research will be briefly reviewed in the next two sections, as will some of the theoretical and modeling work that has been done in these areas. Finally, the criteria for demonstrating communicative cultures that are met (and not met) by these lines of research will be addressed.

3. Song traditions in passerine birds

The idea that the vocal signals of passerines (songbirds) may result from cultural transmission can be traced back at least as early as the study by Marler and Tamura (1964). Since then, numerous authors have studied vocal dialects, song learning, and social influences on vocal signals and signaling (see Krebs and Kroodsma, 1980; Kroodsma and Miller, 1982, 1996; Slater, 1989; Snowdon and Hausberger, 1997). For the present purposes, the focus will be on studies that have linked the social learning of vocal signals to the influence of those signals on courtship and mating success and finally to the transmission of those signals across generations. In particular, work by the Paynes and colleagues on Indigo buntings, *Passerina cyanea*, and by the Grants and colleagues on Darwin's finches, *Geospiza* species, will be discussed, as it offers some of the most long-term and detailed systems of study (and has taken place with wild populations, an added strength). Evidence for culture-like patterns and processes in vocal signals has also been obtained in Black-capped chickadees, *Poecile atricapillus* (Ficken and Popp, 1995), Brown-headed cowbirds, *Molothrus ater* (West et al., 1981, 1983), Chaffinches, *Fringilla coelebs* (Ince et al., 1980; Lynch et al., 1989), European starlings, *Sturnus vulgaris* (Adret-Hausberger, 1986), House finches, *Carpodacus mexicanus* (Mundinger, 1980), Saddlebacks, *Philesturnus carunculatus* (Jenkins, 1977), Stripe-back wrens, *Campylorhynchus nuchalis* (Price, 1998), Village indigobirds, *Vidua chalybeata* (Payne, 1985), different populations and subspecies of White-crowned sparrows, *Zonotrichia leucophrys* (Petrinovich, 1988; Chilton

and Lein, 1996; Bell et al., 1998; Harbison et al., 1999), Wood thrushes, *Hylocichla mustelina* (Whitney, 1992), and Yellow-rumped caciques, *Cacicus cela* (Trainer, 1989).

The Paynes and colleagues have been studying populations of Indigo buntings for over 20 years; they have recorded the vocal repertoires of males and determined their mating success across years. Song traditions are known to have changed over time, although on average a song variant ‘survives’ about three time longer than an individual male bunting, and some variants persisted virtually unchanged for over a decade (Payne et al., 1981). Adult male buntings arriving to the breeding grounds earliest tend to have song variants that are copied the most by younger males (Payne and Payne, 1993). These song variants are stable over a number of generations and social learning processes appear to play the major role in the maintenance of those variants (Payne and Payne, 1993; Payne, 1996; Payne and Payne, 1997). In captive studies, young male buntings will copy more elements of an older male’s song if they can interact with that male than if they cannot (Payne, 1981). Finally, the song variants that male buntings use during the breeding season can influence their mating success (Payne, 1982), although song variants alone do not seem sufficient to explain female courtship decisions and patterns of mating (Payne et al., 1988; Payne and Payne, 1993; see also Baker and Baker, 1988).

Studies with species of Darwin’s finches have found that songs of males most closely resemble those of their fathers and paternal grandfathers, suggesting that song variants represent fairly stable behaviours that are paternally socially transmitted (Grant and Grant, 1996). The particular song variants of males influence female mating decisions (Grant and Grant, 1996). Interestingly, in Darwin’s medium ground finch, *Geospiza fortis*, males with the least common song types survive longer and have higher lifetime reproductive success than males with more common song variants (Gibbs, 1990). This may result from a possible need for dissimilarity in songs of neighboring males for efficient individual recognition in high breeding densities. Furthermore, females avoid mating with males that sing heterospecific songs,

but lack a preference (or develop an ‘anti-preference’) for males with song types that resemble those of their fathers (Millington and Price, 1985; Grant and Grant, 1989, 1997; Gibbs, 1990).

There is thus considerable empirical evidence that vocal signals in some avian species represent communicative cultures. They tend to be extremely stable once acquired within an individual and fairly stable across generations in the population, they can be socially learned and transmitted, and some of the mechanisms of learning have been determined. Theoretical work on the evolution of vocal traditions has indicated that the maintenance of vocal traditions (dialects) in large areas, whose boundaries are fairly sharply delineated from other vocal tradition boundaries, requires extremely low error rates in song learning and very low rates of mortality (Goodfellow and Slater, 1986). Williams and Slater (1990) showed with computer simulations that the size of the vocal repertoire of a given species or population, as well as the number of neighbors surrounding an individual, will affect the extent to which dialect areas can form. Aoki (1989) modeled the evolution of learned song and found that it was facilitated by very strong female preferences for learned, conspecific songs and a low error rate in song learning from fathers to sons. The results of this model suggest that social learning of vocalizations should be rare or non-existent in highly polygynous, lekking species, because fathers in these species do not provide sufficient interaction with sons. Contradicting this prediction, numerous studies have shown social learning of vocal signals in Brown-headed cowbirds, *Molothrus ater*, a brood parasitic species whose males have no contact at all with their offspring (see West and King, 1988, 1996; O’Loghlen and Rothstein, 1993; King et al., 1996).

Many of the empirical studies cited above have linked vocal signals to reproductive outcomes, directly or indirectly. This linking is absolutely necessary to speak of vocal signals as being components of a courtship system that is culturally transmitted. Simply documenting vocal signals in wild populations and how those remain stable or change over generational time does not necessarily mean that one has documented the major

components of a courtship system. In other words, while a socially learned courtship system represents a communicative culture, the reverse is not necessarily true; other aspects of a communicative culture might be alarm, food, or contact calling in social organization. Finally, as argued recently by Nelson (1997), more attention needs to be paid to determining the specific social and ecological contexts that influence vocal development (as in Nordby et al., 1999).

4. Social influences on mating preferences and courtship patterns.

While the discussion in the previous section was on the influence of social learning on vocal signals in avian courtship, this section focuses on social learning of courtship preferences. These preferences can be based upon morphological or behavioural variants of individuals of the opposite sex. For decades, research on sexual imprinting has tested the development of preferences for morphological traits; more recently, work focusing on social learning and preferences for behavioural traits has begun. Imprinting, traditionally defined, refers to learning that is largely irreversible and generally limited to a specific time window during development, the sensitive period (Immelmann, 1972; Hess, 1973). Imprinting is a generalized phenomenon: when an individual is reared with parents of phenotype X, it imprints on the general characteristics of X and not solely on the individuals with which it was raised. Imprinting is an adaptive strategy in that it allows the formation of stable responses to biologically relevant objects.

Sexual imprinting occurs when an individual directs courtship and mating behaviours preferentially to members of a species, population, or group that exhibit traits characteristic of the parental individuals with which it was raised (for reviews see Ten Cate, 1984, 1989; Kruijt, 1985; Bischof, 1994; Ten Cate and Vos, 1999). Sexual imprinting based upon the major histocompatibility complex in house mice, *Mus musculus* (Eklund, 1997; Penn and Potts, 1998), and upon facial features in domesticated sheep and goats

(Kendrick et al., 1998) has been demonstrated experimentally. Typically, however, studies of sexual imprinting have been carried out with avian species. Eggs or very young nestlings are placed into nests of foster parents, often of a closely related species. When the young that have been cross-fostered reach reproductive maturity, their preferences for members of their genetic type relative to their cross-fostered type are measured. Young individuals cross-fostered with adults of different phenotypes later show a sexual preference for individuals with the morphological features of their foster parents in Japanese quail, *Coturnix coturnix japonica* (Gallagher, 1976), mallards, *Anas platyrhynchos* (Klint, 1975; Kruijt et al., 1982), pigeons, *Columba livia*, and Collared doves, *Streptopelia decaocto* (Warriner et al., 1963; Ten Cate et al., 1992), and Zebra finches, *Taenopygia guttata* (Ten Cate, 1984, 1989; Kruijt and Meeuwissen, 1991; Vos, 1994; Weisman et al., 1994). These preferences typically are maintained in an individual for years, often persisting even after breeding season exposure to individuals of the same phenotype as the imprinted individual (but see Kruijt and Meeuwissen, 1991).

The studies reviewed above have tested sexual imprinting based upon morphological characters of the parents. Young individuals are raised either in social environments that contain adults of one set of morphological traits or in social environments that contain adults with a different set of morphological traits, and the preferences in those young for mates with those morphological features are later tested. Far fewer studies have tested the influence of social environments on sexual preferences when the differences in those social environments are behavioural. Increased efforts towards this line of research would be particularly informative to the question of communicative culture. The research could relatively easily combine analyses of social learning influences on the development of signal and response behaviours related to courtship, and of the preferences for those behaviours, in the same individuals.

Some of the most direct evidence for communicative cultures influencing courtship patterns and mating preferences comes from Brown-headed cowbirds, *Molothrus ater*. The vocal sig-

nals of males show populational differences, and the development of those signals is influenced by social learning (Rothstein et al., 1986; King and West, 1988; West and King, 1988, 1996; O’Loghlen and Rothstein, 1993; West et al., 1998). Female cowbirds prefer the songs from males of their own populations relative to songs from males of different populations (King and West, 1988; West et al., 1998). Furthermore, aviary tests have found that cowbirds exhibit positive assortative pairing and mating by population. When given a choice between mates from the same population and mates from a different population in a multiple-choice setting, cowbirds preferentially pair and mate with members of their own population (Eastzer et al., 1985). These mating patterns and preferences can be influenced by the communicative culture in which young individuals develop: sets of young birds exposed to behaviourally distinct populations of adults later show positive assortative mating based on their social environmental background (Freeberg, 1996). The courtship patterns that result from experiences with different social learning backgrounds can be transmitted to further sets of young birds even in the absence of the original adult social models of those behaviourally distinct populations (Freeberg, 1998). Finally, female mating preferences for males of different social backgrounds can be socially learned and transmitted (Freeberg, 1998; Freeberg et al., 1999; for suggestive evidence from wild populations see also O’Loghlen and Rothstein, 1995). To summarize, social learning and transmission appear to pervade the courtship system of cowbirds, from vocal development in males to mating preferences in females to courtship patterns in populations.

Evidence of social learning influencing mating preferences has been found in other species. Clayton (1990) documented an interplay between male morphological and vocal traits and females’ preferences in Zebra finches, *Taeniopygia guttata*, and found that while social experience had little influence on male vocal development, it had a strong influence on females’ preferences for male vocalizations (see also Miller, 1979). Preferences for male song can be influenced by acoustic experience in young female canaries, *Serinus canaria*,

and experience with adult males can influence song preferences in adult females (Nagle and Kreutzer, 1997a,b). On the other hand, Chilton et al. (1990) found little evidence of experiential influence on female mating preferences in White-crowned sparrows, *Zonotrichia leucophrys*.

The studies described above indicate that mating preferences of some species can be influenced by social transmission. This evidence means that our theories of mate choice and sexual selection, which traditionally have assumed innate female preferences, will need to take into account social learning for the taxa that exhibit it (see also Dugatkin, 1996a; Owens et al., 1999; Ten Cate and Vos, 1999). Early models of social learning in courtship and mating preferences found that when mating preferences are very strongly determined by social background, this can lead to rapid population divergence and isolation (Kalmus and Maynard Smith, 1966; Seiger, 1967). Recent models predict that sexual selection can affect how social learning influences mating preferences (Todd and Miller, 1993). Sexual selection itself can be evolutionarily impacted by social learning processes in systems of courtship behaviour (Ten Cate and Bateson, 1988; Laland 1994a,b; Owens et al., 1999). Laland (1994a) showed that when female preferences are influenced strongly by social tradition, the possibility of adaptive male traits spreading is greatly reduced (because of positive frequency dependence; see also Kirkpatrick and Dugatkin, 1994). Further, unlike the earlier studies cited, social learning in mate choice will have little ability to lead to reproductive isolation between groups if there is any regular migration between those groups (Laland, 1994a).

As with the case in studies of song learning, research on the social learning of courtship preferences has only rarely determined the specific behavioural interactions between young and older individuals that influence sexual preferences in those young animals (see also Kruijt, 1985). Experimental work has begun to address this paucity of data, however. Bischof and Clayton (1991) found that in young zebra finch males cross-fostered to Bengalese finch parents, *Lonchura striata*, nestlings that begged for food and were fed more by the foster parents were more strongly im-

printed to Bengalese finches in later tests (frequency of interactions affecting sexual imprinting was also shown by Ten Cate, 1984). Finally, more work testing the influences of siblings and individuals of the same age class on learning in young animals, and the extent to which sexual interactions during adulthood can influence sexual preferences, would prove informative to understanding the establishment and stability of preferences over time (Ten Cate, 1984; Domjan, 1992).

A great deal of recent work has been devoted to the study of mate choice copying, where an individual's (usually, female's) mating preference is immediately modifiable by its observing the mating or mating preference of another individual. Dugatkin (1996a) (p. 87; see also Pruett-Jones, 1992) has defined mate choice copying in a female as occurring when, "the conditional probability of choice of a given male by a female is greater than the absolute probability of choice depending upon whether that male mated previously. Further, the information about a male's mating history (or some part of it) must be obtained by the female via observation." Mate choice copying therefore would occur when a female observes another female courting and/or mating with a male, and her preference to court and mate with that male increases as a result of that observation (note that males can also exhibit mate choice copying). Female mate choice copying increases the variance in male mating success, increasing the opportunity for sexual selection to act (Wade and Pruett-Jones, 1990; Gibson and Höglund, 1992). Female mate choice copying results in an advantage to the most common male types; this makes it more difficult for a novel trait, even if adaptive, to spread in a population (Kirkpatrick and Dugatkin, 1994).

Mate choice copying has been demonstrated in fish and birds (Dugatkin, 1996a; Galef and White, 1998; White and Galef, 1999). These studies indicate that young animals can learn elements of their courtship systems by observing more experienced conspecifics, and have documented some of the necessary and sufficient conditions for this learning to occur. However, the research thus far lends only indirect support for how behaviours in

an individual animal or within an animal population might be maintained. Furthermore, studies have yet to show that preferences established through mate choice copying might be transmitted over generations, an essential characteristic of cultural transmission. As pointed out by Brooks (1998), for mate choice copying to exhibit characteristics of a communicative culture, once a female's preference was shifted by observing another female court a male with a certain suite of behavioural or morphological phenotypes, that shift in preference should remain and should be generalizable to other males possessing similar phenotypes. Indeed, this latter point is assumed by models (e.g. Kirkpatrick and Dugatkin, 1994), but has only recently been experimentally demonstrated (White and Galef, 2000). Future work on mate choice copying as a process of cultural inheritance would need to focus more on behaviours and preferences that last, once established, in an individual and that are transmitted across generations (Brooks, 1996, 1998). The use of populational differences within the same species in behavioural or morphological phenotypes could greatly facilitate this approach.

The work described in these last two sections indicates that social learning can influence the courting and mating behaviours and preferences that an individual develops, and because it affects reproductive outcomes, it can influence the evolution (both genetic and phenotypic) of populations in which it occurs. Communicative cultures related to courtship and mating will influence the evolution and maintenance of variation in systems of courtship behaviour among different conspecific populations. Further, the social transmission of courtship variants necessarily means that the range of species-typical behaviours available for learning by a young individual is limited to the behaviours present in that individual's population. Culture represents a system of generally adaptive behaviours, but also a system to which individuals must adapt (Maynard Smith and Warren, 1982). Thus, the behaviours and preferences of courtship systems can be developmentally constrained by the communicative culture; this would represent a cultural constraint on the development and evolution of courtship behaviours and preferences.

5. Conclusions and future directions

In species in which social learning influences the development of courtship behaviours and preferences, understanding the social transmission of those traits is fundamental to an understanding of the evolutionary processes affecting those populations. Unlike strict genetic transmission, behaviours that are transmitted socially can spread very quickly through populations. The relatively rapid diffusion of social traditions, by affecting the social and potentially physical environment of populations, can alter selection pressures and subsequent evolution (for related discussions, see Cavalli-Sforza and Feldman, 1981; Lewontin, 1983; Boyd and Richerson, 1985; Bateson, 1988; Wcislo, 1989; Laland, 1992). Social transmission represents a mechanism for the inheritance of acquired characters; novel behavioural variants acquired by individuals can be transmitted to future generations. While cultural transmission is often viewed as freeing an individual somewhat from natural selection, it is important to stress that cultural transmission and cultural evolution are still Darwinian processes (Flinn and Alexander, 1982; Richerson and Boyd, 1992).

This paper has presented a definition of a communicative culture to provide a strategy for studying social learning and transmission in systems of courtship behaviour. This strategy is in the form of three criteria to demonstrate the presence of a communicative culture: (1) the behavioural system represents a populationally distinct tradition; (2) it is socially learned; and (3) it is transmitted across succeeding generations of young individuals. Two areas of study that have provided empirical evidence for the social learning of courtship behaviours and preferences were presented; the remainder of the paper suggests future avenues of research that could strengthen our understanding of the influence of communicative cultures on evolutionary dynamics of populations and on developmental processes in individuals.

First and foremost, more studies need to be carried out to test for communicative cultures in relation to systems of courtship behaviour. The bulk of the work done on this question, reviewed briefly above, has been carried out on several

species of passerine bird and, in the case of mate choice copying, a few species of fish. More studies with more vertebrate taxa are needed to determine the prevalence of culture-like processes in non-human animal courtship systems. Have the social learning processes that influence courtship patterns arisen independently in some avian species and perhaps some fish species, or do they possibly represent a phylogenetically older set of general learning rules, such as a 'conformist strategy' (e.g. Wilson, 1975; Mainardi, 1980; Papaj, 1994; Henrich and Boyd, 1998)? Is social learning of courtship systems more widespread than is indicated by the present data, or is it perhaps limited to a few taxa where social learning happens to be less costly developmentally than non-social learning? We can't answer these questions yet, as too few studies with too few species have been performed.

We also need to focus more on the mechanisms by which a young individual develops its courtship system. We need to determine aspects of the social environment that are particularly influential on development in young animals; a communicative culture specifies the behavioural variants of its members and is an historical link across generations, providing a developmental niche for learning (Schleidt, 1985; King and West, 1987; West and King, 1987; Alberts and Cramer, 1988; West et al., 1988, 1997). A young animal has 'to learn the right thing at the right time from the right role model' (Flinn, 1997, p. 34). While teaching may not be a characteristic of animal cultures, it seems likely that young animals actively go about learning their behaviours, and are not simply passive receivers of information. For example, young zebra finch males, *Taeniopygia guttata*, learn more song elements from adults with whom they maintain closest proximity (Mann and Slater, 1995). Further, in the context of how a communicative culture is acquired by a young individual, we need to document not just the communicative signals, but the signaling interactions between individuals (Snowdon, 1988; West and King, 1996).

Active assessment by a young animal of the communicative culture in which it develops likely carries energetic costs in terms of the acquisition

and storage of information. A young animal cannot know all of the features of its communicative culture. Therefore, future work should address the mechanisms by which young animals make decisions based upon incomplete information, and how they begin to learn about the patterns of behaviour in their social environment. This has been modeled for mate and food patch assessment (e.g. Mangel, 1990; Stephens, 1993; Luttbegg, 1996). Few empirical data exist on the strategies used by young animals in learning their courtship behaviours and preferences. For example, what are the mechanisms upon which the social learning of courtship behaviours and preferences is based? Should a young individual imitate successful individuals, avoid learning the behavioural variants of unsuccessful individuals, follow the majority by learning the most common variants, or learn variants based on other criteria such as genetic similarity? Depending upon the species, these four strategies (and there could be dozens more) could result in different patterns of cultural transmission. Theory assumes or predicts that the more an individual is exposed to a certain behaviour, the more likely it will adopt that behaviour (see Pepperberg, 1988; Findlay et al., 1989), or that young and naive individuals that simply engage in more social relations will have greater success and a greater effect on the social traditions of succeeding generations (Ruyle, 1973).

Related to the general issue of determining mechanisms of social learning, future work must also begin searching for developmental constraints on communicative cultures (Ten Cate and Vos, 1999). This effort would make explicit the interactions of genotypes, physical environments, and social environments during ontogeny. As with any phenotype, there will be constraints on what, when, and how an individual socially learns components of its courtship system (Marler et al., 1981; Arnold, 1992b; Oyama, 1993; Flinn, 1997). Determining these constraints would increase our knowledge of how communicative cultures might evolve. Informative to these efforts would be attempts to integrate studies of brain ontogeny into research on communicative cultures. Lumsden and Wilson (1981) discussed the brain as being the fundamental link between the genotype of an

individual and how an individual socially learned its behaviours (and subsequently, how selection might act on it), because the brain would control the 'epigenetic rules' for culture. Indeed, the interactions between environmental stimuli, brain development, and bird song learning have long proved fruitful areas of research (Arnold, 1992a; Brenowitz and Kroodsma, 1996; for neural studies of sexual imprinting see Bischof and Rollenhagen, 1999).

Courtship systems will be comprised of more than just communicative signals. They will also include morphological characters that themselves may not be influenced by social traditions (although the way in which they are used during signaling could well be affected by culture-like processes). Determining how socially learned, non-socially learned, and congenital behavioural and non-behavioural traits of a courtship system interact during development would increase our understanding of the evolution of those systems. Experimental studies on the relations between the process of mate choice copying and heritable variation in body colouration and preferences for that colouration in female mating decisions are advancing our knowledge in this regard (Dugatkin, 1996b, 1998).

Different genetic backgrounds in individuals may result in different communicative cultures. Genetic influences on mating preferences have been documented in numerous species (reviewed in Bakker, 1990). Research has also found populational differences in the extent to which individuals socially learn vocal signals. Sedentary and migratory populations of White-crowned sparrows, *Zonotrichia leucophrys*, and different populations of Brown-headed Cowbirds, *Molothrus ater*, learn their vocalizations at different rates (Nelson et al., 1995; King et al., 1996). Further testing for different learning patterns related to the migratory status of the population would be an important line of research, as the extent of migration may be fundamental to the divergence of communicative cultures in different populations (e.g. Laland, 1994a).

The mechanisms by which an individual acquires its courtship behaviours and preferences are important to know, but an equally important

issue for questions of cultural transmission is how those traits, once acquired by individuals, are maintained in populations (Durham, 1976; Mainardi, 1980; Heyes, 1993; Laland et al., 1993; Tomasello et al., 1993; Galef, 1995, 1996; Laland, 1996; Flinn, 1997). Central to this will be the influences on the communicative culture of the non-cultural environment, including the demographic makeup of the population as well as the physical environment itself (Flinn and Alexander, 1982). For example, Galef et al. (1990) found that preferences for certain food types in Norway rats, *Rattus norvegicus*, were influenced by the number of social models in the local population exhibiting those preferences. Lefebvre and Giraldeau (1994) have found that the number of tutors (social models) and the number of non-model 'bystanders' could influence an individual's ability to learn a novel feeding technique in pigeons, *Columba livia*. The relative numbers of social models and naive individuals in a population may influence the transmission of systems of courtship behaviour as well. Furthermore, the physical environment can influence the development of communicative signals. In striped ground crickets, *Allonemobius fasciatus*, male calls develop differently under different light and temperature regimes (Olvido and Mousseau, 1995). How the environment affects the physiological status of individuals can also influence how behavioural traditions might be maintained in populations. For example, in guppies, *Poecilia reticulata*, hunger level affects mate choice copying (Dugatkin and Godin, 1998) and predation risk affects mate choice strategies (Godin and Briggs, 1996).

Finally, because communicative signals are obviously fundamental to communicative cultures, understanding how selection processes act on those signals within a population is important. While a system of communicative behaviours as described here represents a functional system, it is also a system of signals, cues, and preferences that can be exploited by unintended receivers and signalers, such as predators, competitors for mates, and mates themselves (Otte, 1974; Wiley, 1983; Endler, 1992, 1993; Dawkins, 1993; Ryan and Rand, 1993). Determining how a communicat

culture is maintained and how it changes in the context of different selection pressures acting on the population represents a powerful integration of proximate and ultimate approaches. Moreover, these efforts are essential if we wish to understand the interactions between individual ontogeny, cultural processes, and population dynamics in the development and evolution of systems of courtship behaviour and mating patterns.

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