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## **Social learning and culture in animals**

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**Abstract:** Most animals must learn some of the behaviours in their repertoire, and some must learn most. Although learning is often thought of as an individual exercise, in nature much learning is social, i.e. under the influence of conspecifics. Social learners acquire novel information or skills faster and at lower cost, but risk learning false information or useless skills. Social learning can be divided into learning from social information and learning through social interaction. Different species have different mechanisms of learning from social information, ranging from selective attention to the environment due to the presence of others to copying of complete motor sequences. In vertical (or oblique) social learning, naïve individuals often learn skills or knowledge from parents (or other adults), whereas horizontal social learning is from peers, either immatures or adults, and more often concerns eavesdropping and public information use. Because vertical social learning is often adaptive, maturing individuals often have a preference for it over individual exploration. The more cognitively demanding social learning abilities probably evolved in this context, in lineages where offspring show long association with parents and niches are complex. Because horizontal learning can be maladaptive, especially when perishable information has become outdated, animals must decide when to deploy social learning. Social learning of novel skills can lead to distinct traditions or cultures when the innovations are sufficiently rare and effectively transmitted socially. Animal cultures may be common but to date taxonomic coverage is insufficient to know how common. Cultural evolution is potentially powerful, but largely confined to humans, for reasons currently unknown. A general theory of culture is therefore badly needed.

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## Chapter 20

# Social learning and culture in animals

Carel P. van Schaik

### ABSTRACT

Most animals must learn some of the behaviours in their repertoire, and some must learn most. Although learning is often thought of as an individual exercise, in nature much learning is social, i.e. under the influence of conspecifics. Social learners acquire novel information or skills faster and at lower cost, but risk learning false information or useless skills. Social learning can be divided into learning from social information and learning through social interaction. Different species have different mechanisms of learning from social information, ranging from selective attention to the environment due to the presence of others to copying of complete motor sequences. In vertical (or oblique) social learning, naïve individuals often learn skills or knowledge from parents (or other adults), whereas horizontal social learning is from peers, either immatures or adults, and more often concerns eavesdropping and public information use. Because vertical social learning is often adaptive, maturing individuals often have a preference for it over individual exploration. The more cognitively demanding social learning abilities probably evolved in this context, in lineages where offspring show long association with parents and niches are complex. Because horizontal learning can be maladaptive, especially when perishable information has become outdated, animals must decide when to deploy social learning. Social learning of novel skills can lead to distinct traditions or cultures when the innovations are sufficiently rare and effectively transmitted socially. Animal cultures may be common but to date taxonomic coverage is insufficient to know how common. Cultural evolution is potentially powerful, but largely confined to humans, for reasons currently unknown. A general theory of culture is therefore badly needed.

## 20.1 Introduction

The traditional null model of behavioural ontogeny is that animals acquire their species-specific behavioural repertoires through maturation of genetically anchored developmental programs (instincts), supplemented by individual exploration of environmental affordances (individual learning). The main reason for this position, however, may turn out to be an historical accident: Comparative psychology developed as an experimental, laboratory-based, rather than a field-based naturalistic science. In the wild, opportunities for social learning arise whenever animals interact or even are in mere proximity.

Learning is a change in the brain produced by experience. We usually call this change knowledge or skill, and infer that it occurred by noting a change in behaviour. Social learning is learning under the influence of conspecifics. More formally, social learning, or socially mediated learning, can be defined as changes in an individual's behaviour resulting from attending to another individual's behaviour or its products (Box 1984, Fragasz and Perry 2003). Social learning is different from communication. Both involve responding to conspecifics (see Schaefer, this volume), but communication usually does not involve learning. However, there is some overlap, as in learning through social interaction (see below).

Through social learning, animals can acquire information or skills they would otherwise not have obtained, or acquire routine skills faster. It is therefore not surprising that social learning is the default mode of learning by naïve individuals in those animal species where overlapping generations and long parent-offspring association enable this. But, as we will see, that does not necessarily mean that traditions and cultures are widespread, nor that animals will always rely on cues from conspecifics, even if they are available.

I first examine social learning by asking a number of proximate questions about how (mechanisms), what (content), when (at what age and from whom) and where (contexts). I then turn to ultimate questions, such as its adaptive significance and the factors favouring the evolution of the more advanced sorts of social learning. But we can also ask an additional set of questions, concerning the consequences of social learning at the level of populations and species. An immediate consequence can be culture, whereas in the long run social-learning skills can co-evolve with tendencies to explore and innovate, and thus intelligence.

Throughout, the reader must keep in mind that social learning is studied in very different research traditions that have developed largely independently from each other. Behavioural ecologists have generally focused on

adults gathering ecologically relevant information (horizontal transmission), whereas psychologists (and primatologists and anthropologists) have generally focussed on the mechanisms of immatures acquiring skills (vertical transmission). These traditions complement each other, and I will therefore try to integrate their approaches.

## 20.2 Proximate aspects of social learning

### 20.2.1 How: mechanisms of social learning

Social learning is quite heterogeneous in terms of mechanisms. *Learning by attending to social information* has received most attention. It may be used for the acquisition of social skills through eavesdropping (i.e. observing social interactions between others: e.g. Valone 2007), but it is most studied in the context of acquiring subsistence skills. It encompasses a variety of poorly understood processes, and the technical literature is complicated and confusing. The interested reader is referred to Byrne (2002), Whiten et al. (2004), Subiaul (2007) and Hoppitt and Laland (2008).

For the present purpose, I divide learning by attending to social information into a few major categories (Table 20.1). In the simplest category are social or response facilitation (non-specific increases in activity as a result of the proximity or activity of conspecifics) and selective association (following role models around), the latter perhaps simply as a consequence of gregariousness. These forms of social learning share the property that the presence of others biases the exploratory tendency of the naïve individuals. Yet, this mechanism may be sufficient for young animals to acquire the same diet as their mothers, simply by following her around and thus selectively encountering, and learning about, whatever she eats (van der Post and Hogeweg 2006).

The next major category includes cases where naïve animals use the presence or behaviour of other animals as pointers to a specific site or object upon which to focus their own independent exploration and learning (enhancement). This may help naïve animals to develop preferences or skills by exposing them to the affordances of objects and foods. Enhancement is closely related to social information use (Valone 2007), where animals base decisions to forage or move or their choice of mates on observation of the presence and activity of conspecifics. Such information use becomes enhancement when the animals doing this learn something new in the process.

Indirect forms of enhancement may also be found. Thus, naïve animals may increase exploration upon encountering the feeding sign of con-

specifics. For instance, aye-ayes (*Daubentonia madagascariensis*) engage in tap foraging, in which they tap on branches with a specialized long-nailed finger and listen for cavities. Upon discovery of a cavity, they gnaw a hole and fish out larvae. Young aye-ayes are attracted to the holes made by other aye-ayes, and explore them selectively (Krakauer 2005).

In all these cases, the presence or actions of conspecifics lead naïve animals to learn about the environment, but the latter do not necessarily pay attention to the models' actions. In the following two major categories, they do (Subiaul 2007). In simple observational learning, species-typical actions are copied. For instance, in mate copying, seen in fishes and birds, females copy the mate choice of other females observed to mate with particular (types of) males (Witte 2006). Another form is so-called observational conditioning, in which learners copy the striking responses of models that accompany alarm calls, and learn to associate them with the releasing stimuli (e.g. predator sightings). Many primates learn the proper use of alarm calls this way (Seyfarth and Cheney 1980). Note that in observational conditioning, the naïve animals are socially fine-tuning what are basically instinctive actions, using the reactions of experienced conspecifics to classify or label other animals or objects. The copying of known motor patterns as seen in many birds and some primates (Zentall 2004, Subiaul 2007) is often referred to as contextual or familiar imitation. This is not a trivial ability because it somehow requires a translation from perception into action, and probably relies on dedicated neural mechanisms, such as the presence of mirror neurons, i.e. neurons that fire both when an action is performed and when the same action is observed in others (Rizzolatti 2005).

The final major category of social learning is observation learning through production imitation (also: motor or novel imitation), which refers to the copying of novel actions or action sequences (emulation, the copying of the goals of the model's actions, is probably very similar). This ability is remarkably common among birds (Zentall 2004), but among primates motor imitation has so far only been found in apes while monkeys are capable of contextual imitation at best (Whiten and van Schaik 2007). Subiaul (2007) speculates that this is because production imitation requires neural adaptations that mediate the planning and coordination of gross and fine motor patterns.

As to the cognitive abilities required, there is broad consensus that observational learning is cognitively more demanding than non-observational social learning, and that production imitation is more demanding than context imitation. For instance, human infants develop the ability to copy known motor actions before they can copy novel actions or action sequences (Masur 1988). Moreover, among primates, there are taxonomic

neurobiological differences that support the presence of production imitation in humans but not in monkeys (reviewed in Subiaul 2007). Finally, at least among mammals, the taxonomic distribution of this ability may turn out to be correlated with the presence of mirror-self-recognition, cognitive empathy, and elements of a theory of mind (de Waal 2001, Heyes 2001). However, because documenting the actual abilities involved in social learning requires careful experiments, we know very little about the taxonomic distribution and the link with other cognitive abilities or even brain size.

In addition to learning from social information, Table 20.1 recognises a second major kind of social learning: *learning through social interaction*. This form of social learning overlaps extensively with communication, but differs in that it also involves conditioning (learning) as a result of the individual's social interactions: agonistic and affiliative behaviour, as well as social play (e.g. Pellegrini et al. 2007). Learning through social interactions (or socialisation: Box 1984) is probably the major means by which immature animals acquire social skills, as suggested by social deprivation, which produces socially incompetent adults (Harlow and Harlow 1962) and by interspecific cross-fostering, which shows adjustment to reigning social norms (de Waal and Johanowicz 1993).

Learning through social interaction normally plays no role in the learning of subsistence skills or ecological knowledge, but *teaching*, which does, also belongs in this category. In teaching, the model takes an active role. A behaviour pattern qualifies as teaching if certain actions only occur in the presence of a naïve observer, carry some cost but are not immediately beneficial to the teacher, and if the observer profits from these actions in that it learns these actions faster than it would otherwise do (Caro and Hauser 1992). This does not require that the teacher is aware of the knowledge state of the naïve animal, i.e. that the teaching is intentional, although that would make it more effective. It should therefore be expected in many species, but although it has over the past few years been found in various species, far more striking is its absence in most. The species in which it is present are largely characterised by one or both of the following two conditions: (i) the presence of complex diets, where naïve individuals need help to familiarise themselves with the affordances of their food, usually fast-moving prey or embedded food items that must be extracted; and (ii) the presence of altruistic tendencies on the part of the teacher, be it through high relatedness or prosocial attitudes or both, as in cooperative breeders (Hoppitt et al. 2008, Burkart and van Schaik 2009; Burkart et al. in press).

### 20.2.2 What: the content of social learning

Dawkins (1976) coined the term ‘meme’ for the fundamental unit of socially transmitted information, and although it has led to some theorising, it has not caught on among those studying social learning (Aunger 2007). One reason is the association with selfish genes, which has led to a theoretical focus on parasitic behavioural innovations to the exclusion of the numerous useful ones (see below). Another reason is the strongly anthropomorphic focus, which meant that meme transmission was equated with production imitation, thus ignoring the variability of socially transmitted behaviours found among animals. I will therefore refer to ‘informational variant’ for the general case and use more detailed words where possible.

Here, I propose the following classification of informational variants that can be acquired, with or without modification, through social learning: perishable information, non-perishable information (or labels), skills and knowledge, signal variants, and symbols (after van Schaik et al. 2003). Perishable information refers to the kind of information that is often easily gleaned by associating with another individual, or even observing this individual from afar, summarised as ‘knowing where’. Non-perishable information or labels, on the other hand, is about ‘knowing that’ (also: declarative knowledge). Thus, knowing that a particular kind of red berry is edible is a label, whereas knowing that this week there is a good patch of them at a particular location is perishable information. Similarly, knowing that a particular animal is a predator is a label, but knowing where it roamed yesterday and where it might be today, is perishable information. A skill refers to ‘knowing how,’ e.g. about how to access food, or how to swing to another tree (also: procedural knowledge). Some informational variants may be harder to classify. Thus, remembering that these red berries tend to be available at a particular location at this time of year is either knowledge or skill, though certainly not perishable information.

The final two categories refer to social communication. A signal variant is an alternative way to signal the same particular message. For instance, vocal dialects contain signal variants, because one assumes that the content of the message conveyed is not affected by the change in acoustical features. Other cases concern the non-vocal domain. Thus, orang-utans (*Pongo abelii* and *P. pygmaeus*) produce kiss-squeaks when in distress, and have created geographic variants. In some regions, orang-utans place these kisses on (bundles of) leaves. The meaning is the same, albeit perhaps more pronounced (Hardus et al. 2009). A symbol is a communicative variant that is arbitrary, its meaning having become a local or regional convention, rather than species-wide, as in signals. Thus, orang-utan mothers, in some localities but not others, make acoustically distinct sounds to

call in their infants, but the actual sounds vary among populations (A. Lameira et al. unpubl. data).

Different social-learning mechanisms may be minimally needed to acquire these different classes of variants, with skills almost certainly requiring observational learning. It is not clear how the communicative variants are learned socially, although vocal learning in birds is known to involve dedicated neural circuits (Prather et al. 2008). All information variants beyond perishable information are thought to arise through innovation, either of the inadvertent, accidental kind or by cognitively more demanding processes such as insight. Little is known, however, of the processes that produce innovation.

### **20.2.3 From whom: deployment strategies and transmission biases**

If an animal is learning socially, whom should it pick as a model (Laland 2004)? A crucial distinction here is between (i) vertical or oblique social learning, by immatures from parents (vertical) or other adults (oblique), and (ii) horizontal social learning, which is among peers, and usually studied among adults.

Consider vertical social learning first. A simple prediction is that young animals have more to learn from others than adults, and that the motivation for social learning should therefore decline with age. This is well known, but rarely documented in a way one can compare across species, although interesting taxonomic variation is expected. For instance, in species with extensive cultural repertoires, such as great apes, adults may continue to be interested in, and capable of, social learning (e.g. Whiten et al. 2005), although this is not always the case (see 20.3.3).

A second straightforward prediction is that naïve animals should always be selectively attending in situations where novel skills or information can be acquired. In many species, young behave like apprentices: following their mother or other caretakers around with intense curiosity, and paying special attention when difficult skills are being demonstrated (Fig. 20.1). Foraging skills are often learned because infants scrounge partly processed foods from the mother (Terkel 1996, Jaeggi et al. 2008, Rapaport and Brown 2008), or selectively focus on her activities when she targets foods that are rare or difficult to process (Tarnaud and Yamagiwa 2008, Jaeggi et al. 2010). As a result, long-term studies of the development of maturing individuals show that they tend to acquire the variants used by those with whom they associated the most (Perry and Ordoñez 2006; but see Matthews 2009; see also BOX 20.1).



Other decisions are also relevant. If there is a choice among models, which of those should a naïve animal attend to? One generally expects there to be some transmission bias. The most obvious solution is to focus attention on those individuals that show the best mastery and allow being observed, which is what naïve chimpanzees and capuchin monkeys do in the case of nut cracking (Matsuzawa et al. 2001, Biro et al. 2003; Ottoni et al. 2005) – a tendency known as model-based or prestige bias (Richerson and Boyd 2005). This tendency is also captured in de Waal's (2001) BIOL rule: bonding- and identification-based observational learning. However, this rule additionally postulates a 'desire to be like others' on the part of the naïve immature, i.e. social conformity. This addition may be most pertinent for signal variants and symbols, because they do not differ in content.

It is also possible that the naïve individual is exposed to multiple distinct variants. The null hypothesis then is that an animal simply adopts whatever behaviour is demonstrated most commonly, or is demonstrated by the largest number of models. If the learner can evaluate the value of each variant, she may simply adopt the one or ones she finds satisfactory (known as content bias; cf. Galef 1995). This is evident for labels, involving food choice or predator recognition, but may also be relevant where learners carefully evaluate a new feeding skill. However, suboptimal choices may also ensue. First, animals may be conservative, i.e. have a tendency to stick to the technique they know well, even if other, more efficient techniques are shown to them by others in the group (Biro et al. 2003; Hrubesch et al. 2009). Second, they may display a disproportionate tendency to follow the majority in their choice (positive frequency dependence), i.e. conformity (Efferson et al. 2008). A common cause of conformity is obligate gregariousness, which forces all animals to make the same choices when exploring alternatives require leaving the group (Day et al. 2001). Active conformity is common among humans, partly because it is the optimal decision when information about the variants is poor (informational conformity), and partly because it is a sign of group membership or may be a socially imposed norm (normative conformity: Henrich and McElreath 2007).

Social learning can also be horizontal. In this context, it is possible that new skills or important knowledge are gained (Page and Ryan 2006), but much horizontal transfer also concerns perishable information about the current state of the environment or of conspecifics. Behavioural ecologists often distinguish between public information use and eavesdropping. In the use of public information (also: inadvertent social information), individuals learn about the current state of the local environment by attending to the behavioural decisions or the success rates of others. The information

is gained from inadvertent cues, not signals (see Schaefer, this volume). Examples include foraging animals using the behaviour of others to determine whether a particular food patch is worth visiting or where to settle for breeding (Valone 2007).

Eavesdropping is a form of social learning about the quality of other individuals by attending to their social interactions, e.g. fights, usually focusing on the signals being exchanged. It is social learning because the eavesdropper often subsequently modifies its behaviour, but what is learned is usually perishable information, e.g. the fighting ability of a particular individual or the attractivity of that individual as a mate. Eavesdropping has been demonstrated through elegant experiments (Dabelsteen 2005). It is surprisingly common among birds, and may also be widespread among mammals (Valone 2007). One well-studied example is 'mate choice copying,' where females show a preference for mating with a male that they had just seen successfully mate with another female over other, otherwise similar males (Witte 2006). This makes sense when other information to choose between potential mates is absent; indeed, copying is more common when the males are evenly matched or when females are naïve (Valone 2007).

There is an interesting contrast in the emphases of different research traditions (Bonnie and Earley 2007). Psychologists (and with them primatologists) are generally interested in vertical and oblique social learning, often with a strong focus on mechanisms, and thus also in cultural phenomena in the wild. Many anthropologists have similar interests, although they take the presence of complex social-learning mechanisms for granted, and instead concentrate on context and content biases in the deployment of these social-learning abilities. Behavioural ecologists, in contrast, are rarely interested in mechanisms, and often focus on horizontal social learning of perishable information in field conditions. As a result, they tend to focus on eavesdropping and public information use, rather than culture (Table 20.2).

These different traditions have led to some important gaps in our knowledge. Most importantly, psychologists and primatologists rarely study horizontal transmission, especially not in the wild, whereas behavioural ecologists tend not to know which mechanisms their subjects are using, even when they must often go beyond enhancement (cf. Galef and Giraldeau 2001).

## 20.3 Social learning as an adaptation

### 20.3.1 When is social learning adaptive?

The previous section leaves little doubt that social learning is generally adaptive and that the various social learning mechanisms evolved through natural selection. However, that does not mean that social learning is always the optimum way of acquiring information. Here, I explore in more detail under what conditions the ability to learn socially is adaptive. In general, social learning confers adaptive significance if

$$B_{SL} - C_{SL} > B_{IL} - C_{IL},$$

where B refers to a fitness benefit, C to a fitness cost and the subscripts SL and IL stand for social and individual learning, respectively.

The main reason why social learning is generally adaptive is obvious:  $C_{SL} \ll C_{IL}$ . Social learning frees up individuals from having to decide which environmental stimuli to attend to, thus fundamentally improving the signal-to-noise ratio of environmental inputs for an individual. Moreover, individual learning involves costs (Mery and Kawecki 2004), as well as risks, especially if it involves exploration (Mettke-Hofmann et al. 2006). Social learning thus reduces such costs and risks, while speeding up the acquisition of skills or knowledge, making it an adaptive strategy under a wide range of conditions.

This analysis assumes that the models are indifferent. However, from the demonstrator's perspective, there may also be costs or benefits to being copied. Consider horizontal transmission first. Assume that the possession of the information or the skill provides a clear fitness benefit. Then, if there is negative density dependence in the population, models would lose fitness if they are being copied (i.e. provide public information). Thus, one might expect animals to actively reduce the risk of being copied by making activities inconspicuous to others or even driving others away, unless they benefit from attracting others into their proximity or are surrounded by relatives, or there is group augmentation (Kokko et al. 2001). Similarly, some animals may incur a cost from having their signals intercepted by eavesdroppers. For instance, courtship activities in birds often attract male neighbours, who then interfere with mating (Dabelsteen 2005, Valone 2007). As a result, we expect some signals, e.g. courtship vocalisations, to be highly directed, which they indeed are in red-winged blackbirds (*Agelaius phoeniceus*: Patricelli et al. 2007). Vertical transmission of skills or knowledge, on the other hand, generally involves a stake in the learner's welfare through kinship or group augmentation, making it in the demonstrator's interest to ensure that the information or skill is passed on. Unfor-

tunately, very few studies have specifically tested these straightforward predictions.

### 20.3.2 Vertical social learning

Returning to the learner's perspective, we can ask when skills or information acquired through social learning are adaptive separately for vertical and horizontal social learning. Vertical social learning is most likely to be adaptive because immatures are naïve and must acquire many of their skills through learning. Indeed, maturing individuals in many species may prefer to learn socially. First, such a preference is also suggested by examples of the avoidance of novel foods by immatures until a parent has eaten it (meerkats: Thornton 2008; aye-ayes: Krakauer 2005; callitrichids: Rapa-port and Brown 2008; chimpanzees: Ueno and Matsuzawa 2005), as well as by the very low rates of independent food exploration among immature wild orangutans (Jaeggi et al. 2010). Second, it is strongly suggested by cross-fostering experiments. Such experiments are most feasible in birds, where eggs can be exchanged between nests of different species. Growing up with another species had a dramatic impact on the overall behaviour of the transplanted individuals in cockatoos or titmice (Rowley and Chapman 1986, Slagsvold and Wiebe 2006). These findings support the assumption that especially the young and naïve actually show a preference for social learning over individual exploration. Overall, these findings suggest that our null model of individual learning, with social learning added occasionally, is probably utterly wrong for all species in which vertical learning of skills is important. It is certainly wrong for humans (Meltzoff et al. 2009).

Nonetheless, even vertical social learning may sometimes be maladaptive to the learner (i.e.  $B_{SL} \ll B_{IL}$ ) in some conditions. In humans, young children rely extensively on social learning, cobbling pretty much their whole repertoire together through copying. The adoption of dangerous pastimes, such as rock climbing, or costly customs, such as low fertility, shows that the unquestioning copying of behaviour patterns shown by prestigious role models or the whole community need not be adaptive (Richerson and Boyd 2005). Why are human youngsters so uncritical? The most plausible explanation is that our socially learned skills are so numerous and so complicated that the best strategy for a youngster is to simply copy without much individual evaluation. On average, this tendency is clearly adaptive, although maladaptive habits may also arise (Richerson and Boyd 2005). This argument is supported by comparisons between chimpanzees and children: human children tend to imitate irrelevant details

of a demonstrated task whereas chimpanzees do not (Horner and Whiten 2005), a phenomenon known as over-imitation (Lyons et al. 2007).

### **20.3.3 Horizontal social learning**

Let us now turn to horizontal learning. Here, the asymmetry in knowledge and skills is less obvious than between caretaker and young, and it is more likely that socially acquired information may be misleading, especially when it is perishable. This point is intuitively obvious: because the location of food or the identity of the optimal mate vary over time, simply copying the choices of others will not necessarily produce optimum decisions. Indeed, because public information is often less reliable than individual information, individuals use it as an additional rather than the sole source of information on the environment (Galef 1995, Giraldeau et al. 2002), and tend to ignore public information when they have reliable private information (van Bergen et al. 2004, Valone 2007).

Another reason may be the cost of learning when the animal already possesses a certain skill, e.g. how to remove food in an extractive-foraging task. If another individual shows another technique for the same task, adopting the new technique would be adaptive if the potential increase in future yield rate exceeds the learning costs (which also includes a temporary depression in yield). Animals obviously cannot easily estimate the utility of switching to another technique. Research on captive chimpanzees shows that individuals that have mastered one technique to solve a task are reluctant to invest in learning another technique to solve the same task (Marshall-Pescini and Whiten 2008, Hrubesch et al. 2009). Now that this conservatism has been revealed, it is interesting to find out which conditions may compel individuals to invest in learning new skills.

Rogers (1988) argued that the value of socially learned information inevitably declines, and eventually the benefit of social learning relative to individual learning disappears (see also Boyd and Richerson 1985). This conclusion is too strong. As we saw, it is often adaptive to acquire knowledge (e.g. is this fruit edible?) or skills (how do I extract these seeds?), which are useful, perhaps after some modification or generalisation. Perhaps the safest generalisation at present is that preferential reliance on vertical social learning of skills is often adaptive, whereas preferential reliance on horizontal social learning to acquire perishable information is often maladaptive.

#### 20.3.4 Evolution of social-learning abilities

The simplest forms of social learning require no more than selective association or facilitation, and selection could easily favour such a tendency if the information acquired in this way is on average adaptive. However, under what conditions could selection have favoured the evolution of the cognitively more demanding and therefore more costly observational forms of social learning?

A naïve answer would be that mere gregariousness or living in larger rather than smaller groups provides sufficient conditions for the evolution of observational-learning abilities. However, there is no evidence for an effect of group size on the frequency of social learning, both within (Huffman & Hirata 2003) or among species (Reader & Laland 2002) of primates and among bird species (Lefebvre et al. 1996). Moreover, many group-living lineages, such as equids, ground squirrels or lemurs show no evidence for advanced social learning skills. Finally, a mathematical analysis suggested that the tolerance of models and the duration of close proximity to them are more important for the acquisition of complex skills than their number (van Schaik & Pradhan 2003). Obviously, when teaching is involved, group size becomes even less important.

More likely, the answer has to do with two factors: how easy is it to learn the skills independently, and how tolerant are models? First, acquiring a skill by copying the model's behaviour or goals is needed when the odds are poor that the naïve individual will independently come up with the skill by simply being pointed to the right situation through association or enhancement (cf. Boyd and Richerson 1996). It is therefore likely that selection for enhanced social-learning skills largely took place in an ecological context where invented skills were especially useful, such as for extractive foragers or hunters (the co-evolution between these two cognitive abilities will be explored later). A major role for ecology is plausible because social skills can often be learned through social interactions and eavesdropping (unlikely to require production imitation).

Second, the opportunity for social acquisition of skills will depend on the benefits for models of being copied and how often and how long observational learning is possible. These conditions suggest observational learning abilities in species with slow-paced life history and long associations between parents or caretakers and immatures, which form stable social units with overlapping generations and high social tolerance. There is as yet not enough information on the taxonomic distribution of observational learning to test these suggestions, but the high incidence of simple imitation in birds noted above suggests that tolerant parent-offspring association and difficult diets play a major role.

Animals are expected to use their whole repertoire of social-learning abilities, but will rely on the most demanding ones to learn the most difficult skills. Indeed, in wild Bornean orang-utans, immatures use a variety of mechanisms to learn their skill set (Table 20.3), from proximity to scrounging to production imitation and emulation, often in combination, and also often insert bouts of practice after observing their mother perform a difficult skill (Jaeggi et al. 2010).

### GLOSSARY

**Affordances:** Learned action possibilities, i.e. properties of objects or environments that can be learned about by exploration, and then be used in subsequent behavioural actions.

**Culture:** In the broadest sense, culture is used as socially transmitted information, in the narrower one as socially transmitted technology and norms that involve conformity ('the way we do things here' McGrew 2004). Whiten and van Schaik (2007) separate it from tradition by noting that culture tends to contain multiple traditions in multiple domains.

**Model:** The knowledgeable individual that may (passively) allow a naïve individual to acquire a particular skill or information, or (actively) pass it on through teaching.

**Social learning:** changes in an individual's behaviour resulting from attending to another individual's behaviour or its products

**Tradition:** An enduring distinctive behaviour patterns characteristic of social units and passed on through social learning (Fragaszy and Perry 2003).

**Teaching:** Teaching has the following characteristics: (i) certain actions only occur in the presence of a naïve observer, (ii) these actions carry some cost but are not immediately beneficial to the teacher, and (iii) the observer profits from these actions in that it learns these actions faster than it would otherwise do.

## 20.4 Immediate consequences of social learning: traditions and culture

### 20.4.1 Animal cultures

Geographic variation in animal behaviour is normally explained by invoking genetic or ecological processes. An ecological explanation would claim that all individuals exposed to a geographically localised set of habitat features independently converge on the same behavioural response. A genetic explanation would argue that all individuals in a particular region have a strong genetic predisposition to develop the behaviour. This would generally lead to clear-cut geographic clusters, whose boundaries coincide

with subspecies boundaries or long-term dispersal barriers. However, social learning can also produce geographically varying presence or absence of behavioural variants, otherwise known as traditions or cultures.

Culture has traditionally been considered a major dividing line between humans and animals. Yet, cultural anthropologists cannot really agree on a definition of culture (Durham 1991), except that it pervades all our actions and even our thinking, and have tended to concentrate on the belief systems, social norms and rituals of a society at the expense of its technology and subsistence pattern (McGrew 2004). A simpler biological definition of culture – socially transmitted skills and knowledge – is both consistent with the phenomena captured in human culture and applicable to animals. To satisfy it, animals in nature must acquire an innovative behaviour (i.e., behaviour that did not arise routinely in a given environment but was instead invented by someone) by learning it from others who already possess this innovation.

Because the word culture has long been earmarked for privileged use for the human species, some biologists have proposed to use the term tradition for cultural phenomena among animals. Traditions are defined as enduring distinctive behaviour patterns characteristic of social units and passed on through social learning (Fragaszy and Perry 2003). While this definition of animal cultures averts interdisciplinary spats and can encompass human culture, it also leads us to disregard possible conceptual and phylogenetic continuities. Moreover, the concept of tradition generally requires stability across generations, but animal data usually do not have the time-depth to demonstrate this. Here, I will use the word culture to stress the continuities with those among animals, while acknowledging the radically different uses that evolved among humans.

Social learning does not automatically produce culture. Horizontally transmitted perishable information about environment (public information) or conspecifics (eavesdropping) does not lead to culture because any spatial patterns are transient. Likewise, most vertically transmitted information generally does not produce culture, because animals everywhere will readily stumble upon the same innovation. As a result, culture should largely be limited to taxa that can learn through observation and are intelligent enough to come up with strong innovations (*sensu* Ramsey et al. 2007). Even among the latter taxa, culture in the spatial sense may not arise if the species' social organisation is such that all transmission is strictly vertical. In dolphins (*Tursiops truncatus*), for example, infants learn their foraging specialisations (i.e., innovations) exclusively from their mothers (Mann and Sargent 2003, Krützen et al. 2005), and there may be several different specialisations within a single locality, and indeed in most localities. However, despite the absence of geographic variation, it



would still make sense to call the behaviours involved cultural given that immatures acquire them developmentally through social learning.

Primate fieldworkers developed an approach to bolster the cultural interpretation of geographic variation, called the ethnographic, geographic or group-contrast method, or method of elimination (Boesch 1996, Whiten et al. 1999, van Schaik 2003). A behavioural variant is considered cultural if it is common wherever it occurs, consistent with its spread and maintenance by social learning, but not clearly linked to ecological differences among the areas or genetic differences among the populations. By concentrating on behavioural variants that do not show clear genetic or ecological correlations in their spatial distribution, researchers could eliminate non-cultural explanations. Together, these field-based, non-experimental methods have served to establish the plausibility of culture in chimpanzees (Whiten et al. 1999), cetaceans (Rendell and Whitehead 2001), orang-utans (van Schaik et al. 2003), and capuchin monkeys (Perry et al. 2003). This interpretation was consistent with the demonstration of sophisticated and highly reliable observational forms of social learning in apes, especially chimpanzees (Whiten et al. 2005).

The major weakness to date of these field methods is that they are useful as proof of principle but not to estimate the size of the cultural repertoire and thus to assess the importance of culture in nature (van Schaik 2009). By design, the geographic exclusion method ignores any behaviour that is correlated with ecological variables or genetic discontinuities, e.g. inclusion in the diet of a particular food item, even if the animals are critically dependent on social learning for their maintenance (cf. Humle and Matsuzawa 2002). On the other hand, if it fails to recognise ecological or demographic factors that underlie the behaviour pattern, which therefore need not be socially transmitted, this technique will overestimate cultural repertoires (Laland et al. 2009). That said, most ape researchers would estimate that the 40 or so variants described for chimpanzees and the 30 or so described for orang-utans are likely to be the tip of the cultural iceberg.

It is important that additional techniques be developed to recognise cultural variants in the wild. BOX 20.1 gives an overview of the methods available to date.

**BOX 20.1****Assessing culture**

Some non-experimental approaches to identify socially transmitted variants, based on observations of spatial patterns (Pattern) or evidence for, or indications of, social learning (Process). Based on Perry (2009), Laland et al. (2009), Whitehead (2009) and van Schaik (2009).

**Pattern**

- (1) *Across sites*: the geographic or group-contrast method, assuming no ecological or genetic differences between sites, and assuming within-site homogeneity of the incidence of the behaviour. A quantitative version turns it into a multiple matrix regression, estimating behavioural similarity as a function of genetic similarity and ecological similarity, either for a particular behaviour pattern or a whole repertoire.
- (2) *Across individuals*: multiple matrix regression of behavioural similarity among individuals (of one or more populations) as a function of genetic and ecological similarity and past association (to estimate cumulative opportunities for social learning).
- (3) *Features of behaviours*: Identify the socially learned behaviour patterns in an individual's repertoire, by showing that its emergence is associated with use of opportunities for social learning and practice when non-routine behaviours are performed by models. Criteria include: (1) selective attention, e.g. by peering, suggesting observational social learning; (2) practice subsequent to selective attention; (3) begging and scrounging, suggesting socially induced affordance learning; and (4) in the case of techniques, hand specialisation.

**Process**

- (1) *Documenting ontogeny*: Link patterns of association and selective attention over time to the acquisition of a particular variant, whenever there is within-population variation.
- (2) *Documenting spread*: Examine the spread of an innovation whose origin was witnessed, against null models of association and rate of spread.

**20.4.2 Mapping variation in animal cultures**

To properly assess the distribution of culture in nature, i.e. which species have which components of culture as well as how humans differ from other animals we need to go beyond semantic debates and take a broad perspective. In principle we could estimate the strength of three potentially independent dimensions of socially transmitted innovations: (i) the complexity of the innovation; (ii) the complexity of the social-learning tech-

niques required to acquire the behaviour socially; and (iii) the extent to which a geographic imprint ensues.

At this stage, a simple dichotomy on each dimension will suffice to frame the approach. Thus, innovations can be cognitively simple or cognitively complex, depending on whether they could have arisen by chance and trial and error or instead required some form of insight to have been performed the first time (cf. Whiten and van Schaik 2007). Likewise, they could have been acquired by simple non-observational forms of social learning or by observational forms. Finally, we can divide cultural variants into those that do produce geographic variation with those that do not, either because they are universal and ubiquitous everywhere or are interspersed with other variants at many different sites (due to exclusive vertical learning).

Although this procedure still leaves eight possible states, in practice the number of observed states will be much smaller. As was already noted implicitly, the complexity of innovation and social learning will tend to be correlated, because cognitive abilities limit the complexity of both innovation and social learning, and thus the content and extent of cultural repertoires. The variants that are easily innovated and transmitted through simple mechanisms such as social facilitation or stimulus or local enhancement may be most widespread. They may also be linked to the third dimension because where innovations arise so easily we may not find any geographic variation. As the cognitive complexity of the innovation increases, more dedicated mechanisms of social learning are required for social transmission. These make the most interesting cultural variants, because social transmission is likely to be essential for their spread and maintenance, and geographic variation almost inevitably arises.

This proposal can be linked to the content-based classification proposed earlier (Fig. 20.2). Perishable information cannot produce cultures. Labels are usually simple innovations requiring simple social learning mechanisms and also need not produce geographic variation. Most cases of vertical social transmission in nature may concern the faster than usual acquisition during development of species-wide foraging patterns or predator recognition, i.e. labels (cf. Galef and Giraldeau 2001). In most species, the learning processes involved need not be any different from the ones an animal would use when alone. Still, label variants may arise, as when different easily recognised foods are included in the diet in different places, although such cases will probably be rare.

Skills, signal variants and symbols can more readily produce cultures. Whenever the cultural variant requires innovation, geographic variation is likely, at least for a certain amount of time. Well-known examples are the cultures found among great apes (including humans) and cetaceans, but

also those of capuchin monkeys or rats (Terkel 1996), even though in these cases the social-learning mechanism may involve no more than enhancement.

One extension immediately comes to mind. Cumulative culture refers to innovations that are beyond the reach of individual inventors and arose through the step-by-step accumulation of modifications to the variant that improved its function but moved it further and further away from the original innovation. These skills or social rules could be called cumulative innovations, which are one step up from complex innovations, and may rely on both production imitation and teaching to be transmitted. This gives us a three-step scale of complexity of innovation and social learning (Fig. 20.2).

The value of scheme like that of Fig. 20.2 is heuristic, in that it should serve to focus the debate on the relevant aspects of the whole phenomenon of culture rather than on terminology. For instance, why are there no examples of cultures from such well-studied animals such as baboons, horses, great tits or sticklebacks? The scheme suggests that many of the culturally transmitted innovations in those taxa are labels that leave no geographic imprint. If new work necessitates its revision it will have served its purpose.

## **20.5 Long-term consequences: culture and intelligence**

### **20.5.1 Culture and intelligence**

Most developing animals need environmental inputs to fine-tune their brains so as to acquire the behavioural repertoire most appropriate in the current conditions, a phenomenon called constructive learning (Quartz 2003). Play is an example of active attempts to generate such inputs that serve to train the motor system (Fairbanks 2000). When it comes to acquiring knowledge or specific skills, social learning should improve the signal-to-noise ratio of these inputs because animals learn skills faster when learning socially than when learning (i.e. generating sensory inputs) alone. Indeed, there are clear developmental effects of social learning on an individual's repertoire of cognitive skills, as shown by comparisons among wild great ape populations (van Schaik et al. 2003) as well as the results of social deprivation and enculturation experiments (van Schaik and Burkart unpubl. data). Thus, if there is a niche-construction element to an individual's set of learned skills, and if this set approximates intelligence, intelligence is culturally constructed (Tomasello 1999).

To the extent that this ontogenetic account is correct, culture should in the long run affect intelligence. Species with frequent opportunities for social learning should more readily respond to selection pressures to add cognitive abilities, so that they should end up with larger relative brain size on average than species that have fewer opportunities for social learning. The cultural intelligence hypothesis (van Schaik 2004) therefore predicts a tight positive interspecific correlation between social learning performance and individual learning ability. There is evidence for this at the level of frequencies of innovation and social learning (Reader and Laland 2002) and at the level of level of maximum complexity achieved (van Schaik and Burkart unpubl. data). It also predicts that cultural species are more intelligent, but there is not enough comparative information to test this prediction yet. Thus, culture could provide a compelling explanation for the evolution of intelligence, complementing accounts that focus exclusively on the fitness benefits of enhanced cognitive abilities, such as the social brain or technical intelligence hypotheses (Byrne & Bates 2007).

### **20.5.2 Cultural evolution**

Cultural transmission systems have some properties that are fundamentally different from regular organic evolution, as summarised in Table 20.4 (after Danchin et al. 2004). Whereas mutations are random with respect to fitness, most innovations are not, but instead improve fitness. Moreover, the transmission of favourable variants, slow and noisy in organic evolution since it has to rely on natural selection of individuals across generations, can be fast and precise in the case of social transmission. Cultural selection is therefore truly Lamarckian, and this new system of inheritance can in principle be far more efficient than classic natural selection. It would appear to be the silver bullet toward almost instantaneous adaptation to local conditions, and thus highly adaptive for species that colonise new habitats or encounter temporal changes in their habitats – in other words, pretty much all species. Why, then, is cultural evolution so rare in nature?

We have seen that many species rely on social learning, yet few have traditions and even fewer have cultures, as defined here, and only humans have truly cumulative culture. Thus, the features of this table only apply to very few species, and in its more extreme forms only to humans. Culture is almost synonymous with being human, and may be our most successful adaptation. One reason for this is that the proper adoption of innovations, i.e. potentially novel cultural variants, requires the cognitively most complex forms of observational learning along with teaching. This combina-

tion may be limited to humans. The absence of cumulative culture in great apes or other species capable of observational learning (Whiten et al. 2004) suggests that some factor was added during human evolution. One recent hypothesis is that the pro-active prosociality induced by the adoption of cooperative breeding during human evolution served to add both the teaching component and, in the long run, the increased cognitive demands of observational social learning (Burkart et al. 2009a).

### 20.5.3 Toward a unified science of culture

Cultures can be dynamic, changing continuously due to innovation, forgetting, dropping out of fashion, demographic changes, etc. Cultures can remain stagnant due to lack of innovation, but even when innovations are produced they may not spread due to social conformity or conservatism. Thus, a mature theory of culture should contain the following elements:

- *The rate of innovation:* One obvious factor affecting this rate is population size (Henrich 2004), but this will be affected by the degree of conservatism, which in turn may depend on the presence of environmental crises, such as famine or war, and perhaps on demographic factors, such as the presence of a large bulge of adolescents, more willing than others to try out new innovations.
- *The nature of social transmission mechanisms:* The mechanism may critically affect the spread of innovations and the reliability of their transmission (Boyd and Richerson 1996).
- *Biases in the transmission of innovations:* Strong conformity will tend to slow down cultural change, whereas prestige-based copying will tend to speed it up. The more individual evaluation of novel variants encountered by a naïve individual takes place, the slower cultural change (Richerson and Boyd 2005).
- *Conditions affecting transmission:* The effective size of the social network plays a major role, which is strongly affected by association patterns and social tolerance among individuals (e.g. van Schaik and Pradhan 2003, Henrich 2004), as should social relations between social units (diffusion) and the identity of the dispersing sex. An additional factor is the intrinsic salience of the innovation, which is partly a function of its domain. For instance, orang-utans perceive comfort innovations as much less salient than those linked to feeding or communication (van Schaik et al. 2006).
- *Conditions affecting diffusion:* The degree to which separate populations are open to diffusion of variants from others may be especially impor-

tant where populations are small and poorly networked, and variants are therefore prone to extinction. The presence of dispersal barriers (e.g. due to habitat fragmentation), the sex of the dispersers, and the degree to which dispersers are integrated socially all play a role.

- *Tradeoffs between innovative and social-learning ability*: Exclusive reliance on social learning may interfere with directing attention toward individual exploration, and thus solving problems. For instance, Burkart et al. (2009b) showed that those individual marmosets (*Callithrix jacchus*) that were better at social learning a new foraging task than others were less quick to notice the presence of a hitherto unavailable shortcut to food. Thus, in a population of social-learning specialists, culture may get stuck. However, the presence of different personality types within a population may remove this obstacle to cumulative cultural change.

Such a mature theory of culture would not only explain the taxonomic variation in the presence of culture, repertoire sizes within and across species, or the longevity of individual traditions, but also the relative role of culture in such well-known human phenomena as the upper Paleolithic revolution (Powell et al. 2009) or the adoption of agriculture.

## 20.6 Conclusions and outlook

Every developing animal must acquire a number of skills to be successful in its habitat and social organisation through learning, although species may differ dramatically in the actual number of learned skills. Most come equipped with a set of near-instinctive response predispositions, which may be honed by social learning, and thus produce local diets and niches. Where studied, immatures have a preference for social over individual learning, and adults wherever possible make widespread use of eavesdropping or public information. Moreover, several individuals learn complex skills they would otherwise almost certainly not have acquired. Still, cultural evolution in nature seems largely confined to humans.

Nonetheless, the reader must have noted from the way findings or patterns were formulated that much of our knowledge in this young field is still tentative. At the same time, it is clear that an improved understanding of cultural phenomena in animals is vital for evolutionary biology and especially evolutionary anthropology. Theorising has run well ahead of empirical research.

One important avenue for future research is to unravel the relative importance of genetic endowment, ecological conditions and opportunities

for social learning in bringing about an individual's behavioural repertoire, and to compare the picture across a wide array of species. Tools for this task are as yet inadequate, but they are being developed (Laland et al. 2009; see also BOX 20.1). This analysis needs to be done in a range of species, varying from those with suspected cultural variation, such as great apes and cetaceans, to species for which such variation is thought to be absent, such as many birds and fishes.

Another very important issue is innovation. Little is known about what produces innovation, probably because it is a by-product of individual exploration (perhaps related to personality: Bergmüller, this volume). Yet, the presence of culture relies on it (Fig. 20.2), and cumulative culture is critically dependent on continuing innovation. In order to get some purchase on the role of innovation in the production of animal culture, solid operational definitions are needed. These are being developed (Reader and Laland 2003, Ramsey et al. 2007) and tested (van Schaik et al. 2006, Lehner et al. in press). I expect that a good theory for the conditions that favour or hinder the incidence of innovation and of their spread and maintenance through social learning will contribute to solving the puzzle of the limited taxonomic distribution of culture and the near-absence of cumulative cultural evolution in animals.

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Glossary:

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**Table 20.1** The main kinds of social learning distinguished here.

|  |                                   |  |
|--|-----------------------------------|--|
| <b>Learning by attending to social information</b> | Non-observational social learning | 1. facilitation / gregariousness                     |
|  |                                   | 2. enhancement                                       |
|  | Observational social learning     | 3. contextual imitation / observational conditioning |
|  |                                   | 4. production imitation / emulation                  |
| <b>Learning through social interaction</b>         | 1. interaction conditioning       |  |
|  | 2. teaching                       |  |

**Table 20.2** Comparing anthropological and behavioural-ecology approaches.

| <b>Field</b><br><i>Emphasis</i>           | <b>Anthropology-<br/>Psychology-<br/>Primateology</b> | <b>Behavioural Ecology</b> |
|---|---|----------------------------|
| <i>Direction of transfer</i>              | vertical and oblique                                  | horizontal                 |
| <i>Content</i>                            | labels and skills                                     | perishable information     |
| <i>Method of social learning studied?</i> | yes   | no                         |
| <i>Consequences</i>                       | traditions or culture (often)                         | not so                     |



**Table 20.3** Kinds of learning deployed by orang-utan infants to acquire their diet, and the nature of the foods and the knowledge acquired this way (after Jaeggi et al. 2008, 2010).

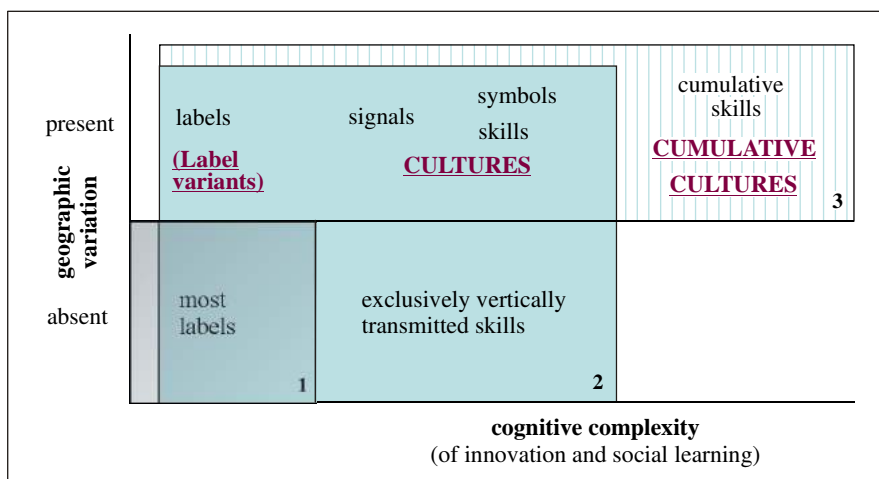
| <i>Social/individual learning?</i> | <b>Independent exploration</b> | <b>Parent-offspring association</b> |                               |                          |            |
|------------------------------------|--------------------------------|-------------------------------------|-------------------------------|--------------------------|------------|
| <i>Mechanism</i>                   | individual trial and error     | proximity and enhancement           | + informational food transfer | + observational learning | + teaching |
| <i>% items in Pongo diet</i>       | < 1%                           | ≈ 54%                               | ≈ 46%                         | ≈ 17%                    | 0%         |
| <i>Food types</i>                  | common and easy-to-process     |                                     | rare and difficult-to-process | extracted                |            |
| <i>Kind of knowledge</i>           | Labels (what?)                 |                                     | Skills (how?)                 |                          |            |

**Table 20.4** The main distinguishing features of regular (organic) and cultural evolution.

|                                     | <b>Organic evolution (Darwinian)</b>  | <b>Cultural evolution (Lamarckian)</b>                           |
|-------------------------------------|---|--|
| <b>Raw material</b>                 | <i>Mutation</i> (non-directed, usually deleterious)                               | <i>Innovation</i> (usually directed, rarely deleterious)         |
| <b>Spread of favorable variants</b> | through <i>differential lifetime reproductive success</i> across many generations | through <i>adoption</i> , potentially within a single generation |



**Fig. 20.1** Social learning in nature is often vertical: immatures learn from their mother, as in this Bornean orang-utan mother-infant pair. Photo © Lynda Dunkel.



**Fig. 20.2** The dimensions of tradition and culture.