

RESEARCH ARTICLE

Social Knowledge and Signals in Primates

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Primates are notable for having a rich and detailed understanding of their social environment and there has been great interest in the evolution and function of social knowledge in primates. Indeed, primates have been shown to have impressive understandings of not only other group members but also the complex relationships among them. To be useful, however, social knowledge requires memories from previous encounters and observations about individual traits that are stable. Here, we argue that social systems or traits that make social knowledge more costly or less accurate will favor signals that either supplement or replace social knowledge. Thus, the relationship between signals and social knowledge can be complementary or antagonistic depending on the type of signal. Our goal in this review is to elucidate the relationships between signals and social knowledge in primates. We categorize signals into three types, each with different relationships to social knowledge. (1) Identity signals directly facilitate social knowledge, (2) current-state signals supplement information gained through social knowledge, and (3) badges of status replace social knowledge. Primates rely extensively on identity information, but it remains to be determined to what extent this is based on receiver perception of individual variation or senders using identity signals. Primates frequently utilize current-state signals including signals of intent to augment their interactions with familiar individuals. Badges of status are rare in primates, and the cases where they are used point to a functional and evolutionary trade-off between badges of status and social knowledge. However, the nature of this relationship needs further exploration. *Am. J. Primatol.* 75:683–694, 2013. © 2012 Wiley Periodicals, Inc.

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INTRODUCTION

If you ask a biologist about “signals,” you may get a very different response depending on whether or not they study primates. Primate researchers have largely focused on either the “meaning” of primate signals and the language-like aspects of their communication [e.g. Harre & Reynolds, 2008] or signals of intent that indicate how the signaler is about to behave [e.g. Silk, 1997]. Nonprimate researchers have focused on signals as indicators of aspects of the quality of the signaler used in competitive [e.g. Clutton-Brock & Albon, 1979] or mate choice situations [e.g. Andersson, 1982]. Only recently have primate researchers begun to focus on such “badges of status,” with several studies finding that primates use badges of status much the same way as other taxa [e.g. Setchell & Wickings, 2005].

While the divergent research interests of primatologists and other biologists might account for some of the different research foci, we feel that an underlying biological difference between primates and other taxa is also at work. Specifically, primates tend to live in stable social groups while nonprimates more often have important interactions (e.g.

mate choice) with unfamiliar individuals. These situations create different cost-benefit structures for using social knowledge to mediate social interactions, with primates being very reliant on social knowledge [Cheney & Seyfarth, 2007]. Thus, primates tend to use signals to *supplement* social knowledge (e.g. signals of intent) while nonprimates tend to use signals as *substitutes* for social knowledge (e.g. badges of status). These differences suggest a relationship between signals and social knowledge that is additive in some situations but mutually exclusive in others. Our goal is to elucidate the relationship between signals and social knowledge, using primates as a case study.

We first define signals and social knowledge using a standard communication framework. We limit

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our focus to signals used in social interactions, and we do not discuss signals in other contexts (e.g. alarm calls, species recognition). Based on this framework, we delimit the factors in primate societies that are likely to limit the utility of social knowledge and explore how signals may (1) directly facilitate social knowledge, (2) supplement knowledge gained through social knowledge, and (3) replace social knowledge in interactions with unfamiliar individuals.

SIGNALS AND SOCIAL KNOWLEDGE

Definitions

Signaling and social knowledge at their core are fundamentally tools for animals to gather information about their social environment. Here, we follow the animal communication literature and define information as a reduction in uncertainty in the recipient [Seyfarth et al., 2010]. Traditionally, studies of communication have classified the transfer of information between parties depending on the relative costs and benefits to the senders (the individuals producing information) and the receivers (the individuals receiving and acting on information) [Bradbury & Vehrencamp, 2011; Scott-Phillips, 2008]. In reality, all animals take on the role of senders and receivers, though the adaptive challenges of producing and interpreting information are substantially different so we will treat senders and receivers as distinct entities for simplicity of discussion.

Broadly, signals can be defined as traits that have evolved because they benefit senders by eliciting favorable responses in receivers [Bradbury & Vehrencamp, 2011; Scott-Phillips, 2008; Tamura & Ihara, 2011]. In practice, however, the term “signal” is often reserved for cases where the fitness of both senders and receivers are increased [Scott-Phillips, 2008]. This is because if receivers are harmed by a signal (e.g. deception), we expect selection to favor receivers that ignore the signals leading to the loss of communication. There is a vast literature on the evolution of signals—with particular emphasis on the factors that maintain honesty and prevent deceptive signals—which we will not cover here [Bradbury & Vehrencamp, 2011; Krebs & Dawkins, 1984; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005]. For our purposes, we will consider signals to be traits that have evolved for the purpose of conveying information that (on average) benefits both senders and receivers.

To fit social knowledge into the predefined communication framework, we need to examine how social knowledge influences the fitness of both senders and receivers. We define social knowledge as the use of knowledge about a particular individual based on

past interactions and observations to guide actions in the present. In the context of social knowledge, we will consider the receiver to be the individual utilizing knowledge and the sender to be the individual that the receiver knows something about. From a mechanistic standpoint, much of social knowledge is perhaps best viewed as a form of eavesdropping. Receivers gather information from social interactions, though the purpose of the interactions is not to inform receivers per se. For example, the purpose of a contest over resources is to access a resource, though contestants and observers may incidentally learn information about the relative qualities of the contestants involved. Such indirect acquisition of social information is a hallmark of primates. For example, in an early experimental study, Bachmann and Kummer [1980] showed that hamadryas males eavesdrop on the interactions between males and females when deciding which female to attempt to interact with. Social knowledge, however, goes a step further than eavesdropping in that receivers can utilize the cumulative sum of information gathered over longer periods of time. For example, male macaques use information about the relative ranks of other males when deciding which males to recruit as allies [Silk, 1999]. As a general rule, we expect receivers to utilize their knowledge to their own benefit (otherwise, the use of such knowledge would be disfavored by selection).

Whether or not senders benefit from the acquisition and use of social knowledge will depend on the circumstances. In some cases, senders can benefit by providing information about themselves. For example, mothers respond to the contact calls of their own infants but ignore other infants [Rendall et al., 2000]. In this case, infants benefit because their mothers know their identity from vocalizations. In many baboons, females with young infants benefit from friendships with adult males who protect them against harassment from other males and high-ranking females [Nguyen et al., 2009; Palombit et al., 1997]. Females, then, would benefit by others knowing about their friendships with adult males. In a more nuanced way, knowledge of other individuals' ranks has a strong influence on the directionality of grooming. Generally, females are more likely to groom “up the hierarchy” [Schino, 2001] meaning that social knowledge about rank benefits higher ranking females and hurts lower ranking females, at least in the context of grooming. Overall, then, social knowledge may be either beneficial or harmful to senders depending on the particular context (e.g. friendships vs. grooming) and the characteristics of the sender (e.g. rank). In a communication framework, social knowledge may mirror either signaling (that benefits the sender) or eavesdropping (that does not) depending on the benefits to the sender.

Limits of Social Knowledge

Advanced social cognitive abilities have allowed primates to navigate the intricate social environments produced by stable groups [e.g. Byrne & Whiten, 1989; Cheney & Seyfarth, 2007]. There are a number of necessary features of social knowledge, however, that limit its utility in certain situations. In defining social knowledge as the use of information about particular individuals gained through previous interactions or observations, we necessarily impose some requirements on receivers in order to make use of social knowledge. First, receivers must be able to individually recognize senders. Without individual recognition, it would not be possible to associate information with particular individuals [Tibbetts & Dale, 2007]. Importantly, recognition needs to be accurate and reliable [Beecher, 1989], as mistaken identities may lead to awkward (and potentially detrimental) social interactions in primates just as they may do in our own lives. Second, information gained about senders in past encounters must be relevant in subsequent encounters [Barnard & Burk, 1979]. Thus, social knowledge is less useful when the relevant state of a sender changes rapidly. The integrity of past information may also be dampened by prolonged delays between social interactions (attenuation) or new experiences (interference) [Dukas, 1999]. Third, memories necessarily require a previous experience or observation. Social knowledge, then, is not useful when interacting with unfamiliar individuals. For many primates, individuals engage in relatively few interactions with unfamiliar individuals, though in some contexts interactions with unfamiliar individuals can have profound fitness consequences (see below).

We have identified three areas that place limits on the usefulness of social knowledge: (1) identifying individuals accurately and reliably, (2) tracking rapidly changing states, and (3) engaging unfamiliar individuals in a first social interaction. In the following sections, we examine how different types of signals (that we call “identity,” “current state,” and “badges of status”) allow primates to overcome the limitations of social knowledge.

Identity Signals Facilitate Recognition

A central challenge in social recognition is to achieve accurate and reliable discrimination among individuals. This challenge is particularly acute in the context of individual recognition, where receivers are tasked with uniquely identifying multiple senders. To reliably identify individual senders, receivers must rely on suites of phenotypes that are both variable among individuals but consistent within an individual over time [Beecher, 1989; Dale, 2006; Dale et al., 2001]. Primates are adept at recognizing individuals via vocalizations, appear-

ance, and/or scent [Cheney & Seyfarth, 1980; Palagi & Dapporto, 2006; Parr, 2011]. Given that recognition behavior is well documented in primates, the presence of identity signatures in a range of primate phenotypes including vocalizations, faces, and scents is almost trivial. The fact that the predictive/discriminatory power of identity signatures varies across traits and species, however, raises important questions: To what extent are senders favored to advertise their identity with easily identifiable identity signals in primates? And, does the evolution of identity signals, as opposed to cues, have any implications for receivers' social knowledge?

Before examining the presence and potential effects of identity signals in primates, we must first define what we mean by identity signaling. To do so, we make a distinction between identity signatures, cues, and signals. As we mentioned in the previous paragraph, identity signatures are common features of many primate phenotypes though identity signatures are not necessarily signals of individual identity. Strictly speaking, we define identity signature as any aspect(s) of a trait or suite of traits that allows for reliable discrimination among individuals. Broadly, the term identity signature could be applied to any trait that allows for individual discrimination though in studies of animal behavior identity signatures typically refer to traits used for social recognition [e.g. Cheetham et al., 2007]. Identity signatures, just as other types of communicative phenotypes, may either be cues or signals [Scott-Phillips, 2008]. We define identity cues as traits that allow for individual recognition, but have not evolved for the purpose of facilitating recognition. Therefore variation in identity cues must be either the result of selection on traits unrelated to recognition or a necessary byproduct of development processes. A clear example of an identity cue is human fingerprints. The unique patterns of swirls can be used to identify individuals, though they have not arisen as a result of a long history of selection for individual identification. Additionally, in this example, senders (those leaving fingers) tend to suffer costs as a result of fingerprint-based identification (such as jail time).

Identity signals are traits that have evolved for the purpose of advertising individual identity [Beecher et al., 1986; Dale et al., 2001; Pollard & Blumstein, 2011; Sheehan & Tibbetts, 2009; Thom & Dytham, 2012]. In the case of identity signals, trait variation used for recognition is the product of selection favoring easily recognizable senders. In this sense, identity signals may be viewed as a sort of nametag, which is worn for purpose of facilitating recognition. Models of identity signal evolution suggest that senders may be favored to advertise their identity with unique, easily identifiable phenotypes when it is costly to be confused with others [Dale et al., 2001].

There is abundant evidence that primates have individually distinctive vocalizations [Chapman & Weary, 1990; Fischer et al., 2001; Macedonia, 1986; Mitani et al., 1996; Rendall et al., 1998]. Our goal is not to review this broad topic but rather highlight a few important points regarding identity signaling: (1) the evidence for identity signals in primates, (2) suggestions for additional tests of identity signaling, and (3) the potential implications of identity signals as opposed to identity cues for receivers.

While the pervasiveness of identity signatures in primate vocalization is suggestive of selection for identity signaling, current data often warrants a cautious interpretation. Statistical analyses of individual identity signatures are designed to identify characteristics that are consistent within an individual and variable across individuals [Beecher, 1989]. Thus, any trait that is consistently different among individuals may lead to statistical support for an identity signature, though these may not necessarily be identity signals. For example, the long calls of Wied's black tufted-ear marmosets (*Callitrix kuhli*) show clear individual differences in any given year, though the differences are not reliable from year to year within the same individual [Jorgensen & French, 1998]. The inconsistency of vocalizations over time in the case of marmosets is counter to the expectations of identity signals, though may still function as useful identity signatures provided that the change in call structure is gradual. Similarly, a recent study of fallow deer found that male roars provided information on both identity and quality [Briefer et al., 2010]. While, quality information was consistent from year to year (i.e. roars changed predictably as males increased and decreased in quality), identity information was variable over time. The longitudinal analysis shows that calls lack consistent identity signatures, suggesting that they are under selection to signal quality rather than individual identity per se (though it is possible to cue in on identity in a given year). Therefore, statistical evidence of individuality is not sufficient evidence of identity signaling. Evidence that individuality is shaped by selection is needed.

Some studies have sought to test the hypothesis that vocalizations are selected to signal individual identity by comparing the level of individuality among calls within a single species. For example, Mitani et al. [1996] demonstrated that pant hoots showed more individually identifiable variation than pant grunts in chimpanzees (*Pan troglodytes*), in agreement with their prediction that identity-signaling requirements differed between the two call types. Rendall et al. [1998] found that individual distinctiveness varied among coos, grunts, and screams in rhesus monkeys (*Macaca mulatta*). Coos had the highest level of individuality and are thought to function as contact calls among dispersed individuals, whereas grunts typically occur in face-

to-face settings [Rendall et al., 1998 and references therein]. Therefore, the higher level of distinctiveness in coos may reflect greater selection for identity signaling in the absence of other identifying information present from visual contact during grunts. Similarly, the level of individuality differs among call types in red-capped mangabeys (*Cercocebus torquatus*), with calls used to mediate social interactions (e.g. contact and threat) showing elevated levels of individuality [Bouchet et al., 2012].

Intraspecific comparisons of individuality in call types are consistent with identity signaling in primates, although other explanations exist. For example, Owren and Rendall [1997] argue that calls such as screams have acoustic properties that make them aversive to the receiver. Consequently, as a byproduct of selection to be aversive, the individuality of screams may have been reduced. More generally, differences in individuality across call types within a species may arise because selection has acted to decrease the individuality of some calls. Thus, variation in individuality across call types does not necessitate that selection has acted to increase the individuality in some calls (as would be required for the distinctive calls to be identity signals).

In order to more fully understand the origin of individuality in primate communication, additional direct tests of the identity-signaling hypothesis are needed in a wide range of taxa and putative signals. In other taxa, tests of identity signaling have employed both experimental and comparative approaches. First, the identity signaling hypothesis predicts that senders benefit from advertising their identity in situations where confusion is costly [Dale et al., 2001; Johnstone, 1997]. A previous test of this hypothesis experimentally altered color patterns in paper wasps to make all the individuals in a group identical except for one individual [Sheehan & Tibbetts, 2009]. Such dramatic phenotypic manipulations are likely to be impractical in primate groups. It may be possible to test the benefits of signaling individual identity through playbacks of calls with experimentally reduced identity information. A second and more tractable approach, with regards to primates, would be to compare identity information among species in a phylogenetically controlled manner. Recent work has shown that marmot species that live in larger groups have more individually distinctive alarm calls than relatives living in smaller groups [Pollard & Blumstein, 2011]. Comparisons of individuality among related species differing in recognition have provided additional evidence for identity signaling in wasps [Sheehan & Tibbetts, 2010], mice [Robertson et al., 2007], and sparrows [Beecher et al., 1986]. Group size varies widely across primates providing ample opportunity for comparative tests of identity signaling in a large, well-studied taxon with a well-supported phylogeny.

While identity signals are predicted to evolve when senders benefit from being recognized, we expect identity signals to have at least two important implications for receivers as well. First, as with other signals [Endler, 1992; Guilford & Dawkins 1991], receiver psychology is expected to shape the evolution of identity signal form. This means that identity signals should be under selection for optimal efficacy both in terms of allowing receivers to discriminate among individuals and remember those individuals. In comparison to identity cues, which have not been shaped by receiver psychology, identity signals are expected to make the task of recognizing easier. By facilitating recognition, it is possible that identity signals may help lessen the cognitive costs associated with social cognition, though this conjecture needs further theoretical consideration. Second, primates have a rich repertoire of social vocalizations that allow them to infer the intentions of others (see next). In addition to the information on intent provided in the vocalizations, listeners also receive information on individual identity. The fact that identity information is present in many primate vocalizations (and facial expressions and scents too) likely makes it easier for receivers to integrate information about current social activities with past social knowledge. For example, if a rhesus coo lacked identity information it would be more difficult for receivers to decide how to respond to the vocalization until they had been able to visually identify the caller as well.

Current-State Signals Supplement Social Knowledge

Many aspects of individuals are labile, making social memory insufficient to guide relevant decisions. Thus, even though a receiver recognizes a sender, information the receiver has previously acquired about the sender may be inaccurate. For example, approaching an animal that is threatening you is probably not a good idea, even if your previous interaction was friendly. The threat acts as a “current-state” signal that is used to convey information about unstable aspects of individuals (i.e. their intentions).

Here, we use the term “current-state signals” to describe signals with a range of meanings (intent, fertility, quality, resources, locations, etc.) that provide information on traits that change regularly. In the next section, we discuss the use of badges of status that convey more stable information and interact differently with social knowledge. We draw a contrast between signals that provide information on fluctuating versus stable characteristics for the purpose of highlighting different effects on social knowledge and signaling at the extremes, though we recognize that the stability of information conveyed in signals varies along a continuum.

Based on our schema, current-state signals typically serve to supplement social knowledge and are often incorporated with social knowledge. For example, an identical threat grunt may elicit very different responses depending on the relative ranks of the sender and receiver. Such a difference requires the integration of the current-state signal and the receiver’s social knowledge gained from previous interactions with the sender. However, because the information in current-state signals is independent from the identity of the individual, they can also be received and responded to by strangers. For example, animals can use intention signals to guide their interactions with unfamiliar immigrants even though this is not typically how they are used.

At the shortest time scale, signals can convey the intentions of the signaler, which may change from moment to moment. In primates, signals of intent are ubiquitous, although research has focused on signals of benign intent and their use in reconciliation [e.g. Cheney et al., 1995]. For example, in macaques, high-ranking females frequently approach lower ranking females that have young infants [Bauers, 1993]. In a hierarchy of females ranked A through L, female B may approach female F who has an infant. Typically, the approach of a high-ranking female is threatening and female F would move away based on the identity of the approacher (i.e. she would move away from female B but not female J). However, female B may give non-threatening contact grunts as she approaches and, in such cases female F is less likely to move away. Such approaches typically end with female B having a nonaggressive interaction with the infant of female F. In a signaling framework, female B provided a signal of benign intent (the grunt) to female F, who modified her response accordingly. However signals of intent can also convey aggressive intent [e.g. Laidre, 2005], submission [e.g. Maestriperi & Wallen, 1997], interest in mating [e.g. Lindburg, 1990], or a preferred direction of movement [e.g. Sigg & Stolba, 1981]. Importantly, primates integrate signals of current intent with social knowledge (rank, previous interactions, etc.) allowing them to adaptively make decisions about social interactions [Laidre, 2005].

Over the time scale of days to weeks, primates have signals that indicate their current reproductive condition. These are most common among female primates that exhibit sexual swellings [see also Semple et al., 2002 for a discussion of copulation calls]. While there is some debate about the adaptive significance of such swellings [Domb & Pagel, 2001; Higham et al., 2008; Hrdy, 1999; Huchard et al., 2009; Nunn, 1999; Pagel, 1994; Stallmann & Froehlich, 2000; Zinner et al., 2002], in a signaling context, the function is clear—the swelling transmits information about the fertility status of the female. Because a female’s fertility can change from day to day, it is insufficient

for males to recognize the female—they need more information to guide their assessment. Thus, fertility signals are a form of current-state signals that provide receivers with information about the reproductive status of individuals.

Some research has suggested that sexual swellings can also act like badges of status (see next section) that indicate the quality of the female [e.g. Domb & Pagel, 2001] although this remains controversial [Zinner et al., 2002]. It is likely that sexual swellings can convey multiple types of information about the sender [Higham et al., 2008] and badge of status properties of swellings may evolve from a current-state signal [Huchard et al., 2009]. We prefer to categorize sexual swellings as current-state signals because they typically have a complementary relationship to social knowledge. However, it remains possible that social knowledge may be insufficient to assess female quality in some situations (e.g. if male tenure is short) and these situations may favor the evolution of swellings that act as badges of status. Such a possibility requires further study.

While fertility signals are only found in females, males can also signal their reproductive condition, particularly when their condition (e.g. fighting ability) changes rapidly. One such case occurs in chacma baboons. Male chacma baboons compete aggressively for high rank that entails mating advantages. Males engage in “wahoo contests” that can last for more than an hour and involve repeated wahoo vocalizations, chasing and fighting. The wahoo vocalizations appear to indicate fighting ability as acoustic properties of the wahoos correlate with rank and degrade with fatigue and age [Fischer et al., 2004; Kitchen et al., 2003]. Chacma males live in stable groups with a relatively small number of resident males that almost certainly recognize each other [Bergman et al., 2006; Cheney et al., 2004]. However, male fighting ability changes rapidly as rank changes are frequent [almost monthly, Kitchen et al., 2003] and tenure as alpha male is short [Hamilton & Bulger, 1990]. Thus, social knowledge may be insufficient to accurately assess potential rival males and the signal serves to supplement social knowledge. The authors of this research describe the wahoo as a signal of male quality and we agree that it is. However, because the aspect of quality being signaled is unstable, in our current framework it is more accurately described as a current-state signal rather than a badge of status, keeping in mind that current-state signals can refer to labile aspects of the sender’s quality. However, to the extent that wahoos are used to assess unfamiliar males (i.e. in neighboring groups or recent immigrants), they may function more as badges of status. As with female sexual swellings, it may be difficult to draw a sharp distinction between current-state and badge of status signals—especially if signals are multimodal and provide multiple messages. However, the extent to which signals provide infor-

mation on unfamiliar individuals or intractable quality, they are likely to interact differently with social knowledge as discussed next.

Territorial calls may be another form of current-state signals [Marshall & Marshall, 1976]. In this case, the signal serves to indicate the location and continued presence of the sender. The signal may be received by familiar individuals, acting as a supplement to the information they have about their neighbors [as in “dear enemies,” Temeles, 1994], or by unfamiliar animals moving through the area. In either case, the signal communicates information about a labile feature of the sender, making it a current-state signal.

Badges of Status Provide Information about Unknown Individuals

In cases where individuals interact with strangers, there is no opportunity to use social knowledge. Instead, assessments must be made based on the phenotype present at the time of the interaction. Many species have evolved “badges of status” (or ornaments) that facilitate such assessments [Andersson, 1986; Rohwer, 1982]. Here, we use the term “badge of status” broadly to refer to any signals that relate to stable aspects of the senders quality regardless of the underlying costs of the signal or the situation it is used in. Assessments of strangers primarily occur in mate choice contexts [e.g. peahens choosing among unknown peacocks as potential mates, Petrie et al., 1991] or in male–male competition [e.g. red deer competing for access to mates, Clutton-Brock & Albon, 1979]. Badges of status are widespread in the animal kingdom, and there is extensive research on their function and evolution with much of the research focusing on the maintenance of signal honesty [reviewed in Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005]. However, much less is known about badges of status in primates. Here, we briefly review the several studies of established and putative badges of status in primates and then describe a few other possibilities.

- (1) *Facial coloration of male mandrills.* This is the most extensively studied primate badge of status. Most research has focused on the red coloration, although the blue coloration also plays a role, and the contrast between the red and blue may be the most salient feature [Renoult et al., 2011]. Research has shown that coloration varies with status and testosterone and females prefer males with redder faces [Setchell, 2005; Setchell & Dixon, 2001; Setchell & Wickings, 2005]. This signal appears to have evolved as a substitute for social knowledge [Setchell & Kappeler, 2003] as mandrills have very large groups where social information may be lacking.

- (2) *Red faces of male rhesus macaques.* The redness of the males' faces is testosterone based, changes seasonally (being redder in the mating season), and is the basis of female preference [Baulu, 1976; Rhodes et al., 1997; Waite et al., 2003]. Macaques have moderately sized but stable groups [Berman et al., 1997], which do not appear to warrant the evolution of a badge of status. However, during the breeding season, groups experience an influx of novel males [Lindburg, 1969], suggesting there is opportunity to choose among (or compete with) unfamiliar males. On the other hand, it may be the case that the redness is used primarily among familiar animals to indicate the male's current condition, making this a current-state signal.
- (3) *Gelada male chest patch.* Geladas have an unusual patch of bare skin on their chest that varies in redness [Bergman & Beehner, 2008]. Among males, the redness correlates with status, with redder males having access to more females [Bergman et al., 2009]. The large, fluid groups of geladas might limit the utility of social knowledge [Le Roux et al., 2011]. Indeed there is experimental evidence that geladas males do not recognize other males that they encounter regularly [Bergman, 2010]. Such a situation certainly favors the evolution of a badge of status.
- (4) *Vervet scrotal coloration.* Adult male vervets have bright blue scrotal skin that varies with status [Isbell, 1995]. Manipulating the color results in more aggression from males and changes in rank, suggesting a role in male–male competition [Gerald, 2001]. Females also attend to differences in scrotal color [Gerald et al., 2010]. However, vervets live in relatively small, stable social groups [Struhsaker, 1967] suggesting little need for badges of status. We propose that either the competitive ability of male vervets changes rapidly enough to warrant a current-state signal (like the chacma baboon wahoo), or that encounters between unfamiliar neighboring (or immigrant) males are important enough to favor a badge of status system.
- (5) *Drill coloration.* The redness of male drill sexual skin appears to act as a badge of status [Marty et al., 2009]. Redder males are higher ranking, and also preferred by females, although the female preference for redness is not independent of the male's rank [Marty et al., 2009]. This signal appears to substitute for social knowledge as encounters with strange males are common in their temporary “supergroups” [Marty et al., 2009].

There are other cases where badges of status are likely. Olfactory signals in lemurs appear to have a badge of status function in addition to a territorial function [Charpentier et al., 2008, 2010]. However, more work is needed to know how such signaling re-

lates to their use of social information. The striking head coloration of uakaris suggests a signaling function that would correspond to their fluid social system [Bowler & Bodmer, 2009]. The same is true for hamadryas male faces and paracallosal skin [Kummer, 1984]. Certainly more work is needed to understand the diversity of badge of status systems within primates.

DISCUSSION

Relationships between Signal Types and to Social Knowledge

Identity and current-state signals

There is considerable potential overlap between identity and current-state signals (Table I). On the sender side, many current-state signals are likely to contain identity information [e.g. threat grunts in baboons Bergman et al., 2003]. However, it remains to be determined to what extent the identity information in current-state signals is a mere byproduct of individual variation or is the result of selection as would be required to qualify as an identity signal. On the receiver side, it is very likely that primates routinely integrate information from identity and state signals [e.g. Higham et al., 2011; Weingrill et al., 2003].

The fact that receivers integrate information from identity and current-state signals may have two important implications for the evolution of current-state signals. First, Silk and colleagues [2000] proposed a model, which showed that low-cost signals can be evolutionarily stable if individual act repeatedly. The empirical example provided in the paper discusses the honesty of grunts and girneys in female rhesus macaques, which are current-state signals advertising benign intent. The presence of social knowledge and repeated interactions, then, appears to aid the evolutionary stability of low-cost current-state signals. Second, signals of a given intensity are typically thought to have a common value across individuals. We can use, for example, the tail length of male widowbird to judge his quality relative to the other males in the population [Andersson, 1982]. However, if we also know information about the identity of a sender, we might consider the deviation of a current-state signal from the norm for

TABLE I. How Social Information is Transferred in Different Situations

Phenotype	Sender-receiver relationship	
	Familiar	Unfamiliar
Stable	Social knowledge/ identity signals	Badges of status
Unstable	Current-state signals	Current-state signals

that sender rather than the population as a whole. Two individuals (A and B) may give threat displays of similar intensity. Based on previous interactions, we may know that A is very quick to threaten and back down while B threatens sparingly and rarely backs down once provoked. In this case, we should interpret the threat displays differently based on our knowledge. Indeed, studies in primates show that familiar and unfamiliar animals do interpret fertility signals differently [Higham et al., 2011; Weingrill et al., 2003]. Because receivers incorporate social knowledge and identity information into the interpretation of current-state signals, selection for senders to follow a uniform signal code may be relaxed in primates. Relaxation on the correlation between signal intensity and quality across individuals may explain, to some extent, the debate surrounding some current-state signals such as sexual swellings in primates [Huchard et al., 2009].

Identity and badge of status signals

Identity and badge of status signals are less complementary. On the sender side, there is some evidence from fallow deer that the aspects of signals that transmit quality information are unreliable indicators of identity information [Briefer et al., 2010]. No work has explored this relationship directly in primates, but there are theoretical reasons that quality and identity signaling may be incompatible. To be useful to the receiver, an identity signal must be both distinct and repeatable while a badge of status must be correlated with the aspect of quality being assessed [Dale et al., 2001]. Thus, it is unlikely that the same feature will satisfy both of these criteria, although senders may utilize separate identity signals and badges of status simultaneously. On the receiver side, identity and badges of status are useful in very different social situations, making it less likely that receivers will rely on both types of information in a given interaction. When they do, we argue that the badge of status is more accurately viewed as a current-state signal.

Current-state and badge of status signals

On the sender side, current-state and badge of status signals are similar in that both may provide information about the quality of an individual, with the key distinction being the stability of that information/characteristic. While this distinction may be somewhat arbitrary, the nature of the distinction is such that signals relating to a single aspect of the sender must be either badge of status or current-state signals (i.e. either the trait is reasonably stable or it is not). Senders may, however, use different current-state signals and badges of status simultaneously. On the receiver side, it is likely that information from current-state signals and badges of status are integrated (e.g. a threat from a male sig-

nalizing high quality may be more intimidating than a threat from a male signaling low quality).

Signals and social knowledge

For identity and current-state signals, the relationship to social knowledge is straightforward—the signals augment the use of social knowledge and facilitate the receiver's response to familiar individuals. In the case of badge of status and social knowledge, the relationship is more antagonistic, with badges of status serving as a substitute for social knowledge in situations where social knowledge is not practical. However, the precise nature of the relationship, both in functional and evolutionary terms, needs further exploration. Here, we present a comparison between two closely related and well-studied species, chacma baboons and geladas, to illustrate the apparent trade-off between badges of status and social knowledge.

Baboons are representative of most Old World monkey societies with closely bonded, philopatric females, and mostly immigrant males that are long-term residents [Seyfarth, 1976]. While chacma baboon groups are among the larger primate groups (up to 120), they are stable and interactions with unfamiliar animals are infrequent [Cheney & Seyfarth, 2007]. Correspondingly, a wealth of observational and experimental data indicate the extent to which chacma baboons use social knowledge to guide their interactions, going well beyond simple recognition of all members of their group [Cheney & Seyfarth, 2007]. For example, female baboons are simultaneously sensitive to both the rank and kin relations of other females in their group, information that may be useful in recruiting and joining alliances [Bergman et al., 2003]. Furthermore, male baboons are sensitive to the relative ranks of others [Kitchen et al., 2005], and respond differently to males that are climbing or falling in the hierarchy [Bergman et al., 2006]. Both males and females have signals of reproductive condition (sexual swellings in females, wahoos in males) that allow males to gain more information about familiar individuals. Baboons are not known to have badges of status. As such, baboons are representative of most primates.

In contrast, geladas live in aggregations of reproductive units [Dunbar, 1983] comprised of 2–10 natal females and 1–4 long-term resident males (1 reproductive male and 0–3 nonreproductive males). Although not well studied, it is likely that social knowledge guides interactions within the small, stable reproductive units. Females have sexual swellings that indicate fertility [Dunbar, 1977], facilitating assessment by familiar males within the reproductive unit [extra-unit copulations are extremely rare, Snyder-Mackler et al., 2012a]. These units form fluid aggregations with other units and prereproductive bachelor males that regularly

number over 500 individuals and can be as large as 1,100 geladas [Snyder-Mackler et al., 2012b]. Experimental work has shown that males fail to vocally recognize other males outside their reproductive unit, even those that they associate with on the majority of days [Bergman, 2010]. Furthermore, bachelor males do not appear to monitor the relationships between males and females in reproductive units, information that could be useful in deciding which males to attack [le Roux et al., 2011]. However, geladas do appear to have a badge of status, the male chest patch that is redder in reproductive males and redder in males with more females in their reproductive unit [Bergman et al., 2009]. Thus, bachelor males may rely on the chest patch rather than social knowledge when deciding which unit males to attempt to displace. As such, with a derived system featuring limited social knowledge and a badge of status, geladas are similar to many nonprimate taxa.

The baboon–gelada comparison, along with the other cases of badges of status in primates, highlights an apparent trade-off between badges of status and social knowledge. A reliance on social knowledge is adaptive in stable groups composed of familiar individuals [Tibbetts & Dale, 2007] while badges of status are adaptive in large fluid social groups [Tibbetts & Safran, 2009]. However, several issues remain unresolved. Most importantly, the functional relationship between badges of status and social knowledge is not clear. Is the apparent trade-off real? Social knowledge and badges may be absent in the same situations simply because they are useful in different situations and they have no direct effect on each other. For example, gills and wings are rarely seen together, but they have no functional relationship to each other. However, given that social knowledge and badges provide largely redundant information about senders (e.g. their status), the presence of one may diminish the relative benefits of the other. In this sense, the distinct use of badges or social knowledge may result from a trade-off between the two. If there is a trade-off, is it the case that social knowledge is superior, and badges of status only evolve when it is not available?

These questions are mirrored in uncertainties about the evolutionary relationship between social knowledge and badges of status. Given the prevalence of stable social groups across primates, the ancestral condition of most anthropoid primates is likely to be a reliance on social knowledge in stable social groups of familiar individuals. Our review suggests that badges of status have evolved primarily in cases where social knowledge is less useful (i.e. large or dynamic social systems). This pattern could result from an evolutionary trade-off between social knowledge and badges of status. Social knowledge may limit the utility of badges of status, blocking their evolution in most primates [as has also been

suggested in sparrows, Rohwer, 1982; Tibbetts & Safran, 2009].

However, an alternate possibility exists; perhaps the evolution of badges of status has facilitated interactions with unfamiliar individuals, allowing the subsequent evolution of fluid social systems in some taxa. For example, the baboon's wahoo may facilitate interactions between both familiar and unfamiliar animals, setting the stage for the evolution of a more fluid system where males frequently interact with unfamiliar males, using wahoo displays to assess each other. In this case, a current-state signal would be an evolutionary precursor to a badge of status [cf. Huchard et al., 2009 who propose a similar transition with female swellings without invoking social knowledge]. More broadly, such a scenario would suggest that a reliance on social knowledge constrains the evolution of social systems because primates tend to lack the types of signals that facilitate interactions with unfamiliar individuals. We look forward to further exploration of these issues.

SUMMARY

The relationship between signals and social knowledge is either complementary or antagonistic depending on the type of signal. With respect to social knowledge, we describe three classes of signals. (1) Identity signals directly facilitate social knowledge, (2) current-state signals supplement knowledge gained through social knowledge, and (3) badges of status replace social knowledge. Among animals, primates are unusually reliant on social knowledge in guiding their day-to-day interactions. As such, primates rely extensively on identity information, but it remains to be determined to what extent this is based on receiver perception of individual variation or senders using identity signals. Primates frequently utilize current-state signals including signals of intent to augment their interactions with familiar individuals. Badges of status are rare in primates, and the cases where they are used point to a functional and evolutionary trade-off between badges of status and social knowledge. However, the nature of this relationship is needs further exploration.

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