Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis

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Although monitoring social information is a key aspect of the social complexity hypothesis, surprisingly little work has compared social knowledge across different species of wild animals. In the present study, I use playback experiments to test for individual recognition in wild male geladas (*Theropithecus gelada*) to compare with published accounts of social knowledge in chacma baboons (*Papio ursinus*). Geladas and baboons are closely related primates living in socially complex groups that differ dramatically in group size—geladas routinely associate with more than 10 times the number of conspecifics than do baboons. Using grunts from non-rival males to simulate approaches, I examined the strength of a subject male's response when the 'approach' was from the direction of (i) non-rival males (control), or (ii) rival males (a more salient stimulus if playback grunts are not recognized by the subject). I compared responses separately based on the degree of social overlap between the caller and the subject. Responses indicate that male geladas, unlike baboons, do not use vocalizations to recognize all of the individuals they regularly encounter. This represents, to my knowledge, the first documented evidence of 'missing' social knowledge in a natural primate population. The sharp distinction between baboons and geladas suggests that geladas are either unable or unmotivated to keep track of the individual identity of other males in their multi-level society—even males with whom they have a large degree of social overlap. Thus, these results are consistent with the central assumption of the social complexity hypothesis that social cognition is costly.

Keywords: comparative cognition; social knowledge; individual recognition; social intelligence; vocalization; cognitive evolution

1. INTRODUCTION

According to the social complexity hypothesis, the intricacies of social life act as a selective pressure that favours the evolution of greater cognitive abilities (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988). Although aspects of this hypothesis remain somewhat controversial (Holekamp 2007), the social complexity hypothesis has received support from three types of evidence. First, across many taxa, increased sociality is associated with increased brain size, suggesting coevolution between these two traits (e.g. Barton 1996; Perez-Barberia *et al.* 2007). Given that brain size (or the relative size of parts of the brain) has been shown to relate to specific cognitive abilities (Reader & Laland 2002), the link between sociality and brain size predicts that more social species (i.e. species with social relationships that are more enduring, more numerous or more structured than less social species) should have greater cognitive abilities than less social species. Indeed, evidence for socially linked cognitive differences has been found in corvids (Bond *et al.* 2003). Second, many social species demonstrate sophisticated cognitive abilities (such as transitive inference and hierarchical classification) in the social realm (Cheney & Seyfarth 2007), suggesting that such complex cognition might be necessary for some social interactions. For example, female baboons classify other females simultaneously according to both individual attributes (rank)

and higher order groups (matriline; Bergman *et al.* 2003). Third, within a population, baboons (*Papio* spp.) with stronger social bonds (as measured by grooming rates and proximity) have higher offspring survival (Silk *et al.* 2003, 2009), indicating that adept social skills may confer a fitness advantage. These lines of evidence provide strong, but indirect, support for the social complexity hypothesis.

Missing from our current understanding of the social complexity hypothesis is a comparative understanding of how animals use social cognition in natural settings. Documenting the social information that individuals have (i.e. social knowledge) is a key aspect of social cognition, yet surprisingly little work has focused on comparative social knowledge in wild populations. Certainly, social knowledge has been studied across a variety of species, but very few studies have explicitly compared social knowledge in pairs of closely related species that differ in their sociality (see below for exceptions). Furthermore, most studies of social knowledge have focused on documenting the presence or absence of a particular type of social knowledge in a single species rather than testing for *differences in knowledge* across taxonomic groups. Only when we know how and why social knowledge differs across species, will we be able to fully understand the evolutionary relationship between social complexity and cognitive abilities.

Individual recognition (i.e. when one individual recognizes another according to distinctive characteristics) is the best-documented type of social knowledge, occurring

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in a wide range of taxa, from invertebrates (e.g. wasps, Tibbetts 2002) to vertebrates (e.g. lizards, Carazo *et al.* 2008; and mammals, McComb *et al.* 2000). Much of the work in mammals is based on playback experiments that test for vocal recognition. At the upper limit, African elephants (*Loxodonta africana*) have unusually large recognition networks, with adult females recognizing up to 100 other adult females (McComb *et al.* 2000). Individual recognition has been most widely demonstrated in primate species (reviewed in Tomasello & Call 1997). Primates have been repeatedly shown to respond differently to the vocalizations of specific individuals within their social group and even in neighbouring social groups (Cheney & Seyfarth 1982).

The best comparative data on individual recognition (or, at least discrimination) come from mother–infant studies (e.g. pinnipeds, Insley *et al.* 2003; swallows, Medvin *et al.* 1993; and ground squirrels, Schwagmeyer 1988). These studies take advantage of the special relationship between mothers and their infants. For example, mothers should be highly motivated to respond to the calls of their own offspring, but not those of other unrelated infants. This protocol has been used to demonstrate that there is variation in the presence or absence of discrimination across species for both mothers discriminating infants and infants discriminating mothers. This variation maps onto aspects of social structure and provides evidence that sociality and discrimination abilities can coevolve. Note that while such studies indicate variation in discrimination ability, only a few studies have actually found individual recognition of offspring by showing discrimination within groups of offspring (e.g. Rendall *et al.* 1996; Draganoiu *et al.* 2006; Muller & Manser 2008).

However, mother–infant recognition requires at most the recognition of only a few individuals and is not an open-ended system that could lead to the evolution of sophisticated cognitive abilities. More relevant to the social complexity hypothesis is the variation in recognition ability that involves the identification of many individuals. Currently, there is very little evidence of variation in such abilities across species. One of the few exceptions derives from a recent study of meerkats (*Suricata suricatta*; Schibler & Manser 2007). In a habituation–dishabituation experiment, meerkat subjects did not respond to alarm calls based on the identity of the caller. The authors contrast their results to those from a similar study (albeit using a different methodology) conducted on vervet monkeys (*Chlorocebus pygerythrus*), where vervets were found to respond to alarm calls primarily based on the identity of the alarm caller, thus allowing them to ignore unreliable callers (Cheney & Seyfarth 1988). The differences between vervets and meerkats are intriguing but difficult to interpret because of the different methods used in each experiment. More importantly, these results are difficult to interpret in a comparative framework because vervets and meerkats differ in so many aspects of their ecology and social structure.

A recent comparative study of individual recognition in ants (Dreier & d'Ettorre 2009) improves on the meerkat–vervet comparison. First, it compares two closely related species and thus eliminates many potential taxonomic confounds. Second, it compares species using similar methodologies, thus increasing the chances that different responses are owing to differences in cognitive abilities and not methodology. The ant comparison found that individual recognition occurs in species (*Pachycondyla villosa* and *Pachycondyla inversa*) with complex social interactions (i.e. dominance hierarchies) but is absent in a species (*Lasius niger*) that lacks these interactions. These results suggest that complex social interactions can select for greater social knowledge (although it remains possible that the reverse may have occurred, i.e. that differences in recognition led to the evolution of complex social interactions).

These data on individual recognition in ant species raise several new questions. First, do some species keep track of more individuals than others, and if so, why? Second, do we see quantitative differences in social knowledge among large-brained animals like primates? The social complexity hypothesis seeks to explain the evolution of sophisticated cognitive abilities and, therefore, social complexity should be cognitively challenging even among cognitively advanced species. Here, I examine individual recognition in wild geladas (*Theropithecus gelada*) for comparison with previously published findings from chacma baboons (members of a sister genus, *Papio*; Page *et al.* 1999).

Both baboons and geladas share many morphological and behavioural attributes and live in complex societies with socially differentiated relationships. However, the two genera differ markedly in their social structure. Baboons (with the exception of *Papio hamadryas*, Kummer 1968) live in stable matrilineal, multi-male/multi-female social groups with no discernable substructure and little or no interaction between groups. By contrast, geladas live in much larger and more fluid multi-level societies (Kawai *et al.* 1983; Dunbar 1984, 1993). At the most basic level of gelada society is the one-male unit, composed of a leader male, one or more follower males (together, leader and follower males will hereafter be referred to as *unit males*), several adult females and their offspring. Younger adult males that do not yet have a one-male unit live in all-male groups (bachelor groups). One-male units that share a home range and frequently intermingle (47–76% of the time, §2) are called a *band*, and temporary aggregations of units from one or more bands are called a *herd*. Herds can number over 1000 animals (Kawai *et al.* 1983).

We know from previous research that baboons have extensive knowledge about other members of their group (reviewed in Cheney & Seyfarth 2007). Although the goal of these studies was not to explicitly test for individual recognition, in most cases, individual vocal recognition was required to obtain the predicted results (e.g. females, Bergman & Beehner 2003; Cheney & Seyfarth 1999; and males, Crockford *et al.* 2007). For example, in a study that examined whether male baboons keep track of temporary relationships (in this case, consortships) between males and females, Crockford *et al.* (2007) played male grunts and female copulation calls from different locations to male subjects. Each subject heard three trials that differed in (i) the identity of the male caller (i.e. the female's consort partner versus another high-ranking male), or (ii) the timing of the playback relative to a consortship (i.e. while the male and female were in consort versus shortly after the consortship had ended). Note that the same vocalizations were played

in both parts of the second comparison. They found that the subjects responded strongly only when playbacks simulated temporary separation of current consort partners (Crockford *et al.* 2007), presumably because the male subject might be interested in this now-available, oestrous female. Such results would only be possible if the subject males recognized the grunts of the caller males. My goal here is to document the extent of individual recognition for male geladas in increasingly larger subgroups, starting with the one-male unit. I will then examine individual recognition in the larger band and then the herd. In contrast to baboons (and most other primates), geladas live in extremely large and fluid societies where individual recognition may not extend to all the animals they regularly encounter.

I tested for vocal recognition in male geladas by playing a series of low-pitched grunts to simulate the benign approach of another male to the subject. This is the same playback design used previously in baboons to explore the nature of male–male relationships (Bergman *et al.* 2006). The experimental design in geladas took advantage of the competitive relationship between bachelor males and unit males. Unit males intermingle frequently and peacefully with other unit males, and both inter- and intra-unit sneak copulations are rare (Dunbar 1986). By contrast, unit males have a low tolerance for the close presence of bachelor males. If bachelor males are to gain reproductive access to females, they must challenge (and defeat) a leader male to take control of the one-male unit. Not surprisingly, unit males are vigilant when bachelor males approach (Mori 1979), but show little or no response when unit males approach (T. J. Bergman 2006, personal observation). I, therefore, predicted that the simulated approach of an *unknown* male (even when the male was another unit male) should elicit strong responses from male subjects (all of which were unit males), since any unknown male has the potential to be a bachelor rival. By contrast, I predicted that the same male subjects should respond weakly to simulated approaches of *known* unit males. I compare responses separately for subject–caller pairs based on their degree of social overlap across the study period, which ranges from 100 per cent (members of the same unit that spend every day together) to 0 per cent (males from different areas that have never encountered one another). I expect to find individual recognition among males within the unit (small, stable social groups). However, I am more interested in whether individual recognition occurs in caller–subject pairs that have intermediate overlap (i.e. members of the same band or herd). Do the same subjects' responses resemble within-unit pairs (suggesting recognition) or unknown pairs (suggesting lack of recognition)?

2. MATERIAL AND METHODS
(a) *Gelada social system*
All census observations indicated that members of the same unit are always together. By contrast, members of units from neighbouring bands could be found in the same herd together as little as 6 per cent of observation time (see below) and probably had very few social interactions. Two intermediate levels between the unit and the herd exist. Although rare, there are *teams* of one-male units that

generally are found in close association with each other, and it is thought that these teams are the result of recently fissioned units (Dunbar 1984). Units (and teams) join together to form bands that typically number approximately 250 individuals. These are long-term (but fluid) associations that share a home range. Members of the same band are typically found together a majority of the time (see below) and are often in close proximity (less than 5 m).

Among adult males, leader males account for the vast majority of matings. Males remain leaders of a unit for an average of 3.2 years (based on observing 34 leader males for an average of 1.6 years per male, or 54.6 male years, T. J. Bergman 2010, unpublished data). Follower males are typically older males that are deposed unit leaders that remain in the group but lack reproductive access to females. Females in a unit remain together following changes in the leader male, and it is thought that unit females are closely related (Dunbar 1984).

Young males leave their natal unit before maturity and join an all-male group where they remain for several years before attempting to take over a unit. Males of different one-male units are frequently in close proximity (less than 5 m) with little vigilance towards other unit leaders or followers (T. J. Bergman 2006, personal observation). By contrast, bachelor males are typically peripheral to the group. The approach of a bachelor towards the one-male units is associated with considerable vigilance and agitation among unit males (Mori 1979).

(b) *Study site*
Research was conducted in the Simien Mountains National Park, Ethiopia, from August 2006 to May 2007 in the Sanka-ber area, where the gelada population totals approximately 1200 individuals spread out across four bands that occasionally intermingle in the same herds. Two of these bands have been under intensive behavioural study since January 2006 and are fully habituated to human observers on foot (approach distances less than 3 m). Research was conducted in high grasslands where visibility typically extends to several kilometres, making it easy to monitor the location of geladas.

(c) *Experimental design*
Following a protocol used previously in chacma baboons (Bergman *et al.* 2006), I used grunts of unit males to simulate the close approach of an individual to the subject male. In both studies, the stimulus vocalization was used only to indicate the presence of the caller, and therefore needed to be a benign, non-threatening call. For baboons and geladas, grunts are quiet vocalizations, used in affiliative contexts (Aich *et al.* 1990; Palombit *et al.* 1999). Grunts are the most common vocalization for both unit males and bachelor males (T. J. Bergman 2006, unpublished data). Thus, even though grunts are typically directed at animals within a unit or bachelor group, unit males frequently hear the grunts of extra-unit males. Furthermore, gelada grunts (figure 1) resemble baboon grunts that are harmonically rich and relatively easy to identify individually (Aich *et al.* 1990; Owren *et al.* 1997; Rendall 2003). For all playback trials, I used a natural sequence of two to four short grunts and one to two prolonged grunts ('prolonged moan'; Aich *et al.* 1990; figure 1). Grunt sequences were recorded opportunistically during behavioural observations from less than 7 m using a Sennheiser ME-66 directional microphone and a Marantz PMD 660 digital recorder. Calls were recorded
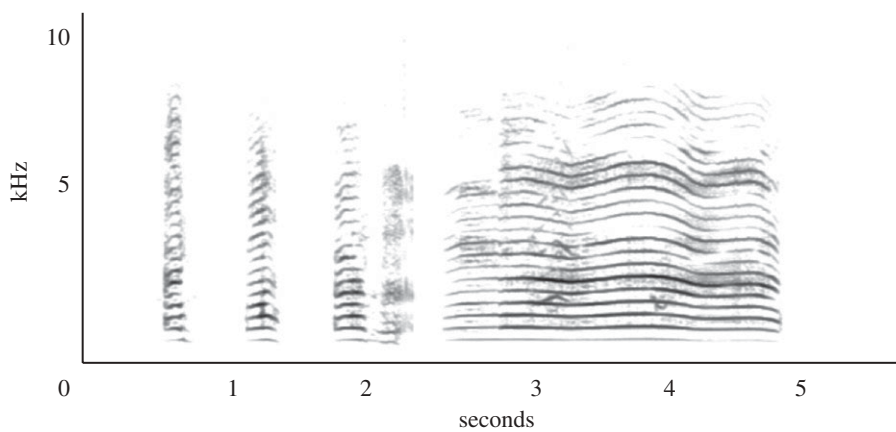
Figure 1. Spectrogram of a playback sequence of three short grunts and one prolonged grunt. Note geladas frequently produce vocalized inhalations during grunt sequences, and one can be seen between the third short grunt and the prolonged grunt. Spectrogam created using PRAAT 5.1.02 for Macintosh with a Gaussian window of 0.05 s.

as WAV files and edited using DSP-QUATTRO 2.1 for Macintosh. Grunts from 15 callers (13 leader and two follower males) were used to create the sequences and each sequence was played to 1–3 unit male subjects. All sequences were matched for duration (approx. 4.5 s, figure 1) and adjusted by ear to match the amplitude of natural grunts.

In designing this playback experiment, I considered the following: unit males should respond differently to the simulated approach of a known versus an unknown male (even when the unknown male is a unit male). The simulated approach of a known unit male does not represent a threat to the subject; however, the simulated approach of an unknown unit male *might* be a threat because it might be a bachelor male. Thus, the 'cautious' response would be for the subject to move away or orient towards the speaker in an attempt to gain more information about the caller's identity. Thus, I predicted that the grunts of unknown unit males would elicit strong responses (i.e. longer duration of orienting towards the speaker), while the grunts of known unit males would elicit weak responses (i.e. shorter duration of orienting or no response at all).

Complicating the playback design somewhat, I reasoned that male subjects may not respond to *all* unknown male callers the same. For example, if males do not individually recognize other males within their band or herd, then presumably these males frequently hear the vocal approach of unknown males. Therefore, to increase the salience of the vocal stimulus, I varied the direction that the 'approaching' male is coming from. Unit males continuously monitor the location of bachelor males (Mori 1979) and thus might respond differently to unfamiliar males depending on the direction from which they appeared to be approaching. Evidence from territorial birds (e.g. Stoddard *et al*. 1991) and chacma baboons (Crockford *et al*. 2007) indicates that subjects respond differently to simulated vocalizations depending on the location of the 'caller'. Therefore, I used a paired design, playing the same vocalization to the same subject from two different locations (on different days, separated by at least 3 days): (i) from the direction of other unit males (control sequence), and (ii) from the direction of a bachelor group (a more salient stimulus if the playback grunts are not recognized). This restricted all playback trials to subjects that were positioned at the edge of the band sitting closest to the bachelors, so that in one direction the nearest animals were bachelors and in the opposite direction the nearest animals were unit males. The only factor differentiating the two trials was the location of the speaker, and thus the likelihood that the approaching male could be a bachelor if the grunts were unfamiliar to the subject. Because *in all cases* the playback grunts were those of unit males, a weak response to the simulated grunts in both directions would suggest that the grunts were familiar to the subject. On the other hand, a strong response to the simulated grunts from the direction of the bachelors but a weak response from the direction of other units would indicate that the grunts were unfamiliar to the subject.

To detect the limits of individual recognition, I used subject–caller pairs with varying degrees of social overlap. 'Overlap' between a male subject and the male caller was calculated as the number of days the two were present at the same sleeping site divided by the number of days the sleeping site was known for the subject. I measured unit overlap for the 6.5 months preceding the initiation of playback experiments (from 12 August 2006 to 28 February 2007). Outside of units, these values ranged from 0–92%; the highest degree of overlap (92%) was between males from the only team in our study population. Aside from this team, overlap for males in the same band ranged from 47–76%. Individual males from different bands overlapped with other unit males in the same herd from 6–16%. For a subset of experiments, I also used calls from completely unknown males, recorded from a location 30 km away from the boundary of the study herd's range (i.e. 0% overlap).

All trials were conducted under the following conditions: (i) a single bachelor group was present (within 500 m) but out of sight from the subject, and (ii) the male caller was present (within 500 m) but out of sight from the subject (with the exception of the 0% overlap animals who were never present). In all trials, the speaker was hidden behind an object large enough to hide a male gelada, speaker–subject distance was between 5 and 10 m, and the calls were played only if the subject had not oriented towards the speaker in the preceding minute. Although my ability to conduct trials was limited by natural circumstances, I attempted to balance the number of times that a subject's first trial came from each direction (towards the bachelors or towards the unit males). Sixteen subjects first heard grunts towards the bachelors, and 11 subjects first heard grunts away from the bachelors.

I conducted 58 trials including 27 complete pairs (i.e. grunts being played from both directions); the remaining

four unpaired trials were not included in analyses. Trials included 18 subjects (12 leaders and six followers); nine subjects appeared in two pairs of trials with different degrees of overlap with the caller. Initial trials indicated a lack of recognition beyond the band, so trials were concentrated among categories with more overlap and distant categories were combined for analyses. The 27 pairs represented eight *within-unit* pairs (including six leader and follower males from the same unit and two pairs from the same team), 10 *within-band* pairs and nine *distant* pairs (including six from the same herd but not the same band, and three from a completely different area).

(d) *Analysis*
All playback experiments were videotaped with a Canon ZR80 camcorder and videos were scored on a computer with a frame-by-frame analysis (using iMovie '08) by two independent observers. Values were averaged for both observers (they never differed by more than 5%). Measurements include (i) the duration of orienting towards the speaker in the minute following the onset of the playback vocalizations and, (ii) any movement of more than 5 m in the minute following the playback (Bergman *et al.* 2006). Observers also recorded whether the subject grunted before the end of the playback sequence, possibly in response to the playback. Because geladas in the same unit often exchange grunts (Richman 1987), a subject's grunts immediately after a playback were taken as evidence of recognition of the caller. Responses were analysed using SPSS for Mac v. 17.0 with statistical significance set at 0.05.

3. RESULTS
The duration of orienting towards the speaker for trials involving follower males (either as subjects or callers, $n = 18$) did not differ from trials without follower males (Mann–Whitney $U = 258.5$, $p = 0.20$). The duration of orienting also did not differ between first and second trials (Mann–Whitney $U = 318$, $p = 0.41$).

Subjects moved away from the area within 1 min following playback grunts in only 14 trials. Eight of these 14 trials involved grunts played from the direction of the bachelors, thus the likelihood of moving did not differ based on the direction ($\chi_1^2 = 10.3$, $p = 0.59$). Moving away from the area following the playback experiment did not appear to be informative and was not analysed further.

Following all simulated approaches, subjects oriented towards the speaker in 38 of 54 trials (70%), and the mean ($\pm$ s.d.) duration of looking towards the speaker was 2.52 ± 3.47 s. Using a Wilcoxon signed-ranks test, I analysed each caller–subject pair to compare orienting responses based on the direction of the speaker. Overall, subjects looked towards the speaker for longer when the call came from the direction of the bachelors ($n = 27$, $Z = -3.2$, $p = 0.002$). For *within-unit* pairs, subjects' responses were generally weak, and the direction of the speaker had no effect on response ($n = 8$, $Z = -0.14$, $p = 0.89$; figure 2a). Responses were significantly stronger when the call came from the direction of the bachelors for both *within-band* ($n = 10$, $Z = -2.52$, $p = 0.01$, figure 2b) and for *distant* pairs ($n = 9$, $Z = -2.19$, $p = 0.03$; figure 2c). Note that we placed the two males from the same team in the within-unit category, but the
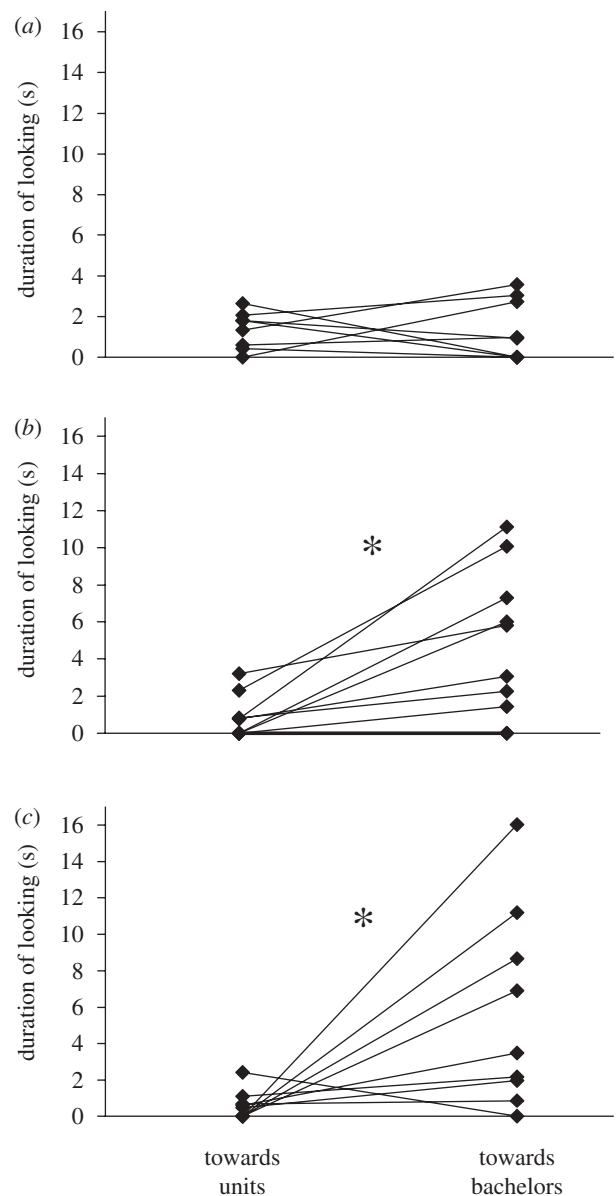

Figure 2. Summary of the time subjects looked towards the speaker in paired playback trials. On different days, each subject heard the same animal's vocalization from the direction of the bachelor group ('towards bachelors') or from the direction of the unit males ('towards units'). Subjects and callers were either (*a*) in the same unit or team (*within unit*), (*b*) in a different unit but in the same band (*within band*), (*c*) or from different bands or herds (*distant*). Asterisk indicates significant differences at $p < 0.05$.

results did not change if we placed these males in the within-band category (data not shown).

Because recognition appears to end at some point between the unit and the herd, I further explored the within-band category to look for evidence of recognition among band members with high degrees of overlap. I divided the within-band category (without teams) in half based on overlap. Even among the high-overlap group (overlap range 0.64–0.76), responses were significantly stronger when the call came from the direction of the bachelors ($n = 5$, $Z = -2.02$, $p = 0.04$). In addition to categorical analyses, I also used linear regression to continuously compare the degree of overlap with responses to the experiments. For this analysis, my
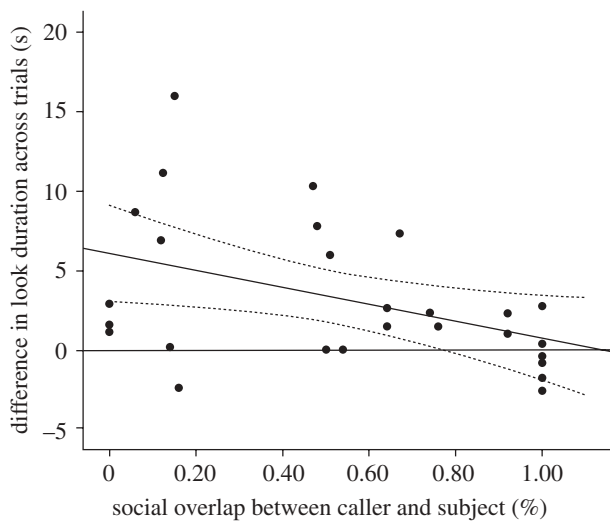
Figure 3. Scatter plot of responses to playbacks against overlap between the subject and the caller. Each point represents a caller-subject pair. The response variable is the duration (in seconds) of looking when the call is played from the direction of the units subtracted from the duration of looking when the call is played from the direction of the bachelors (positive values indicate lack of recognition). Solid line is from linear regression and dashed lines indicate 95% confidence intervals for this regression.

dependent variable was the look duration when calls were played from the direction of the units subtracted from the look duration when calls were played from the direction of the bachelors. Note that this value should be zero in the cases of recognition and positive (indicating longer looks in the direction of the bachelors) when there was no recognition. The independent variable was the degree of social overlap between the subject and the caller. Although there was a significant negative relationship such that response differences decreased as overlap increased ($n = 27$, $r^2 = 0.19$, $p = 0.025$; figure 3), this relationship disappeared when I removed the within-unit trials from the analysis ($n = 21$, $r^2 = 0.05$, $p = 0.3$). Importantly, in the analysis including all trials, the regression line crossed 0 (suggesting recognition) at beyond 100 per cent overlap and the 95% confidence interval for the regression line crossed 0 at 77 per cent overlap (figure 3). Thus, the data are consistent with recognition only at the very highest levels of overlap.

Subjects grunted before the end of the playback grunts in four trials, all of which were within-unit trials. Grunts were significantly more likely in within-unit trials than they were in other trials (Fisher exact test, $p = 0.006$), supporting the results from the looking responses that showed recognition within units.

4. DISCUSSION
Results from this study demonstrate that individual recognition can vary quantitatively in an open-ended system across primate species. Gelada males recognize by voice only *some* of the males that they regularly encounter. Specifically, males only recognize other males in their unit (and possibly their team). When male subjects heard the simulated approach of a male within their own unit or team, they did not attempt to acquire additional information about this male—even when he

'approached' from a side where bachelors were present. In some cases, subject males even grunted in response to this 'approach', a behaviour commonly observed during natural interactions between males in the same unit. Although this result is unsurprising given the strength and stability of relationships within gelada units, it indicates that gelada grunts contain sufficient acoustic information for individual recognition.

By contrast, vocal recognition for males did not extend beyond the unit. Gelada males did not vocally recognize *any* other males—even males from their own band with whom they had extensive social overlap (up to 76%). When male subjects heard the simulated approach of a male outside their unit, they only responded strongly if he 'approached' from the side where bachelors were present. Importantly, they responded the same whether the male was a band member (that they could potentially recognize) or a completely unknown animal. In these trials, subjects responded in the same way that they would have if the caller was a bachelor male (recall that male 'callers' in these experiments were never bachelors). This unexpected result contrasts with much of the current data from other primates, including studies on the closely related chacma baboons, who vocally recognize all of the animals they encounter regularly (members of their own group), and vervet monkeys, who vocally recognize not only members of their own group but also members of neighbouring groups with whom they have little contact (Cheney & Seyfarth 1982). In summary, geladas do not individually recognize the animals that surround them day to day, and thus this is, to my knowledge, the first evidence of 'missing' social knowledge in a wild primate.

How do these results fit in with the social complexity hypothesis? At the present time, several possibilities emerge. First, geladas may not keep track of other males because they are *unable* to do so. This hypothesis indicates that the numbers of animals geladas regularly encounter exceed their recognition capacity. A chacma baboon group typically has 2–15 males, and, rarely, as many as 20 males (Hamilton *et al*. 1976; Cheney *et al*. 2004; Hamilton & Bulger 1992). Conversely, gelada bands typically number over 30 adult males, and a herd can have over 100 males (Kawai *et al*. 1983; Dunbar 1984). It is possible that that geladas are unable to recognize more than 20–30 individuals, a result that would validate the assumption that tracking social information can be cognitively challenging, providing support for the social complexity hypothesis.

Second, geladas may not keep track of other males because they are unmotivated to do so. At present, I am unable to rule out a motivational rather than cognitive difference between baboons and geladas. Gelada unit males may not have incentive to learn about other males in their bands. Unlike baboons, where males in the same group actively compete for dominance rank and access to females, gelada males from different units are not in competition with one another and lack consistent dominance relationships (Dunbar 1984). Thus, gelada males may have the cognitive capacity to learn about other members of their band or herd, but they lack the *motivation* to do so. This explanation suggests that males with motivation (i.e. bachelor males) might demonstrate the ability to keep track of other males. Bachelor males face the problem of choosing which leader males to challenge in takeover

attempts and, as such, might benefit from having information about their potential opponents—such as how many females are in the unit, the current condition of the leader male and possibly even the strength of the social relationship between the leader male and his females. Unfortunately, it is not possible to assess recognition in bachelors using the same playback design because they respond equally strongly to all males outside of their bachelor group (T. J. Bergman 2006, personal observation). At present, I am in the process of using other methods to gather information on bachelor social knowledge. If bachelor males do have widespread individual recognition, this would support a motivational, rather than cognitive, difference between baboon and gelada males. It is important to note, however, that differences in motivation (versus differences in ability) would suggest that wild animals may optimize social cognition by ignoring some social information that is available to them.

Results from this study suggest that the gelada social group might be smaller and simpler than previously thought. There is some uncertainty about which level of a multi-level, fission–fusion society is comparable to the 'group' in other primate taxa (Dunbar 1995). The gelada band has been called the *ecological* equivalent of the baboon group (Dunbar 1984), yet the *cognitive* equivalent might actually be the one-male unit or team (Dunbar 1995). The limits of social knowledge may be one method of delineating the 'group' boundary for multi-level societies such as that found in geladas and hamadryas baboons. Results presented here match Dunbar's (1995) cognitive group size and suggest that the one-male unit (or possibly team) represents the gelada 'group'—and is analogous (and probably homologous) to the baboon group. If this is the case, then the band may not be a true social entity, but rather a simple aggregation of animals based on predator protection and/or limited sleeping sites. However, even if gelada social groups are relatively small and simple, the results presented here still stand in sharp contrast with other primates. Geladas have ample opportunities to learn to recognize other animals in their band, but they do not. Unique among primates, they fail to recognize animals that they encounter at a close distance on most days.

It is surprising that the approach of an unfamiliar male could cause so little reaction in gelada males; responses were weak when unknown males 'approached' from the direction of the unit males. Such a lack of concern about a potentially unknown male lies in sharp contrast to baboons and most other primates (Kitchen *et al.* 2003, 2004; Fisher *et al.* 2004). Perhaps, this difference may result from another unique feature of a harem-based system—mainly, that unit males do not represent a threat to other unit males. This difference suggests that geladas have evolved a greater tolerance for the close proximity of unfamiliar animals, a behavioural characteristic also found in bonobos (*Pan paniscus*) as compared with their close relatives, the common chimpanzees (*Pan troglodytes*; Hare *et al.* 2007). It remains to be determined whether this heightened tolerance for conspecifics in geladas might be associated with greater socio-cognitive abilities as it is in bonobos (Hare *et al.* 2007).

Unit males appear to monitor bachelors in much the same way they might monitor a predator. Animals do not need to have social knowledge (such as individual recognition) to avoid predators. They merely need to monitor their location. Similarly, with the exception of their own unit, males do not appear to learn the identity of other males around them. Rather, they simply keep track of the current location of the bachelors. This suggests that, just as some ecological situations can have social aspects (e.g. cache pilfering in jays; Dally *et al.* 2005), social problems can mirror ecological tasks. There has been considerable discussion of the relative importance of ecological and social factors in driving cognitive evolution (e.g. Shultz & Dunbar 2006). However, before we attempt to further assess the relative importance of ecological and social selective pressures in cognitive evolution using indirect measures (e.g. group size and brain size), perhaps we would do better to first focus on the specific types of information that animals use in natural settings.

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