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Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*)

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Abstract Behavioral flexibility is considered by some to be one of the hallmarks of advanced cognitive ability. One measure of behavioral flexibility is how subjects respond to novel objects. Despite growing interest in comparative cognition, no comparative research on neophilia in wild primates has been conducted. Here, we compare responses to novel objects in wild chacma baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*). Baboons and geladas are closely related taxa, yet they differ in their ecology and degree of social tolerance: (1) baboons are habitat and dietary generalists, whereas geladas have one of the most specialized primate diets (90% grass); (2) baboons exhibit an aversion toward extra-group individuals, whereas geladas typically exhibit an attraction toward them. Using subjects of all age and sex classes, we examined responses to three different objects: a plastic doll, a rubber ball, and a metal can. Overall, baboon subjects exhibited stronger responses to the objects (greater neophilia and exploration) than gelada subjects, yet we found no evidence that the geladas were afraid of the objects. Furthermore, baboons interacted with the objects in the same way they might interact with a potential food item. Responses were unrelated to sex, but immatures showed more object exploration than adults. Results corroborate novel object research conducted in captive populations and suggest that baboons and geladas have differences in behavioral flexibility (at least in this cognitive domain) that have been shaped by ecological (rather than social) differences between the two species.

Keywords Novel objects · Neophilia · Exploration · Primate · Neophobia · *Theropithecus gelada* · *Papio ursinus* · Baboon · Cognition

Introduction

Recent literature reflects a growing interest in the relationship between behavioral flexibility and cognitive processes (Reader and Laland 2003; Lefebvre et al. 2004; Roth and Dicke 2005; Sol et al. 2005). Because responses to novel objects can provide an assay of some aspects of behavioral flexibility, comparative novel object research has the potential to address fundamental issues about the evolution of cognitive abilities. For example, the hypothesis that ecological complexity favors the evolution of greater cognitive ability (Parker and Gibson 1977; Milton 1988) is supported by the existing comparative data on novelty behavior. Across a range of taxa, less fear of or greater attraction to novel stimuli (less neophobia and greater neophilia, respectively) has been associated with (1) more omnivorous diets (Glickman and Sroges 1966; Clarke and Lindburg 1993), (2) greater ecological plasticity (Greenberg 1984, 1990; Martin and Fitzgerald 2005), (3) extractive foraging (Day et al. 2003), and (4) habitat complexity (Mettke-Hofmann et al. 2002).

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In addition to the comparative evidence for ecological correlates, many within-species studies indicate that social and/or demographic factors are reliable predictors of object exploration. First, studies across a wide variety of taxa report differences in responses to novel stimuli based on age (Glickman and Sroges 1966; Fragaszy and Mason 1978; Joubert and Vauclair 1986; Henrich 1995; Visalberghi et al. 2003; Kendal et al. 2005), despite broadly similar ecological conditions (e.g., diet and habitat) for adults and immatures. Second, results from several studies indicate that responses to novelty are related to dominance rank, although which rank is more likely to initiate object interaction varies among studies (subordinates: Menzel 1966, 1971; Katzir 1982; Stahl et al. 2001; Stöwe et al. 2006b; dominants: Drea 1998). Finally, responses to novel objects differ across social contexts (effect of companion presence: Stöwe et al. 2006a; effect of companion type: Fragaszy and Mason 1978; Drea 1998; Stöwe et al. 2006b). Taken together, these within-species results suggest that differences in social factors might also determine differences in object exploration between species. However, no study has explicitly related differences in neophilia and neophobia to social differences between species. This is surprising given that social complexity (like ecological complexity) is thought to be a major factor driving cognitive evolution (Jolly 1966; Humphrey 1976; Byrne and Whiten 1988).

Furthermore, despite the importance that ecology and social context play in responses to novel objects, few between-species comparative studies have been conducted on wild animals living in their natural habitat (Greenberg 1989; Webster and Lefebvre 2001; see also novel foods: Cambefort 1981). Non-captive research might be particularly necessary for primates, who are reported to respond more strongly to novel objects when in captivity (Visalberghi et al. 2003). In fact, innovation, which is believed to be linked to neophilia (Day et al. 2003; Reader and Laland 2003), is also more common in captivity, perhaps because captive animals have more 'spare time' (Reader and Laland 2003). This suggests that if species demonstrate different responses to novel objects in captivity, the difference could be due, at least in part, to differences in how the species respond to captivity itself. Thus, as a first step in addressing how natural selection shapes species-typical responses to newly discovered objects, studies should be conducted under natural conditions (for a similar argument in other cognitive studies, see Laidre 2007).

To study how social setting and ecology shape species-typical responses to novelty, we compared responses to novel objects in chacma baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*) in their natural habitats. *Papio* and *Theropithecus* are closely related members of the Old World monkeys (Cercopithecoidea), and some phylogenetic analyses report the two genera as sister taxa (Page et al. 1999). However, despite their close phylogenetic relationship, these two genera exhibit dramatic differences in diet, habitat complexity, and social organization. First, all members of *Papio* are considered dietary generalists and eat a wide variety of foods including clumped resources such as fruits and seeds and opportunistic resources such as small insects and vertebrates (Rowell 1966; Altmann and Altmann 1970; Norton et al. 1987; Altmann 1998). In contrast, the diet of geladas is extremely specialized, consisting of over 90% grass (Dunbar 1977; Dunbar and Bose 1991; Iwamoto 1993; Hunter 2001). Second, *Papio* baboons are found in a broad array of habitats including open grassland, savannah, delta, mountains, semi-desert, and closed forests (Rowell 1966; Altmann and Altmann 1970; Aldrich-Blake et al. 1971; Whiten et al. 1987; Cowlishaw 1997; Henzi and Barrett 2005), whereas geladas are habitat specialists whose range is narrowly restricted to the high-elevation grasslands of Ethiopia (Crook 1966; Yalden et al. 1977; Mori and Belay 1990). Therefore, if ecological complexity (i.e., more varied diet and broader habitat tolerance) favors responsiveness to novelty, we predict that *Papio* baboons should be more likely to exhibit object neophilia and exploration than geladas.

The two genera also exhibit dramatic differences in social organization. Gelada society has a multi-level organization (Dunbar 1984, 1993). At the most basic level is the one-male unit (OMU), composed of a leader male, one or more follower males, several adult females, and their offspring. Only leader males have been observed to mate, and females remain together following changes in the leader male. OMUs that share a home range are called a band, and frequently one or more bands may join together to form a herd that can number over 1,000 animals (personal observation). Encounters between OMUs and between bands do not involve any vigilant behavior. Rather, geladas often move towards extra-group animals, and such groups fission and fuse seamlessly (Dunbar 1983). Conversely, the majority of *Papio* baboons (all except hamadrays baboons who have a derived multi-level society that differs dramatically from gelada society: Grüter and Zinner 2004) have discrete mixed-sex groups of around 30–100 individuals, comprising related females (and their offspring) and unrelated males. Female baboons form stable matrilineal hierarchies (Silk et al. 1999), whereas males compete for dominance rank and access to females (Bulger 1993). Individuals mainly interact with members of their own group and rarely interact with or remain in proximity to extra-group animals. In fact, inter-group encounters are characterized by high tension, vigilance, nervousness, and aggression (including male vocal displays, and chases), terminating when one or both groups move quickly away (Hamilton et al. 1975; Cheney and Seyfarth 1977; Henzi et al. 1998; Kitchen et al. 2004).

In sum, geladas are socially more neophilic and less neophobic than baboons. Social neophilia might relate to object neophilia: A growing body of research on behavioral syndromes and animal personality indicates that many behaviors are consistent across contexts (Sih et al. 2004; Dingemanse and Reale 2005). For example, an individual's response to novel objects and environments correlates with their response to conspecifics (Dingemanse and Reale 2005). If such context generality holds here, we predict that geladas will show greater object neophilia and exploration than baboons.

Over and above any taxonomic differences, demographic factors may influence novelty behavior. For example, both baboons and geladas exhibit the conserved Old World monkey behavioral pattern whereby males disperse from their natal group at maturity and females remain natal (di Fiore and Rendall 1994). Dispersal, or the tendency to seek out a new group, may be related to a predisposition toward novelty seeking (Fraser et al. 2001; Dingemanse et al. 2003). If this predisposition carries over to responses to objects (as discussed above), we expect large sex differences in responses to novel objects, with males of both species showing greater neophilia and object exploration, particularly among juveniles. Additionally, based on results from previous studies (Glickman and Sroges 1966; Fragaszy and Mason 1978; Joubert and Vauclair 1986; Henrich 1995; Visalberghi et al. 2003; Kendal et al. 2005), we expect juveniles will have stronger neophilic and exploration responses than adults. Finally, we look at responses across age to see if responses develop differently in baboons and geladas. For example, because the relatively simple habitat of geladas might limit any benefits to exploration, this behavior might be expected to decrease with age in geladas, but not baboons.

Methods

Study subjects—*Papio*

Trials on baboons were conducted on a single group in the Okavango Delta of Botswana by DMK from April–June 2006. Since 1978, the study group has been observed intermittently (e.g. Bulger and Hamilton 1987), and since mid-1992 the group has been under continuous observation on an almost daily basis (Cheney et al. 2004). All members of the group are fully habituated to human observers on foot. At the time of the study, the group ranged from 67 to 74 individuals, with 9–10 adult males, 22 adult females, and 36–42 immatures.

The site is extremely remote and the chacma baboons rarely encounter humans other than the researchers. However, they do occasionally pass through the research camp where they have a limited opportunity to see human-related objects (unlike many baboons living with some exposure to human habitation—particularly ones around tourist campsites—this group does not have access to garbage).

Study subjects—*Theropithecus*

Trials on geladas were conducted in the Simien Mountains National Park of Ethiopia by TJB from April—June 2006. Research was conducted in the Sankaber area, where the gelada population totals approximately 1,200 individuals (spread out across four bands). Two of these bands have been under intensive behavioral study since October 2005 and are fully habituated to human observers on foot. Despite different study durations for baboons and geladas, human observers can approach individuals from both study populations to within 2–3 m.

Like the baboon subjects, geladas occasionally encounter some human-related objects scattered throughout the park (mainly scraps of cloth and plastic bags).

Novel object experiments

Using individuals from these two populations as subjects, we compare responses to three novel objects: a plastic doll (30 cm, light-skinned, blond, with red, pink, and white clothing), a rubber ball (yellow, 6.5 cm diameter), and a clean, empty metal can (red, 6.0 × 13.0 cm). Identical objects were used for both baboon and gelada trials. These objects were chosen to represent a variety of colors and shapes.

Trials were conducted as part of ongoing, long-term behavioral research that includes following and observing the subjects for several hours a day while frequently filming their behavior. Therefore, the only aspect of the trials that differed from ongoing behavioral observation was the presence of the novel object. Additionally, neither population has ever been provisioned and, therefore, they do not associate observers with food. Finally, despite dramatic dietary differences, both geladas and baboons are similarly selective in their interaction with natural objects. That is, generally neither species approaches or manipulates non-food items such as sticks or rocks while moving through their habitat (personal observation).

As the study group was foraging through an area, one of the three objects was placed ahead of the moving group. The object was placed behind a natural visual barrier (rock, bush, tree, etc.) and in position long before any animals arrived (see S1–S2 for exemplars). Subjects never observed placement of the object.

Objects were placed in such a way that only an individual that approached to within a few meters would have visual access to the object. This placement protocol helped minimize the number of individuals that might see the object for any given trial. The subject for each trial was the first individual to look at the object (i.e., make a noticeable head turn towards the object), and subjects were tested only once per object. Responses from any additional individuals that looked at the object during that trial were discarded, and these individuals were not allowed to be subjects in future trials for that particular object. Although some gelada subjects were not individually known, members of the same band were never tested twice for the same object.

Subjects for each trial were necessarily opportunistic, but every attempt was made to balance the number of subjects from each age, sex, and taxon category that encountered each object. Ages of baboons were known, but geladas were assigned an age category (young, medium, or old juvenile, subadult, or adult) based on size and developmental characteristics (Dunbar and Dunbar 1975). We conducted trials until we had at least five subjects in each cell (Table 1), with the exception of adult males who only make up a small proportion of the group for either species and, consequently, were rarely the first to discover an object.

Novel object responses

Subjects were filmed (with a Canon ZR700 mini-DV camera) from a distance of 10–15 m as they approached the object, and filming continued until all animals had left the area. For all subjects, we analyzed the video using a frame-by-frame analysis to score: (1) the distance to the object when first seen and the closest distance the subject got to the object, (2) the latency to approach the object, (3) how long a subject remained within 2 m of the object, (4) the duration of looking at the object, (5) the duration (if any) of handling the object, and (6) time to resume previous activity (usually foraging) after seeing the object. Distances were estimated from the video (based on the known size of the subject), and tests with video of objects separated by known distances showed that estimates were accurate (<10% error). DMK and TJB independently scored trials from video for both baboons and geladas. In no case did scores differ by more than 5%, and in all cases scores were averaged from the two independent video analyses.

We categorized the six behavioral responses to the novel objects as indicating either neophilia or neophobia (below). Generally, neophilia makes animals more likely to rapidly interact with novel objects while neophobia reduces this tendency. However, despite being associated with contrary responses to novelty, neophilia and neophobia are not opposite ends of a motivation continuum. In other words, animals can simultaneously exhibit both high neophobia and high neophilia; therefore, we recognize that a perfect separation of neophobia and neophilia may not be possible (Greenberg 2003).

Neophilia and exploration

Neophilia and object exploration were measured using the following variables: (1) how far the subject moved toward the object after seeing it (expressed as distance moved toward object/distance from object when first seen), (2) duration of handling the object (touching or manipulating object with hands), and (3) duration of looking at the object. Because these variables are inherently correlated (i.e., an animal has to approach an object to handle it), they were combined in a factor analysis, resulting in a single factor (hereafter, Interaction with Object) with an Eigenvalue greater than 1.0. Factor 1 explained 63% of the variance in the data and each of the variables had high loading scores on Factor 1 (approach object: 0.77, duration handle: 0.72, duration look: 0.87). A separate factor analysis within each species produced similar results, as did analyses of each variable independently (data not shown).

It is possible that animals look at an object due to anxiety, making ‘look’ a measure of neophobia. However, looking at the object was positively correlated with approaching ($r = 0.55$, $P < 0.001$) and handling the object ($r = 0.48$, $P < 0.001$). Thus, in this study, looking appears to indicate attraction rather than fear.

Neophobia

We examined three of the above measurements that could indicate neophobia. First, we expected that animals with higher neophobia would exhibit greater latency to approach

Table 1 Number of trials for subjects in different categories

Age	Sex	Ball		Can		Doll		Total	
		Baboon	Gelada	Baboon	Gelada	Baboon	Gelada	Baboon	Gelada
Immature	Female	5	7	5	9	8	6	18	22
	Male	7	6	13	9	7	6	27	21
Adult	Female	5	7	7	6	13	13	25	26
	Male	3	3	3	3	2	4	8	10
Total		20	23	28	27	30	29	78	79

the object (hereafter, Latency to Approach). We measured Latency to Approach as the time between onset of the subject looking toward the object and the moment they made their first movement towards the object (43 subjects that did not approach the object were excluded from this analysis). Second, subjects that are fearful of novel objects might move away from them (unlike most captive situations, our subjects were free to leave the area if they did not want to be near the object). Therefore, we measured how long a subject remained within 2 m of the object after first seeing it (Time Spent Close to Object). For subjects that never approached to within 2 m of the object, we recorded how long they remained at or within the distance at which they first spotted the object. Third, because animals might be anxious about the object but still remain close to it, we also measured how much time passed between an animal seeing the object and their return to their previous activity (Time to Resume). We expected that longer Time to Resume would reflect greater neophobia.

Some of our measures of neophobia could simply indicate lack of interest. Here we use the relationship between our measures of neophobia and neophilia to differentiate fear from lack of interest. If *fear of the object* determines a subject's response, then we expect the same subjects to show short Time Spent Close to Object, long Time to Resume, long Latency to Approach, and low neophilia (i.e., Interaction with Object). Alternatively, if subjects are not afraid of an object but additionally are not *interested in the object*, these measures should not be consistently related.

Data analysis

We used general linear models (GLM; SPSS 11 for Mac) to test effects of four categorical independent variables—*taxon* (baboon or gelada), *age class* (immature—subadult or younger—or adult), *sex* (male or female) and *object* (ball, can, or doll)—on four dependent variables (Interaction with Object, Latency to Approach, Time Spent Close to Object, and Time to Resume). Because the two species might interact differently with objects of different color and shape, we also entered a *taxon by object* interaction into the neophilia analysis. Alpha was set at 0.05.

Results

Interaction with object

Taxon, object, and the taxon by object interaction were significant predictors of response to trials (Table 2); baboon subjects interacted with the objects much more (i.e., stronger neophilia and exploration) than gelada subjects, but only for the doll and ball (Fig. 1a). Of the baboon subjects, 30% handled the object including sniffing, manipulating, inspecting, and biting the ball and the doll, sometimes for extended periods of time (but never for longer than 1 min). Conversely, only 4% of gelada subjects handled the object, and most of these only touched or briefly picked up the object. Although individuals of both species typically only glanced at the can, a few baboon subjects sniffed and picked up the can.

Subjects' responses were not related to sex (Table 2). Even within juveniles, responses did not differ by sex ($F_{1,86} = 0.41$, $P = 0.53$). In contrast, age class was a significant predictor of response (Table 2); immature subjects showed more neophilia and exploration than adults (Fig. 1b).

Because we found that responses were less neophilic in adults than in juveniles and less neophilic in geladas than in baboons, we investigated whether the differences between taxa might emerge during development owing to different

Table 2 Results of GLM analyses

Independent variable	Sum of squares	*df*	Mean square	*F*	*P*
Dependent variable: Interaction with Object					
Overall model	50.13	7	7.16	10.08	<0.001
Intercept	<0.01	1	<0.01	0.01	0.94
Taxon	14.25	1	14.25	20.05	<0.001
Object	17.77	2	8.88	12.5	<0.001
Age class	8.08	1	8.08	11.37	0.001
Sex	0.82	1	0.82	1.15	0.29
Taxon × object	10.77	2	5.38	7.58	0.001
Dependent variable: Latency to Approach					
Overall model	225.25	5	45.05	3.58	0.005
Intercept	174.41	1	174.41	13.84	<0.001
Taxon	133.53	1	133.53	10.60	0.002
Object	66.34	2	33.12	2.63	0.08
Age class	11.58	1	11.58	0.91	0.34
Sex	1.77	1	1.77	0.14	0.71
Dependent variable: Time Spent Close to Object					
Overall model	5,596.54	5	1,119.31	4.05	0.002
Intercept	23,584.09	1	23,584.09	85.41	<0.001
Taxon	3,650.57	1	3,650.57	13.22	<0.001
Object	165.00	2	82.50	0.30	0.74
Age class	1,932.19	1	1,932.19	7.00	0.009
Sex	84.67	1	84.67	0.31	0.58
Dependent variable: Time to Resume					
Overall model	2,032.02	5	406.41	5.27	<0.001
Intercept	5,267.41	1	5,267.41	68.30	<0.001
Taxon	63.65	1	63.65	0.83	0.37
Object	667.83	2	333.92	4.33	0.02
Age class	1,311.33	1	1,311.33	17.00	<0.001
Sex	55.31	1	55.31	0.72	0.4

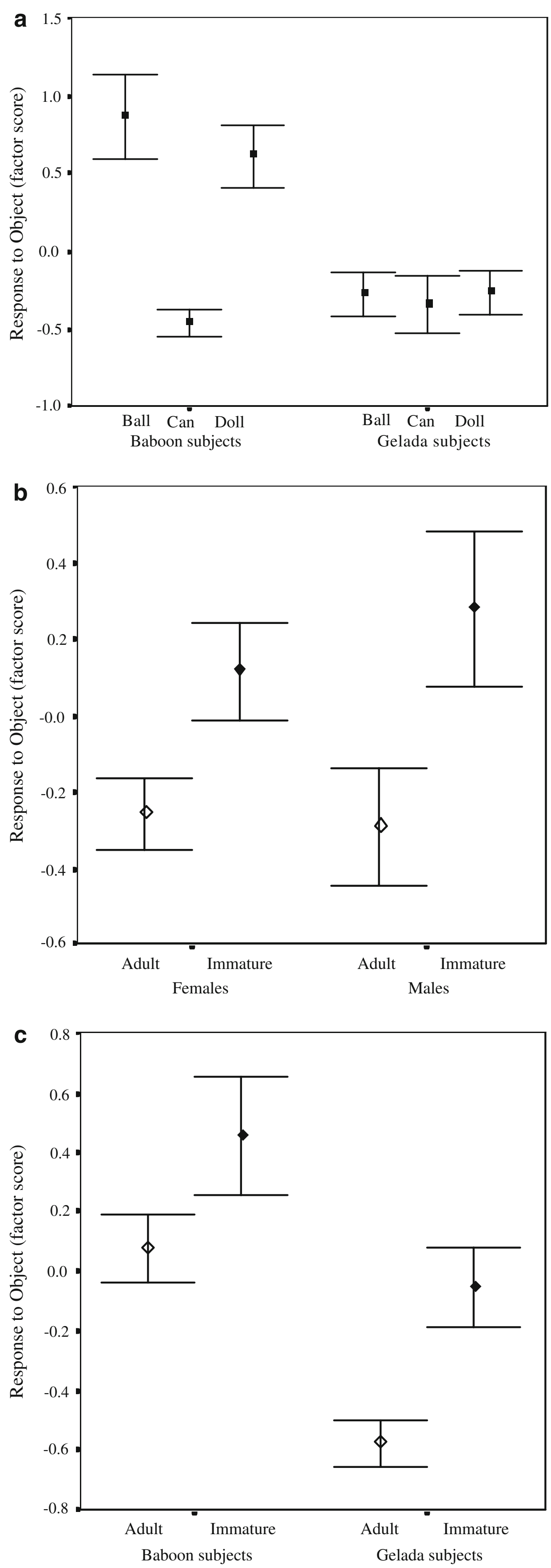

Fig. 1 Mean (± standard error) Interaction with Object factor scores. Novel objects included a ball, can, and doll. Larger values for factor scores indicate stronger responses (see Methods). **a** Grouped by taxon and object, **b** grouped by age class and sex, **c** grouped by taxon and age class

experiences. To address this possibility, we conducted a post-hoc analysis comparing Interaction with Object in adults and immatures for baboons and geladas separately. In geladas, immatures responded more strongly than adults (ANOVA, $F_{1,77} = 9.94$, $P = 0.002$), but in baboons this difference was not significant ($F_{1,76} = 2.25$, $P = 0.14$, Fig. 1c). Despite this difference in development, an analysis restricted to immature subjects showed that baboons still had stronger responses than geladas ($F_{1,86} = 4.34$, $P = 0.04$, Fig. 1c).

Latency to Approach

Only taxon was a significant predictor of subjects' Latency to Approach (Table 2), with geladas having a longer latency to approach the objects than baboons (Fig. 2). Object had no significant effect on Latency to Approach, but the can elicited the longest latencies (Fig. 2). Age and sex were not related to latencies (Table 2).

Time Spent Close to Object

Only taxon and age class were significant predictors of subjects' Time Spent Close to Object (Table 2). Immature subjects of both taxa spent more time close to the object than adults (Fig. 3). Despite the fact that gelada subjects interacted less with the object (see above), they actually spent more time close to the object than baboon subjects (Fig. 3). Based on inspection of the videos, we noticed no obvious signs of anxiety in geladas or baboons while in proximity to the object.

Time to Resume

Only age class and object were significant predictors of subjects' Time to Resume (Table 2). Immature subjects of both taxa took longer to resume their previous activity than adults, and time to resume was shorter for subjects interacting with the can than with other objects (Fig. 4).

Discussion

We observed clear differences in responses to novel objects between wild baboons and geladas. Such differences in neophilia and exploration in closely related taxa suggest a relationship between ecology and behavior in these two genera.

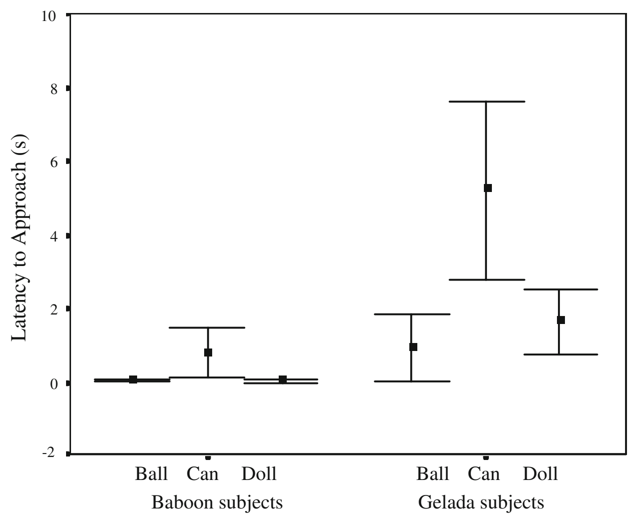

Fig. 2 Mean (± standard error) Latency to Approach (s) for baboon and gelada subjects, separated by object

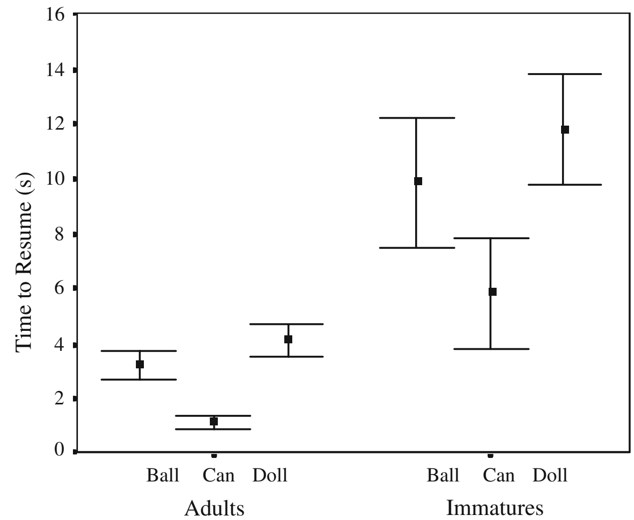

Fig. 4 Mean (± standard error) Time to Resume previous activity (s) for immature and adult subjects, separated by object

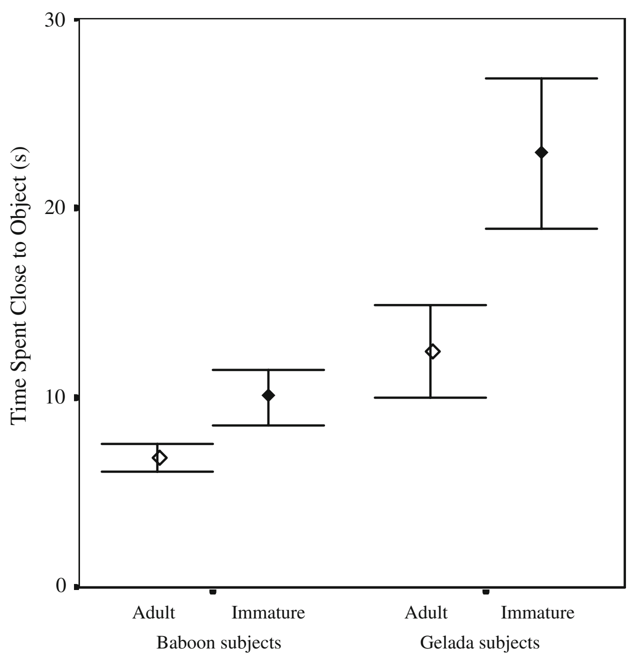

Fig. 3 Mean (± standard error) Time Spent Close to Object (s) for baboon and gelada subjects in different age classes (adult, immature)

Gelada subjects, members of a genus characterized by a much less complex diet and habitat than baboons, exhibited comparative disinterest in all objects (i.e., lower scores on factor 1 than baboons, see Methods); conversely, baboon subjects were likely to approach, handle, and manipulate objects. Whereas the strongest responses by geladas rarely included contact with the objects, baboons interacted with the novel objects as they might a potential food item—frequently sniffing it, putting it in their mouth, and attempting to pull it apart. Moreover, baboons interacted least with the metal can. Although the ball might look like an oversized fruit and the doll might represent a small animal (it is similar in size and shape to juvenile vervet monkeys, an occasional food item for baboons), the metal can has little resemblance in size, shape, or color to any natural food item. This pattern matches findings in capuchins, who were more attracted to novel foods than to novel objects (Visalberghi et al. 2003). It appears that geladas are responding to the ball, the can, and the doll as novel objects, whereas the baboons respond to the ball and the doll as novel food items. As such, our findings may have relevance for research on novel foods (e.g., Cambefort 1981).

Although firm conclusions necessitate replication with other populations of geladas and baboons, there are several possible explanations for why geladas and baboons might have different responses to novel objects. First, differences might arise because geladas and baboons have different experiences and thus learn to respond differently to novel objects. This hypothesis is supported by variation across age, showing that immatures respond more strongly than adults—but only in geladas. However, it is unlikely that experience explains all of the species differences because, even when analyses were restricted to immatures, baboons responded more strongly than geladas. Furthermore, in locations where geladas and baboons are sympatric (such as the Simien Mountains National Park), they still adhere to their remarkably different diets (personal observation), suggesting that baboon-gelada differences are not solely due to learned differences. Furthermore, geladas and baboons raised in captivity have different dietary preferences (K. Fereday, personal communication). Together with growing evidence for heritability of exploratory behavior (e.g., Dingemanse et al. 2002), these observations suggest that the reduction in object neophilia and exploration in geladas has accompanied the evolution of a specialized, graminivorous diet rather than just arising as a consequence of different individual experiences. This hypothesis is in line with previous comparisons of neophilia and neophobia among other closely-related taxa that differ in diet specificity (Clarke and Lindburg 1993; Webster and Lefebvre 2000) or habitat complexity (Greenberg 1990; Mettke-Hofmann et al. 2002).

Our results from two taxa of wild primates are also consistent with results from captive studies on responses to novelty in primates—mainly in that species with more complex diets exhibit a higher degree of neophilia (Glickman and Sroges 1966; Day et al. 2003). Therefore, our results support the use of captive populations for determining species differences in responses to novel objects. However, more within-species comparisons with wild populations are needed to validate this approach. To date, neophilia has only been systematically compared in captive and non-captive subjects of one primate species, *Cebus apella,* where novel objects generated more interest among the captive subjects (Vitale et al. 1991; di Bitetti and Janson 2001; Visalberghi et al. 2003).

It is also possible that the taxon differences in response to novelty are due, in part, to different levels of experience with human-related objects. Some of the chacma baboons may have previously seen balls and cans (they occasionally pass through the research camp where human-related objects are seen). By contrast, geladas are extremely unlikely to have ever seen any of the three objects despite frequent encounters with humans. However, we think this explanation is unlikely for two reasons. First, although the ball and can may not necessarily be "novel" for all baboons, the placement of these objects along natural foraging routes represents a novel situation because human-related items are never found in these remote areas. Second, responses to the objects do not track differences in exposure. If previous experience determines responses to objects (with responses either increasing or decreasing with greater exposure), we would expect baboon subjects to exhibit a similar response to the ball and the can. However, baboons exhibited a strong response toward the ball and doll and a weak response toward the can. Furthermore, baboon and gelada subjects showed similar (i.e., equally weak) responses to the can, despite having different levels of familiarity with cans.

Although we found differences in how quickly geladas and baboons approached and moved away from the objects, we found little evidence that neophobia was shaping responses. First, baboons and geladas were equally quick to resume normal behavior after encountering the object. Second, geladas were slow to approach objects but also slow to move away from objects. Rather than demonstrating any particular fear or interest in the object, this result probably reflects an overall slower pace of movement among geladas. During foraging, geladas typically sit upright on their haunches and shuffle slowly across the ground pulling up handfuls of grass as they go. Consequently, after seeing the object in our experimental trials, many of our gelada subjects continued to forage on grass near the object. In contrast, baboons have greater day ranges (1–9 km, mean of 5 km, Dunbar 1992) than geladas (1.5–2.5 km, Iwamoto and Dunbar 1983; Hunter 2001), and thus cover more ground at a faster rate while foraging (personal observation). Because the majority of our trials for both species were conducted while subjects were foraging, baboons were less likely to sit near the object for long periods of time. However, the possibility that our study did not detect some level of neophobia among geladas cannot be completely ruled out.

The social factors considered in this study were less important than ecological factors in determining responses to novel objects for baboons and geladas. First, because males in both species disperse to new groups upon reaching maturity, we expected males to exhibit greater overall neophilia than females. However, we found no sex differences in responses to novel objects; males were not more likely to explore new objects—even among juvenile males nearing transfer age. Previous primate studies have found sex differences in responses, but only in cases where males and females exhibit dietary differences (e.g., capuchins: Visalberghi et al. 2003). Second, if social factors are important determinants of neophilia, then the geladas—who are socially more neophilic—should have exhibited stronger responses to novel objects than the baboons. Yet, baboons were much more likely to interact with novel objects than geladas were, suggesting that interaction with novel objects remains distinct from interaction with novel individuals. Although this finding contradicts the 'context generality' proposed for personality traits (Dingemanse and Reale 2005), it is consistent with other research showing that behaviors such as boldness are context dependent (Coleman and Wilson 1998). More cross-species tests of context generality are needed to generate firm conclusions.

Consistent with previous studies (Glickman and Sroges 1966; Fragaszy and Mason 1978; Joubert and Vauclair 1986; Henrich 1995; Visalberghi et al. 2003), immature geladas spent more time interacting with novel objects than did adults. Greater neophilia and exploration in immatures may be related to play behavior (Glickman and Sroges 1966), which might be critical to developing the brain and muscles (e.g., Byers and Walker 1995), improving cognitive and social skills (e.g., Fairbanks 1993; Lewis 2000), or training animals to cope with unexpected behavior (e.g., Spinka et al. 2001). Additionally, immatures are less-skilled foragers than adults (e.g., Johnson and Bock 2004), thus manipulation of novel objects could simply reflect exploration of their environment while they search for and attempt to identify appropriate foods.

While previous research has indicated the importance of dominance rank in determining responses to novel objects, we did not design our study to test this factor because of the difficulty identifying rank among gelada subjects (juvenile ranks were unknown and it is difficult to compare ranks of adults across one male units). However, at least among baboons, rank did not appear to be as important as age. The rank of female baboons are stable throughout their lives, while males rise in rank as they mature, yet both males and females showed similar declines in neophilia with age (data not shown).

Theropithecus gelada represents the last extant species of a genus once found throughout eastern and southern Africa (Jolly 1972). Today, geladas are endemic to Ethiopia and found only in a few areas throughout the northern highlands, and in one isolated population south of the Rift Valley in Arsi province (Mori and Belay 1990). *Papio*, by contrast, is thought to be expanding its range throughout Sub-Saharan Africa—perhaps at the expense of *Theropithecus* (Iwamoto 1979). Neophilia may be related to innovation (Day et al. 2003), and evidence from other primate and bird species suggests that those species with enhanced innovation propensities tend to be more successful establishing themselves in novel environments (Sol and Lefebvre 2000; Lefebvre et al. 2004; Martin and Fitzgerald 2005; Sol et al. 2005; but see Reader and MacDonald 2003). Likewise, the greater neophilia and exploration for *Papio* baboons compared with geladas may reflect a propensity for innovation and thus explain the ability of baboons to invade nearly every possible habitat in Sub-Saharan Africa.

Whether the stronger neophilia and potentially enhanced innovative skills of baboons relative to geladas also indicate enhanced cognitive processes is completely speculative at this point. The social knowledge and cognitive abilities of baboons have been studied extensively (reviewed in Cheney and Seyfarth 2007); however, we know comparatively little about the cognitive capacities of geladas. On one hand, the specialized diet and habitat of geladas may not have selected for sophisticated cognitive mechanisms related to innovation and learning. To the extent that neophilia and exploration are linked to innovation and learning (Day et al. 2003), our novel object experiments support this hypothesis. Additionally, gelada brains are relatively smaller than baboon brains despite similarities in body size (Harvey et al. 1987); however, whether overall brain size (or more specific areas such as the neocortex) accurately reflects cognitive ability is debatable (reviewed in Barton 2006).

On the other hand, it is possible that geladas have little behavioral flexibility in the foraging domain, but might share similar cognitive abilities with baboons in the social domain. Gelada social organization is at least as complex as baboon societies (Dunbar and Dunbar 1975; Mori 1979), and behavioral observations of geladas suggest a high degree of social tolerance (Dunbar and Dunbar 1975; Ohsawa 1979), complex reproductive decisions (Dunbar 1984), and highly sophisticated vocal communication (Richman 1976; Kawai 1979; Aich et al. 1987; Aich et al. 1990). Certainly, geladas and baboons represent an interesting comparison for cognitive research if we are to understand the relative importance of ecological versus social factors in shaping the evolution of cognitive processes.

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